Stanford



Paula V. Welander

Senior Associate Dean for Research and Professor of Earth System Science

Bio

BIO

Paula Welander is a microbiologist who received her undergraduate degree from Occidental College in Los Angeles. She pursued her PhD studies in microbiology at the University of Illinois at Urbana-Champaign and completed her postdoctoral studies at MIT in the Departments of Biology and of Earth, Atmospheric, and Planetary Sciences. Paula joined the Stanford faculty in 2013 where her current research program is focused on understanding the biosynthesis and physiological function of “molecular fossils” or biomarkers in extant bacteria.

ACADEMIC APPOINTMENTS

- Professor, Earth System Science
- Member, Bio-X

ADMINISTRATIVE APPOINTMENTS

- NASA Astrobiology Postdoctoral Fellow, Massachusetts Institute of Technology, (2012-2012)
- Research Scientist, Massachusetts Institute of Technology, (2011-2012)
- NSF Minority Postdoctoral Fellow, Massachusetts Institute of Technology, (2008-2011)
- National Science Foundation Graduate Research Fellow, University of Illinois at Urbana-Champaign, (2002-2005)
- Graduate College Fellow, University of Illinois at Urbana-Champaign, (2001-2007)
- Research Associate I, Beckman Research Institute, City of Hope, (1999-2001)
- Research Assistant I, California Institute of Technology, (1998-1999)

HONORS AND AWARDS

- Margaret Supple COLLEGE Faculty Fellow, Stanford University (2026)
- John M. Hayes Award, Geochemical Society (2024)
- Excellence in DEI Award, Stanford University (2022)
- Excellence in Teaching Award, Stanford University (2019)
- Faculty Early Career Development (CAREER) Award, National Science Foundation, Division of Earth Sciences (2018)
- Geobiology and Geomicrobiology Division Award for Outstanding Research (pre-tenure), Geological Society of America (2018)
- Hoagland Award Fund for Innovations in Undergraduate Teaching, Stanford University (2017)
- Terman Fellow, Stanford University (2014)
- Gabilan Faculty Fellow, Stanford University (2013)
- NASA Astrobiology Postdoctoral Fellowship, NASA Postdoctoral Program (2012)

- OGD 2010 Best Paper Award, Geochemical Society (2011)
- NSF Minority Postdoctoral Research Fellowship, National Science Foundation (2008)
- Mame Shiao Debbie Award, University of Illinois at Urbana-Champaign (2006)
- Outstanding Teaching Assistant, University of Illinois at Urbana-Champaign (2005-2006)
- Recipient, Gordon Conference Minority Student Travel Grant (2003)
- NSF Graduate Research Fellowship, National Science Foundation (2002)
- Graduate College Fellowship, University of Illinois at Urbana-Champaign (2001)
- Recipient, Declined, NIH MCB Training Grant Fellowship, University of Illinois at Urbana-Champaign (2001)
- Recipient, Howard Hughes Medical Institute Undergraduate Research Grant (1998)
- Fellow, Richter Fellowship (1997)
- Undergraduate Research Academic Support Program Grant, Occidental College (1997)
- Recipient, Cal Grant (1995 – 1998)

BOARDS, ADVISORY COMMITTEES, PROFESSIONAL ORGANIZATIONS

- Member, American Society of Microbiology (2002 - present)
- Member, American Geological Union (2013 - present)
- Member, European Association of Geochemistry (2013 - present)
- Editorial Board Member, Geobiology Journal (2014 - present)
- Member, Society for Advancement of Chicanos and Native Americans in Science (SACNAS) (2016 - present)

PROFESSIONAL EDUCATION

- Ph.D., University of Illinois at Urbana-Champaign, Urbana, IL , Microbiology (2007)
- M.S., University of Illinois at Urbana-Champaign, Urbana, IL , Microbiology (2003)
- B.A., Occidental College, Los Angeles, CA , Kinesiology (1998)

LINKS

- Welander Lab: https://welanderlab.sites.stanford.edu/
- Stanford Earth Profile: https://earth.stanford.edu/people/paula-welander

Research & Scholarship

CURRENT RESEARCH AND SCHOLARLY INTERESTS

Earth’s history is marked with periods of dramatic atmospheric and climate fluctuations that have greatly affected life and its evolution. Much of our knowledge of how the biosphere responded to these ancient events stems from studies of faunal and floral fossils revealing profound changes in the abundance and diversity of macroscopic organisms. However, much less is known about microbial community responses to such dramatic environmental changes. This is one of the great challenges of geomicrobiology - how do we study microbial communities in the context of Earth’s distant past?

Although microbes do not readily leave diagnostic morphological fossils, subtle microbial signatures are recorded in sedimentary rocks spanning billions of years. One such group of biosignatures are well-preserved lipid compounds that have specific biological origins and can function as biomarkers for the occurrence of specific microbes or environmental conditions at the time of deposition. However, many questions remain about the extant sources and the biosynthetic pathways of these lipids in modern organisms. In my research group, we focus on improving our understanding of the taxonomic

distribution, the biosynthesis, and physiological function of biomarker lipids in extant microbes. Below are three biomarker areas that we are currently exploring in the Welander group:

1. Bacterial production of eukaryotic biomarkers. Eukaryotic biomarkers are specific lipid molecules that are considered diagnostic for certain eukaryotic organisms – from multicellular animals like sponges to unicellular eukaryotes such as protist. However, some bacterial species have been shown to produce these “eukaryotic” lipids and there are several open questions regarding how bacteria synthesize and utilize these lipids. We have identified unique bacterial proteins in aerobic methanotrophs for the synthesis of tetrahymanol, a cyclic triterpenoid primarily produced by ciliated protists, and sterols, essential lipids found in almost all eukaryotic cells. We are currently exploring the biochemical mechanisms behind these unique bacterial proteins and are also investigating the physiological function of these "eukaryoitc" lipids in a variety of bacteria.

2. Identification of orphan biomarker sources. Orphan biomarkers are lipids identified in ancient or modern sediments for which there are no extant sources or the extant sources are not consistent with their occurrence in a specific environment or time period. One example is isoarborinol, an unusual pentacyclic triterpenol whose only known extant sources are certain flowering plants. Through our work, we have identified two novel arborinol lipids structurally similar to isoarborinol, which we named eudoraenol and adriaticol, in the marine bacterium Eudoraea adriatica. We are currently investigating the phylogenetic distribution of eudoraneol cyclase homologs in environmental metagenomes and are utilizing an E. coli heterologous expression system developed in our lab to express these cyclases in the lab.

3. Lipid biosynthesis in archaea. Glycerol dialkyl glycerol tetraethers (GDGTs) are unique archaeal membrane lipids that can function not just as biomarkers for archaea but can also be used as paleotemperature proxies. However, the pathway for GDGT synthesis has not been fully characterized and we have been attempting to identify the missing synthesis proteins in the thermoacidophile Sulfolobus acidocaldarius. Thus far, we have identified a novel protein, calditol synthase (Cds), necessary for modifying the glycosylated membrane head groups of Sulfolobus. We have also identified two novel proteins, GDGT-ring synthases, required for introducing the cyclopentane rings within the core GDGT structure. We are currently characterizing these GDGT biosynthesis proteins and continue to search for other unknown tetraether lipid biosynthesis proteins in archaea and bacteria.

Teaching

COURSES

2026-27

- Citizenship in the 21st Century: COLLEGE 102 (Win)
- Preparing for Faculty Careers: EDUC 343C (Spr)

2025-26

- Citizenship in the 21st Century: COLLEGE 102 (Win)
- Preparing for Faculty Careers: EDUC 343C (Spr)

2024-25

- Citizenship in the 21st Century: COLLEGE 102 (Win)

2023-24

- Citizenship in the 21st Century: COLLEGE 102 (Win)
- Research Proposal Development and Delivery: EPS 307, ESS 307 (Spr)

STANFORD ADVISEES

Doctoral Dissertation Reader (AC)

Jessica Bullington, Casey Decosto, Valerie Martin, Benjamin Shapero, Miles Tuncel

Postdoctoral Faculty Sponsor

Lizett Gonzalez Carreon, Nathan Marshall, Esther Munoz

Doctoral (Program)

Madelyn Foulkes, Charles Hu

GRADUATE AND FELLOWSHIP PROGRAM AFFILIATIONS

- Biology (School of Humanities and Sciences) (PhD Program)

Publications

PUBLICATIONS

- **Characterization of aliA and aliB deletion mutants reveals a dominant role of AliA in Haloferax volcanii lipoprotein lipidation.** *The Journal of biological chemistry*
  Hong, Y., Garcia, A., Kopelev, S., Cote, J. A., Pfeiffer, F., Welander, P., Schulze, S., Pohlschroder, M.
  2026: 113477

- **A sterol reductase responsible for the unusual 8(14)-unsaturation in bacterial sterol production and degradation.** *Journal of bacteriology*
  Lee, A. K., Giner, J. -., Welander, P. V.
  2026: e0013426

- **A lipid compendium of a metabolically compromised bacterium provides insights into lipid acquisition, biosynthesis, and metabolism.** *bioRxiv : the preprint server for biology*
  Chatterjee, P., Shin, H. E., Tuncel, M. I., Paddy, I. A., Lee, A. K., McCausland, J., Welander, P. V., Jacobs-Wagner, C., Dassama, L. M.
  2026

- **The Origin of Life in the Light of Evolution.** *ArXiv*
  Kaçar, B., Williams, T. A., Eme, L., Gogarten, J. P., Sanchez-Baracaldo, P., Spang, A., Aylward, F. O., Travisano, M., Welander, P. V., Huber, J. A., Cooper, V. S., Turner, P. E., Lyons, et al
  2026

- **Uncovering the prevalence, key biogenesis enzymes, and biological significance of archaeal lipoproteins.** *Nature communications*
  Hong, Y., Makarova, K. S., Garcia, A. A., Xu, R., Pfeiffer, F., Welander, P. V., Pohlschroder, M.
  2025; 16 (1): 8411

- **The evolutionary history and modern diversity of triterpenoid cyclases.** *Molecular biology and evolution*
  McShea, H. S., Viens, R. A., Olagunju, B. O., Giner, J. L., Welander, P. V.
  2025

- **A geranylgeranyl reductase homolog required for cholesterol production in Myxococcota.** *Journal of bacteriology*
  Lee, A. K., Welander, P. V.
  2025: e0049524

- **Identification of two archaeal GDGT lipid-modifying proteins reveals diverse microbes capable of GMGT biosynthesis and modification.** *Proceedings of the National Academy of Sciences of the United States of America*
  Garcia, A. A., Chadwick, G. L., Liu, X. L., Welander, P. V.
  2024; 121 (26): e2318761121

- **Editorial: Emergence of dynamic membranes - role of terpenoids in the evolution of membrane organization and regulation** *FRONTIERS IN ECOLOGY AND EVOLUTION*
  Nettersheim, B. J., Hoshino, Y., Welander, P. V.
  2024; 12

- **Tetraether archaeal lipids promote long-term survival in extreme conditions.** *Molecular microbiology*
  Liman, G. L., Garcia, A. A., Fluke, K. A., Anderson, H. R., Davidson, S. C., Welander, P. V., Santangelo, T. J.
  2024

- **Novel sterol binding domains in bacteria.** *eLife*
  Zhai, L., Bonds, A. C., Smith, C. A., Oo, H., Chou, J. C., Welander, P. V., Dassama, L. M.
  2024; 12
- **De novo cholesterol biosynthesis in bacteria.** *Nature communications*
  Lee, A. K., Wei, J. H., Welander, P. V.
  2023; 14 (1): 2904
- **Sterol methyltransferases in uncultured bacteria complicate eukaryotic biomarker interpretations.** *Nature communications*
  Brown, M. O., Olagunju, B. O., Giner, J. L., Welander, P. V.
  2023; 14 (1): 1859
- **Reply to Oren et al., "New Phylum Names Harmonize Prokaryotic Nomenclature".** *mBio*
  Sharma, G., Islam, S. T., Rahi, P., Silby, M. W., Giovannelli, D., Welander, P. V., Ehling-Schulz, M., Chaudhry, V., Molloy, E., Hertweck, C., Mundra, S., Kalia, V. C., Lal, et al
  2022: e0232322
- **Genomic Features of the Bundle-Forming Heliobacterium Heliophilum fasciatum.** *Microorganisms*
  Bender, K. S., Madigan, M. T., Williamson, K. L., Mayer, M. H., Parenteau, M. N., Jahnke, L. L., Welander, P. V., Sanguedolce, S. A., Brown, A. C., Sattley, W. M.
  2022; 10 (5)
- **Identification of a protein responsible for the synthesis of archaeal membrane-spanning GDGT lipids.** *Nature communications*
  Zeng, Z., Chen, H., Yang, H., Chen, Y., Yang, W., Feng, X., Pei, H., Welander, P. V.
  2022; 13 (1): 1545
- **Lipid biomarkers: molecular tools for illuminating the history of microbial life.** *Nature reviews. Microbiology*
  Summons, R. E., Welander, P. V., Gold, D. A.
  2021
- **Anaerobic 3-methylhopanoid production by an acidophilic photosynthetic purple bacterium.** *Archives of microbiology*
  Mayer, M. H., Parenteau, M. N., Kempher, M. L., Madigan, M. T., Jahnke, L. L., Welander, P. V.
  2021
- **Enantioselective Total Synthesis of the Archaeal Lipid Parallel GDGT-0 (Isocaldarchaeol).** *Angewandte Chemie (International ed. in English)*
  Falk, I. D., Gál, B. n., Bhattacharya, A. n., Wei, J. H., Welander, P. V., Boxer, S. G., Burns, N. Z.
  2021
- **Deciphering the evolutionary history of microbial cyclic triterpenoids** *FREE RADICAL BIOLOGY AND MEDICINE*
  Welander, P. V.
  2019; 140: 270–78
- **Soil exchange rates of COS and (COO)-O-18 differ with the diversity of microbial communities and their carbonic anhydrase enzymes** *ISME JOURNAL*
  Meredith, L. K., Ogee, J., Boye, K., Singer, E., Wingate, L., von Sperber, C., Sengupta, A., Whelan, M., Pang, E., Keiluweit, M., Brueggemann, N., Berry, J. A., Welander, et al
  2019; 13 (2): 290–300
- **GDGT cyclization proteins identify the dominant archaeal sources of tetraether lipids in the ocean.** *Proceedings of the National Academy of Sciences of the United States of America*
  Zeng, Z. n., Liu, X. L., Farley, K. R., Wei, J. H., Metcalf, W. W., Summons, R. E., Welander, P. V.
  2019
- **Calditol-linked membrane lipids are required for acid tolerance in Sulfolobus acidocaldarius.** *Proceedings of the National Academy of Sciences of the United States of America*
  Zeng, Z., Liu, X., Wei, J. H., Summons, R. E., Welander, P. V.
  2018
- **C-4 sterol demethylation enzymes distinguish bacterial and eukaryotic sterol synthesis.** *Proceedings of the National Academy of Sciences of the United States of America*
  Lee, A. K., Banta, A. B., Wei, J. H., Kiemle, D. J., Feng, J. n., Giner, J. L., Welander, P. V.

2018; 115 (23): 5884–89

- **Microbial communities and organic biomarkers in a Proterozoic-analog sinkhole.** *Geobiology*
  Hamilton, T. L., Welander, P. V., Albrecht, H. L., Fulton, J. M., Schaperdoth, I., Bird, L. R., Summons, R. E., Freeman, K. H., Macalady, J. L.
  2017; 15 (6): 784-797
- **Synthesis of arborane triterpenols by a bacterial oxidosqualene cyclase** *PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES OF THE UNITED STATES OF AMERICA*
  Banta, A. B., Wei, J. H., Gill, C. C., Giner, J., Welander, P. V.
  2017; 114 (2): 245-250
- **Fractionation of the methane isotopologues (CH4)-C-13, (CH3D)-C-12, and (CH3D)-C-13 during aerobic oxidation of methane by Methylococcus capsulatus (Bath)** *GEOCHIMICA ET COSMOCHIMICA ACTA*
  Wang, D. T., Welander, P. V., Ono, S.
  2016; 192: 186-202
- **Sterol Synthesis in Diverse Bacteria** *FRONTIERS IN MICROBIOLOGY*
  Wei, J. H., Yin, X., Welander, P. V.
  2016; 7
- **A distinct pathway for tetrahymanol synthesis in bacteria** *PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES OF THE UNITED STATES OF AMERICA*
  Banta, A. B., Wei, J. H., Welander, P. V.
  2015; 112 (44): 13478-13483
- **Methane Oxidation and Molecular Characterization of Methanotrophs from a Former Mercury Mine Impoundment.** *Microorganisms*
  Baesman, S. M., Miller, L. G., Wei, J. H., Cho, Y., Matys, E. D., Summons, R. E., Welander, P. V., Oremland, R. S.
  2015; 3 (2): 290-309
- **Elucidation of the Burkholderia cenocepacia hopanoid biosynthesis pathway uncovers functions for conserved proteins in hopanoid-producing bacteria** *ENVIRONMENTAL MICROBIOLOGY*
  Schmerk, C. L., Welander, P. V., Hamad, M. A., Bain, K. L., Bernards, M. A., Summons, R. E., Valvano, M. A.
  2015; 17 (3): 735-750
- **Diverse capacity for 2-methylhopanoid production correlates with a specific ecological niche** *ISME JOURNAL*
  Ricci, J. N., Coleman, M. L., Welander, P. V., Sessions, A. L., Summons, R. E., Spear, J. R., Newman, D. K.
  2014; 8 (3): 675-684
- **Identification and quantification of polyfunctionalized hopanoids by high temperature gas chromatography-mass spectrometry.** *Organic geochemistry*
  Sessions, A. L., Zhang, L., Welander, P. V., Doughty, D., Summons, R. E., Newman, D. K.
  2013; 56: 120-130
- **Molecular indicators of microbial diversity in oolitic sands of Highborn Cay, Bahamas** *Geobiology*
  Edgecomb, V. P., Bernhard, J. M., Beaudoin, D., Pruss, S., Welander, P. V., Shubotz, F., Mehay, S., Gillespie, A. L., Summons, R. E.
  2013; 11: 234-251
- **Discovery, taxonomic distribution, and phenotypic characterization of a gene required for 3-methylhopanoid production.** *Proceedings of the National Academy of Sciences of the United States of America*
  Welander, P. V., Summons, R. E.
  2012; 109 (32): 12905-10
- **Identification and characterization of Rhodopseudomonas palustris hopanoid biosynthesis mutants** *Geobiology*
  Welander, P. V., Doughty, D. M., Wu, C. H., Mehay, S., Summons, R. E., Newman, D. K.
  2012; 10: 163-177
- **Identification of the bacteriochlorophylls, carotenoids, quinones, lipids, and hopanoids of Candidatus Chloracidobacterium thermophilum** *Journal of Bacteriology*
  Garcia Costas, A. M., Tsukatani, Y., Rijpstra, W. I., Schouten, S., Welander, P. V., Summons, R. E., Bryant, D. A.
  2012; 194: 1158-68

- **Using Taguchi-based statistics to produce robust PCR results** *Bioprocessing*
  Welander, P., Cantin, E., Lundberg, P.
  2011; 10: 22-26
- **Identification of a methylase required for 2-methylhopanoid production and implications for the interpretation of sedimentary hopanes.** *Proceedings of the National Academy of Sciences of the United States of America*
  Welander, P. V., Coleman, M. L., Sessions, A. L., Summons, R. E., Newman, D. K.
  2010; 107 (19): 8537-42
- **Hopanoids play a role in membrane integrity and pH homeostasis in Rhodopseudomonas palustris TIE-1.** *Journal of bacteriology*
  Welander, P. V., Hunter, R. C., Zhang, L., Sessions, A. L., Summons, R. E., Newman, D. K.
  2009; 191 (19): 6145-56
- **The continuing puzzle of the great oxidation event** *Current Biology*
  Sessions, A. L., Doughty, D. M., Welander, P. V., Summons, R. E., Newman, D. K.
  2009; 19: R567-R574
- **Mutagenesis of the C1 oxidation pathway in Methanosarcina barkeri: new insights into the Mtr/Mer bypass pathway** *Journal of Bacteriology*
  Welander, P. V., Metcalf, W. W.
  2008; 190: 1928-1936
- **Tumor necrosis factor (TNF) protects resistant C57BL/6 mice against herpes simplex virus-induced encephalitis independently of signaling via TNF receptor 1 or 2** *Journal of Virology*
  Lundberg, P., Welander, P. V., Edwards, 3rd, C. K., van Rooijen, N., Cantin, E.
  2007; 81: 1451-1460
- **Loss of the mtr operon in Methanosarcina blocks growth on methanol, but not methanogenesis, and reveals an unknown methanogenic pathway** *Proceedings of the National Academy of Sciences*
  Welander, P. V., Metcalf, W. W.
  2005; 102: 10664-10669
- **Herpes simplex virus type 1 DNA is immunostimulatory in vitro and in vivo** *Journal of Virology*
  Lundberg, P., Welander, P., Han, X., Cantin, E.
  2003; 77: 11158-11169
- **A locus on mouse chromosome 6 that determines resistance to herpes simplex virus also influences reactivation, while an unlinked locus augments resistance of female mice** *Journal of Virology*
  Lundberg, P., Welander, P., Openshaw, H., Nalbandian, C., Edwards, C., Moldawer, L., Cantin, E.
  2003; 77: 11661-11673