Project Summary

Overview

The species compositions of ecological communities often depend on history. Even for the same environmental conditions, small differences in initial species compositions can cause communities to assemble into different discrete states. These alternative community states can differ dramatically in the identities and abundances of the species that comprise them. Thus, chance events early in the history of a community can have large effects on its structure and function. Because the populations within real communities are almost never completely isolated nor evolutionarily static, alternative community states are impacted both by interactions across spatial scales and by trait evolution. Here, I propose to study how rapid evolution alters alternative community states at both single-community and metacommunity (a network of interconnected communities) scales. Under the guidance of Dr. Tadashi Fukami at Stanford University, I will use both laboratory experiments and mathematical models to address this question in a well-described and ideally suited study system: microbes in *Diplacus aurantiacus* nectar. I will address two main questions: (Q1) How does rapid trait evolution affect the compositions of alternative single-community states and their prevalence across a metacommunity? (Q2) Under what conditions do rapid evolution and gene flow alter how alternative metacommunity states affect species coexistence? This project will also help broaden the participation of underrepresented groups through (1) mentorship of an undergraduate research team and (2) a paid internship program for formerly incarcerated research scholars.

Intellectual Merit

A major criticism of community ecology has been its inability to explain much of observed variation in community structure and function. Part of the problem is that chance events can cause communities to assemble into disparate alternative community states. Due to complicated connectivity patterns among individual communities, these alternative states can operate at multiple spatial scales, with interactions that can qualitatively alter outcomes. Additionally, models assuming static species traits often do not capture the full dynamical picture of our evolutionarily labile systems. This is especially true when evolution is on the same timescale as ecology, since intertwining ecological and evolutionary processes can greatly affect communities and ecosystems. Yet we know little about how alternative community outcomes are affected by rapid evolution, and how they interact across spatial scales. By studying the effects of rapid evolution on alternative community states across scales, I can help explain the history- and scale-dependent variation in communities that has long been a criticism of the field of community ecology.

Broader Impacts

Broader Impacts of this work fall into two main categories. First, I will work with community-building groups and training programs at Stanford to recruit a diverse team of at least 3 undergraduates that will be paid to carry out the proposed laboratory experiments. Students will gain experience with microbiological lab techniques, data entry, and basic computer programming. Second, I will partner with existing prison-to-university pipelines to create a paid STEM internship program for formerly incarcerated undergraduate scholars. The ultimate aim of this program is to help address a pressing social issue that disproportionately affects underrepresented minorities. This structured, quarterly program would provide scholars with mentorship and hands-on scientific experience to help them build their own careers. The projects will primarily be computational or theoretical, so scholars will gain concrete skills in computer programming, statistics, and mathematics. For both undergraduates and the STEM scholars, students will also develop broadly transferable career skills, such as teamwork, technical writing, and problem solving.

Effects of rapid evolution on alternative community states at multiple spatial scales

Introduction

History often plays a strong role in shaping which species coexist and where. Even for the same environmental conditions, species interactions can often allow for multiple different discrete states, or alternative community states (ACS), into which a given community can assemble (Fukami, 2015; Scheffer et al., 1997). Which ACS is realized depends on initial community conditions (e.g., species compositions). ACS can operate locally (i.e., on a single habitat patch) and underlie substantial differences in community structure, such as those caused by the takeover of an invasive species (Schooler et al., 2011). ACS can also operate regionally across metacommunities (networks of connected patches), and feedbacks between local and regional ACS can change outcomes based on a single spatial scale alone (Shurin et al., 2004). Multi-scale ACS can influence global patterns of community function (e.g., tree cover; Staver et al., 2011) and human diseases affected by gut microbes (Costello et al., 2012).

Species' traits underlie many of the ecological processes that generate ACS, so trait change could alter the species compositions of ACS or cause communities to shift between states (Dakos et al., 2019). When trait evolution is rapid (on the same timescale as population dynamics), it can generate feedbacks between trait change, population dynamics, and species interactions, which can change both the dynamical properties (Yoshida et al., 2003) and final states (Duffy and Sivars-Becker, 2007) of communities. Mounting evidence indicates these "eco-evo dynamics" are common (Kinnison et al., 2015; Schweitzer et al., 2014) and can alter community properties such as the ability of species to coexist (Kremer and Klausmeier, 2017; Lankau and Strauss, 2007; Vasseur et al., 2011). Moreover, eco-evo dynamics often operate at various spatial scales, resulting in across-scale feedbacks (Pelletier et al., 2009; Ware et al., 2019). **Yet we know little about how rapid evolutionary trait change affects ACS, especially across multiple spatial scales** (Dakos et al., 2019). The limited evidence to date supports it having a strong role in shaping multi-scale ACS and their ecological consequences (Wittmann and Fukami, 2018), but empirical data are especially lacking.

The proposed research will examine the effects of rapid trait evolution on ACS at multiple spatial scales. I will address two main questions: **(Q1) How does rapid trait evolution affect the compositions of ACS and their prevalence across a metacommunity? (Q2) Under what conditions do rapid evolution and gene flow alter how regional ACS affect species coexistence?** By addressing these questions using experiments and theory, I aim to generate new insights into how communities are shaped by historically contingent ecological–evolutionary processes across scales.

Study system

In flowers of the shrub *Diplacus aurantiacus*, resident communities of nectar microbes (the bacterium *Acinetobacter nectaris* and yeast *Metschnikowia reukaufii*; hereafter simply "bacteria" and "yeast", respectively) demonstrate multi-scale ACS and the potential for rapid evolution. Local ACS occur because whichever species arrives first to a new flower inhibits the other, resulting in individual flowers being either bacteria- or yeast-dominated (Chappell and Fukami, 2018; Tucker and Fukami, 2014). Yeast's relative inability to disperse without pollinators and pollinators' preference for yeast-dominated plants cause regional ACS, resulting in bacteria-dominated or mixed-species plants (Toju et al., 2018). Rapid evolution in yeast is supported by ongoing work showing variation among wild strains for two traits affecting local ACS: (1) how well late-arriving yeast tolerate early-arriving bacteria ("bacteria tolerance") and (2) how well early-arriving yeast inhibit late-arriving bacteria ("bacteria inhibition") (C. Chappell & T. Fukami, unpublished data). In bacteria, there is less evidence for a similar capacity to rapidly evolve. This may be a result of greater immigration of bacteria from the surrounding landscape, since strong gene flow

from a larger population facing different selection pressures can inhibit local adaptive evolution (Holt and Gaines, 1992; Holt and Gomulkiewicz, 1997). Rarely does a study system have multiple well-described traits that affect ACS, and even more rare is evidence that any of these traits can rapidly evolve. Combined with the ability to quickly replicate the process of generating alternative communities, this nectar microbe system presents an excellent opportunity to study rapid evolution's effects on ACS.

Research Objectives and Methods

Question 1: How does rapid trait evolution affect the compositions of ACS and their prevalence across a metacommunity?

Hypotheses: Rapid trait evolution by one species will increase the prevalence of the community state where that species is most abundant. It will also change the composition of one community state, but the precise effect will depend on which trait is evolving.

Rationale: Because yeast is better understood than bacteria regarding its traits that affect ACS, this hypothesis will be tested using evolution in yeast only. When yeast can evolve bacteria tolerance, this should allow high-tolerance yeast strains to persist at higher densities when bacteria arrive first. Bacteria tolerance evolution should therefore reduce average differences between yeast and bacteria abundance in bacteria-dominated communities. This will make ACS more similar, increasing community evenness and decreasing among-community variation. Alternatively, rapid evolution of bacteria inhibition in yeast should cause the opposite effects because it should allow high-inhibition yeast strains to better monopolize patches when they arrive first. Evolution of either trait should increase metacommunity-wide yeast abundance, which I expect to increase the likelihood of the yeast-dominated community state. Lastly, when either trait can evolve, I predict "eco-evolutionary feedbacks": Changes in relative species abundances will alter selection, causing evolution of the trait, which will in turn affect relative species abundances.

Methods overview: I will use laboratory experiments of metacommunities to assess how rapid evolution affects local ACS across space. Before starting, I will assay yeast strains for two ACS-affecting traits (bacteria tolerance and bacteria inhibition), using a subset of the 102 strains archived by the Fukami lab (Figure 1a). These assays will inform the evolution treatments: I will vary the ability of yeast to rapidly evolve either trait by manipulating their starting among-strain variation (Figure 1b). Reproduction in the focal yeast species is almost entirely clonal (Herrera et al., 2014), so rapid trait evolution by yeast will most often occur through changes in relative frequencies of strains that differ in their trait values. This is a common way to manipulate the capacity for evolution in clonal organisms (Yoshida et al., 2003). Additionally, I will vary the starting proportion of communities dominated by yeast versus bacteria (Figure 1c). This will help demonstrate whether there are feedbacks between trait evolution and relative species abundances.

Trait assays: To construct a set of yeast strains with variation in ACS-affecting traits, I will conduct trait assays on archived yeast strains. A phylogeny has been constructed for these 102 strains (Dhami et al., 2018), and most have both gene-expression and metabolomic data. I will first choose 24 strains that are spread evenly along the phylogeny and have diverse gene expression and metabolomic profiles. I will assay traits in these strains by either (for bacteria tolerance) introducing them to a bacteria-dominated community or (for bacteria inhibition) introducing bacteria to a community dominated by that yeast strain (Figure 1a). I will estimate abundances of both yeast and bacteria using qPCR 96 hours after the first microbe introduction; this is about the length of time an individual *D. aurantiacus* flower is open. Abundance estimates based on qPCR will be developed in collaboration with Dr. Bart Lievens (Katholieke Universiteit Leuven, Belgium), as his lab has previously developed qPCR primers for the species of

interest (Colda et al., 2021). Bacteria tolerance values will be $\log(\hat{y})$, where $\hat{y}$ is yeast abundance in the final community. Bacteria inhibition will be $-\log(\hat{b})$, where $\hat{b}$ is final bacteria abundance. I will replicate these assays 4 times for each strain.

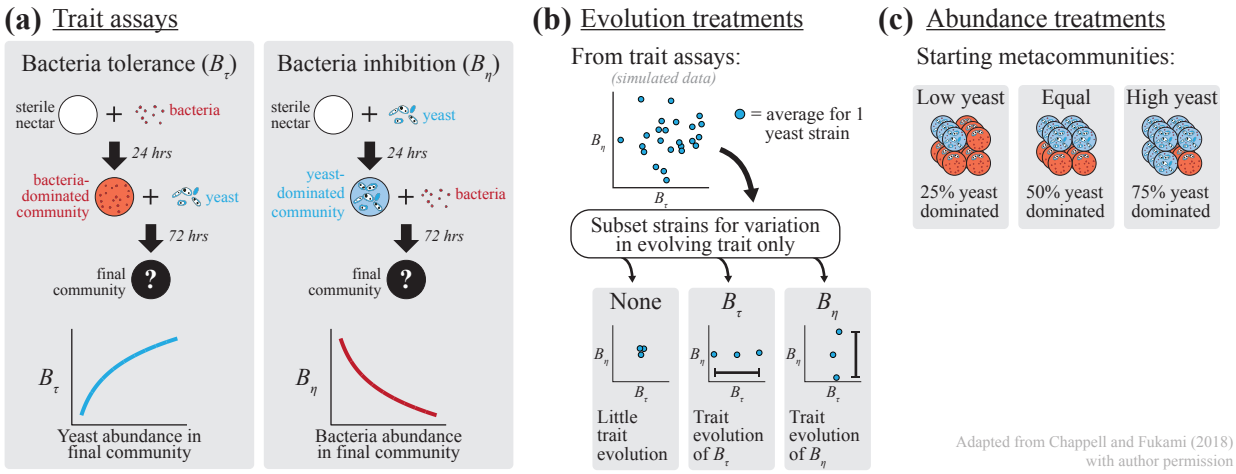

Figure 1. (a) Trait assays and (b,c) experimental treatments for Question 1.

Experimental treatments: I will have 3 evolution treatments and 3 abundance treatments. From the 24 initially assayed yeast strains, I will select strains so they represent the 3 evolution treatments: (1) low standing variation for both traits, (2) high variation for bacteria tolerance, and (3) high variation for bacteria inhibition (Figure 1b). There will always be 3 strains per treatment, and the among-strain average for the traits will be the same for all treatments. I will always use the same strain of bacteria. I will also run these experiments with each selected strain of yeast individually to rule out effects of non-assayed traits in one or more strains. The abundance treatments will be (1) 75%, (2) 50%, and (3) 25% of starting communities dominated by yeast, while the others are dominated by bacteria (Figure 1c). Communities dominated by each species will have the dominant species added first, followed by the other 48 hours later.

Experimental metacommunities: To replicate metacommunity dynamics, I will use microcosm experiments based on methods used previously by the Fukami lab (Dhami et al., 2018; Peay et al., 2012). I will have 24 nectar communities, half of which will be inoculated with microbes based on the treatment. Microbes colonizing new, sterile nectar is central to the dynamics of interest, so the other half of the communities will be started with sterile nectar 48 hours later. Staggering the start times means that we can terminate communities 96 hours after they start while retaining microbes in the system by simply replicating pollinator-mediated microbe dispersal: inserting an initially sterile pipet tip into half the tubes (randomly selected) every 24 hours. I will estimate bacteria and yeast-strain abundances by using qPCR on the nectar of terminated communities. Experiments will run for 32 days, as this is the typical amount of time individual *D. aurantiacus* plants bloom each season. I will have 4 replicates per treatment. The resulting dataset will consist of bacterial and yeast-strain abundances by community, time, treatment, and repetition.

Analyses: I will first estimate average community evenness using the Berger-Parker index (Colwell, 2009) and among-community variation using the Bray and Curtis (1957) index. I will use autoregressive mixed (ARM) models (Phillips et al., 2021) to assess whether evolution treatments affect these indices through time. I will have a fixed effect of time, and random intercepts and slopes grouped by evolution and abundance treatments; random intercepts estimate overall differences among treatments, while random slopes estimate how treatments affect time trends. Next, I will fit the experimental data to a mechanistic statistical model to delve deeper into potential feedbacks between population dynamics, selection, and trait

change. The model will fit yeast-strain-specific values for bacteria tolerance and bacteria inhibition and species-specific dispersal rates. From the model estimates, I can compute selection coefficients through time (Ives et al., 2020) for the yeast strains and thus examine links between selection, trait change, and metacommunity dynamics.

Question 2: Under what conditions do rapid evolution and gene flow alter how regional ACS affect species coexistence?

Hypothesis: Coexistence can be maintained despite regional ACS that promote exclusion when maladaptive gene flow mediates a tradeoff between dispersal ability and local adaptive evolution.

Rationale: Dispersal among flowers and plants is greater overall and less dependent on pollinator visits for bacteria than yeast. This causes pollinator-mediated regional ACS to more likely exclude yeast from plant metacommunities than bacteria (Toju et al., 2018). Yet, experiments indicate that bacteria may be less able than yeast to evolve better tolerance to arriving late (C. Chappell & T. Fukami, unpublished data), perhaps because of strong gene flow from disparate environments. I expect that yeast exclusion due to regional ACS can be reduced when yeast can rapidly evolve traits that affect ACS since it should allow them to better monopolize when arriving early and persist when arriving late. However, since yeast is an inferior disperser, evolution by bacteria must be comparatively limited for evolution to allow yeast to persist.

Methods overview: I will use a mathematical model to investigate the effects of rapid local evolution and gene flow on the coexistence consequences of regional ACS. Using a model here will allow me to explore dynamics at a larger scale than would be feasible in the field or lab and to assess the consequences of a range of values for parameters for which we have little empirical data. The model will be conceptually based on that by Tucker and Fukami (2014), where bacteria inhibits yeast by pH reduction, and both uptake amino acids as a limiting resource. The version here will differ in that it will use a discrete-time formulation and include multiple communities and many strains of both yeast and bacteria. I will explicitly simulate (a) dispersal within the metacommunity, (b) immigration from outside the metacommunity, and (c) generation of phenotypic variation via mutation from ancestral strains.

Dispersal and immigration: The metacommunity will consist of many individual communities all connected by dispersal, and immigration from outside the metacommunity can bring in new strains. Dispersal and immigration will be primarily pollinator independent for bacteria and pollinator dependent for yeast. I will simulate the processes generating regional ACS by having pollinator visits to plants decrease as the proportion of its flowers dominated by bacteria increases (Toju et al., 2018). I will simulate a range of values for the sensitivity and longevity of pollinator avoidance of bacteria-dominated plants because, although we know this effect can last for months (Toju et al., 2018), we do not have detailed information on associated pollinator behavior. Because trait values of immigrants are also largely unexplored, I will simulate across a range of means and variances for immigrant traits for both species.

Mutation and evolution: I will model evolution using a clone-based, adaptive dynamics approach (sensu Abrams, 2001). For this method, each clone's population growth rate is based on their fixed trait values, and evolution occurs as a result of differential population growth among clones. Clones give rise to daughter clones with a probability μ, and daughter clone trait values are ~Normal(ν_i, σ_i) where ν_i is the mother's trait i value. Trait assays will inform values of σ_i for yeast. I will search for literature on trait variability in bacteria (e.g., Álvarez Pérez et al., 2021) but may need to report results for simulations across a range of plausible values.

Significance

Community ecology has long been critiqued for its lack of general principles (Lawton, 1999), and this is partially due to how often community outcomes depend on historical events (Fukami, 2015). Another source of unexplained variation is the across-scale interactions that occur as an emergent property of community connectivity (Leibold et al., 2004; Shurin et al., 2004). Moreover, across the field of ecology, increasing evidence supports the need to re-evaluate classic models while incorporating evolution (Fussmann et al., 2007). This is especially true for eco-evo dynamics that occur when evolution is on the same timescale as ecology, since they can greatly affect predicted outcomes compared to when we assume static species traits (Duffy and Sivars-Becker, 2007; Kremer and Klausmeier, 2017; Lankau and Strauss, 2007; Vasseur et al., 2011; Yoshida et al., 2003). Yet we know little about how alternative community outcomes are affected by rapid evolution, and how they interact across scales. This research will study how rapid evolution affects ACS at both the community and metacommunity scale. By combining experimental and theoretical approaches, I aim to inform general predictions of history's role in shaping how species covary across space in evolutionarily labile systems.

Broader Impacts

Undergraduate mentorship

The ample resources for undergraduate research at Stanford will help me both carry out the experiments and promote diversity and inclusion. Like the experiments during my PhD, I will need a team of at least 3 students to conduct the proposed experiments. By reaching out to community-building groups for underrepresented minorities (e.g., Stanford Black Bioscience Organization, Biomedical Association for the Interest of Minority Students), I can recruit a diverse team to carry out the work and gain microbiological laboratory experience. I will also hire students from low-income backgrounds through the Federal Work-Study program, and work with students to apply for summer funding through the SSRP-Amgen Scholars Program. The resources provided by Stanford's Vice Provost for Undergraduate Education (e.g., their "Best Practices in Mentoring") will help me to maintain healthy, productive student–mentor relationships. I am excited to help train and mentor undergraduate students while contributing to a more representative ecology and evolutionary biology.

Internships for formerly incarcerated people

Mass incarceration is one of the most destructive social justice issues in America, resulting in millions of people, mostly those of color, being ensnared in the carceral system and discriminated against well after they leave prison (Alexander, 2010). For formerly incarcerated people, STEM education and experience is an effective way to reduce recidivism (Erisman and Contardo, 2005) and allow them to build careers. My plan is to create a paid internship program that will provide hands-on scientific experience for formerly incarcerated undergraduate students. These scholars will be selected by working alongside existing prison-to-university pipelines (e.g., Berkeley Underground Scholars, Princeton's Prison Teaching Initiative, STEM Opportunities in Prison Settings) to recruit up to three scholars per quarter, each with a passion for science. Scholars will then work with a mentor (me or another volunteer from the Fukami lab) to choose and refine a scientific question that they will pursue over the course of a school quarter. At the end of this period, scholars will communicate their findings by creating a poster for an undergraduate symposium (e.g., Stanford Research Conference).

The scientific topics will usually be theoretical or computational biology because I have expertise in these areas and because the ability to work remotely would greatly broaden the areas in which scholars can live. Scheduled meetings will be held every week to provide consistent mentorship throughout the process, and

monthly technical reports will provide opportunities for more detailed feedback. Through the program, scholars will have gained a range of transferable career skills, including teamwork, technical writing, problem solving, computer programming, data science, and mathematics. I will also provide continuing guidance on the graduate school admissions process, which can be frustratingly opaque for those without mentorship within academia. Stanford's prominent place in Silicon Valley makes it especially well placed to find job opportunities for those with computer programming and applied research experience. The ultimate goal is to provide mentorship and STEM experience for formerly incarcerated people for them to better build their own careers. I am currently working with Dr. Kyle Cole (Director, Office of STEM Outreach, Stanford) to develop this project and search for additional sources of funding (e.g., Federal Work-Study, SSRP-Amgen Scholars).

Training Objectives and Career Goals

My ultimate goal is to become a professor at a research university, where I can build a research program at the interface of ecology and evolution. During my PhD, I used theory, experiments, and population genomics to address questions of how ecology and evolution interact. Despite the breadth of this research, I have not yet pursued questions of how dynamical processes interact across scales. This is an especially interesting topic because scale is a long-standing problem in both ecology and evolution (Eldredge, 1985; Levin, 1992) that remains relevant in the eco-evolutionary literature (Ware et al., 2019). Thus, the most conceptually exciting component of this project is the explicit multi-scale nature of the nectar-microbe study system. This project would also allow me to develop new skills, including (1) building a system-specific model from the ground up, (2) fitting experimental data to a mechanistic model, and (3) working with microbes in the laboratory. Thus, the proposed project would provide an excellent opportunity to gain new skills and to view scientific problems through a wider conceptual lens.

Sponsoring Scientist and Host Institution

I propose this project with Dr. Tadashi Fukami. His experience generating syntheses about historical contingency will help me conceive broader insights into how history shapes communities. Moreover, his lab's nectar-microbe system is well-suited for ecological and evolutionary experiments at multiple scales, and their archive of well-described yeast strains with genetic and metabolomic profiles will help me choose candidate strains. Dr. Daniel S. Fisher (Applied Physics, Stanford) has also expressed interest in collaborating on this project. His expertise with sophisticated quantitative analysis of the interplay of ecology and evolution will be invaluable for understanding the complex patterns this project will generate.

Timetable

My NSF PRFB would start in July 2022, and Figure 2 shows the schedule of major anticipated outcomes.

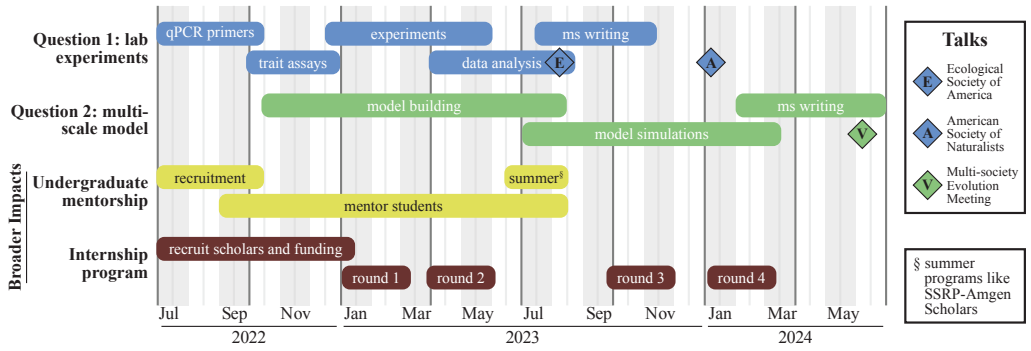

Figure 2. Timeline for my proposed NSF PRFB including talks planned.

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Data Management Plan

Data and Materials Produced

The trait-assay and experiment portions of this project will generate many (~ 750) samples of nectar from the excess not used for qPCR. They will each be small (< 10 μL) and contain microbes that could be useful later for other analyses (e.g., genomics). Data from assays and experiments will consist of bacteria and yeast-strain abundances (for assays) by assay type, strain, and repetition, or (for experiments) by treatment, repetition, community, and time. All components of this project will produce software: For assays and experiments, software will be used for analyses. For the theory part, software will be used for simulations.

Standards, Formats, and Metadata

Bacteria and yeast-strain abundances will be stored in *.csv files since they are a ubiquitous and open format. Raw qPCR output will be stored in *.eds and *.txt files, as these are the formats used by the ABI StepOnePlus real-time PCR system to store experiment and setup files, respectively. I will generate metadata using the Ecological Metadata Language (EML) via the eml package in R. Software for this project will use a combination of R and C++ code (*.R, *.h, and *.cpp files) that will be organized into R packages. The required DESCRIPTION files will provide high-level metadata for software, which I will supplement with README files in the major sub-directories.

Data and Sample Storage

Nectar samples will be stored at –80ºC in the Fukami lab for at least 3 years past the fellowship end date. Data from assays and experiments will be entered into paper lab notebooks, which will be retained by the Fukami lab for the same period of time. Every week, data will be input to Excel spreadsheets and exported to *.csv files, and paper notebooks will be scanned to png images to retain the raw data. All data will be stored on my personal laptop, personal network-attached storage (NAS), Google Drive, and Stanford's networked file system. Software will use git version control and will be backed up similarly to data, except for using GitHub instead of Google Drive. Backups to NAS will be automatically done every day via Time Machine, Google Drive every day via the desktop app, and GitHub every time I update software via the push command. I will manually back up to Stanford's system every week using a custom bash script. This design exceeds the typical 3-2-1 rule used for backups.

Data Archiving and Sharing

All assay and experimental data (raw qPCR output and *.csv files of species and strain abundances) will be made publicly available on Dryad upon publication. All software (for assays, experiments, and theory) will be publicly available on GitHub from the start of the associated project and will be published on Zenodo upon publication. Both Zenodo and Dryad provide open-source, archival storage and persistent identifiers for citing. Based on recommendations by the Open Knowledge Foundation and Open Source Initiative, I will use the MIT license for software and Creative Commons CCZero (CC0-1.0) license for research datasets from this project. Publications will also be deposited onto ResearchGate to improve access to resulting manuscripts.

Roles and Responsibilities

I will be primarily responsible for data collection, management, analysis, and dissemination. Tadashi Fukami will assist in data collection training, and will be in charge of archiving physical samples. The staff at Stanford's University IT Core Infrastructure are responsible for Stanford's networked file system.

Dissertation Abstract

Interactions between ecological and evolutionary processes in experimental, theoretical, and wild populations

Increasing evidence points to the importance of interacting ecological and evolutionary processes in shaping populations, species, and communities. For my dissertation work, I address topics within this larger theme using a combination of theory, experiments, and population genomics. Through these diverse approaches, I hope to glean new insights into how ecology and evolution interact to shape biodiversity at various scales. This work is through three major projects:

First, I used a general theoretical model to assess how coevolution should affect coexistence among competing species. In contrast to previous models, I allowed species to make evolutionary "investments" in two types of traits: those that stabilize coexistence and those that destabilize it. I found that coevolution should often result in mixed communities, where some species invest in stabilizing (e.g., niche partitioning) and others in destabilizing (e.g., aggressive resource defense) traits—or where some invest in both and others in neither. Investments by one species affect the fitness landscape and resulting investments by other species, with potential positive feedback loops. This adds to the evidence that evolution can often inhibit coexistence, and further complicates the question of how so many species coexist in nature.

Second, I studied how genotypic variation is maintained in a host–parasitoid system despite hosts rapidly evolving parasitoid resistance. Studies of rapid evolution interacting with ecological processes ("eco-evo dynamics") rarely explore how the variation allowing for this evolution can persist despite strong selection. In pea aphids, resistance to parasitoids can evolve rapidly, which causes feedbacks between host–parasitoid dynamics and resistance evolution. To study these dynamics, I designed laboratory experiments and constructed a mathematical model of the system. I found that variation in this rapidly evolving trait is maintained through (1) costs to resistance and (2) dispersal of aphids across habitat patches with varying parasitoid abundances. This is a rare empirical demonstration of a mechanism causing balancing selection that allows for persistent eco-evo dynamics.

Third, I am investigating the effects of extreme population fluctuations on genome evolution in a wild population. Existing studies on how population dynamics affect genome evolution are constrained by the scale and detail of data: They lack either whole genome sequencing or detailed population surveys. In Lake Mývatn, Iceland, an aquatic fly (*Tanytarsus gracilentus*) has population fluctuations of ~5 orders of magnitude. Researchers have estimated abundances and archived samples for *T. gracilentus* as part of the Mývatn monitoring program since 1977. In collaboration with Dr. Árni Einarsson (Director, Mývatn Research Station), this ongoing work will use a 40-year, whole-genome-sequencing time series paired with detailed ecological data to assess how population fluctuations structure genomic diversity. I will specifically look for effects of population crashes on (1) nucleotide diversity across the genome, (2) abundances of transposable elements, and (3) signatures of selection. I also developed and published software that can simulate DNA sequencing data from populations with complex ecological and evolutionary histories, and will use simulations from this package to test the effectiveness of candidate bioinformatic pipelines on this unusual dataset.