Title

Soil microbes and their response to experimental warming over time: A meta-analysis of field studies

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Authors

Romero-Olivares, AL
Allison, SD
Treseder, KK

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Abstract

Numerous field studies have found changes in soil respiration and microbial abundance under experimental warming. Yet, it is uncertain whether the magnitude of these responses remains consistent over the long-term. We performed a meta-analysis on 25 field experiments to examine how warming effects on soil respiration, microbial biomass, and soil microbial C respond to the duration of warming. For each parameter, we hypothesized that effect sizes of warming would diminish as the duration of warming increased. In support of our hypothesis, warming initially increased soil respiration, but the magnitude of this effect declined significantly as warming progressed as evidenced by the two longest studies in our meta-analysis. In fact, after 10 years of warming, soil respiration in warmed treatments was similar to controls. In contrast, warming effect sizes for fungal biomass, bacterial biomass, and soil microbial C did not respond significantly to the duration of warming. Microbial acclimation, community shifts, adaptation, or reductions in labile C may have ameliorated warming effects on soil respiration in the long-term. Accordingly, long-term soil C losses might be smaller than those suggested by short-term warming studies.

1. Introduction

To predict the effects of global warming on ecosystems, researchers have manipulated soil and air temperatures in numerous field experiments (Carey et al., 2016). Although some warming experiments have lasted over a decade (Dorrepaal et al., 2009; Melillo et al., 2011, 2002; Rousk et al., 2013), the majority have been shorter. Therefore, the long-term effects of field experimental warming on ecosystem functions have been challenging to examine. Here we focus on microbial responses to warming, because their contributions to soil CO_2 respiration can influence future trajectories of climate change (Wieder et al., 2013). In an earlier meta-analysis, Rustad et al. (2001) noted that warming generally increased soil respiration across 16 field studies. Nevertheless, at that time, these studies represented relatively short warming periods of six years or less. Whether soil respiration remains elevated or returns to baseline levels under longer-term warming has been subject to debate. Some studies have reported a decrease in warming effects over time (Luo et al., 2001; Melillo et al., 2002), whereas others have documented no significant change (Schindlbacher et al., 2011). Thus, an examination of the temporal trends in responses of ecosystems to warming should shed light on long-term feedbacks between soils and climate (Allison and Treseder, 2011; Pold and DeAngelis, 2013).

Warming might initially stimulate decomposition by enhancing the metabolism of decomposers, provoking increases in microbial CO_2 production (Lloyd and Taylor, 1994). This could lead to soil C losses, higher soil respiration rates, and an overall positive feedback to global warming (Jenkinson et al., 1991). However, this response can be transient (Luo et al., 2001). For example, in Prospect Hill at Harvard Forest, soil respiration rates in warmed plots were higher than those in the controls for the first few years, but the warming effect declined over time and eventually became non-significant (Giasson et al., 2013; Melillo et al., 2002). Several mechanisms could drive this pattern by altering microbial C use as warming proceeds (Allison et al., 2010b; Bradford et al., 2008; Frey et al., 2013; Pritchard, 2011; Rousk et al., 2012; Sierra et al., 2010). These include acclimation of individual microbes (Allison et al., 2010b; Crowther and Bradford, 2013; Malcolm et al., 2008; Tucker et al., 2013; Yuste et al., 2010), shifts in microbial communities (Bárcenas-Moreno et al., 2009; Luo et al., 2014; Rousk et al., 2012; Treseder et al., 2016; Wei et al., 2014), and evolutionary adaptation of microbial populations to higher temperatures (Romero-Olivares et al., 2015). In addition, labile C pools in the soils could become depleted owing to higher microbial activity (Bradford et al., 2008; Eliasson et al., 2005; Kirschbaum, 2004; McHale et al., 1998). These mechanisms are non-exclusive, and their influence may vary among seasons (Contosta et al., 2015), ecosystems, and across time scales.

To improve predictions of long-term consequences on soil C, we must determine whether warming effect sizes on soil respiration and microbial abundance diminish over time, and how quickly this occurs. Meta-analysis is a rigorous statistical tool that can address these questions; it combines quantitative data from previously published studies to reach conclusions with greater statistical power. For example, several meta-analyses have determined that experimental warming generally increases soil respiration, soil microbial abundance, net N mineralization, decomposition, soil microbial C and N, net primary production, and photosynthesis (García-Palacios et al., 2015; Lu et al., 2013; Rustad et al., 2001; Zhang et al., 2015). A recent meta-analysis also showed that the temperature sensitivity of soil respiration does not change with experimental warming in many ecosystems (Carey et al., 2016). Although these meta-analyses have contributed greatly to our knowledge of the response of ecosystems to warming, none has focused on trends over time.

Toward this end, we used meta-analysis to analyze the effect of field experimental warming over time on soil respiration, fungal biomass, bacterial biomass, and soil microbial C. We chose these parameters because they govern large ecosystem-scale processes affected by global warming, such as CO_2 inputs to the atmosphere through soil C losses (Allison et al., 2010a; Šantručková and SiraŠicraba, 1991; Wang et al., 2003). We compiled data from field-based experimental warming studies that varied in duration from 1 to 15 years. We asked, how do warming effects change as duration of warming increases? We hypothesized that warming effects on each parameter would diminish as duration of warming increased.

2. Materials and methods

2.1 Literature survey

We searched the ISI Web of Science and Google Scholar for published papers reporting the response of soil fungal and bacterial biomass, soil respiration, and soil microbial C to experimentally warmed soils and its respective controls. We performed separate literature searches for each of the following terms: “soil microb* experimental warming”, “soil fung* experimental warming”, “soil bacter* experimental warming”, “soil resp* experimental warming”. In addition, we manually searched for papers published in previous meta-analyses (Arft et al., 1999; García-Palacios et al., 2015; Lu et al., 2013; Rustad et al., 2001; Wu et al., 2011; Zhang et al., 2015) and review papers (Allison and Treseder, 2011; Giasson et al., 2013; Pold and DeAngelis, 2013). To complete our data collection, we used the geographic coordinates of the experimental plots as search terms, to account for all published studies conducted in the same experimental plots but missed by our initial search terms. Our literature search included papers published (or accepted for publication) between January 1994 and July 2015. We excluded studies manipulating factors other than temperature, unless a split-plot design was used and a single subplot for the temperature effect was present.

A total of 52 studies met our search criteria, representing 25 field warming experiments across 11 different types of ecosystems, and a total duration of warming ranging from 1 to 15 years (Table 1). Measurements that were taken from the same unique set of field plots were considered as belonging to the same experiment.

2.2 Data acquisition

For each experiment, we recorded the mean, standard deviation (SD), standard error (SE), and sample size (n), of both warmed and control plots, for fungal and bacterial biomass, soil respiration, and soil microbial C. The data were extracted directly from tables, published supplementary material, and from graphs using Plot Digitizer 2.6.6 (http://plotdigitizer.sourceforge.net). In addition, we recorded the type of warming (e.g., infrared heater, open top chamber, closed top chamber, buried heating cables), the duration of warming, and other information such as type of ecosystem, mean annual temperature, mean annual precipitation, magnitude of soil warming, change in soil moisture, and geographic coordinates (Table 1). If SEs were presented instead of SDs, we used the formula SD = SE ($n^{1/2}$) to obtain SDs. Any unidentified error bars were assumed to represent SE (Peng et al., 2014).

2.2.1 Soil respiration, fungal & bacterial biomass, and soil microbial C

Soil respiration was measured in all studies by an in situ CO_2 flux chamber, with one exception where authors used a gas headspace with isotope mass spectrometer. To measure fungal biomass, authors used a variety of techniques; total phospholipid fatty acids (PLFA) analysis was the most common (19 out of 21 experiments used this method). The remaining two experiments used either total fatty acids methyl esters (FAME) or microscopy (i.e. hyphal lengths). Similarly, bacterial biomass was quantified through PLFA, in all but one experiment where microscopy was the preferred quantification method. Moreover, soil microbial C was measured through chloroform fumigation extraction in all studies.

2.3 Statistics

We used meta-analysis to determine warming effects on soil respiration, fungal biomass, bacterial biomass, and soil microbial C. For each experiment and each response variable, we calculated the effect size as the natural logarithm of the response ratio (lnR). First, we averaged all sampling time points per year within each experimental plot, to remove seasonal-level variation. Then, with the averaged data, we calculated the response ratio of the mean of the treatment group (warmed) divided by the mean of the control group (unwarmed). An lnR of 0 indicates that warming had no effect on the response variables. We also calculated the variance (V_R) using the means, n, and SD of both treatments (Suppl. Table 1). To calculate lnR and V_R, we used MetaWin software (Rosenberg et al., 2001).

We tested our hypothesis for each soil parameter separately. In each case, we used a linear mixed-effects model fitted with a restricted maximal likelihood (REML) approach (“nlme” R package) (R Core Development Team, 2009) (Suppl. R code). This structure allowed us to account for non-independence of repeated measurements within experiments, by essentially nesting measurements within experiment. Experiments were defined as unique sets of field plots. For each test, warming effect size (lnR) of soil respiration (or fungal biomass, bacterial biomass, or microbial C) was the dependent variable, duration of warming was the independent variable, and experiment ID was a random effect. In separate analyses, we tested if the magnitude of soil warming (or change in soil moisture) also influenced the effect size of soil respiration. Specifically, we tested whether lnR (dependent variable) was significantly related to magnitude of warming, duration of warming, or the interaction between magnitude and duration (independent variables). Similarly, we tested for significant relationships between lnR (dependent variable) and change in soil moisture or duration of warming (independent variables). In the latter case, we did not test for an interaction between change in soil moisture and duration of warming, because substantial (>10%) declines in soil moisture were only reported for studies that lasted 6 years or less. For all analyses, data were weighted by the reciprocal of V_R, which is a standard approach for meta-analyses (Gurevitch and Hedges, 1999). Significant decreases in lnR with duration of warming would support our hypothesis.

3. Results

Soil respiration was measured in 19 experiments. In support of our hypothesis, warming effect sizes declined significantly with duration of warming (Fig. 1, t = –2.230, P = 0.031). Initially, warming increased soil respiration by 46 ± 8% across studies (y-intercept of linear mixed-effects model, P < 0.001). Yet, the magnitude of this warming effect decreased over time, so that after 10 years, soil respiration in the warmed treatments was near that of the controls. The attenuation of the warming effect is also evident within individual studies. Specifically, in all but one of the studies with ≥4 years of measurements (i.e. MRS, Niinistö et al., 2004), warming effect sizes tended to decline over time (Fig. 2). When magnitude of warming and duration of warming were both included as independent variables, magnitude of warming was not significantly related to lnR of soil respiration (t = −0.471, P = 0.640), nor was there a significant interaction between magnitude and duration of warming (t = 1.732, P = 0.091); duration of warming remained significant (t = –2.723, P = 0.010). Likewise, change in soil moisture did not significantly influence lnR of soil respiration (t = 1.507, P = 0.1514), and duration of warming still had a significant effect (t = -2.508, P = 0.016) when soil moisture was included in the model.

Fungal and bacterial biomass was reported in 10 and 9 experiments respectively, ranging from 1 to 13 years after warming began. There was no indication, however, of significant declines in effect size with duration of warming for either fungi (Fig. 3, t = –1.529, P = 0.157) or bacteria (Fig. 4, t = –0.109, P = 0.916). Microbial C was measured at 1 to 15 years of warming, across nine experiments. Again, effect sizes of microbial C did not decrease with duration of warming (Fig. 5, t = 1.464, P = 0.169). As such, we rejected our hypothesis with respect to fungal biomass, bacterial biomass, and microbial C.

4. Discussion

In our meta-analysis of field experiments, we found that warming effects on soil respiration diminished significantly over time, with declines most evident after a decade of warming (Fig. 1). Although increases in soil respiration are often observed within the first few years of warming (Flanagan et al., 2013; Melillo et al., 2002; Niinistö et al., 2004; Peng et al., 2015; Peterjohn et al., 1994), our results suggest that this response is transient. We found two lines of evidence for attenuation of warming effects on soil respiration. First, effect sizes declined significantly with warming duration when data from all studies were combined. Second, this trend was apparent within individual studies in which soil respiration had been measured over four years or more (Fig. 2). In fact, despite temporal variations, in seven of the eight studies that met this criterion, the warming effect size on soil respiration tended to decrease with time. In fact, the study in which soil respiration increased after ≥4 years, authors acknowledged that in the fourth year of warming, measurements were taken in warmer days compared to year two and three. This difference amplified the results between control and treatment “such that the response in the fourth year became equivalent to that of the first” (Niinistö et al., 2004). Altogether, our results suggest that long-term effects of warming on soil C dynamics may be weaker than suggested by initial responses.

Our meta-analysis is the first to focus on changes in warming effect sizes on soil respiration throughout the duration of field experiments lasting more than 10 years. Previously, Rustad et al. (2001) noted that the mean effect size of warming on soil respiration tended to be smaller (albeit non-significantly) in studies that lasted more than three years. Nevertheless, at that time, the longest studies included in that comparison were five years. Lu and collaborators (2013) contrasted effect sizes on soil respiration for short-term (<5 years) versus intermediate-term (5–10 years) studies. They reported that the mean effect size of soil respiration did not differ significantly between the two categories. Moreover, Zhou et al. (2016) found no significant relationship between warming duration and effect size of soil respiration in studies with ≤6 years of warming. In the current meta-analysis, the decrease in effect sizes for soil respiration was most striking after 10 years of warming (Fig. 1), which highlights the importance of longer-term studies. The attenuation in effect size of warming is especially noticeable in the two longest studies, Prospect Hill (PH) (Melillo et al., 2002) and Kessler’s Farm Field (KFF) (Belay-Tedla et al., 2009; Li et al., 2013; Luo et al., 2009; Wan et al., 2005; Zhang et al., 2005) (Fig. 2). In both cases, effect sizes remained positive during the first 10 years; negative effect sizes were only observed after 10 years. Regarding microbial abundance, meta-analyses by García-Palacios et al. (2015), Wang et al. (2014), and Zhang et al. (2015) detected no significant effects of duration on effect sizes for fungal abundance, bacterial abundance, microbial biomass, or microbial C. These findings are similar to ours.

What might have driven this attenuation of the warming effect on soil respiration? Researchers have previously suggested that acclimation of soil microbes (Bradford et al., 2010; Crowther and Bradford, 2013; Malcolm et al., 2008; Tucker et al., 2013; Yuste et al., 2010), shifts in microbial community composition (Luo et al., 2014; Treseder et al., 2016; Wei et al., 2014), evolutionary adaptation of microbes (Romero-Olivares et al., 2015; Wallenstein and Hall, 2012), or depletion of labile C (Bradford et al., 2008; Eliasson et al., 2005; Kirschbaum, 2004; McHale et al., 1998) can be responsible. Any combination of these mechanisms could have influenced the temporal trends in soil respiration. Even though mean effect sizes for fungal biomass, bacterial biomass, and microbial C did not shift significantly with warming duration (Figs. 3–5), we cannot rule out acclimation, community shifts, or evolutionary adaptation in the microbial community, since each could alter microbial respiration rates without changing biomass.

Root respiration is a component of soil respiration rates reported in studies in our meta-analysis. Although most studies do not isolate the response to warming of the different components of soil respiration (i.e., microbial respiration vs root respiration), some short-term studies have reported decreases in root respiration rates in response to warming (Zong et al., 2013) or no significant responses (Vogel et al., 2014). Nevertheless, it is challenging to partition root versus microbial respiration in a manner consistent enough to support a meta-analysis (Kelting et al., 1998; Sapronov and Kuzyakov, 2007). Consequently, we cannot discard the possibility that changes in the response of root respiration might have contributed to decreases in the response of soil respiration to long-term warming.

Because warming can increase evapotranspiration, it is possible that soil respiration and microbial biomass responses were affected by soil drying (Verburg et al., 1999). Although effects of soil moisture on microbial community composition and functioning might be an important factor, we did not observe any significant relationships between soil moisture change under warming and the soil respiration response, either on average or over time. Several studies have suggested a link between warming, reductions in soil moisture, and reductions in soil respiration at specific sites (Allison and Treseder, 2008; Bronson et al., 2008; Liu et al., 2009; Suseela et al., 2012) but this mechanism was not consistent across our larger dataset. Therefore soil drying does not appear to play a major role in the attenuation of soil respiration response to warming.

Our meta-analysis demonstrates that the increases previously reported in soil respiration in response to short-term warming (Bokhorst et al., 2007; Contosta et al., 2011; Flanagan et al., 2013; Niinistö et al., 2004; Schindlbacher et al., 2012; Wan et al., 2005) might be ephemeral as previously suggested (Eliasson et al., 2005; Luo et al., 2001; Oechel et al., 2000). Collectively, our results and these ideas suggest that ecosystems will lose soil C most quickly in the first several years after warming, and more slowly thereafter. Therefore, release of CO_2 to the atmosphere may not be as extreme as suggested by short-term warming experiments. Nevertheless, our study was restricted by the scarcity of long-term warming experiments and equivocal responses of microbial biomass. As current warming experiments progress, repeated measurements of soil respiration and microbial abundance would be highly valuable.

4.1 Conclusions

Our meta-analysis shows that soil respiration decreases after long-term warming and suggests that soil C losses might not be as substantial as previously suggested by short-term warming experiments. We suggest that microbial community shifts, evolutionary adaptation, and/or depletion of labile soil C might be contributing to the attenuation of the effect size on soil respiration over time. These mechanisms should be further explored in laboratory and field settings, especially in long-term field warming experiments. We emphasize the importance of long-term warming studies, because 1) declines in mean effect sizes on soil respiration were most evident after 10 years, 2) short-terms studies might be misinterpreted by temporal variations, and 3) long-term studies provide more data to partition temporal from long-term trends. Future research should incorporate microbial parameters obtained from long-term warming experiments to provide concise projections of the effects of climate change on the global C cycle.

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Figure legends

Figure 1. Effect sizes of soil respiration versus duration of warming, as the natural log of warming:control treatments (lnR). Where lnR is less than 0, soil respiration decreased with warming. Where lnR is greater than 0, soil respiration increased. Effect sizes decreased significantly with duration of warming, across all studies. Symbols are experiment IDs (Table 1). Line is best fit.

Figure 2. Effect sizes of soil respiration versus duration of warming for experiments with measurements in at least four years. Letters indicate experiment IDs (Table 1). Lines are best-fit.

Figure 3. Effect sizes of fungal abundance versus duration of warming, as the natural log of warming:control treatments (lnR). Where lnR is less than 0, fungal abundance decreased with warming. Where lnR is greater than 0, fungal abundance increased. There was no significant relationship between effect size and duration of warming. Symbols are experiment IDs (Table 1).

Figure 4. Effect sizes of bacterial abundance versus duration of warming, as the natural log of warming:control treatments (lnR). Where lnR is less than 0, bacterial abundance decreased with warming. Where lnR is greater than 0, bacterial abundance increased. There was no significant relationship between effect size and duration of warming. Symbols are experiment IDs (Table 1).

Figure 5. Effect sizes of microbial C versus duration of warming, as the natural log of warming:control treatments (lnR). Where lnR is less than 0, microbial C decreased with warming. Where lnR is greater than 0, microbial C increased. There was no significant relationship between effect size and duration of warming. Symbols are experiment IDs (Table 1).

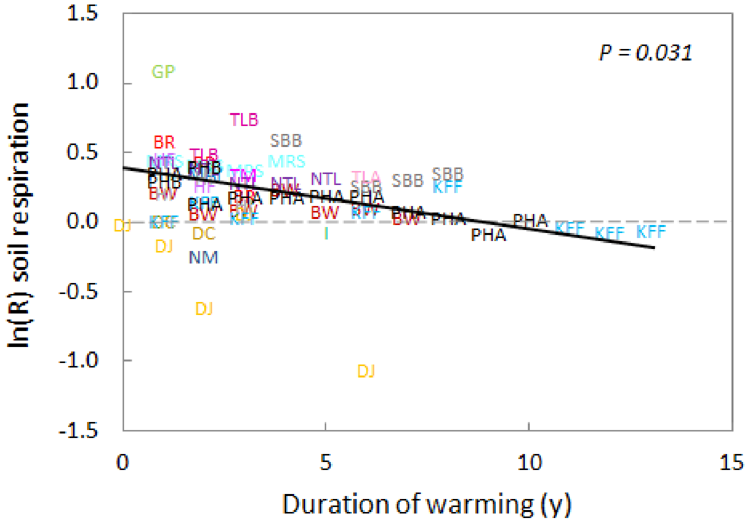
P = 0.031
ln(R) soil respiration
Duration of warming (y)
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
0
5
10
15
GP
TLB
BR
SBB
MRS
NTL
TLA
PHA
KFF
BW
HF
DJ
DC
NM
I

Figure 1.

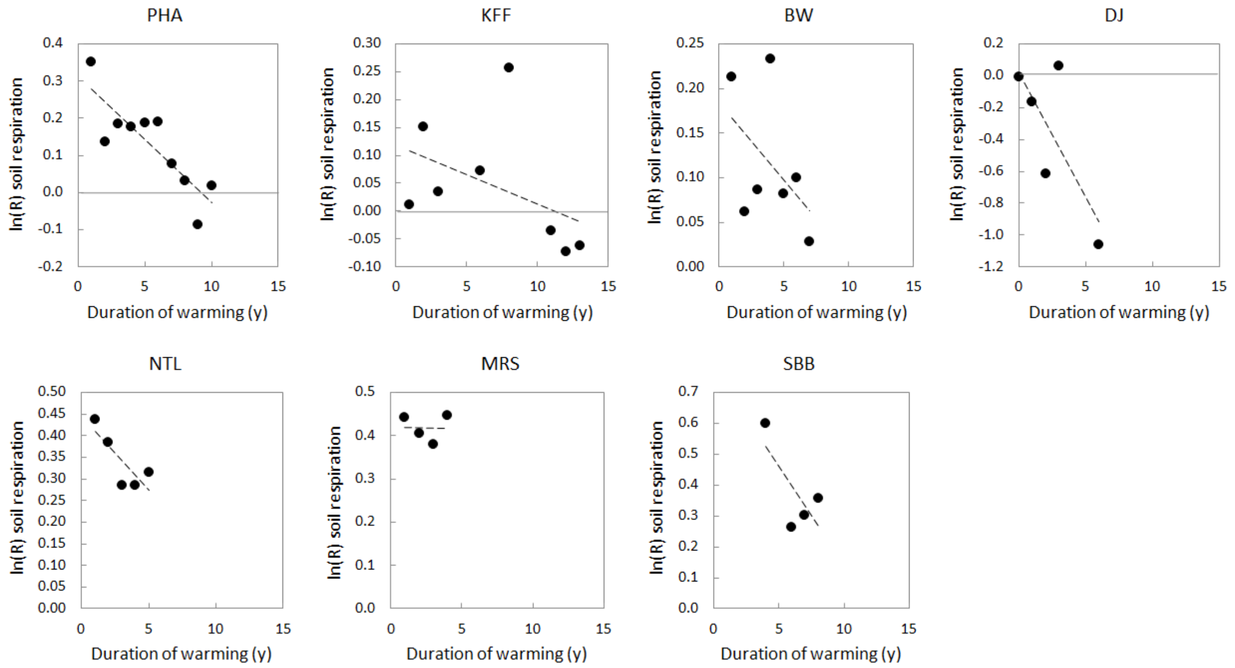
PHA
KFF
BW
DJ
NTL
MRS
SBB
ln(R) soil respiration
Duration of warming (y)
0
5
10
15

Figure 2.

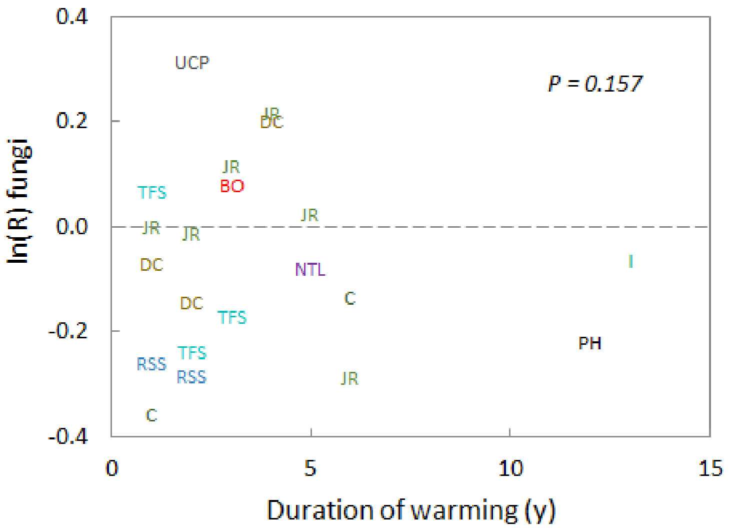
P = 0.157
0.4
0.2
0.0
-0.2
-0.4
0
5
10
15
ln(R) fungi
Duration of warming (y)
UCP
JR
DC
JR
BO
TFS
JR
JR
JR
DC
NTL
I
C
DC
TFS
PH
TFS
RSS
RSS
JR
C

Figure 3.

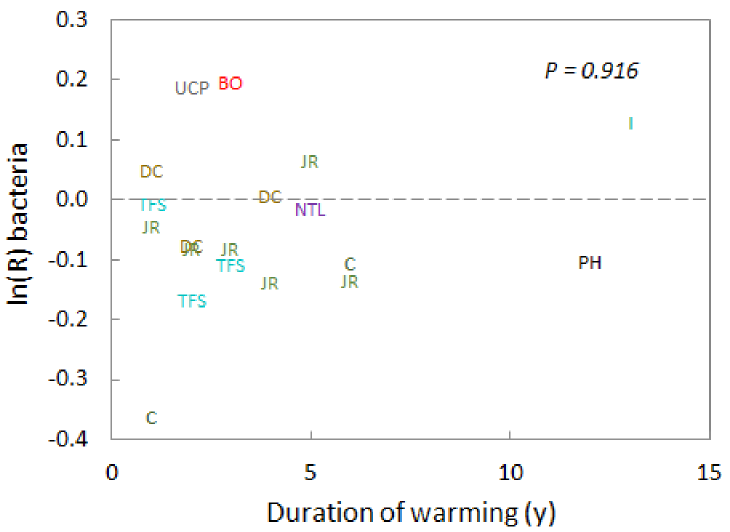
P = 0.916
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.4
ln(R) bacteria
UCP
BO
I
JR
DC
TFS
DC
NTL
JR
DC
JR
JR
TFS
C
PH
JR
JR
TFS
C
0
5
10
15
Duration of warming (y)

Figure 4.

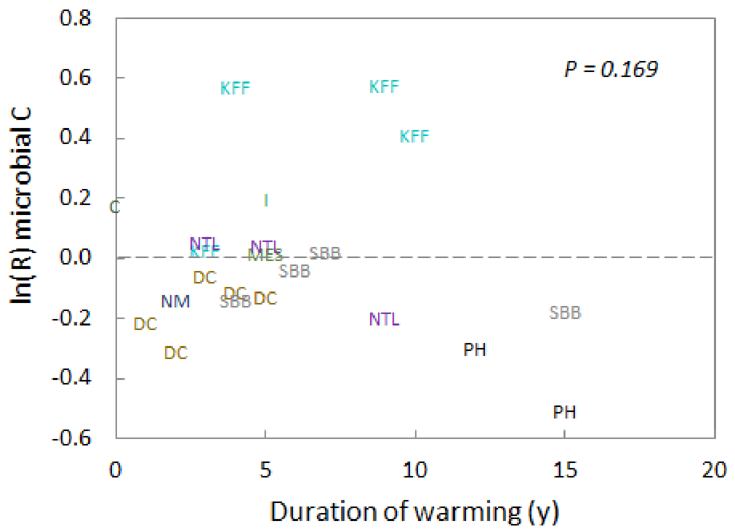
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
0
5
10
15
20
ln(R) microbial C
Duration of warming (y)
P = 0.169
KFF
KFF
KFF
C
I
NTL
KFF
NTL
MES
SBB
DC
SBB
NM
DC
SBB
DC
DC
DC
NTL
SBB
PH
PH

Figure 5.