

## Teaching Interests

An integral part of our job as evolutionary biologists is not only the education of the students who will be the future of our discipline, but also of the students who will be the future teachers, doctors, politicians, and members of the general public. I have extensive teaching experience, and have made concerted efforts to continuously improve my effectiveness as an educator. Beyond the requisite work as a teaching assistant in graduate school, I have engaged in a number of activities to enhance my teaching skills. On several occasions I gave a week of guest lectures in the undergraduate genetics course at the University of Georgia. I completed a teaching apprenticeship program to develop inquiry-based techniques for a large undergraduate evolution course. I was a graduate student mentor, and worked one-on-one with several undergraduate research students, one of whom even presented her work at an international meeting. I volunteered in other programs, including weekly presentations for a botany course at a local high school and presenting a workshop on inquiry-based learning to members of an NSF PRISM workgroup. In addition to this experience as a graduate student, I worked for a year as a professor in Mexico City, teaching Plant Evolution at the National Autonomous University of Mexico (UNAM) and English at a private school. I was named head professor of the course at UNAM, for which I wrote the syllabus, coordinated lectures and laboratories between myself and another professor, organized and ran a 3-day field trip, and wrote and presented in Spanish a semester of lectures on plant evolution.

I firmly believe that efforts to directly involve students in their education can have profound impacts on students' learning and interest in a subject. This is even true in large classes: I successfully developed a lecture on genetic drift using M&M candies, distributed among nearly 200 students, to simulate random changes in gene frequencies. And though orchestrating random mating, founder effect, and population bottlenecks in a room of 200 students requires extensive organization and planning, it is relatively easy to incorporate the same kinds of techniques as part of everyday lectures – asking students to interpret data in the light of the information they have just learned or challenging students to come up with experiments to distinguish between alternative hypotheses. Additionally, I believe that one of our greatest challenges as educators is to ensure that students, and the public in general, understand what science is and how it works. It is not difficult to bring the scientific method to bear in the classroom; rather than present lists of information for students to memorize and later forget, we can present a subset of the same information in the context of the experiments and hypotheses that generated it.

As a member of the faculty of the Department of Plant Sciences, I would welcome involvement in a wide range of subjects, from introductory botany to plant morphology, genetics, or evolution. Additionally, I would look forward to developing a variety of advanced courses or graduate seminars including population or quantitative genetics, molecular evolution, phylogenetics, or the genetics of adaptation.

## Research Interests

My research interests revolve broadly around the study of plant adaptation, an idea that I approach from three distinct perspectives. The main thrust of my current research takes a population genetic approach to elucidate models of divergence, local adaptation, and hybridization among populations and between species. Additionally, I have great interest in using plant domestication as a model for the study of plant adaptation, and have undertaken field, laboratory, and computational work to study domestication and the idea of preadaptation to domestication. Finally, at a broad scale, I look at patterns across numerous angiosperm species using comparative phylogenetics to investigate adaptation at a macroevolutionary level. In the sections below, I describe these areas of research and the directions they will take in the future.

## Population Genetics Modeling of Plant Evolution

Adaptation does not happen in a vacuum. Myriad other processes concurrently affect the genetic variation of natural populations of plants, including gene flow, drift, vicariance, population growth, and speciation. The standard neutral model is thus often woefully inappropriate as null model for testing selection. Instead, tests for selection need a null model that can incorporate other processes; recent advances in the computational and statistical tools available to population geneticists have begun to make this a feasible undertaking. Here I describe my current research working with these tools to describe evolutionary histories of plant populations.

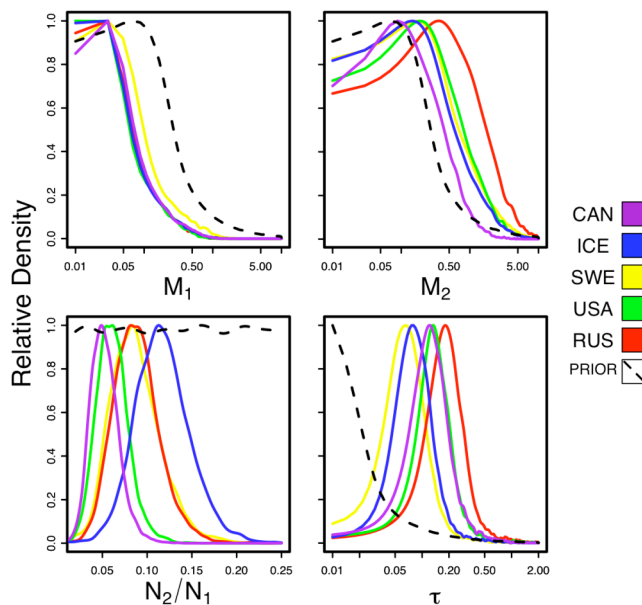


Fig. 1. Estimated posterior probability of divergence time ( $\tau$ , units of  $4N$  generations), migration rates ( $M_1$  and  $M_2$ ), and population size ( $N_2/N_1$ ) between a German population of *A. lyrata* and five colonized populations. Dotted lines show the prior probability distribution.

## Demography and Local Adaptation in *Arabidopsis lyrata*

In contrast to its sister taxon *Arabidopsis thaliana*, *A. lyrata* is self-incompatible and highly outcrossing in most populations. Also in contrast with *A. thaliana*, *A. lyrata* appears to maintain large, long-term stable populations, making it an excellent model for studying population subdivision and local adaptation. In collaboration with several other researchers, I have used population genetic tools to analyze a large dataset of nuclear loci and develop models of the demographic histories of *A. lyrata* populations, and using these models to then test for local adaptation [1; numbers refer to the CV]. Making use of approximate Bayesian approaches to coalescent simulation and population genetic inference, I estimated the parameters of a simple divergence with migration model between ancestral and colonized populations of *A. lyrata* (Fig. 1). I

then used these estimated demographic model to simulate data under a neutral null model of demography and divergence alone. Comparing observed patterns of polymorphism in our data to the expectations under these null models, I was able to identify a list of candidate loci for local adaptation. While some of these loci (such as FCA, a flowering time gene) are not surprising as candidates, the search highlighted several additional loci for which we had *no a priori* expectation of selection. I firmly believe that such bottom-up approaches [2] will become increasingly useful at identifying candidate or outlier loci – these same models have already proven useful for identifying transposable element families that have recently undergone recent transposition or selection in these populations [11].

### Speciation and divergence in *Zea*

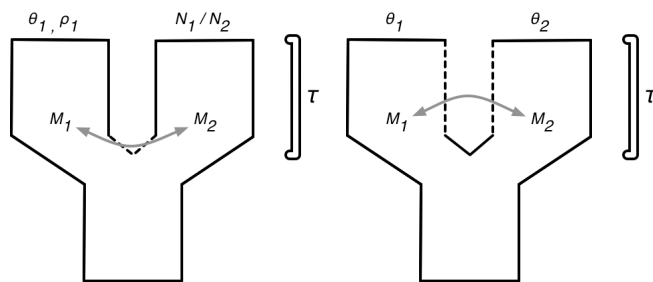


Fig. 2. Two of several alternative models of divergence and speciation. *Left* Divergence in the face of introgression, followed by isolation. *Right* Divergence in isolation followed by subsequent introgression.

Population divergence and local adaptation are thought to be important factors in the formation of new plant species, but until recently it has not been possible to fit realistic models of divergence and speciation to empirical data. Using a large set of sequence loci sampled from all of the diploid species of the genus *Zea* as well as three subspecies of *Zea mays*, I am currently working to parameterize models of divergence and speciation for maize and its wild relatives. Using an approximate Bayesian rejection-sampling approach, I can

explicitly test support for alternative models of speciation and divergence (Fig. 2). Preliminary evidence supports alternative models for different levels of divergence (subspecies vs. species), but also clearly reveals the presence of recent introgression among several of taxa, suggesting the possibility that cultivated maize may act as a bridge for introgression among taxa. Finally, having a null model in hand again allows us to identify outlier loci that show either substantially greater or less introgression than the majority of the data. Such loci could potentially be playing significant roles in adaptation and divergence in these taxa. The results from this work call into question not only the adequacy of some long held beliefs about the process of divergence but also highlight the potential role of cultivated species in changing the adaptive landscape of their wild relatives.

### Future Directions

I foresee that most of my future work will continue to involve the development and use of statistical population genetic methods to elaborate evolutionary models of plant populations. The flexibility of these techniques allows them to be harnessed to address an amazing diversity of questions, including the identification of candidate loci. As computational capabilities continue to improve and sequence data becomes more abundant, the power and promise of these methods will only increase.

## Genetics of Plant Domestication

One of Darwin's fundamental insights was the necessity of variation for evolution and adaptation, an idea later codified explicitly by Fisher and Wright. Nonetheless, Darwin believed that domestication increased the variability of plant species, and argued that variation could not have been the causal reason that some species were never successfully domesticated. We now know that selection necessarily depletes diversity, and several lines of theoretical and empirical work suggest a pivotal role for genetic diversity in population response to natural selection. I am interested in both ends of this process: how adaptation affects diversity in cultivated species, and how diversity and other factors determine the domestication success of wild species.

### Tomatillo and Chaya: Genetic Diversity and Domestication

The tomatillo (*Physalis philadelphica*, Solanaceae), best known for its use in green salsa, provides an ideal system in which to study genetic diversity and domestication. I have taken the first steps to developing the tomatillo as a model system, investigating the effects of selection on species-wide patterns of genetic diversity. While most studies comparing phenotypic to genotypic diversity find evidence of local adaptation on quantitative traits, I showed that  $Q_{ST}$ - $F_{ST}$  comparisons are able to differentiate between traits thought to be under selection during domestication (germination timing and fruit size), and those unlikely to have been targeted by domestication (leaf morphology) [12].

In contrast to the self-incompatible weedy tomatillo, the domestication of chaya (*Cnidoscolus aconitifolius*, Euphorbiaceae) follows that of other long-lived vegetatively propagated crops. While its wild ancestor is morphologically and genetically diverse, I have shown that chaya has been reduced to a few clonal types as a result of domestication practices [7], and has lost most of its sexual reproductive capacity [8]. Chaya thus provides an excellent example of 'instantaneous' adaptation: an individual favored genotype spreading asexually under strong selection, such that the ability to reproduce sexually itself becomes disadvantageous.

### Preadaptation to Domestication

Though Darwin explicitly argued against the idea that certain species were preadapted to domestication, this idea has persisted in the literature as an explanation for the relatively small number of successful modern domesticates. I have used two alternative approaches to investigate the possibility of preadaptation to domestication.

First, making use of nearly a century of plant cytogenetic data, I compared genome-wide rates of recombination between wild and domesticated species [6]. Utilizing phylogenetic comparative methods, I tested the predictions of alternative hypotheses about the evolution of recombination under domestication. My results show no preadaptive role for recombination, but strongly support population genetic predictions about the effects of strong selection.

Second, realizing that effective population size ( $N_e$ ) is a major determinant of genetic diversity and strongly correlated with the efficacy of selection, I used computer simulations to study the preadaptive role of effective population size in domestication [13]. Taking advantage of an extensive body of maize literature, I was able to construct a forward population genetic model of domestication, the results of which show a significant effect of  $N_e$  on domestication

success. Most importantly, I found that differences in  $N_e$  on the scale of those observed among species in the genus *Zea* are sufficient to explain differential domestication success.

### **Future Directions**

I will continue work on plant domestication, focusing especially on the idea of preadaptation to domestication. I plan to refine my computer models of effective population size, incorporating new parameters and testing the range of values under which  $N_e$  plays an important role in domestication. As more genetic and genomic data become available for crops and their wild ancestors, I will test the predictions of this preadaptive hypothesis comparing diversity across a number of plant taxa. And finally, I would like to continue to develop tomatillo as a model system in which to study preadaptation to domestication: improving sampling among wild relatives and developing new markers to eventually allow the kind of population modeling I have done in other species.

### **Macroevolutionary Patterns**

I have always been intrigued by the power of evolutionary biology to explain patterns of diversity in the world around us; it is thus no surprise that some of the adaptive and evolutionary scenarios that most catch my interest are those that apply across large groups of species. Here I briefly discuss two projects in which I use phylogenetic comparative methods to investigate patterns of variation among plant species.

Angiosperm species are known for their surprising variation in genome size. Less well appreciated, however, is the remarkable variation in genome-wide recombination rates that exists among the same species. Although previous workers have argued that there is no relationship between genome size and recombination rate, I took advantage of two large datasets on genome size and recombination rate to show the existence of a significant positive phylogenetic correlation between the two [3]. I argue, however, that there is little evidence to support any purported adaptive role for this correlation, and that processes of genome size change and the mechanics of crossing over are sufficient to explain these observations.

Conservation geneticists have long been concerned with the effects of low genetic diversity in endangered species, and a recent analysis (Spielman et al. 2004 PNAS) suggests a lack of genetic diversity as a causal factor in extinction. This work ignores the numerous examples of endangered taxa with high diversity [e.g. 9] and factors such as habitat loss that contribute to extinction. In collaboration with a graduate student at UGA, I have compiled large databases of genetic diversity to test these predictions in a phylogenetic context. Preliminary analysis of a subset of the data suggests little to no association between extinction risk and genetic diversity after correcting for phylogeny.

### **Future Directions**

Though not the main focus of my research, I will continue to be interested in and work with broad patterns of variation across plant and animal taxa. The conceptual simplicity of the methods and wide interest of the results make this kind of work particularly suited for new graduate students or advanced undergraduates interested in pursuing research opportunities in plant evolutionary biology.