Seasonal climate variations promote bacterial α-diversity in soil

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Abstract

Ecological theory suggests that temporal environmental fluctuations can contribute greatly to diversity maintenance. Given bacteria's short generation time and rapid responses to the environmental change, seasonal climate fluctuations are very likely to play an important role in maintaining the extremely high α-diversity of soil bacterial community, which has been unfortunately neglected in previous studies. Here, with in-depth analyses of two previously published high-quality soil bacterial datasets at global scale, we found that soil bacterial α-diversity was positively correlated with both seasonal variations of temperature and precipitation. Furthermore, piecewise structural equation models showed that seasonal variations of temperature or precipitation directly promoted soil bacterial α-diversity in each dataset. Our findings implied that fluctuation-dependent mechanisms of diversity maintenance presumably operate in soil bacterial communities and highlighted that both the average values and temporal variations of abiotic environmental factors should be considered when investigating soil bacterial community composition in the future.

The extraordinarily high α-diversity of soil bacterial communities has fascinated and puzzled microbial ecologists [1, 2]. In contrast to the considerable advances in characterizing soil bacterial biogeographic patterns across spatial and environmental gradients (e.g. [3, 4]), little attempt has been made to infer the underlying mechanisms of diversity maintenance. The high spatial heterogeneity of soil was generally thought as an important factor in maintaining bacterial α-diversity [5]; surprisingly, temporal environmental fluctuations promoting diversity maintenance firstly suggested by Hutchinson was rarely mentioned, which is one of the most influential ideas in community ecology [6, 7]. The fluctuation-dependent coexistence mechanisms are particularly important for micro-organisms due to their short generation time and rapid responses to environmental changes [8, 9]. Temporal changes in temperature and precipitation can significantly alter soil physiochemical and nutritional status, which jointly enhance temporal environmental fluctuations in soil, and drive the seasonal species turnover in bacterial community [10]. However, in nearly all of the bacterial biogeographic studies, only the mean annual temperature (MAT) and annual precipitation (AP) were chosen as climatic predictors of soil bacterial community diversity and composition, whereas seasonal climate variations were unfortunately neglected. Here we tested the prediction that seasonal climate variations promote soil bacterial α-diversity derived from the fluctuation-dependent coexistence theory, with two previously published surveys covering wide geographic and climatic gradients: global topsoil microbiome (hereafter "topsoil data") [4] and global soil atlas (hereafter "atlas data") [11]. Details of data acquisition, processing, and statistical analyses were provided in supplementary methods.

The climate data were obtained from the WorldClim database (http://www.worldclim.org), whereby the standard deviation of monthly mean

temperature and the coefficient of variation of monthly precipitation were used to represent temperature seasonality (TS) and precipitation seasonality (PS), respectively. Soil bacterial α-diversity was measured as the number of observed phylotypes (hereafter richness). As predicted, richness of soil bacteria significantly increased with TS and PS in both datasets (Fig 1a-d; linear regression, $p < 0.05$). Piecewise structural equation model was then fitted to infer how geographic (absolute attitude), climatic (MAT, AP, TS, PS) variables and soil physiochemical properties (pH and C/N ratio, the most important two soil physiochemical factors in determining bacterial diversity and composition) interact to determine richness of soil bacteria. The modeling results demonstrated significant direct effect of PS (Fig 2a; standardized coefficient $\beta = 0.206$, $p < 0.001$) in promoting richness of soil bacteria in topsoil data, and TS (Fig 2b; standardized coefficient $\beta = 0.188$, $p < 0.001$) in atlas data. Note that the average of TS was significantly larger in atlas data, whereas the average of PS was significantly larger in topsoil data (Fig 1e, f; Mann-Whitney test, $p < 0.001$). It is highly possible that TS and PS simultaneously promote soil bacterial α-diversity, but their effects are more likely to be detected when samples with high levels of seasonal variations are included.

Theoretically, there are two classes of fluctuation-dependent coexistence mechanisms: the storage effect and relative nonlinearity of competition [7, 9]. The storage effect mediates coexistence via temporal niche partitioning [7], and its operation requires that (1) species differ in their responses to environments, which results in (2) the relative strength of interspecific and intraspecific competition varying with fluctuating environments; and that (3) there are mechanisms buffering population from extinction under unfavorable conditions [7], such as a variety of physiological stress-resistance and dormancy mechanisms of soil bacteria [12]. There

has been much experimental evidence that soil bacteria show diverse responses to moisture and temperature gradients. For example, a collection of soil bacterial isolates exhibited a wide range of responses to moisture gradient, and the derived niche parameters suggested a potential of coexistence via partitioning the moisture niche axis [13]. In addition to dry- and wet-adapted bacteria, stress-tolerant and opportunistic strategies of soil bacteria in response to drought or raining events were also discovered, as well as sensitive taxa [12, 14]. Likewise, both warm- and cold-responsive taxa were identified [15], and soil bacterial communities can rapidly diverge under contrasting experimental temperature treatments [16]. Besides evidence strongly supporting differential responses to moisture and temperature (requirement 1) discussed above, repeated reports of seasonal turnover in soil bacterial community structure (e.g. [10]) implied altered competitive intensities among soil bacteria under fluctuating environments (requirement 2); although distinguishing whether it is due to the fluctuating temperature and moisture *per se*, and/or the accompanying seasonal changes in availability of various resources was difficult. So far, rigorously testing of the storage effect has been restricted to simplistic microcosms [17, 18]; although being presumably important, its role in maintaining soil bacterial α-diversity in natural system remains unexamined yet.

By contrast, relative nonlinearity of competition might not be the major mechanism responsible for the promoting effect of seasonal climate variations on the soil bacterial α-diversity. Coexistence via relative nonlinearity of competition is based on that the per capita growth rates of species are different nonlinear functions of limiting resource [7, 8, 19]. Such nonlinearity can result in the fluctuation of limiting resource, and the stable coexistence can achieve when each species is disadvantaged relative to the others in the fluctuation environment caused by itself, but not

necessarily requires fluctuation of external conditions [7, 8, 19]. On the other hand, previous modeling investigations emphasizing the importance of relative nonlinearity of competition merely focused on microorganisms in homogenous aquatic systems [8, 9], and their implications cannot be directly generalized to the soil environment with high spatial heterogeneity, where the resources are not simultaneously accessible to all species.

In conclusion, our findings supported the idea that seasonal temperature and precipitation variations promote soil bacterial α-diversity via fluctuation-dependent mechanisms of diversity maintenance. Our study benefited from applying classic ecological theories to interpret pattern and get mechanistic insight [20], and highlighted the importance of considering both the average values and temporal variations of abiotic environmental factors to understand the soil bacterial community composition. Further experimental studies designed to investigate the specific coexistence mechanisms will shed new light on the diversity maintenance of soil bacterial communities in the future.

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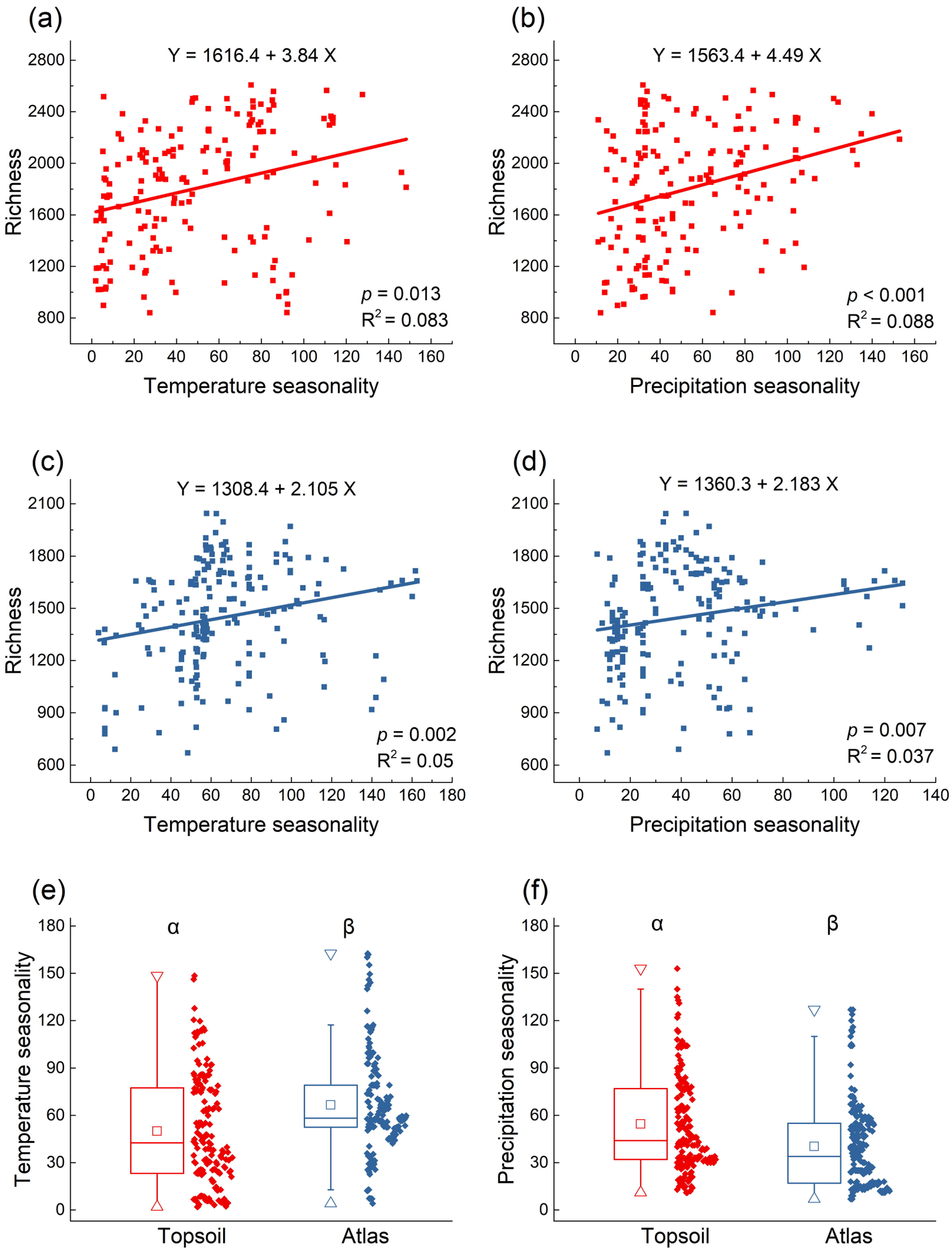
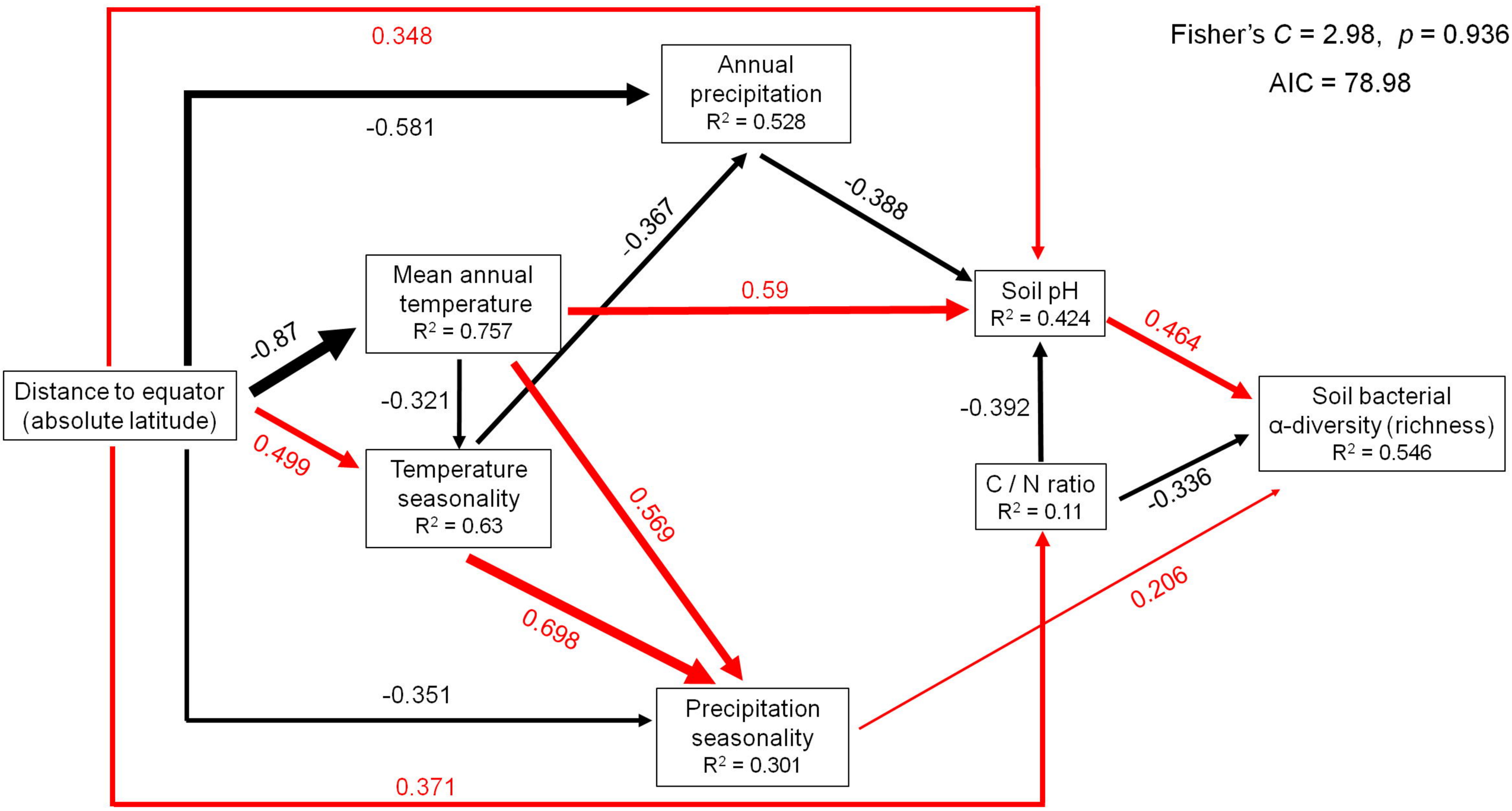
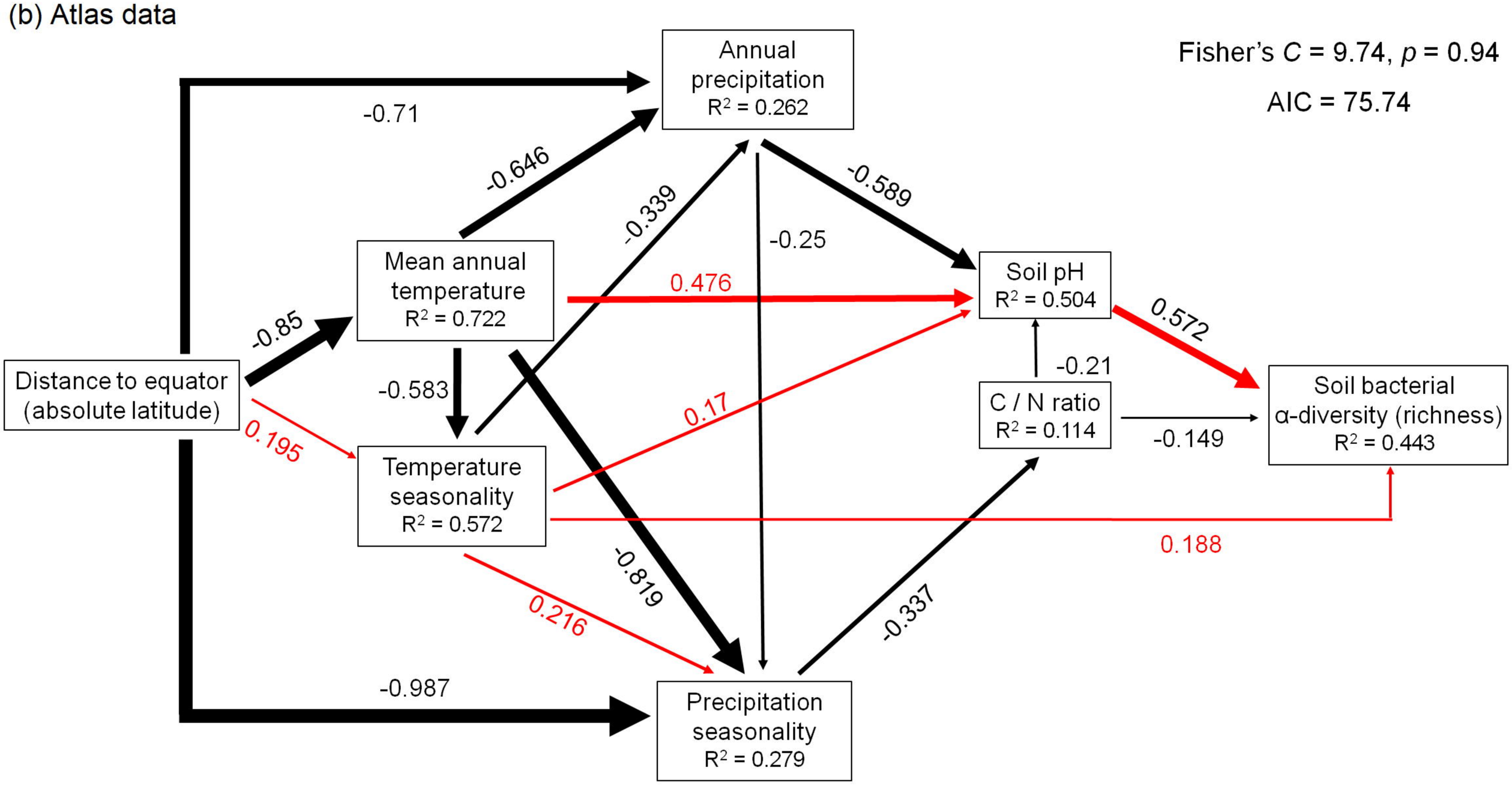
Figure legends

Fig 1 The relationships between soil bacterial richness (the number of observed phylotypes) and temperature (a, c) or precipitation seasonality (b, d), with the extent of climatic seasonality captured (e, f) in topsoil and atlas data. The colors represent different datasets (topsoil data: red, atlas data: blue). In panels (e, f), the lower and upper ends of the boxes represent 25% and 75% of the range, respectively; lines in the boxes indicate medians; triangles indicate maximums and minimums; squares indicate mean values; and whiskers represent ±1.5 × the interquartile range (IQR, defined as the upper quartile minus the lower quartile); different letters denote significant differences in climatic seasonality between two datasets (Mann-Whitney test, $p < 0.001$).

Fig 2 Structural equation models (piecewise SEM) of geographic (absolute latitude), climatic (mean annual temperature, annual precipitation, temperature seasonality, precipitation seasonality) variables, and soil physiochemical properties (pH, C/N ratio) as predictors of soil bacterial richness for topsoil data (a) and atlas data (b). Red arrows represent positive paths, and black arrows represent negative paths; only significant paths were shown ($p < 0.05$). Standardized effect sizes of path coefficients were reported and indicated by path thickness. Shipley's test of directed separation: Fisher's C statistic (if $p > 0.05$, then there are no missing associations and the model reproduces the data well) and AIC were used to evaluate the overall fit of the model. Details of model evaluation and coefficients estimation were provided in supplementary methods and results.


(a)
Y = 1616.4 + 3.84 X
Richness
Temperature seasonality
p = 0.013
R2 = 0.083
(b)
Y = 1563.4 + 4.49 X
Richness
Precipitation seasonality
p < 0.001
R2 = 0.088
(c)
Y = 1308.4 + 2.105 X
Richness
Temperature seasonality
p = 0.002
R2 = 0.05
(d)
Y = 1360.3 + 2.183 X
Richness
Precipitation seasonality
p = 0.007
R2 = 0.037
(e)
α
β
Temperature seasonality
Topsoil
Atlas
(f)
α
β
Precipitation seasonality
Topsoil
Atlas

(a) Topsoil data



(b) Atlas data