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Annual to decadal temperature adaptation of the soil bacterial community after translocation across an elevation gradient in the Andes

Running title: Decadal thermal-adaptation of bacterial growth

Nottingham, A.T.[1,2*], Hicks, L.C.,[1,3] Meir, P.[1,4], Salinas, N.[5], Zimmerman, M.[6], Bååth, E.[3]

1) School of Geosciences, University of Edinburgh, Crew Building, Kings Buildings, Edinburgh, EH9 3FF, United Kingdom
2) School of Geography, University of Leeds, Leeds, UK
3) Section of Microbial Ecology, Department of Biology, Ecology Building, Lund University, SE-223 62 Lund, Sweden
4) Research School of Biology, Australian National University, Canberra, Australian Capital Territory, 2601, Australia
5) Instituto de Ciencias de la Naturaleza, Territorio y Energias Renovables, Pontificia Universidad Catolica del Peru, Av. Universitaria 1801, San Miguel, Lima 32, Peru
6) University of Natural Resources and Applied Life Sciences, in Vienna, Austria
* corresponding author

ABSTRACT

The response of soil microbial activity to climate warming has been predicted to have a large destabilising effect on the carbon cycle. However, the nature of this feedback remains poorly understood, especially in tropical ecosystems and across annual to decadal timescales. We studied the response of bacterial community growth to 2 and 11 years of altered temperature regimes, by translocating soil across an elevation gradient in the tropical Andes. Soil cores were reciprocally translocated among five sites across 3 km in elevation, where mean annual temperature (MAT) ranged from 26.4 to 6.5°C. The bacterial community growth response to temperature was estimated using a temperature Sensitivity Index (SI): the log-ratio of growth determined by leucine incorporation at 35°C:4°C. Bacterial communities from soil translocated to their original site (controls) had a growth response assumed to be 'adapted' to the original MAT. Translocating soil downslope (warming) resulted in an increased SI relative to their original growth response, and *vice versa* under cooling, indicating community-level adaptation over the incubation period to the altered MAT. The average level of adaptation (i.e., the extent to which SI converged on the control values) was 77% after 2 years, and was complete after 11 years. The adaptive response was greater when soil was warmed rather than cooled: instances of complete adaptation of SI occurred in soils after 2 years when warmed, but only after 11 years when they were cooled. Taken together, our results show that the majority of the growth adaptation to warming by the bacterial community occurs rapidly, within 2 years, whilst growth adaptation to cooling occurs within a decade. Our analysis demonstrates rapid warm-adaptation of bacterial community growth, with potential consequences for the temperature sensitivity of soil carbon cycling in response to future climate warming.

Keywords: climate warming; microbial community; microbial growth; Ratkowsky model; soil carbon; tropical forest

1. Introduction

Climate warming is predicted to stimulate microbial activity, resulting in increased degradation of soil carbon (C) and causing a positive feedback for further climate change (Davidson and Janssens, 2006). However, the magnitude of this feedback depends on changes in the temperature sensitivity of microbial growth – the magnitude of the change in microbial community activity with warming. There is now widespread evidence that both the function and composition of microbial communities change under warming (Bradford, 2013; Romero-Olivares et al., 2017; Bååth, 2018; Nottingham et al., 2019b). However, studies of warming effects on soil microbial processes have reported divergent responses that vary across temporal and biogeographical scales (Romero-Olivares et al., 2017) and with scarce information available for tropical ecosystems, despite the very large soil carbon stores in these regions (Jackson et al., 2017; Wood et al., 2019). Our ability to predict the response of the soil C cycle to climate warming is especially limited by a lack of information on the temperature sensitivity of microbial processes across annual-to-decadal timescales and in tropical ecosystems.

Here we focus on the characterisation of the temperature response of microbial (specifically, bacterial) community growth, which can be directly determined by laboratory incubations (Bååth, 2018). The temperature response of microbial community growth and respiration follow the square root relationship (Ratkowsky et al., 1982), which can be used to assess the community-level metabolic response to warming (Bååth, 2018). Using this approach, it has been shown that higher mean annual temperature (MAT) results in microbial community growth and respiration better adapted to higher temperatures and *vice versa*, where 'adaptation' is indicated by relatively faster activity at temperatures closer to MAT, with the minimum temperature of activity (T_{min}) increasing with increasing MAT (Rousk et al., 2012; Bååth, 2018; Nottingham et al., 2019a; Li et al., 2021). The mechanisms behind this altered temperature sensitivity of microbial growth may include: i) physiological changes resulting in short-term acclimation by existing microbial taxa, which have been shown across ambient temperature ranges for fungi (Crowther and Bradford, 2013) but not for bacteria other than from heat-shock responses to very high temperatures (Leroi et al., 1994); ii) genetic adaptation resulting in microbial populations with altered genotypes, which has been demonstrated in some instances for bacteria under optimal growth conditions (Bennett et al., 1990), although not in others (Bennett and Lenski, 1997); or iii) species sorting where species inherently adapted to higher temperature conditions will outcompete less well-adapted species (Donhauser et al., 2020) and become dominant in that bacterial community. Irrespective of the underlying mechanism, whether by genotypic or by community compositional change, for this study we use the terminology 'community adaptation', to describe better performance (indicated by relatively faster growth rates) with shifts in temperature, in accordance with terminology used elsewhere (Bradford, 2013; Bååth, 2018).

The overall microbial growth response to temperature, or 'community adaptation' to temperature, depends on both the duration and the magnitude of temperature change. Large and long-term temperature gradients (e.g. across gradients in MAT) have been related to large changes in the minimum and optimum temperatures of bacterial community growth in soil (T_{min} and T_{opt}, respectively) (Bååth, 2018). For example, these growth responses have been demonstrated across a latitudinal gradient of -4°C to 9°C in MAT in the Antarctic (Rinnan et al., 2009) and an elevation gradient of 6.5°C to 26.4°C in MAT in the tropics (Nottingham et al., 2019a). However, it remains unclear how rapidly microbial activity-temperature relationships respond to changing thermal regimes. Short-term laboratory studies suggest a lag in the microbial community temperature adaptation with warming, if the incubation temperature is below T_{opt}. For example, no increase in T_{min} for growth was found after one to two months at 25°C compared to 5°C, while increasing temperature to levels near or higher than T_{opt} for growth (around 30°C), resulted in rapid community adaptation to temperature (Bárcenas-Moreno et al., 2009; Birgander et al., 2013). On the other hand, four years of 5ºC *in situ* warming in a temperate climate zone resulted in increased T_{min}, indicating that temperature adaptation can occur under field conditions and over a longer time period (Rousk et al., 2012). With smaller temperature increases under field conditions, however, community adaptation to temperature has not been detectable for bacterial growth (Rinnan et al., 2009; Rinnan et al., 2011; Birgander et al., 2018) or respiration (Schindlbacher et al., 2015; Carey et al., 2016). The direction of the temperature change, whether increasing or decreasing, may also be of importance. Higher temperatures may result in a faster turnover of the bacterial community compared to lower temperatures; such a response has been used to explain more rapid community adaptation during warmer conditions in laboratory studies (Dıaz-Raviña and Bååth, 1996; Ranneklev and Bååth, 2001). The same response can also explain earlier findings that microbial growth adaptation is determined by peak summer temperatures rather than cooler winter temperatures (van Gestel et al., 2013).

The effect of warming on the soil C cycle and microbial communities is especially poorly understood in tropical forest ecosystems (Wood et al., 2019). Tropical soils account for a third of global C stocks (Jackson et al., 2017), which together with rapid C turnover due to high temperatures result in a substantial contribution of tropical soils to the global terrestrial C cycle (Pan et al., 2011). Recent experimental evidence suggests a high sensitivity of lowland tropical forest soil carbon to two years of warming (Nottingham et al., 2020), but it remains unclear whether and how microbial communities modulate this response across annual-to-decadal time-scales. Studies of elevation gradients in tropical and subtropical forests have shown that long-term (i.e. >1000 yrs) temperature differences can drive changes in the microbial community (Looby et al., 2016; Nottingham et al., 2018), although for many sites elevation-related variation in other factors such as rainfall, geology and plants are more important for determining community composition (Geml et al., 2014; Singh et al., 2014;

Selmants et al., 2016). The experimental translocation of soil across tropical elevation gradients, to impose temperature change (Tito et al., 2020), has also been shown to change the microbial community composition after 10 months (Looby and Treseder, 2018) and five years (Nottingham et al., 2019b); whether these community shifts under short to medium term (e.g. 1-10 yrs) temperature change are associated with altered growth-adaptation of the community is not yet clear. While the *in situ* microbial community growth response is adapted to long-term differences in temperature (Nottingham et al., 2019a; Donhauser et al., 2020), there has been no test of the microbial growth response to temperature changes across annual to decadal time scales, a timescale particularly important in the context of expected rate of temperature change this century (Mora et al., 2013).

We studied the bacterial community growth response ('community-adaptation') to 2 and 11 years of ± 20^{o}C temperature change by reciprocal translocation of soil cores to both warmer and cooler conditions along an elevation gradient in Peru, from the Andes to western lowland Amazonia. We expected that the 'control' soil bacterial communities translocated at their site of origin would be adapted to local temperature conditions - for example, relatively faster growth at warmer temperatures for sites with higher MAT - similar to that found earlier for undisturbed soils along this elevation gradient (Nottingham et al., 2019a). We then hypothesized that: 1) bacterial communities from soil cores transferred from low temperature/high elevation sites, to high temperature/low elevation sites, will become increasingly well adapted over time to higher temperature conditions and *vice versa*; 2) the bacterial community growth adaptation to temperature will be greater following 11 years compared to 2 years of temperature change; and 3) transferring soil cores from low to high temperature environments will change the temperature sensitivity of the bacterial community more rapidly than moving from high to low temperature.

2. **Materials and Methods**

2.1. Soil translocation experiment and soil sampling

Intact soil cores were reciprocally translocated among five sites along a tropical elevation gradient situated on the eastern flank of the Peruvian Andes, spanning a MAT range of 20ºC (6.5 - 26.4ºC; Table 1) (Nottingham et al., 2015). The lower four sites are under continuous forest cover, from the lowland Amazon rainforest (site TAM at 210 m above sea level; m asl) to upper montane cloud forest (site WAY at 3025 m asl). The upper site is above the timberline, in high elevation grassland (site TC at 3650 m asl) (Table 1). MAT decreases with increasing elevation across the gradient, exhibiting little seasonal variation in temperature (Rapp and Silman, 2012). Mean annual precipitation (MAP) peaks at mid-elevation, 5302 mm year^{-1} at 1500 m. Precipitation is distinctly seasonal across the gradient, with a dry season from May-September and a wet season from November-March (Rapp and Silman, 2012). Despite distinct wet and dry seasons, there is little seasonal variation in soil moisture (Girardin et al., 2013), and evidence to date indicates that plants and soils at all sites are rarely moisture limited over the seasonal cycle (Zimmermann et al., 2010; van de Weg et al., 2014). Further description of soil, climate and floristic composition at these sites are reported elsewhere (Girardin et al., 2010; Rapp and Silman, 2012; Jankowski et al., 2013; Oliveras et al., 2014; Nottingham et al., 2018).

Soil cores were translocated in two sets, with translocation downslope imposing an experimental warming treatment and translocation upslope an experimental cooling treatment. The first set were translocated in 2008 and sampled 11 years later in 2019 (11-year treatment). The second set were translocated in 2013 and sampled two years later in 2015 (2-year treatment). At each site, twelve intact monoliths of mineral soil (10 cm diameter and 50 cm depth for the 10-year treatment and 30 cm depth for the 2-year treatment) were excavated. Soil cores were re-installed at sites across the gradient, by carefully inserting the cores into holes cut into the soil using a hand auger. This included soil cores re-installed at the same elevation (i.e. at their site of origin) to control for any disturbance effects. The cores were located in three separate subplots situated outside the perimeter of 1 ha permanent study plots at each site, with the exception of the 3650 m site, where translocated cores were situated in three subplots within a smaller fenced area (approximately 8 m x 8 m) to protect from disturbance. These subplots acted as individual spatial replicates, such that twelve cores were re-installed at each elevation site (4 soils x 3 replicates). The same sites were used for both sets of translocation treatments, except that for the 2-year translocation study we replaced the 1000 m site with a higher site at 3650 m in order to increase the temperature range (Table 1).

Soil cores were collected in October 2015 (2-year translocation) and December 2019 (11-year translocation). Soil was removed from the cores and mixed before subsamples from each core were collected. These samples were then stored in a dark/cool (~15ºC) room until transportation to the laboratory (Lund, Sweden). The soil was then stored for up to 2 weeks at 17ºC until analyses.

2.2. Bacterial community growth adaptation to temperature

The temperature adaptation of the bacterial community growth was determined by measuring instantaneous growth rates at different temperatures (Pietikäinen et al., 2005; Rinnan et al., 2009), using the leucine (Leu) incorporation method (Bååth et al., 2001). The method provides an estimate of community growth at different temperatures, providing a standardised comparison across treatments and studies. Soil (1 g dry weight) was mixed with 20 ml 17ºC distilled water, vortexed for 3 min and centrifuged at 15ºC for 10 min. The supernatant, with an extracted bacterial suspension, was transferred (1.5 ml) into microcentrifugation vials, which were pre-incubated in water baths for 1h (at 4ºC) or 0.5h (at 35ºC) before 2µl ^{3}H-leucine (1-[4,5-^{3}H] leucine, 37 MBq ml^{-1} and 5.74 TBq mmol^{-1}, Perkin-Elmer, USA) together with unlabelled Leu was added (resulting in 275 nM in the bacterial suspension). After 6.5 h (4°C) or 2 h (35°C), trichloroacetic acid was added to terminate growth. Washing of bacteria and measurement of radioactivity was conducted following Bååth et al. (2001). All samples for each replicate were processed on the same day.

2.3. Calculations and statistics

The log ratio incorporation of Leu at 35°C and 4°C, respectively, was used as a temperature Sensitivity Index (SI) of the degree of bacterial community adaptation to temperature, where:

$$\text{SI} = \log\text{ (Leu incorporation at 35°C/ Leu incorporation at 4°C)} \qquad \text{(eq. 1)}$$

Higher ratios indicate relatively faster growth at higher temperatures (i.e. better adaptation) and *vice versa*. We used linear regression to test the response of temperature change (translocation) on SI, given that a previous study demonstrated a strong linear relationship between SI and temperature ($R^2 = 0.88$, $P < 0.001$; Nottingham et al. (2019a). A similar temperature sensitivity index for bacterial growth was previously shown to correlate closely with T_{min} for bacterial growth for the elevation gradient studied here (Nottingham et al., 2019a). We calculated T_{min} for soil bacterial growth by using the linear relationship between T_{min} and MAT demonstrated in the same previous study (Fig. 2a in Nottingham et al. (2019a); $R^2 = 0.89$, $P < 0.001$), where:

$$T_{min}\ (°\text{C}) = -10.0 + 0.33 * \text{MAT}\ (°\text{C}) \qquad \text{(eq. 2)}$$

We used this relationship ($\text{MAT} = (T_{min}+10.0)/0.33$) to estimate T_{min} values corresponding with empirically-determined SI values for control soils translocated to the site of origin (Fig. 1) following 2-years ($\text{SI}=0.38+0.067*\text{MAT}$; rearranged, $\text{MAT}=(\text{SI}-0.38)/0.067$; thus combined with eq. 2 and solved for T_{min}, $T_{min} = 4.93*\text{SI}-11.87$) and 11-years ($\text{SI}=0.51+0.068*\text{MAT}$; rearranged, $\text{MAT}=(\text{SI}-0.51)/0.068$; thus combined with eq. 2 and solved for T_{min}, $T_{min} =4.85*\text{SI}-12.47$) (see upper axis, Fig. 1; second y-axes, Figs 2 and 3).

To examine the average level of change in SI across all soils, and under both warming and cooling, we used relative response (RR) quotients. The use of RR quotients enabled us to compare relative temperature responses across all soil types, minimizing variation from any indirect effects of temperature on other covarying properties among soils (e.g. substrate availability), and to compare responses across different translocation durations (2 yrs and 11 ys).

The RR of SI was determined by:

$$\text{RR of SI} = \log\left[\text{SI at destination } (i=1\text{-}3) / \text{SI at origin } (i=1\text{-}3)\right] \quad \text{(eq. 3)}$$

Errors were determined based on the standard error (SE) of the three replicates, whereby each translocated soil core (i=1-3 replicate core at destination site) was paired with a control core (i=1-3 replicate core at origin site). To evaluate whether temperature change affected the RR of SI, we used linear models of RR of SI against the temperature shift (temperature at destination minus temperature at origin). We used models including warming and cooling responses together and warming and cooling separately. To evaluate whether the change in RR of SI with temperature change under warming or cooling was different after the different time periods (2 years, 11 years) and for soils at origin ('fully adapted' controls), we used ANCOVA. All analyses were performed in R (version 4.0.2).

3. Results

The original bacterial community was assumed to be adapted to the prevailing temperature regime across the elevation gradient. This assumption was supported by a linearly-increasing temperature Sensitivity Index (SI) of bacterial growth with increasing MAT for soil cores kept at their original site both after 2 and 11 years ($R^2 = 0.89$ and 0.83, respectively, Fig. 1). At the high elevation site (MAT 6.5°C) the SI was around 0.9 and increased to 2.2 at the low elevation site (MAT 26.4°C). This is equivalent to an increase in T_{min} for bacterial growth from around -

8°C to -1°C (calculated from eq. (2)) across this elevation gradient with 20°C difference in MAT. Both sampling events resulted in approximately the same slope (2 years, 0.067; 11 years, 0.068; Fig. 1) for the dependence of SI on MAT.

Cooling - by translocation of soil upslope - generally resulted in bacterial growth adapted to lower temperatures (i.e. denoted by a decreased SI relative to SI at origin), while warming by translocation of soil downslope generally resulted in growth adapted to higher temperatures (i.e. denoted by an increased SI relative to SI at origin). For all soils, the SI was correlated with MAT of the new sites following translocation (Figs. 2 and 3).

To illustrate the effect of two years of warming on the temperature sensitivity (SI or T_{min}) of growth, soil from the high elevation site (TC, MAT 6.5°C) translocated to the lowest elevation site (TAM, 26.4°C MAT) had a SI for bacterial growth that increased from 0.9 to around 2.2 (refer to end of solid line in Fig. 2A where MAT of new site = 26.4°C; equivalent to T_{min} increasing from -8°C to approximately 0°C). The SI of TC soil translocated to the two sites with intermediate MAT (WAY, 11.1 and SP, 17.4°C) also increased from the SI value at origin (TC), but to a lesser extent (solid line in Fig. 2A where MAT of new sites = 11.1 and 17.4 °C).

To illustrate the effect of two years of cooling, for the soil from the lowest elevation site (TAM, MAT 26.4°C) translocated to the highest elevation site (TC, MAT 6.5°C), the SI decreased from approximately 2.0 to 1.3, indicating bacterial community adaptation to cooler conditions (Fig. 2D). Similarly, for the two sites with intermediate MAT (WAY and SP, Fig. 2B, C), translocation to sites with higher MAT usually resulted in higher SI (adaptation to warmer conditions) and *vice versa*.

Two years after translocation, the average slope of SI against MAT of the translocation site across all soils (Fig 2; 0.053 ± 0.006) suggested 77% of adaptation had occurred, although there was an uneven effect of cooling and warming. Warming had a stronger effect after two years because the slope was steeper for bacterial communities originating from low temperature conditions translocated to higher MAT (soil from upper two sites with slopes 0.072, 0.053; Fig. 2A, 2B), than for communities translocated from high to low MAT (soil from lower two sites, with slopes 0.041, 0.044; Fig. 2C, 2D, e.g. compare Fig. 2A and D).

Eleven years after translocation, the SI data suggest that the adaptation of bacterial growth to the new temperature regime had increased and was near-complete in all sites. The average slope of SI against the MAT of the translocation site across all soils (0.069 ± 0.006) was the same as the slope for the controls (0.068 ± 0.003) (Fig. 3). For soil from the highest site under forest (WAY) translocated to the low elevation site (TAM) (i.e. warmed by 15°C), SI increased from 1.3 to 2.4; the latter being similar to the SI of bacterial growth at the low elevation site (Fig. 3A). Bacterial growth in soil from the low elevation site (TAM) translocated to the high elevation site (WAY) became fully adapted to the new conditions, decreasing SI from around 2.1 to 1.2 (Fig. 3D). The bacterial growth rates from soils of the two intermediate elevation sites also appeared to fully adapt to the new temperature regimes, irrespective of whether MAT was increased or decreased by translocation (Fig. 3B, C). Thus, the slope for soils from the lower warmer elevations (i.e. that had been cooled), had converged on the controls to a greater extent after 11 years compared to after 2 years (compare Fig 2C and 2D with Figs 3C and 3D; slopes changed from 0.041 and 0.440 to 0.062 and 0.062).

To further examine the average response of SI across all soils to warming and cooling, we used relative response quotients (RR). The relative change in the temperature sensitivity of bacterial growth (RR of SI) was correlated with the change in temperature for soils after 2 years and 11 years (Fig. 4, see insert for average response across warming and cooling). The trajectory of the slope over time tended towards the slope for controls (complete adaptation), increasing from 2 years (0.0160 ± 0.0018; $R^2 = 0.70$, $P < 0.001$), 11 years (0.0184 ± 0.0017; $R^2 = 0.77$, $P < 0.001$) and controls (0.0208 ± 0.0013; $R^2 = 0.82$, $P < 0.001$); where a slope of zero represents no adaptation (dashed line, Fig 4) and a slope of 0.0208 represents 100% adaptation ('control' slope, calculated by comparing responses in non-translocated control soils at site of origin). The RR-SI data (combining cooling and warming responses) suggest that 77% ± 14% of adaptation had occurred after 2 years and 88% ± 15% after 11 years (Fig.4 insert; % calculated by the ratio of slopes for respective treatments and controls), which is consistent with our earlier analysis showing 77% of adaptation after 2 years and complete after 11 years (Figs. 2-3).

The response of RR-SI to temperature change was different under warming and cooling (Fig. 4). Under warming, the relationship between the RR of SI and temperature change was not dependent on the length of incubation (ANCOVA covariate (time) effect $P = 0.62$; pairwise comparisons: control vs. 2 years, $P = 0.60$; control vs. 11 years, $P = 0.69$). The slope of the relationship under warming was similar after 2 years (0.0258 ± 0.0053; $R^2 = 0.57$, $P < 0.001$), 11 years (0.0192 ± 0.0059; $R^2 = 0.40$, $P < 0.01$) and for controls (0.0217 ± 0.0013; $R^2 = 0.52$, $P < 0.001$) (see warming responses in Fig. 4). While under cooling, the relationship between the RR of SI and temperature change was dependent on the length of incubation (ANCOVA covariate (time) effect, $P = 0.02$; pairwise comparisons: control vs. 2 years, $P = 0.07$; control vs. 11 years, $P = 0.42$). Under cooling, the relationship after 2 years (0.0159 ± 0.0059; $R^2 = 0.31$, $P = 0.02$) was different from that after 11 years (0.0192 ± 0.0059; $R^2 = 0.40$, $P < 0.01$) and controls (0.0211 ± 0.0039; $R^2 = 0.51$, $P < 0.001$).

In summary, the temperature response of growth for translocated soils converged towards that of the natural soils found at the destination site of translocation - soil bacteria grew relatively faster at high temperatures if translocated downslope (higher MAT) and *vice versa*. The extent of growth adaptation increased over time and was greater under warming compared to cooling; adaptation was complete (no difference in SI for translocated soils vs. controls) after 2 years of warming but not cooling, and complete after 11 years, both for warming or cooling. By directly comparing the change in slopes for SI, we found 77% of complete adaptation had occurred after 2 years (Fig. 2) and 100% after 11 years (Fig. 3). In a separate analysis using relative response across all soils to warming and cooling together, we found that 77 ± 14% had occurred after 2 years and 88 ± 15% after 11 years (Fig. 4). Thus, averaging across warming and cooling responses, both analyses supported that most (over 70%) of the adaptation had occurred after 2 years, and this continued to increase, converging towards the controls after 11 years.

4. Discussion

Temperature adaptation of bacterial growth following temperature manipulation under field conditions has rarely been studied. Of the studies that have been performed, overall, they support our results by showing that the extent of this adaptive growth response depends on the magnitude of the temperature change and duration of incubation period. Although warming experiments in cold Antarctic or sub-Arctic environments found no community adaptation, this is most likely due to the small temperature increases imposed in the studies – for example by 1°C for three years (Rinnan et al., 2009) and by 1-2°C for 17 years (Rinnan et al., 2011) – or due to shorter periods of warming, for example 3°C of winter-warming for only two years (Birgander et al., 2018). In contrast, experimental soil warming by 5°C for 3-4 years in a temperate forest resulted in a significantly higher T_{min} for bacterial growth, indicative of adaptation to warmer temperatures (Rousk et al., 2012). The present translocation study, which imposed large temperature changes of 4-20°C, found a 0.3°C increase in T_{min} per degree warming, which is similar to the 0.2°C increase in T_{min} per degree warming in Rousk et al. (2012). The changes in SI following transfer to the next site downslope (i.e. an increase in MAT from 4.6 to 9.0°C) all resulted in increased SI (0.1 to 0.3, equivalent to an increase in T_{min} of 0.7 to 2°C), thereby suggesting that temperature adaptation may occur at annual time scales with temperature changes of 4ºC or greater. Our data therefore suggest that these results are well suited to predict soil bacterial growth responses to the 4ºC warming expected in tropical regions this century (Mora et al., 2013).

The growth adaptation of the bacterial community we observed was most likely to principally result from community compositional shifts rather than genetic changes within species. While it is possible that altered temperature sensitivity of growth could arise from physiological changes through genetic adaptation within species, which can occur over months (e.g. > 200 generations in bacteria, albeit at optimal temperatures for growth) (Bennett et al., 1990), other cases of no such adaptation to natural temperature regimes within a species have been found (Bronikowski et al., 2001). One should also bear in mind that in natural soil conditions the growth and turnover for bacterial species during 2 years at low temperatures - for example at the TC site with a MAT of 6.5ºC - is too slow to allow the hundreds of generations necessary for significant change (Bennett et al., 1990; Bååth (1998) estimated 20 generations per year are expected at 10ºC). We thus suggest that the growth response resulting from genetic changes within a species would be very minor relative to those arising from community compositional shifts, as discussed by Bárcenas-Moreno *et al.* (2009). There is substantial evidence showing that warming causes community compositional shifts within months to years, which have been related to changes in microbial growth (Bárcenas-Moreno et al., 2009; Rousk et al., 2012) and respiration (Bradford et al., 2010; Zhou et al., 2012). For example, 26 years of experimental soil warming resulted in community compositional shifts alongside changes in biomass and respiration rates (Melillo et al., 2017) and a metanalysis of warming experiments found long-term (>10 year) attenuation of respiration rates and microbial biomass linked to either community shifts, adaptation and substrate depletion (Romero-Olivares et al., 2017). Indeed, a previous study of soil from this translocation experiment found a community compositional shift after 5 years of temperature change (Nottingham et al., 2019b). Although elsewhere there have been exceptions: across a geothermal gradient in sub-arctic grassland (ambient MAT around +5ºC), >50 years of +6ºC warming did not result in any adaptive change in community composition or growth (Walker et al., 2018), pointing to a need for further study at long timescales. Taking the consensus of evidence for timescales relevant for our experiments, we suggest a dominant role for community compositional shifts in explaining the adaptive growth change we observed, following both 2 and 11 years of translocation.

The temperature response of growth was faster when soil was warmed (translocation downslope) rather than cooled (translocation upslope) after 2 years (compare Figs. 2A and 2B with 2C and 2D, and compare warming and cooling slopes in Fig. 4), which can be explained by higher turnover rates of the bacterial community at higher temperatures. Consistent findings have been shown in terms of soil respiration, where there were larger responses to warming than to cooling following soil translocation across gradients of 3.3ºC MAT in temperate forest (Luan et al., 2014) and 10.9ºC MAT in Australian tropical forest (Zimmermann et al., 2015). Similar results were also found for the same tropical forest gradient under study here (Zimmermann et al., 2009), although these soil respiration responses may have been confounded by differences in substrate availability, with higher organic matter content in the higher elevation soils (Zimmermann et al., 2009; Zimmermann et al., 2012; Nottingham et al., 2015). Direct evidence supporting our results was presented by Dıaz-Raviña and Bååth (1996), who showed that tolerance of microbial communities to metal pollutants developed more rapidly at higher temperatures. This result is further supported by a study in a hot desert ecosystem, showing that the nature of the community temperature adaptation to temperature is more strongly determined by peak seasonal temperature than mean annual temperature (van Gestel et al., 2013). In this latter hot desert ecosystem, bacterial growth was adapted to warm conditions (>40ºC) even in winter when temperatures were <10ºC, clearly indicating that cold conditions during winter did not affect temperature adaptation at the same rate as warm temperatures during summer. Collectively, these results suggest that the bacterial community adaptation response to warmer temperatures is equivalent to the response to cooler temperatures but over longer-periods of time. Under warmer temperatures, the rate of microbial community turnover is higher, providing more opportunities for changes in the community to occur.

To better understand the consequences of these results for the temperature response of the soil carbon balance requires further study of fungal community growth. Fungal growth has been reported to have a lower T_{min} than bacterial growth (Pietikäinen et al., 2005; Birgander et al., 2018) and increased ratios of bacterial to fungal growth rates have been reported at temperatures above 30ºC (Pietikäinen et al., 2005). However, the opposite pattern was shown in a previous study of this Peruvian elevation gradient, which found evidence for long-term microbial growth adaptation – for both bacteria and fungi – to the prevailing local temperature regime with the ratio of bacterial to fungal growth decreasing at higher temperatures (Nottingham et al., 2019a). Further study is required to resolve these opposing results on bacterial to fungal growth relationships, especially across warmer temperature ranges.

Our study has demonstrated the use of translocation experiments as a powerful approach to assess the nature and dynamics of microbial temperature adaptation in soil. Translocation experiments may be used as a powerful complement to *in-situ* warming experiments in order to understand the response of tropical soils to future climate change. However, *in-situ* warming experiments will of course be needed to enable improved prediction of the consequences of future climate warming; especially for lowland sites with high MAT, where translocations to sites with higher MAT cannot be used to test responses to warming. Our result of more rapid adaptation under warming than cooling also demonstrates that, for experiments that aim to measure the temperature sensitivity of community activity without incurring compositional changes, cooling rather than warming manipulations may be preferable (Karhu et al., 2014).

The square-root model on which our findings are based (Ratkowsky et al., 1982), and alternative models (e.g. Macromolecular Rate Theory, Hobbs et al. (2013); (Alster et al., 2018)), improve on predictions solely based on Q_{10} functions and Arrhenius kinetics. Arrhenius theory accurately predicts simple chemical reactions and enzyme kinetics and can be useful to describe relative differences in apparent temperature sensitivities of soil processes across standard temperature ranges (Davidson et al., 2006). However, the theory can fail to predict more complex biologically-mediated soil processes in field experiments (e.g. Nottingham et al. (2020)). The relationships between microbial growth temperature sensitivity (e.g. T_{min}) and temperature change reported here - and in related work (Bååth, 2018; Nottingham et al., 2019a) - offer a starting point for better representation of microbial growth responses in models, and thus to improve our understanding of how terrestrial ecosystems interact with climatic change.

In summary, we provide new evidence in support of adaptation of microbial growth to warming and go further to demonstrate that these changes occur relatively quickly, and more rapidly under warming compared to cooling. We show that, for bacteria, 11 years was enough to achieve the same community adaptation as in the original local soils, and that most of this adaptation had occurred after just two years. Together, our results point towards an important role for microbial temperature responses in mediating changes in the carbon cycle under warming, and importantly, occurring within annual-to-decadal time-scales.

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Table 1. Site characteristics and soil properties (MAT = mean annual temperature, MAP = mean annual precipitation). Data represent mean (SE within parenthesis; n=3).

	Translocation duration	**Elevation** (m asl)	**MAT** (°C)	**MAP** (mm yr^{-1})	**Soil pH**
Tambopata (TAM)	2 and 11 yrs	210 m	26.4	1900	4.0 (0.05)
Tono (TON)	11 yrs	1000 m	21.0	3100	3.8 (0.10)
San Pedro (SP)	2 and 11 yrs	1500 m	17.4	5302	4.3 (0.06)
Wayqecha (WAY)	2 and 11 yrs	3025 m	11.1	1560	4.4 (0.21)
Tres Cruces (TC)	2 yrs	3650 m	6.5	760[a]	4.9 (0.03)

a) Measured at Ajanaco, 3450 m asl (Oliveras et al., 2014)

Legends

Fig. 1. Bacterial community growth adaptation in native soils (controls) along an elevation transect in the Andes. Community adaptation was expressed as a temperature Sensitivity Index (SI) (eq. 1), where a higher value indicates a bacterial community adapted to higher temperature conditions and *vice versa*. Only soil cores incubated at their original site (controls) are shown, which reflect the inherent community adaptation to MAT at that site. Filled symbols and solid line = control soils corresponding to the 2 years translocation study, open symbols and stippled line = control soils corresponding to the 11 years translocation study (bars indicate SE, n = 3). T_{min} for growth given on the top x-axis was calculated from Nottingham *et al.* (2019a) according to $T_{min} = -10.0 + 0.33 * MAT$, see Materials and Methods.

Fig. 2. Bacterial community growth adaptation 2 years after translocating soil cores along an elevation transect in the Andes. Community adaptation was expressed as a temperature Sensitivity Index (SI) (eq. 1), where a higher value indicates a bacterial community adapted to higher temperature conditions and *vice versa*. Open symbols and stippled lines indicate temperature sensitivity of bacterial communities of soil cores incubated at their original site (controls, given in each graph, from Fig. 1), while closed symbols and solid lines indicate soil cores transferred to different sites (bars indicate SE, n = 3). The solid lines are coloured according to the soil origin: A) TC (black; MAT 6.5°C), B) WAY (red; 11.1°C), C) SP (blue; 17.4°C), D) TAM (green; 26.4°C); for abbreviations, see Table 1. The thin horizontal line in each panel shows the temperature sensitivity of soil cores extracted and re-installed at their original or 'origin' site. T_{min} for growth was calculated from Fig. 1., see Materials and Methods. We predicted that under 'no adaptation' the solid regression line for translocated soils would follow the horizontal line, while under 'complete adaptation' the solid line would follow the stippled line.

Fig. 3. Bacterial community growth adaptation 11 years after translocating soil cores along an elevation transect in the Andes. Community adaptation was expressed as a temperature Sensitivity Index (SI) (eq. 1), where a higher value indicates a bacterial community adapted to higher temperature conditions and *vice versa*. Open symbols and stippled lines indicate the temperature sensitivity of bacterial growth in soil cores incubated at their original site (controls, given in each graph, from Fig. 1), while closed symbols and solid lines indicate soil cores transferred to different sites (bars indicate SE, n = 3). The stippled lines are coloured according to the soil origin: A) WAY (black; MAT 11.1°C), B) SP (red; 17.4°C), C) TON (blue; 20.7°C), D) TAM (green; 26.4°C); for abbreviations, see Table 1. The thin horizontal lines in each panel show the temperature sensitivity of soil cores transferred to their original site. T_{min} for growth was calculated from Fig. 1., see Materials and Methods. We predicted that under 'no adaptation' the solid line would follow the horizonal line, while under 'complete adaptation' the solid line would follow the stippled line.

Fig. 4. The average response of the temperature Sensitivity Index SI (RR-SI: relative response quotient of SI) across all soils and under both warming and cooling together. Points represent pair-wise comparison between the SI of bacterial growth in soil at the destination site relative to soil at the site of origin (eq. 3), where for controls, the SI at destination is based on comparison of SI among non-translocated control soils. The lines are linear regressions of RR-SI against temperature shift between destination and origin sites, with 95% confidence intervals. The dashed line (at RR-SI = 0) represents the response in RR-SI if no adaptation occurred. The rate of adaptation over time depended on whether soils were cooled or warmed: there was an effect of translocation time on the RR-SI under cooling (P = 0.02) but there was no effect under warming (*P* = 0.61; ANCOVA, Table S1). Based on the average slope under warming and

cooling together, the adaptive changes increased from 2 years (blue line) < 11 years (red line) < controls (black line) (insert).

Fig. 1.

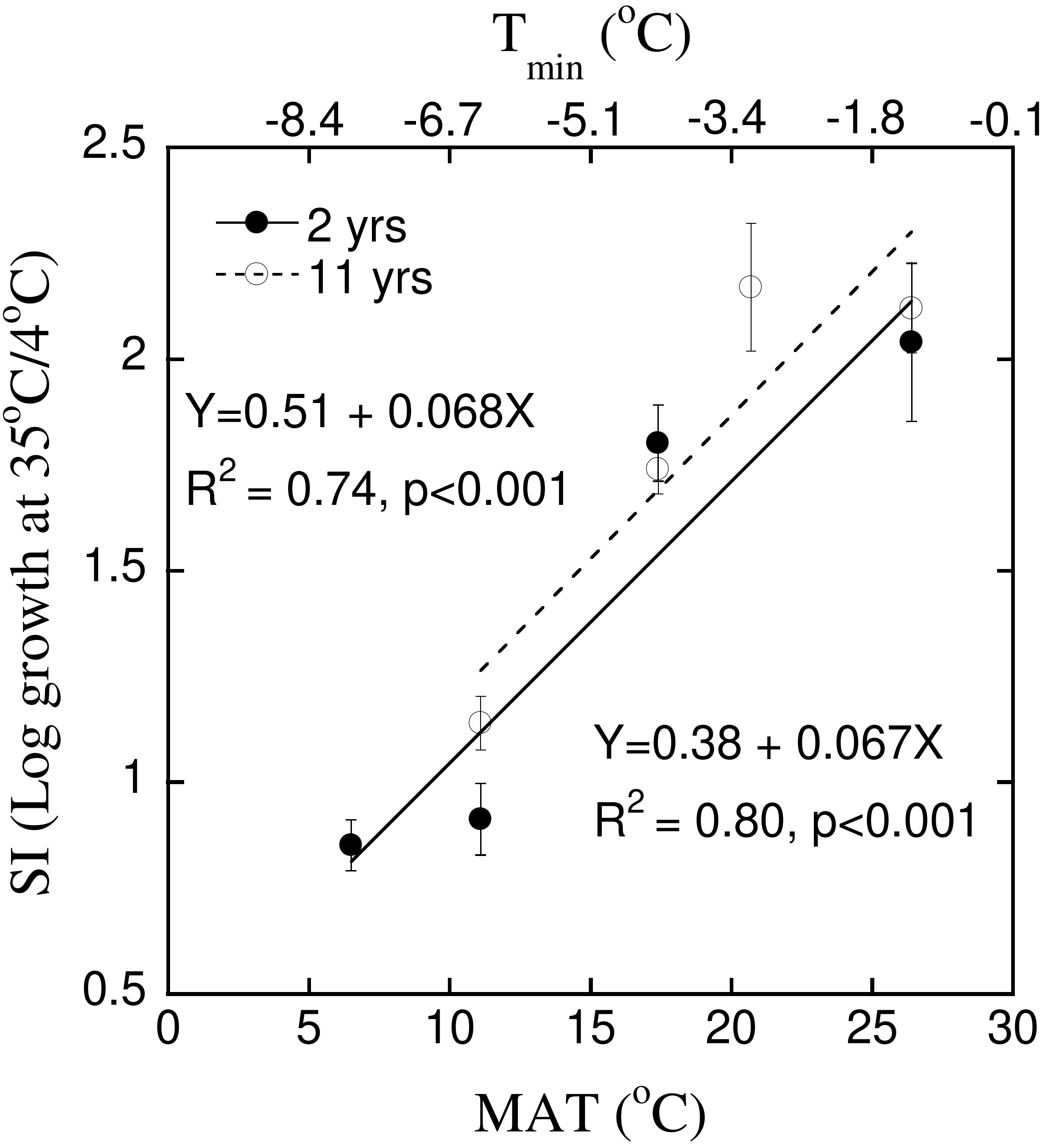

T_min (°C)
-8.4
-6.7
-5.1
-3.4
-1.8
-0.1
2 yrs
11 yrs
Y=0.51 + 0.068X
R² = 0.74, p<0.001
Y=0.38 + 0.067X
R² = 0.80, p<0.001
SI (Log growth at 35°C/4°C)
2.5
2
1.5
1
0.5
0
5
10
15
20
25
30
MAT (°C)

Fig. 2

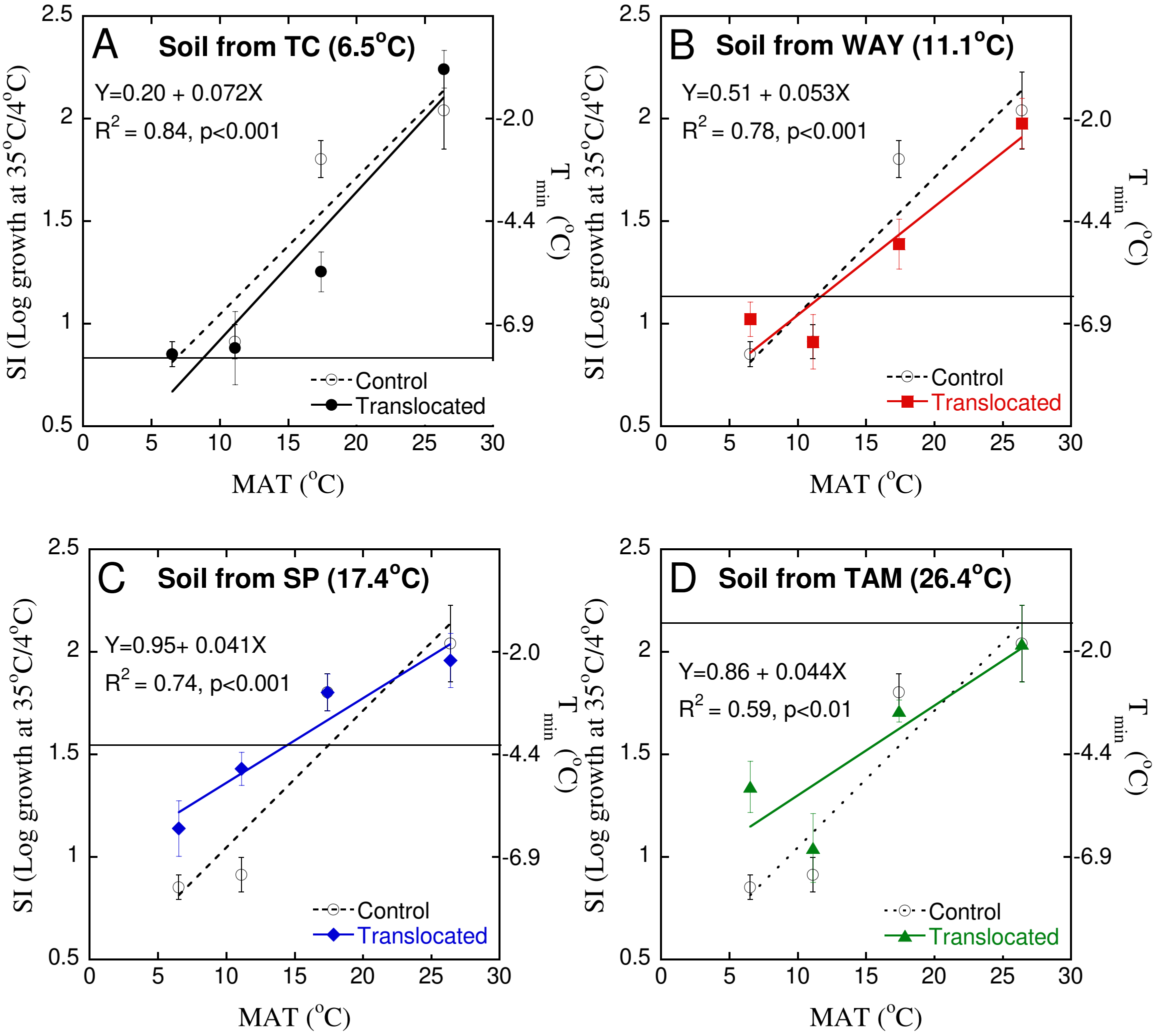

A
Soil from TC (6.5°C)
Y=0.20 + 0.072X
R² = 0.84, p<0.001
Control
Translocated
B
Soil from WAY (11.1°C)
Y=0.51 + 0.053X
R² = 0.78, p<0.001
Control
Translocated
C
Soil from SP (17.4°C)
Y=0.95+ 0.041X
R² = 0.74, p<0.001
Control
Translocated
D
Soil from TAM (26.4°C)
Y=0.86 + 0.044X
R² = 0.59, p<0.01
Control
Translocated
SI (Log growth at 35°C/4°C)
MAT (°C)
T min (°C)
0.5
1
1.5
2
2.5
0
5
10
15
20
25
30
-2.0
-4.4
-6.9

Fig. 3.

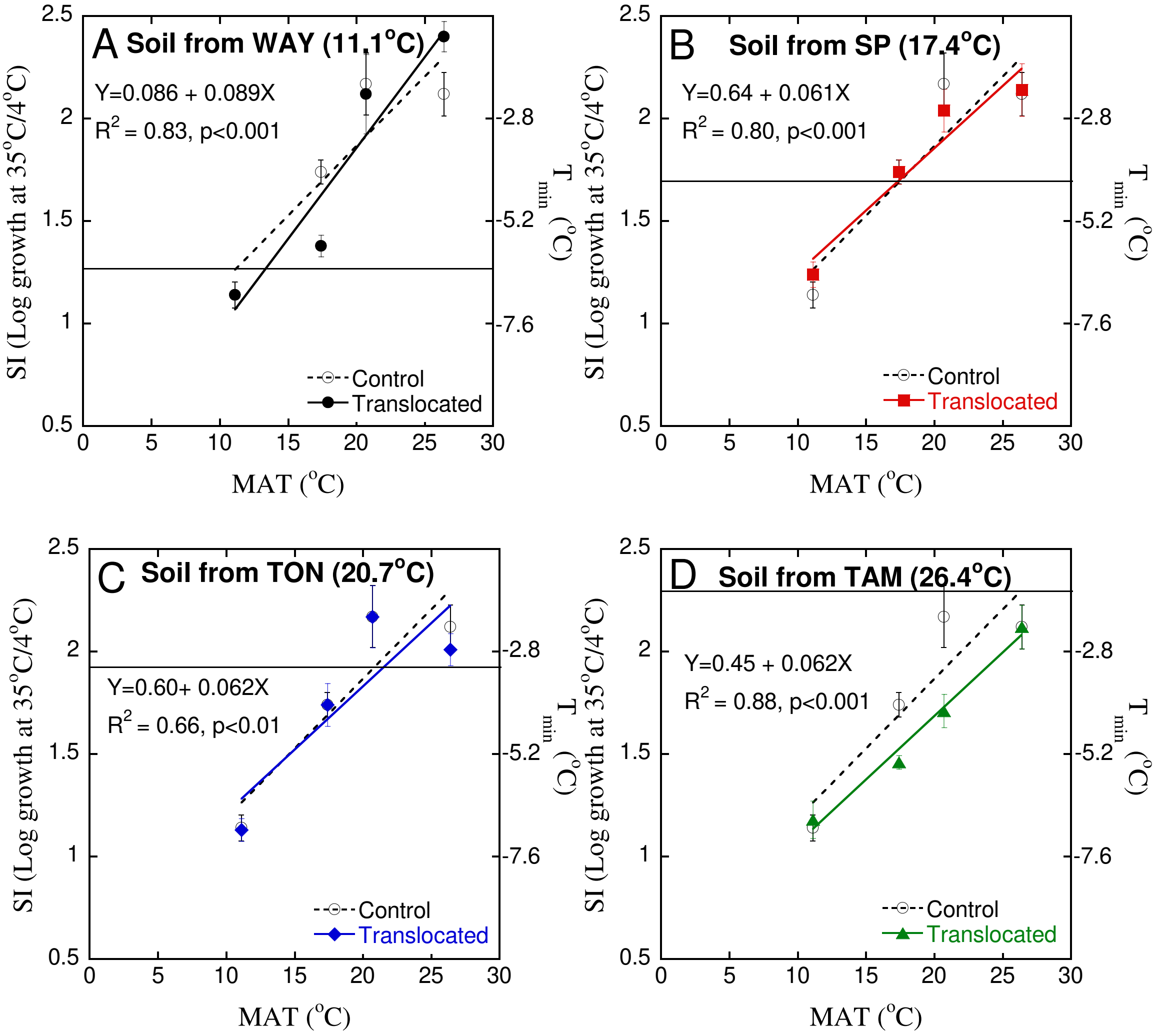
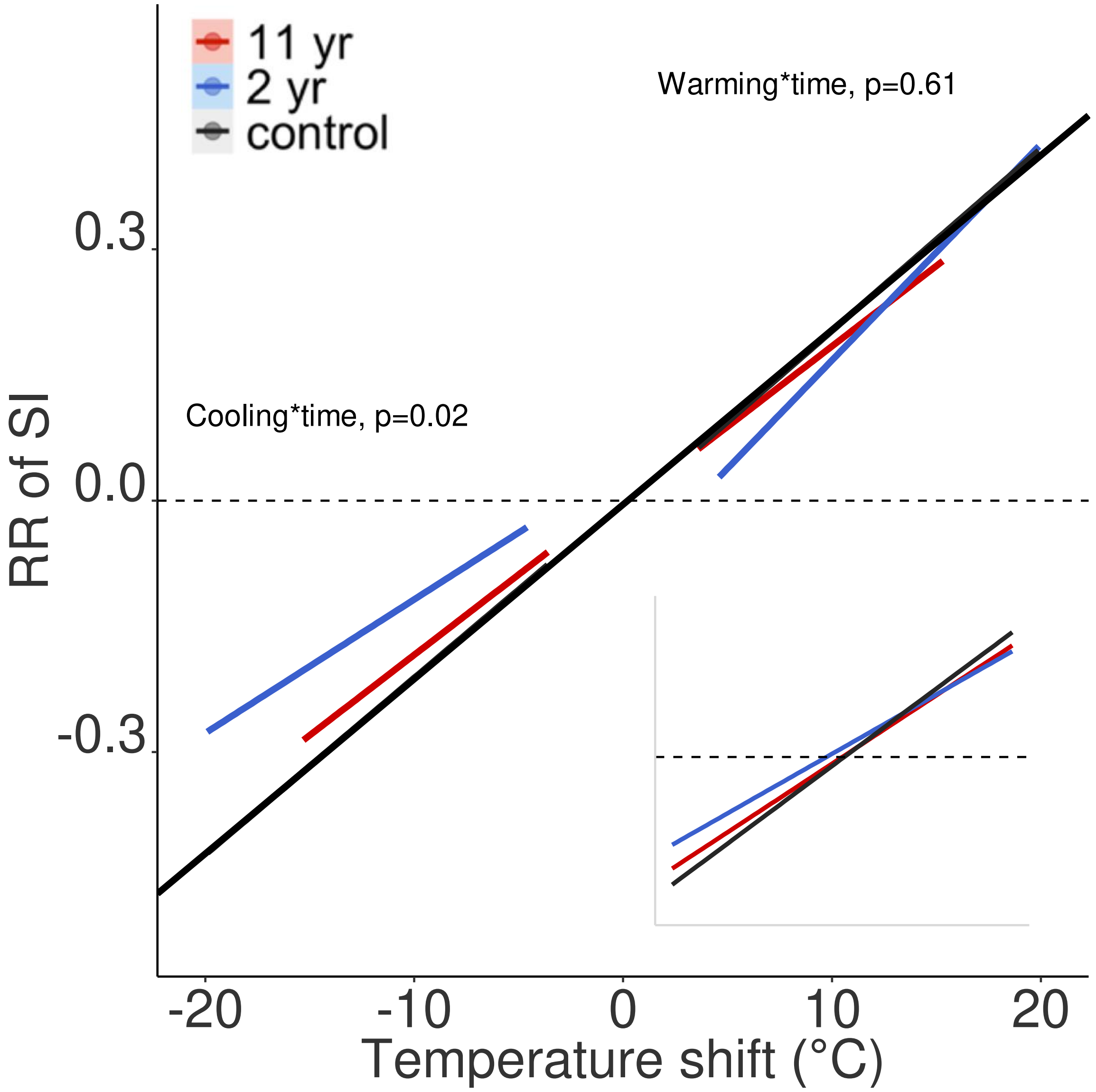

A Soil from WAY (11.1°C)
Y=0.086 + 0.089X
R2 = 0.83, p<0.001
B Soil from SP (17.4°C)
Y=0.64 + 0.061X
R2 = 0.80, p<0.001
C Soil from TON (20.7°C)
Y=0.60+ 0.062X
R2 = 0.66, p<0.01
D Soil from TAM (26.4°C)
Y=0.45 + 0.062X
R2 = 0.88, p<0.001
Control
Translocated
SI (Log growth at 35°C/4°C)
Tmin (°C)
MAT (°C)
0.5
1
1.5
2
2.5
-2.8
-5.2
-7.6
0
5
10
15
20
25
30

Fig. 4


11 yr
2 yr
control
Warming*time, p=0.61
Cooling*time, p=0.02
RR of SI
0.3
0.0
-0.3
-20
-10
0
10
20
Temperature shift (°C)