the western Pacific (~25% Pacific volume), although there are indications that similar trends extended farther east (*15*). The modern rate of Pacific OHC change is, however, the highest in the past 10,000 years (Fig. 4 and table S3).

The current response of surface temperatures to the ongoing radiative perturbation is substantially higher than the response of the ocean's interior, due to the long whole-ocean equilibration time. However, on longer time scales the oceanic response is likely different, as seen in our records where past changes in IWT were much larger than variations in global surface temperatures. The large variations in IWT and inferred OHC during the Holocene and Common era, when global temperature anomalies were relatively small, imply elevated sensitivity to climate conditions in the high latitudes, which, on a multidecadal scale, likely enables the ocean to mediate perturbations in Earth's energy budget.

References and Notes

1. H. Wanner *et al.*, *Quat. Sci. Rev.* **27**, 1791–1828 (2008).
2. L. Leduc, R. Schneider, J.-H. Kim, G. Lohmann, *Quat. Sci. Rev.* **29**, 989–1004 (2010).
3. D. R. Easterling, M. F. Wehner, *Geophys. Res. Lett.* **36**, L08706 (2009).
4. S. Levitus, J. Antonov, T. P. Boyer, C. Stephens, *Science* **287**, 2225–2229 (2000).
5. S. Levitus *et al.*, *Geophys. Res. Lett.* **39**, L10603 (2012).
6. J. Hansen *et al.*, *Science* **308**, 1431–1435 (2005).
7. R. A. Fine, R. Lukas, F. M. Bingham, M. J. Warner, R. H. Gammon, *J. Geophys. Res.* **99**, 25063–25080 (1994).
8. A. Gordon, *Oceanography* **18**, 14–27 (2005).
9. L. D. Talley, J. Sprintall, *J. Geophys. Res.* **110**, C10009 (2005).
10. W. Zenk *et al.*, *Prog. Oceanogr.* **67**, 245–281 (2005).
11. S. Wijffels, J. Sprintall, M. Fieux, N. Bray, *Deep Sea Res. Part II Top. Stud. Oceanogr.* **49**, 1341–1362 (2002).
12. J. Sprintall, S. E. Wijffels, R. Molcard, I. Jaya, *J. Geophys. Res.* **114**, C07001 (2009).
13. Y. Rosenthal *et al.*, *Geophys. Geochem. Geosys.* **12**, 1–17 (2011).
14. A. Morley *et al.*, *Earth Planet. Sci. Lett.* **308**, 161–171 (2011).
15. Supplementary materials are available on *Science* Online.
16. B. K. Linsley, Y. Rosenthal, D. W. Oppo, *Nat. Geosci.* **3**, 578–583 (2010).
17. M. Mohtadi *et al.*, *Paleoceanography* **26**, PA3219 (2011).
18. J. Xu, A. Holbourn, W. Kuhnt, Z. Jian, H. Kawamura, *Earth Planet. Sci. Lett.* **273**, 152–162 (2008).
19. S. Steinke *et al.*, *Global Planet. Change* **78**, 170–177 (2011).
20. H. Dang, Z. Jian, F. Bassinot, P. Qiao, X. Cheng, *Geophys. Res. Lett.* **39**, 1–5 (2011).
21. V. Masson *et al.*, *Quat. Res.* **54**, 348–358 (2000).
22. P. A. Mayewski *et al.*, *Quat. Res.* **62**, 243–255 (2004).
23. H. C. Bostock *et al.*, *Quat. Sci. Rev.* **74**, 35–57 (2013).
24. S. A. Marcott, J. D. Shakun, P. U. Clark, A. C. Mix, *Science* **339**, 1198–1201 (2013).
25. C. Mauritzen, A. Melsom, R. T. Sutton, *Nat. Geosci.* **5**, 905–910 (2012).
26. D. W. Oppo, Y. Rosenthal, B. K. Linsley, *Nature* **460**, 1113–1116 (2009).
27. M. E. Mann *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **105**, 13252–13257 (2008).
28. A. Moberg *et al.*, *Nature* **433**, 613–617 (2005).
29. T. M. Smith, R. W. Reynolds, T. C. Peterson, J. Lawrimore, *J. Clim.* **21**, 2283–2296 (2008).
30. A. J. Orsi, B. D. Cornuelle, J. P. Severinghaus, *Geophys. Res. Lett.* **39**, 1–7 (2012).

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Supplementary Materials

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Reconstructing the Microbial Diversity and Function of Pre-Agricultural Tallgrass Prairie Soils in the United States

Noah Fierer,[1,2]* Joshua Ladau,[3] Jose C. Clemente,[4] Jonathan W. Leff,[1,2] Sarah M. Owens,[5,6] Katherine S. Pollard,[3,7] Rob Knight,[8,9] Jack A. Gilbert,[5,10] Rebecca L. McCulley[11]

Native tallgrass prairie once dominated much of the midwestern United States, but this biome and the soil microbial diversity that once sustained this highly productive system have been almost completely eradicated by decades of agricultural practices. We reconstructed the soil microbial diversity that once existed in this biome by analyzing relict prairie soils and found that the biogeographical patterns were largely driven by changes in the relative abundance of Verrucomicrobia, a poorly studied bacterial phylum that appears to dominate many prairie soils. Shotgun metagenomic data suggested that these spatial patterns were associated with strong shifts in carbon dynamics. We show that metagenomic approaches can be used to reconstruct below-ground biogeochemical and diversity gradients in endangered ecosystems; such information could be used to improve restoration efforts, given that even small changes in below-ground microbial diversity can have important impacts on ecosystem processes.

After the European settlement of the midwestern United States in the mid-19th century, the tallgrass prairie ecosystem was profoundly altered by the removal of key animal taxa (including bison), fire suppression, and the plowing under of native grasses. Together these land-use changes contributed to the most substantial decline of any major ecosystem in North America (*1*, *2*). This ecosystem, which once covered nearly 10% of the contiguous United States (>65 million ha), has been reduced to a small fraction of its historical extent (*3*). Cultivation and row crop agriculture, now practiced across most of the tallgrass prairie biome, not only replaced species-rich plant communities with monoculture croplands, but also drastically altered the physicochemical and biological characteristics of prairie soils. Except for a few prairie relicts that have never been tilled, the soils currently found throughout the region bear little resemblance to their pre-agricultural state (*4*–*7*). We confirmed the effect of cultivation on soil microbial communities by directly comparing bacterial communities in cultivated soils with paired uncultivated soils collected from throughout the native tallgrass prairie range (table S1), and found that the cultivated soils harbored bacterial communities that were significantly distinct in composition from those found in the corresponding native prairie soils (fig. S1).

Owing to the historical and biological importance of the native tallgrass prairie, there have been various attempts to predict the historical distributions of plants and animals across this ecosystem [e.g., (*8*)]. However, comparable reconstructions of below-ground microbial diversity have, to our knowledge, never been attempted, hindering our understanding of how soil microbes may have once influenced plant production, nutrient retention, and soil carbon dynamics in this ecosystem. By coupling metagenomic sequence data, which capture the phylogenetic and functional diversity of existing soil microbial communities (*9*, *10*) found in tallgrass prairie remnants, to spatially explicit models (*11*), which predict the structure

[1]Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO 80309, USA. [2]Cooperative Institute for Research in Environmental Sciences, University of Colorado, Boulder, CO 80309, USA. [3]The Gladstone Institutes, University of California, San Francisco, CA 94158, USA. [4]Department of Genetics and Genomic Sciences and Department of Medicine, Mount Sinai School of Medicine, New York, NY 10029, USA. [5]Institute of Genomic and Systems Biology, Argonne National Laboratory, Argonne, IL 60439, USA. [6]Computation Institute, University of Chicago, Chicago, IL 60637, USA. [7]Institute for Human Genetics and Division of Biostatistics, University of California, San Francisco, CA 94143, USA. [8]Department of Chemistry and Biochemistry, University of Colorado, Boulder, CO 80309, USA. [9]Howard Hughes Medical Institute, Boulder, CO 80309, USA. [10]Department of Ecology and Evolution, University of Chicago, Chicago, IL 60637, USA. [11]Department of Plant and Soil Sciences, University of Kentucky, Lexington, KY 40546, USA.

*Corresponding author. E-mail: noah.fierer@colorado.edu

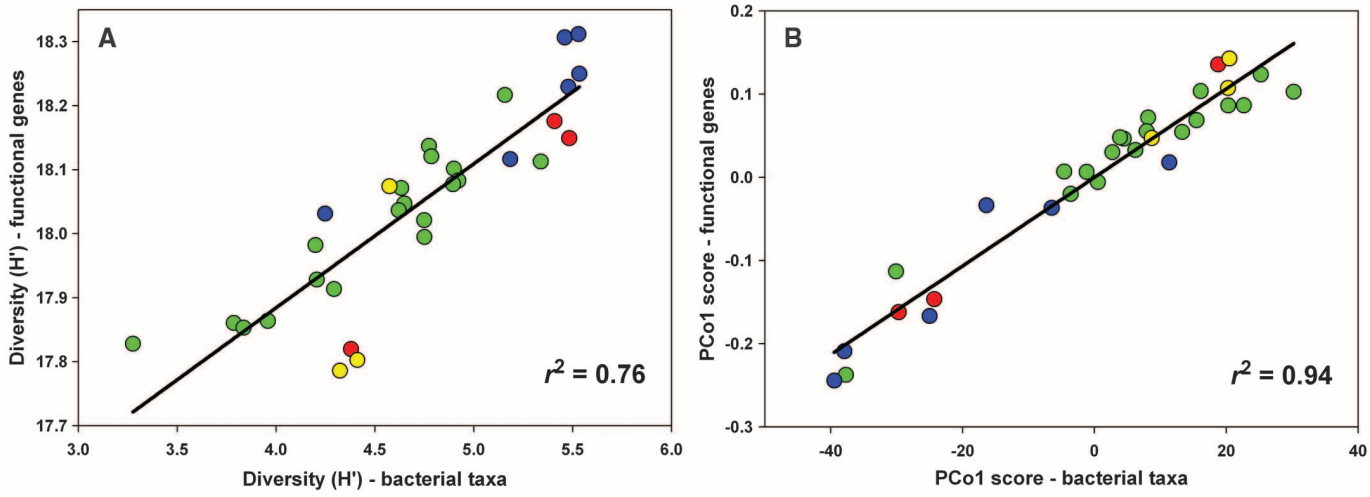


Fig. 1. Relationships between taxonomic and functional diversity (A) and community similarity patterns (B) across the 31 sites, with *x* axes showing taxonomic comparisons and *y* axes showing comparisons based on functional genes. Points are colored according to latitude (red, <35°N; yellow, 35° to 40°N; green, 40° to 45°N; blue, >45°N). The Shannon index (*H*′) and the Bray-Curtis index of community similarity were used as measures of α diversity and β diversity, respectively. The general β diversity patterns are shown here using the principal coordinates score for the first axis; Mantel tests conducted directly from the distance matrices confirm the significance of the correlation shown in (B) (Mantel $r = 0.95$, $P < 0.001$).

of soil microbial communities across environmental gradients, we can reconstruct these communities across the historical extent of the tallgrass prairie ecosystem.

We collected surface soils (top 10 cm) from 31 remnant native prairie sites (found primarily in cemeteries or nature preserves) that were carefully selected to span the range of climate conditions found throughout the tallgrass prairie ecosystem (fig. S2 and table S1). To the best of our knowledge, none of the sampled sites were ever tilled and all were dominated by native tallgrass prairie plant species (e.g., *Andropogon*, *Panicum*, and *Sorghastrum*) when soil samples were collected at the height of the growing season. To characterize the bacterial and archaeal communities, we pyrosequenced a polymerase chain reaction (PCR)–amplified region of the 16*S* rRNA gene (*12*) and compared relative diversity levels across the samples by standardizing sequencing depth to 940 reads per sample (*13*). Microbial α diversity (measured using the Shannon index, *H*′) was not uniformly distributed across the tallgrass prairie (Fig. 1A and table S2). However, none of the measured edaphic variables were significantly correlated with taxonomic diversity ($P >$ 0.1 in all cases). Instead, taxonomic diversity was most strongly correlated with precipitation levels (table S3), just as moisture availability is often a strong predictor of plant and animal diversity at comparable spatial scales (*14*).

To complement the taxonomic analyses and to characterize microbial functional diversity, we used shotgun metagenomics to determine the diversity of known protein-coding genes in each community (*10*, *12*). All samples were compared at an equivalent survey depth of 1.8 million randomly selected annotated reads per sample. Although these annotations are based only on previously described genes and much of the functional diversity contained within soil [or other environments where the majority of taxa have not been well characterized (*15*)] is therefore missed, we did find that the functional diversity that could be annotated within the microbial communities correlated well with taxonomic diversity (Fig. 1A). There has been considerable debate in the field of ecology as to how the taxonomic diversity of communities relates to the observed functional, or trait-level, diversity (*16*); we found a strong positive correlation between the functional and taxonomic diversity of soil microbial communities (Fig. 1A). This pattern is also commonly observed in plant and animal communities (*17*, *18*). Therefore, the abundant soil microbial taxa do not appear to exhibit a high degree of functional redundancy (or equivalence), as is often assumed (*19*); reductions in taxonomic diversity were associated with decreases in the breadth of functional traits contained within these soil communities.

To extend our results beyond the 31 soils directly assayed, we constructed spatially explicit models of the taxonomic and functional diversity

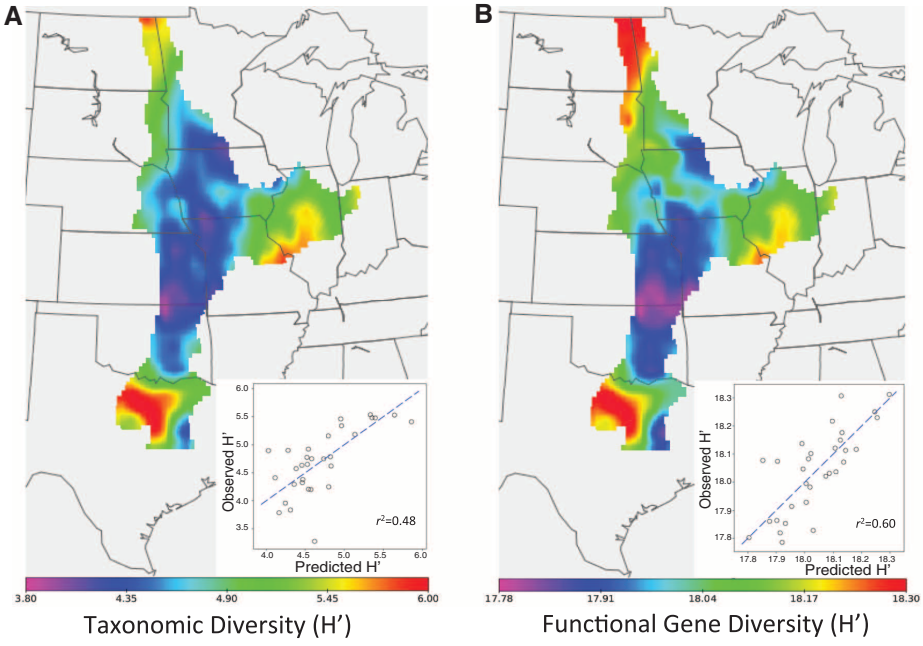
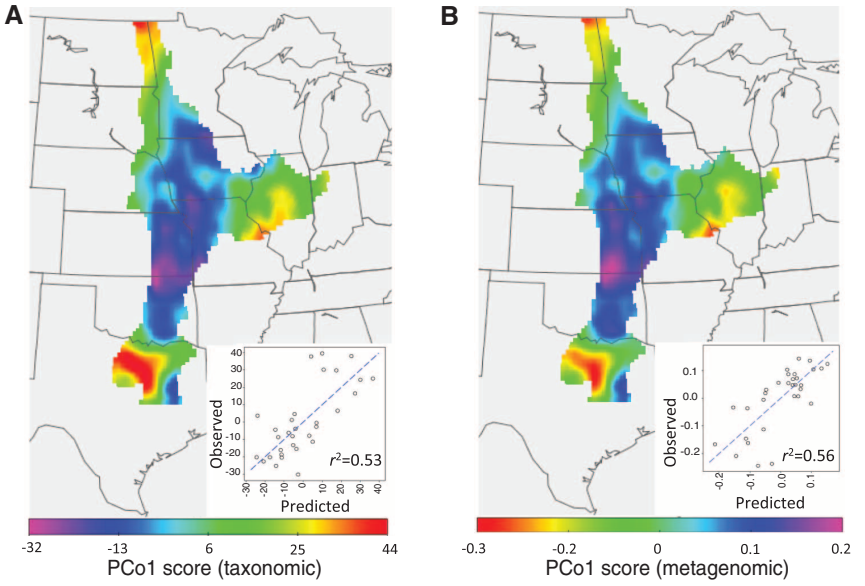
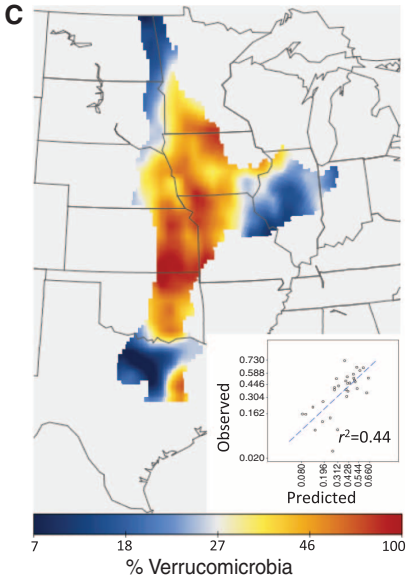


Fig. 2. Predicted diversity patterns (calculated using the Shannon index, *H*′) of bacterial taxa (A) and functional genes (B). Inset plots show the cross-validation results, comparing observed and predicted diversity values for the 31 sampled locations.





D

Gene Category	Relative abundance (% of reads)	Correlation (r) with % Verrucomicrobia
Fatty acid biosynthesis	0.71	0.89
Fructose, mannose metabolism	1.01	0.87
Peroxisome	0.07	0.84
Pentose phosphate pathway	1.42	0.81
Tyrosine metabolism	0.37	0.81
Lipopolysaccharide biosynthesis	0.27	0.80
Valine, leucine, isoleucine biosynthesis	0.90	-0.91
Cell division	0.04	-0.85
Nicotinate, nicotinamide metabolism	0.41	-0.85
Nitrogen metabolism	1.76	-0.84
Porphyrin, chlorophyll metabolism	0.63	-0.82
Bacterial toxins	0.07	-0.82
Valine, leucine, isoleucine degradation	0.36	-0.80

Fig. 3. Maps showing bacterial community types based on their taxonomic composition (A) or functional gene composition (B). Locations similar in hue indicate those communities that are more similar in composition. (**C** and **D**) The patterns shown in (A) and (B) appear to be largely driven by variation in verrucomicrobial abundances (% of reads) (C). Shown in (D) are functional gene categories strongly correlated with verrucomicrobial abundances, only including those gene categories represented by >0.001% of the shotgun metagenomic reads with *r* values greater than 0.8 or less than −0.8.

of soil bacterial communities throughout the historical extent of the native tallgrass prairie using a species distribution modeling approach (*20*, *21*). These models were based solely on climatic variables (tables S3 and S4), not soil characteristics, because we do not know what soil characteristics would have been found across the biome >150 years ago when the native tallgrass prairie ecosystem was still intact (current soil maps are not likely to reflect historical soil properties that have been profoundly altered by decades of cultivation). The best-fit models of Shannon diversity were able to predict >50% of the variance in bacterial taxonomic and functional diversity across the sampled sites (table S3), a predictive power similar to comparable models of regional plant or animal diversity (*20*), with soils from the middle latitudes having less taxonomic and functional diversity than those in the northernmost and southernmost portions of the range (Fig. 2). This pattern contrasts with the biogeographical patterns observed in many plant and animal communities where diversity often peaks in the middle of biomes, which suggests that the "mid-domain effect" (*22*), or related explanations for such diversity gradients, may not be broadly applicable across the tree of life.

The taxonomic composition of the microbial communities and their functional attributes varied considerably across the 31 sampled tallgrass prairie sites. Communities that were taxonomically similar were also similar with respect to their functional characteristics as these two distinct measures were well correlated (i.e., communities that shared many taxa in common also shared many functional attributes) (Fig. 1B). Model predictions of the patterns in community similarity show that the soils in the central portion of the tallgrass prairie range harbored communities that were taxonomically (Fig. 3A) and functionally (Fig. 3B) distinct from those found on the edges of the range. The relative abundances of many taxa changed across the sampled soils (table S2), but the α diversity patterns (Fig. 2) and the patterns in community similarity (Fig. 3) were both closely tied to changes in the relative abundance of Verrucomicrobia (Fig. 3C and table S2), the dominant bacterial phylum across the collected soils (fig. S2 and table S2). Although often underestimated (*23*), Verrucomicrobia represented >50% of the bacterial 16*S* rRNA sequences in the prairie soils from the mid-latitudes but only <15% of the sequences on the edges of the range (Fig. 3C and table S2). These patterns in verrucomicrobial abundances were nearly identical whether abundances were determined by the PCR-based 16*S* rRNA gene analyses or by analyzing the 16*S* rRNA genes recovered from the shotgun metagenomic data (fig. S3); this finding provides independent evidence for the high relative abundances of Verrucomicrobia in many of these soils.

Verrucomicrobia are clearly dominant in the tallgrass prairie soils, but their ecology remains poorly understood because members of this group are difficult to culture and study in the laboratory (*23*, *24*). The Verrucomicrobia identified from the prairie soils were not diverse; only five phylotypes accounted for >75% of the verrucomicrobial sequences from this data set (fig. S4). All of the more abundant verrucomicrobial taxa were classified as belonging to the *Spartobacteria* class, but the taxa were not closely related to previously cultivated verrucomicrobial isolates (fig. S4), making it difficult to determine the ecological attributes of these taxa. Our understanding of soil microbial communities in prairie soils will clearly benefit from efforts to directly determine the phenotypes of the Verrucomicrobia that dominated the majority of the native tallgrass prairie soils.

Although the ecological attributes of these verrucomicrobial taxa cannot be directly assessed with these data, we used a niche-modeling approach in combination with the shotgun metagenomic data to gain some insight into the ecology of the Verrucomicrobia and to try to explain the distribution patterns shown in Fig. 3C. We found that spatial variability in the abundance of Verrucomicrobia could be predicted from climatic conditions (table S3) and that this group was most abundant in soils exposed to intermediate temperature and precipitation conditions (Fig. 3C and fig. S2). However, this correlation with climatic conditions may represent only a distal control on their distribution patterns. The shotgun metagenomic data lend support to the hypothesis that Verrucomicrobia are relatively slow-growing taxa

that thrive under conditions of limited nutrient availability (*25*, *26*). Specifically, verrucomicrobial abundances were positively correlated with a variety of genes associated with carbohydrate metabolism but were negatively correlated with genes associated with nitrogen metabolism and cell division (Fig. 3D). Verrucomicrobia may thus represent a large component of below-ground communities in regions where changes in the quantity or quality of plant organic matter inputs constrain the growth of more copiotrophic taxa. This hypothesis is congruent with results indicating consistent declines in the relative abundances of Verrucomicrobia when soils from across North America were amended with nutrients (*27*). Likewise, this hypothesis is consistent with recent genomic information obtained from *Spartobacteria aquaticum*, an aquatic Verrucomicrobia that is within the same class as the dominant soil Verrucomicrobia observed here, that appears to specialize on the degradation of more recalcitrant carbon compounds (*28*).

Our reconstructions of microbial diversity and functional capabilities across the tallgrass prairie ecosystem could be used to guide and monitor the hundreds of prairie restoration efforts currently underway throughout the midwestern United States (*29*). Maps of the soil microbial communities that once existed in this ecosystem may provide targets to help improve the long-term success of prairie restoration efforts, as restoration efforts are often more successful when they also try to restore below-ground communities (*30*). Such information may be particularly important if the goal is to restore key ecosystem functions, such as soil carbon sequestration, that are strongly controlled by the below-ground communities. Likewise, deviation in soil microbial communities from the predicted pre-agricultural state could be used to quantify the extent of degradation experienced by soils throughout the native prairie range. More generally, this work demonstrates that we can use recent advances in high-throughput microbial community characterization to reconstruct the biogeographical patterns in the diversity and functional capabilities of microbes across a nearly extinct ecosystem. This approach could be extended more broadly to quantify how historical changes in environmental conditions may have altered the diversity and function of below-ground communities in other systems or to determine how human-induced climate change may alter ecosystem properties in the future.

References and Notes

1. P. Sims, P. Risser, in *North American Terrestrial Vegetation*, M. Barbour, W. Billings, Eds. (Cambridge Univ. Press, New York, 2000), pp. 325–356.
2. F. Samson, F. Knopf, W. Ostlie, *Wildl. Soc. Bull.* **32**, 6–15 (2004).
3. F. Samson, F. Knopf, *Bioscience* **44**, 418–421 (1994).
4. V. J. Allison, Z. Yermakov, R. M. Miller, J. D. Jastrow, R. Matamala, *Soil Biol. Biochem.* **39**, 505–516 (2007).
5. D. R. Huggins *et al.*, *Soil Tillage Res.* **47**, 219–234 (1998).
6. K. Jangid *et al.*, *Soil Biol. Biochem.* **42**, 302–312 (2010).
7. S. G. Baer, D. J. Kitchen, J. M. Blair, C. W. Rice, *Ecol. Appl.* **12**, 1688–1701 (2002).
8. E. J. Martinson *et al.*, *Phys. Geogr.* **32**, 583–602 (2011).
9. S. G. Tringe, E. M. Rubin, *Nat. Rev. Genet.* **6**, 805–814 (2005).
10. N. Fierer *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **109**, 21390–21395 (2012).
11. N. Fierer, J. Ladau, *Nat. Methods* **9**, 549–551 (2012).
12. N. Fierer *et al.*, *ISME J.* **6**, 1007–1017 (2012).
13. See supplementary materials on *Science* Online.
14. B. A. Hawkins *et al.*, *Ecology* **84**, 3105–3117 (2003).
15. J. A. Gilbert, R. O'Dor, N. King, T. M. Vogel, *Microb. Inform. Exp.* **1**, 5 (2011).
16. H. Hillebrand, B. Matthiessen, *Ecol. Lett.* **12**, 1405–1419 (2009).
17. O. L. Petchey, K. J. Gaston, *Ecol. Lett.* **5**, 402–411 (2002).
18. S. Díaz, M. Cabido, *Trends Ecol. Evol.* **16**, 646–655 (2001).
19. M. Bradford, N. Fierer, in *Soil Ecology and Ecosystem Services*, D. Wall, Ed. (Oxford Univ. Press, Oxford, 2012), pp. 189–198.
20. J. Franklin, J. Miller, *Mapping Species Distributions: Spatial Inference and Prediction* (Cambridge Univ. Press, New York, 2010).
21. J. Ladau *et al.*, *ISME J.* **7**, 1669–1677 (2013).
22. R. K. Colwell, D. C. Lees, *Trends Ecol. Evol.* **15**, 70–76 (2000).
23. G. T. Bergmann *et al.*, *Soil Biol. Biochem.* **43**, 1450–1455 (2011).
24. S. J. Joseph, P. Hugenholtz, P. Sangwan, C. A. Osborne, P. H. Janssen, *Appl. Environ. Microbiol.* **69**, 7210–7215 (2003).
25. U. N. da Rocha, F. D. Andreote, J. L. Azevedo, J. D. van Elsas, L. van Overbeek, *J. Soils Sed.* **10**, 326–339 (2010).
26. P. H. Janssen, P. S. Yates, B. E. Grinton, P. M. Taylor, M. Sait, *Appl. Environ. Microbiol.* **68**, 2391–2396 (2002).
27. K. S. Ramirez, J. M. Craine, N. Fierer, *Glob. Change Biol.* **18**, 1918–1927 (2012).
28. D. P. Herlemann *et al.*, *mBio* **4**, e00569-12 (2013).
29. J. Harris, *Science* **325**, 573–574 (2009).
30. P. Kardol, D. A. Wardle, *Trends Ecol. Evol.* **25**, 670–679 (2010).

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Supplementary Materials

www.sciencemag.org/content/342/6158/621/suppl/DC1
Materials and Methods
Figs. S1 to S4
Tables S1 to S4
References (*31*–*50*)

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Structural Basis for flg22-Induced Activation of the *Arabidopsis* FLS2-BAK1 Immune Complex

Yadong Sun,[1]* Lei Li,[2]* Alberto P. Macho,[3] Zhifu Han,[1]† Zehan Hu,[1] Cyril Zipfel,[3] Jian-Min Zhou,[2]† Jijie Chai[1]†

Flagellin perception in *Arabidopsis* is through recognition of its highly conserved N-terminal epitope (flg22) by flagellin-sensitive 2 (FLS2). Flg22 binding induces FLS2 heteromerization with BRASSINOSTEROID INSENSITIVE 1–associated kinase 1 (BAK1) and their reciprocal activation followed by plant immunity. Here, we report the crystal structure of FLS2 and BAK1 ectodomains complexed with flg22 at 3.06 angstroms. A conserved and a nonconserved site from the inner surface of the FLS2 solenoid recognize the C- and N-terminal segment of flg22, respectively, without oligomerization or conformational changes in the FLS2 ectodomain. Besides directly interacting with FLS2, BAK1 acts as a co-receptor by recognizing the C terminus of the FLS2-bound flg22. Our data reveal the molecular mechanisms underlying FLS2-BAK1 complex recognition of flg22 and provide insight into the immune receptor complex activation.

Innate immunity in higher eukaryotes relies on the perception of conserved signature components of pathogens, termed pathogen-associated molecular patterns (PAMPs), by plasma membrane–localized pattern recognition receptors (PRRs). In plants, PRRs are mainly receptor kinases (RKs) or receptor-like proteins, and several of them carry leucine-rich repeats (LRRs) in their ectodomains for PAMP recognition. Upon recognition of PAMPs, PRRs initiate an array of shared immune responses, leading to PAMP-triggered immunity (*1*).

Present in most higher plant species and critical for antibacterial immunity (*1*), flagellin-sensitive 2 (FLS2) is an LRR-RK and acts as the PRR for bacterial flagellin by recognizing the epitope flg22 (*2*–*6*). Direct recognition of flg22 by FLS2 is sufficient for inducing immune responses, establishing FLS2 as a flagellin receptor (*7*). Flg22 binding nearly instantly triggers FLS2 association with the LRR-RK BRI1-associated kinase 1 (BAK1) (*8*, *9*). BAK1 also interacts with the LRR-RK

[1]School of Life Sciences, Tsinghua University, Beijing 100084, China, and Tsinghua-Peking Center for Life Sciences, Beijing 100084, China. [2]State Key Laboratory of Plant Genomics and National Center for Plant Gene Research, Institute of Genetics and Developmental Biology, Chinese Academy of Sciences, Beijing 100101, China. [3]The Sainsbury Laboratory, Norwich Research Park, Norwich NR4 7UH, UK.

*These authors contributed equally to this work.
†Corresponding author. E-mail: chaijj@mail.tsinghua.edu.cn (J.C.); jmzhou@genetics.ac.cn (J.-m.Z.); hanzhifu@mail.tsinghua.edu.cn (Z.Han)

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Reconstructing the Microbial Diversity and Function of Pre-Agricultural Tallgrass Prairie Soils in the United States

Noah Fierer, Joshua Ladau, Jose C. Clemente, Jonathan W. Leff, Sarah M. Owens, Katherine S. Pollard, Rob Knight, Jack A. Gilbert and Rebecca L. McCulley (October 31, 2013)

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Editor's Summary

Prairie Redux

Tallgrass prairie is extinct across much of its former range in the midwestern United States, but relicts preserved in cemeteries and nature reserves allow functional comparison of former grassland soils with modern agricultural soils. **Fierer *et al.*** (p. 621; see the Perspective by **Scholes and Scholes**) took matched soil samples from sites representing the gamut of climate conditions and modeled the combination of genomic analysis and environmental data to resurrect the historical prairie soil communities, identifying the nutrient-scavenging Verrucomicrobia as keystone bacteria in functioning prairie.

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