

Frontiers in Tropical Marine and Terrestrial Microbial Ecology



Smithsonian
Tropical Research Institute

SYMPOSIUM | NOVEMBER 29, 2022

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Agenda

SYMPOSIUM | NOVEMBER 29, 2022

- //// 8:00am COFFEE AND PASTRIES
- 🔊 9:00am WELCOME REMARKS | Joshua Tewksbury, Director STRI
- 🔊 9:25am **Erin Spear** | Terrestrial microbial ecology at STRI
- 🔊 9:30am **Matt Leray** | Marine microbial ecology at STRI
- 9:40am **Laetitia Wilkins** | Introducing the new Max Planck Research Group “Eco-Evolutionary Interactions”
- 10:05am **Laura Bogar** | Symbiotic economies? Examining resource movement in ectomycorrhizal mutualism between trees and fungi
- //// 10:30am COFFEE BREAK
- 10:45am **Michael Kühn** | Exploring the microenvironment of aquatic symbiosis
- 11:10am **Justin Shaffer** | Bacterial endosymbionts of seed-associated fungi: Context-dependent survival and germination for infected seeds
- 11:35am **Adrienne Correa** | Thank you for biting: Guild-specific effects of non-lethal consumption on resource species
- //// 12:00pm LUNCH
- 1:00pm **Katie Gold** | Plant disease sensing: studying plant-pathogen interactions at scale
- 1:25pm **Lucía Pita** | The holobiont as an ecosystem: understanding animal-microbe interactions in their natural context
- 1:50pm **Leho Tedersoo** | Molecular view on fungi globally
- 2:15pm **Mohammad ‘Monir’ Moniruzzaman** | Giant virus-protist associations across the spectrum of viral symbiosis
- 2:40pm **Talia Karasov** | The effect of host genetic diversity and surrounding microbiota on pathogen spread
- //// 3:05pm COFFEE BREAK
- 3:20pm **Michelle Hersh** | How does landscape fragmentation affect fungal community structure?
- 3:45pm **Alison Gould** | Shedding light on microbial symbiosis: lessons from a bioluminescent coral reef fish
- 4:10pm **Cathy Collins** | Context-dependent impacts of disease caused by generalist seed pathogens
- 4:35pm **Linda Wegley Kelly** | Diel dynamics of microbial biogeochemistry in coastal marine systems
- 🔊 5:00pm CLOSING REMARKS
- 🗨️ 5:05pm CLOSING RECEPTION



Photo credit: Cornell CALS marketing | Katie Gold

Speakers & Abstracts

Dr. Laetitia Wilkins

Max Planck Institute for Marine Microbiology, Germany



► Introducing the new Max Planck Research Group “*Eco-Evolutionary Interactions*”

Abstract

I will introduce the research goals of our new “free-floating” Max Planck Research Group “*Eco-Evolutionary Interactions*”. We work on three major research axes: (I) Modeling the symbiotic macroevolution in lucinid clams and their bacterial partners across the Isthmus of Panamá; (II) Inferring their ecological history using biogeochemistry in lucinid clam shells (contemporary and fossilized); and (III) Running common garden and translocation



The marine lucinid clam *Codakia distinguenda* lives in a nutritional symbiosis with sulphur-oxidizing bacteria housed in its gills. Photo credit: Laetitia Wilkins

experiments to manipulate symbiosis and understand short-term adaptation. Many of the ideas and working hypotheses in our research group were conceived during the 2018 and 2019 workshops organized at STRI by the #istmobio research group. The #istmobio is a project funded by the Gordon & Betty Moore Foundation that leverages a natural experiment, the Isthmus of Panama, for the long-term study of host-microbe ecology and evolution.

Bio

Dr. Laetitia Wilkins studies how the closure of the Isthmus of Panamá affected the evolution of marine microbial symbioses. This natural experiment provides great insight into evolutionary processes of eukaryote and microbial adaptation and speciation. Her group uses molecular genetic tools and combines them with experimental set-ups and biogeochemistry to learn how populations cope with environmental change.

Dr. Laura Bogar

University of California, Davis,
USA



► Symbiotic economies? Examining resource movement in ectomycorrhizal mutualism between trees and fungi

Abstract

Ectomycorrhizal symbiosis is an essential mutualism by which most temperate trees access nutrients, helping to regulate carbon and nitrogen movement in forests. In other root mutualisms, reciprocal trading of plant carbon for fungal resources is thought to support a “symbiotic economy” that may stabilize these symbiotic partnerships. In ectomycorrhizal symbiosis, however, research has revealed inconsistent relationships between carbon investment, nitrogen provisioning, and plant benefit. To investigate this, we incorporated competition and soil resources into a 10-month split-root microcosm study using *Pinus muricata* seedlings with *Thelephora terrestris*, *Suillus pungens*, or no ectomycorrhizal fungus, under two nitrogen concentrations in artificial soil. We used stable isotope enrichment to track



Suillus mushroom, pine roots with *Suillus* fungus, and pine seedlings in ^{13}C CO_2 chamber. Photo credits: Laura Bogar & Callie Chapelle.

plant photosynthate and fungal nitrogen, finding that reciprocal carbon-for-nitrogen movement occurred only for *T. terrestris*. For *S. pungens*, plant carbon and fungal nitrogen were not coupled, although plants preferentially allocated carbon to *S. pungens* rather than *T. terrestris* under low nitrogen conditions. Our results suggest that the movement of carbon and nitrogen in ectomycorrhizal symbiosis depends strongly on environmental and competitive context, as well as on the identities of the interacting species. Predicting resource movement between forest trees and ectomycorrhizal fungi will require better understanding of this context dependency across species and environments.

Bio

Dr. Laura Bogar uses RNA sequencing (gene expression, community characterization), physiological measurements, and stable isotope enrichment to understand mycorrhizal systems, coupled with field sampling to elucidate the implications for landscape and ecosystem processes. Notably, she used experimental manipulations and carbon-13 labeling to demonstrate that plants can actively structure ectomycorrhizal fungal communities and reward better mutualists.

Dr. Michael Kühl

University of Copenhagen,
Denmark



► Exploring the microenvironment of aquatic symbiosis

Abstract

Symbiotic interactions in aquatic organisms such as reef-building corals and didemnid ascidians take place in a multispecies assemblage spanning different compartments that together form the holobiont. Such compartmentalization affects the fitness landscape and creates a variety of microenvironments within organisms, with different physicochemical conditions that provide unique niches for microbiomes of distinct composition and function, and which remain largely unstudied at appropriate scale. The small dimensions and dynamic changes of such microenvironments (e.g., due to animal behavior) and the presence of strong gradients of key physical (light, temperature) and chemical variables (e.g. O₂, pH, CO₂) complicates their experimental investigation and characterization of microbiomes.



The microenvironmental landscape of a *Fungia* coral. Photo credit: Maja Friis

However, application of microsensors and novel imaging techniques in combination with microvolume sampling is starting to alleviate the large knowledge gaps on the role of microenvironments and compartments for the holobiont and its resilience to environmental stress. I will show examples of such experimental tools and their application for exploring the microenvironmental landscape and linking structure and function in marine photosymbioses.

Bio

Dr. Michael Kühl's studies the microenvironmental controls and microbial interactions in aquatic communities and ecosystems, but also in medical biofilms and chronic infections. To do so, his group employs emerging tools such as microsensors and imaging techniques for biogeochemical analysis of microenvironments, and mass transfer and metabolic rates. Dr. Kühl's work is highly interdisciplinary and leverages cutting edge sensor chemistry, photonics, 3D bioprinting and advanced imaging approaches.

Dr. Justin Shaffer

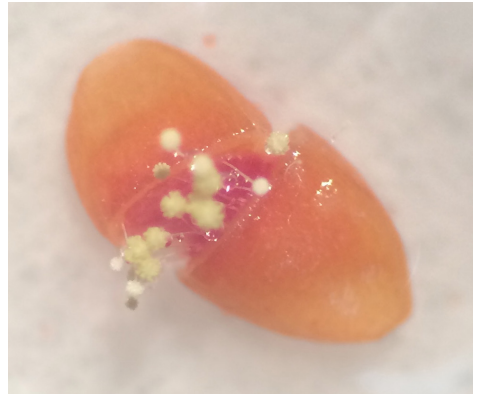
University of California, San Diego,
USA



► Bacterial endosymbionts of seed-associated fungi: Context-dependent survival and germination for infected seeds

Abstract

Soilborne microorganisms and in particular fungi influence the survival of seeds in the soil seed bank, which may alter community-level patterns of tree diversity through both space and time in tropical forests. These seed-associated fungi can alter seed germination and the mortality of apparently dormant seeds, although outcomes are not consistently predictable. Although host- and environmental factors explain some of this variation, the role of additional co-occurring microbes has been shown to be



Tetrazolium-stained *Cecropia* seed with fungal fruiting bodies. Photo credit: Justin Shaffer

important in other systems, and may play a role here. For example, plant-associated fungi often harbor endohyphal bacteria that influence fungal phenotypes and the outcomes of plant-fungus interactions. In this presentation, I summarize the results from experiments quantifying the effects of endohyphal bacteria on interactions between fungi and seeds of Neotropical pioneer trees, which are colonized by fungi naturally in forest soil. Specifically, I will discuss the effects of endohyphal bacteria on seed colonization by fungi and the germination and viability of colonized seeds.

Bio

Dr. Justin Shaffer's work revealed the widespread abundance and diversity of bacteria that inhabit the tissues of plant-associated fungi, their close relationships to known free-living bacteria, and their ability to influence the outcome of plant-fungus interactions, namely seed survival, and germination. He is also the lead author on a recent paper utilizing multi-omics profiling to reveal how microbial and metabolite composition, as well as microbe-metabolite co-occurrence patterns, are shaped by host-association and the environment across Earth's biomes.

Dr. Adrienne Correa

Rice University, USA



► Thank you for biting: Guild-specific effects of non-lethal consumption on resource species

Abstract

Symbioses between habitat-forming species, such as corals, and microorganisms underpin the biodiversity, productivity, and stability of ecosystems. Consumers shape communities of these foundational resource species through trophic interactions, but some outcomes of these interactions are rarely examined. I will summarize ongoing research by my group exploring the extent to which common reef-associated consumers (corallivores and herbivores) disperse live coral symbionts in their feces as they move across reefs, and the impacts of these feces on recipient coral hosts. Such research avenues expand our understanding of the ecological roles of consumers



A corallivore butterflyfish (*Chaetodon lunulatus*) dispersing live coral symbionts across a reef. Photo credit: Alex Veglia

on coral reefs: although herbivores support coral dominance through removal of macroalgal competitors, they also disperse potential coral pathogens. Corallivore predation can wound corals, yet their feces contain live beneficial coral-associated dinoflagellates and bacteria, supporting the hypothesized role of corallivores in coral symbiont dispersal. The ability of various coral life stages to acquire and establish symbionts from consumer feces is also under investigation. Studying how different trophic guilds of consumers contribute to microbiota dispersal and assembly in hosts can ultimately be leveraged in ecosystem management and restoration efforts, for example through the identification of trophic guilds that may promote or harm resource species under different environmental contexts.

Bio

Dr. Adrienne Correa's applies interdisciplinary approaches to quantify how microorganisms influence hosts and ecosystem-level processes, particularly under environmental stress. Her primary research interests include the diversity and evolutionary histories of marine microorganisms; the context-dependent roles of dinoflagellate symbionts, bacteria and viruses in host health and disease; and the influence of microbes on ecosystem function and persistence.

Dr. Katie Gold

Cornell University, USA



► Plant disease sensing: studying plant-pathogen interactions at scale

Abstract

Plant disease threatens crop production sustainability worldwide, resulting in \$220B lost and the application of over 8B pounds of pesticides annually. The consequences of plant disease go far beyond yield reduction and financial loss, and include critical indirect effects along global economic fabrics, food chains, and ecosystems such

as harvest quality, food safety, and biodiversity loss. A more strategic approach to management is needed to reduce the negative consequences of both plant disease and its mitigation to ensure long-term agricultural sustainability in a changing climate. The nascent discipline of plant disease sensing, or the science of using proximal and remote sensing to detect disease, offers opportunity to extend monitoring to previously unachievable resolutions, a basis to construct multi-scale, early warning networks, all while adding a dynamic new dimension to ag-systems biology. Despite its revolutionary potential, plant disease sensing remains a discipline underdeveloped with challenges facing both fundamental study and field application alike. In this talk, Dr. Gold will discuss her lab's use of multi-scale and multi-modal sensing to detect and differentiate asymptomatic plant disease in



Capturing spectral measurements of a grape leaf using a Leaf Clip and Reflectance Probe.
Photo credit: Cornell CALS marketing.

vineyards, lessons learned from the trenches, and future perspectives on global disease surveillance with soon-to-be-launched hyperspectral satellite systems.

Bio

Dr. Kaitlin (Katie) Gold specializes in the use of in situ and imaging spectroscopy (hyperspectral imaging) deployed at a range of spatial scales, from proximal, autonomous rovers to spacecraft, to characterize asymptomatic disease physiology and the impacts of management intervention on early grape disease detection. She studies the fundamental and applied science of plant disease and plant-microbe interaction sensing to improve integrated disease management.

Dr. Lucía Pita

Institute of Marine Science
(ICM-CSIC), Barcelona, Spain



► The holobiont as an ecosystem: understanding animal-microbe interactions in their natural context

Abstract

Symbiosis – “living together” – with microbes contributes to animal ecological success and is a source of evolutionary innovation. The host and its microbiota form a functional unit called the “holobiont”, which can be regarded as a miniature ecosystem of complex host-microbe and microbe-microbe interactions that result in new functions.



The activity of microbes living in association with sponges influences nutrient cycling in marine ecosystems. Photo credit: Jordi Regàs

It is highly debated how these complex holobionts evolved and are maintained. Holobionts do not occur as isolated units, but are affected by their environment and are embedded in a community of holobionts, in a larger ecosystem. Like a Russian doll. We are lacking fundamental understanding of underlying mechanisms of holobiont homeostasis in a changing environment. This knowledge is essential to understand the role of the microbiome in stress and disease. In my talk, I will first introduce the microbial diversity harbored in sponges and how microbial metabolism occurring inside the sponge, coupled with the animal activity, scales up and influences nutrient cycling in the ecosystem. Then, I will focus on our work aiming at revealing the role of sponge immunity as guardian of sponge-microbe interactions. Finally, I will discuss how the holobiont concept has changed our perspective on how marine animals face the environmental stress caused by the climate crisis.

Bio

Dr. Lucía Pita's research combines molecular work (RNA-Seq, amplicon sequencing) with an experimental approach to disentangle the relative role of environment-host-and microbial factors in the functioning of the holobiont with a particular focus on the interaction between marine sponges and bacteria. Now Junior group leader at the Institute of Marine Science (CSIC) in Barcelona, her group focuses on the influence of host immunity on animal-microbe interactions in a changing environment.

Dr. Leho Tedersoo

University of Tartu, Estonia



► Molecular view on fungi globally

Abstract

Global patterns in plant and animal diversity have intrigued naturalists since the times of von Humboldt, but until the last two decades such information about microorganisms including fungi has been impossible to achieve. Here I show how cutting-edge molecular identification tools can boost our understanding about the structure and function of the microbiome and their global distribution patterns. By combining long-term material collections by a large international collaborative network and modern



Isalo massif in Madagascar, the first collection location for the Global Soil Mycobiome project in 2010.

Photo credit: Leho Tedersoo

molecular and bioinformatics tools, we are getting closer to understanding the global patterns in distribution of microorganisms as well as their drivers, endemism and vulnerability to global change.

Bio

As an accomplished mycologist and soil ecologist, Dr. Leho Tedersoo's research interests include the global biodiversity and biogeography of mycorrhizal fungi, including endemism and vulnerability to drought, temperature, and land-cover change, as well as the relationship between mycorrhiza types and the functioning of soils. He is a leader in the field, contributing to best practices in metabarcoding and sequence-based identification of fungi, and an annotation tool for assigning ecological guild to fungi (FungalTraits).

Dr. Mohammad ‘Monir’ Moniruzzaman

University of Miami, USA



► Giant virus-protist associations across the spectrum of viral symbiosis

Abstract

Viruses shape the evolution and ecology of myriad microbial lineages in the biosphere. One of the most compelling viral groups that have recently garnered great interest is the ‘giant viruses’; also known as Nucleocytoplasmic large DNA viruses (NCLDV). NCLDVs are a diverse group of eukaryotic viruses with large virion sizes that can reach up to 1.5 μm , genomes as large as 2.5 million base pairs, and hundreds of genes with complex evolutionary histories. However, little is known about the impact of NCLDVs on the ecological and evolutionary trajectories of their hosts, even though they are ubiquitous in the biosphere and infect diverse ecologically important protist lineages. I have leveraged large-scale genomics and metagenomics to understand how NCLDV-host interactions shape the genomes of both partners. I have found that NCLDVs harbor numerous genes involved in cellular metabolism, which has the potential to modulate host metabolic programs during infection, with profound implications for global biogeochemistry. In contrast, hosts frequently ‘adopt’ the NCLDV genomes via endogenization, which creates opportunities for functional and regulatory innovations. These results pave the way to study diverse outcomes of NCLDV-host symbiosis, ranging from mutualism to antagonistic interactions.

Bio

Mohammad ‘Monir’ Moniruzzaman’s research focusses on understanding the ecological and evolutionary outcomes of virus-microbe interactions in the ocean. He employs laboratory experiments and bioinformatic approaches to study the dynamics of giant virus – host interactions during algal blooms, to characterize the molecular underpinnings of ‘virocell’ metabolism, and to assess the impact of endogenous giant viruses on the physiology and genome evolution of their eukaryotic hosts.

Dr. Talia L. Karasov

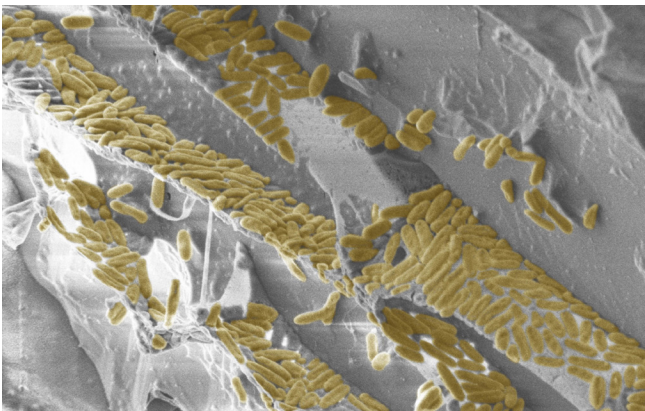
University of Utah, USA



► The effect of host genetic diversity and surrounding microbiota on pathogen spread

Abstract

What determines when a plant population will be overtaken by pathogen and when the population will persist in health? Across geographic regions, plants are colonized by distinct pathogenic and commensal microbes, but the factors driving this variation are largely unknown. I will present two studies that explore the abiotic and biotic factors that influence the abundance of pathogens in populations of the model plant *Arabidopsis thaliana*. In the first study, we characterize the distribution and evolution of common bacterial pathogens from the genus *Pseudomonas* across 300 *A. thaliana* populations in Europe. In the second study, we assess how surrounding microbes and host genetic diversity influence the pathogen distribution. In these studies, we discovered marked, geography-dependent differences in microbiome composition within *A. thaliana* populations and find water availability to be a significant predictor of these differences. We further find evidence that host plant genetics and viral elements act to suppress outbreaks of the *Pseudomonas* pathogen.



Scanning Electron Microscopy (SEM) image of *Pseudomonas*. Photo credit: Sonja Kersten & Juergen Berger

Bio

Dr. Talia Karasov's work explores the interplay between plant genetic diversity and the evolution and spread of microbes, using genomics, population genetics, microscopy, and metabolomics. Using shotgun metagenomics to assess the microbial composition and load of the phyllospheres of wild *Arabidopsis* populations, she demonstrated that high microbial loads are typically associated with the proliferation of a single, likely pathogenic, taxon.

Dr. Michelle Hersh

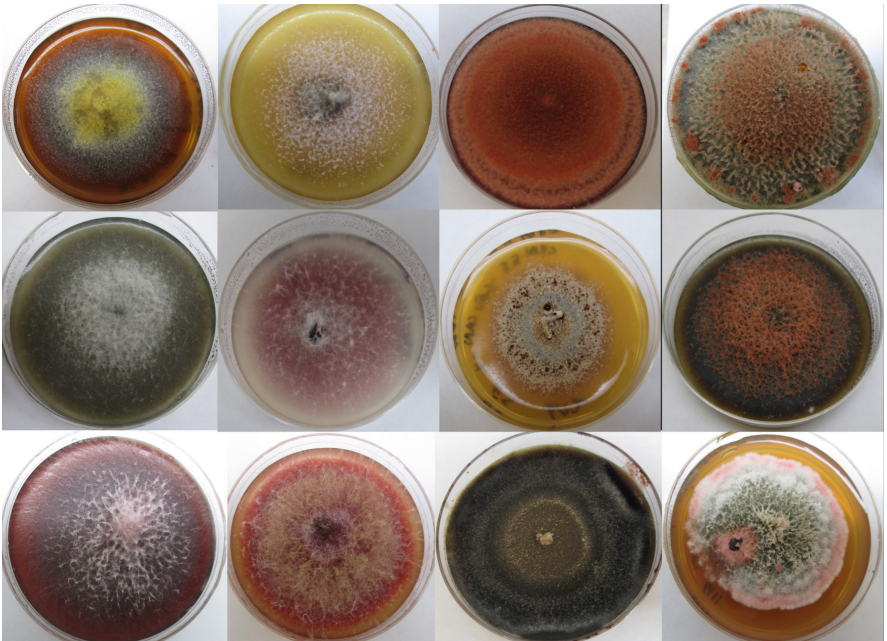
Sarah Lawrence College, USA



► How does landscape fragmentation affect fungal community structure?

Abstract

Seed pathogens can be an important control on plant populations, including but not limited to the negative feedbacks that help maintain plant diversity. At the same time, habitat fragmentation can have many predictable impacts on ecosystem structure and functions, both biotic and abiotic. Our group is exploring how interactions



Fungal pathogens isolated from seeds to explore the effects of landscape fragmentation on plant and fungal communities. Photo credit: Michelle Hersh

between plants and their seed pathogens can be altered by fragmentation. To begin to address this, we assayed fungal communities in buried seeds across an experimentally fragmented landscape in Lawrence, Kansas. Seeds were buried for a calendar year; after excavation we used a combination of culture-based and culture-independent methods to determine fungal community structure and are now starting to analyze the data. We sequenced 1,342 fungal isolates from seven species of plant seeds and are in the process of using amplicon sequencing to look at ~800 seed samples from eleven plant species. We are exploring these datasets to examine the relative influence of host identity, landscape location (large-interior, large-edge, small patch, matrix), soil moisture, plant species richness, plant community composition, and soil temperature on fungal community structure and richness. Does the fungal community change as the landscape fragments, and how?

Bio

Dr. Michelle Hersh's research focuses on the connections between biodiversity and disease. She has used mathematical modeling and empirical work to evaluate how infection by a single and multiple generalist pathogens can impact seedling survival in temperate forests. Her current research explores how landscape fragmentation alters seed fungal communities and the impacts of these changes on plant diversity. She has also been involved in research on tick-borne pathogen communities and most recently, bacterial pathogen pollution in urban waterways.

Dr. Alison Gould

California Academy of Sciences,
USA



► Shedding light on microbial symbiosis: lessons from a bioluminescent coral reef fish

Abstract

Microbial symbiosis has gained recognition as one of the most important forms of species interaction to have shaped biodiversity across the tree of life; virtually all organisms depend on bacteria for their success. However, in order for microbial symbiosis to evolve, the association must be stably re-established by each new host generation. The mechanisms that promote host-symbiont specificity remain largely uncharacterized and can be context-specific. The highly specific, bioluminescent symbiosis between coral reef fish in the *Siphamia* genus and a luminous member of the *Vibrio* family, *Photobacterium mandapamensis*, is providing new insights on the mechanisms that regulate the formation and maintenance of microbial



Bioluminescent symbiosis between a coral reef fish in the *Siphamia* genus and a luminous member of the *Vibrio* family, *Photobacterium mandapamensis*.

Photo credit: Alison Gould

symbiosis from an evolutionary scale down to the molecular level. Ultimately, this experimentally tractable, binary association can help disentangle the ecological and physiological complexities underlying the establishment, persistence, and evolution of host-microbe specificity, providing a more complete understanding of the universal principles that govern microbial symbiosis.



Siphamia. Photo credit: Alison Gould

Bio

Dr. Alison Gould's research focusses on the bioluminescent symbiosis between coral reef fish in the genus *Siphamia* and luminous bacteria. Her work integrates natural history and ecology with genomics to understand how the highly specialized association evolved and how host-symbiont specificity is maintained over time and space.

Dr. Cathy Collins

Bard College, USA



► Context-dependent impacts of disease caused by generalist seed pathogens

Abstract

Soil-borne fungal pathogens play a key role in maintaining plant diversity via plant-soil feedbacks. For negative feedbacks to increase diversity, pathogen impacts must be specialized, reducing fitness of the host plant more than neighboring



Exposing seeds to fungal pathogens to explore the effects of temperature on disease severity. Photo credit: Karl Rabe

species. Yet many soil-borne fungi are generalists: they are both geographically widespread, and infect many plant host species. Anthropogenic disturbances like landscape fragmentation may favor generalists and alter habitats in ways that shift the outcome of host-pathogen interactions. As part of a larger study on how landscape fragmentation shapes plant and fungal communities, our group is exploring how environmental conditions influence disease severity. Do generalist fungal pathogens have differential impacts depending on seed species, environmental conditions, or both? To address this question, we focus on ten fungi taxa cultured from grass and herb seeds buried for one year in an experimentally fragmented landscape. For each putative pathogen taxon (12 isolates of each), we quantified disease impacts on seeds of 12 plant species at two temperatures. Fungal growth rate and host-susceptibility varied

among species, and disease severity increased in temperatures characteristic of small fragments. We use our results as a framework to explore the consequences of context-dependent disease for understanding pathogen-mediated plant coexistence in heterogeneous habitats.

Bio

Dr. Cathy Collins investigates the influence of landscape fragmentation on community assembly and interspecific interactions. She is currently exploring how plants inhabiting large versus small habitat fragments, which differ in temperature, light, and soil moisture, are affected by phytopathogens, as well as the importance of specialist versus generalist pathogens. This work includes characterizing the fungal pathogen communities, seed viability across microclimates, and assessing plant–soil feedbacks.

Dr. Linda Wegley Kelly

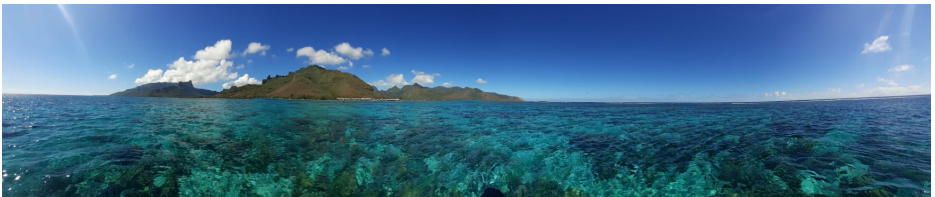
Scripps Institution of Oceanography,
USA



► Diel dynamics of microbial biogeochemistry in coastal marine systems

Abstract

Coastal marine environments maintain their own unique planktonic microbiomes and distinct biogeochemical properties compared to the surrounding ocean waters. Benthic primary producers, such as macroalgae, seagrasses, and corals contribute significantly to microbial ecology in coastal waters by manipulating key environmental parameters, like carbon substrate availability and oxygen concentrations, that influence the growth and metabolism of microbes. Microorganisms comprise the majority of biomass in the water column and their role in the decomposition of dissolved organic substrates is critical for the transformation and recycling of mineral nutrients. For example, day and night populations of coral reef microbes differ compositionally and encode significantly different metabolic profiles. Specific bacterial taxa involved in nitrogen and sulfur cycling demonstrate distinct temporal patterns, indicating that microbial roles in nutrient transfer may track the diel metabolism of reef benthic communities. Active research in my lab seeks to characterize the diverse assemblages of organic substrates released into coastal marine waters by benthic primary producers, and identify microbial metabolisms involved in nutrient transformations and recycling in these environments.



Marine water column overlying a coral reef benthic habitat. Photo credit: Shayle Matsuda

Bio

Dr. Linda Wegley Kelly is an environmental microbiologist with expertise in marine biogeochemistry, untargeted metabolomics and microbial genomics. Dr. Wegley's research program combines molecular approaches with chemistry and microbial ecology to understand the role of microbes in reef biogeochemistry, including nutrient recycling and the balances of both organismal and ecosystem-level production, calcification and respiration.



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