



INDIANA UNIVERSITY
ENVIRONMENTAL RESILIENCE INSTITUTE
Office of the Vice President for Research

29th October 2018
Department of Biological Science
Florida State University

To the Chair and Members of the Search Committee,

I am writing to apply for the position of Assistant Professor in the Department of Biological Science.

I am a mathematical biologist working at the frontier of eco-evolutionary dynamics. I develop mathematical models at the intersection of ecology and evolution to understand how their interaction shapes observed ecological and genetic patterns. Originally trained in mathematics and theoretical physics, I bring strong quantitative skills and a novel theoretical perspective to the challenges facing modern biology.

The importance of mathematical biology has grown rapidly with the abundance and quality of DNA sequence data, allowing us to view the biological world in unprecedented genetic detail. Mathematical models are needed to link this rich data resource to hypotheses about the ecology and evolution of natural and laboratory populations. At present, most models of DNA sequence evolution focus on genetic processes and do not account for ecology (e.g. complex demography or density-dependent selection). Yet ecological processes profoundly influence genetic evolution, and *vice versa*. Making sense of this interplay is one of the great challenges of modern biology, and is the overarching theme of my research program.

I believe there is enormous potential to advance our understanding of the collective dynamics of evolving biological communities by drawing on modern stochastic modeling techniques more typically associated with mathematics and physics. I started pursuing this vision in my PhD, where I used ideas borrowed from statistical mechanics – the study of populations of interacting physical particles – to develop novel models of how ecological communities are structured. These models offer new insights into the key determinants of community structure, and have successfully reproduced important aspects of global vegetation patterns. This novel approach potentially offers an alternative to complex dynamic vegetation models currently used in climate modeling.

In my postdoc at the University of Arizona, I expanded my research program to include evolutionary dynamics. To give one example, I have argued that the remarkably high genetic variation observed in wild *Drosophila* populations is most likely a result of a combination of familiar evolutionary-genetic factors such as dominance with previously overlooked ecological factors such as seasonally oscillating population size. I am now an expert in both ecological and evolutionary theory, giving me a solid foundation for research at their intersection.

The research strengths of the Biology Department synergize well with my research program. I would particularly value interactions with the Travis and Levitan labs on eco-evo and density-dependent selection, with the Okamoto and Burgess labs on population dynamics, with the Inouye lab on selection in heterogeneous environments, with the Rokyta lab on adaptive evolution and mutational fitness effects, with the Houle and Hughes lab on a range of issues in quantitative genetics, and with the Beerli and both Lemmon labs on genetic and genomic inference. I enjoy working with more empirically-focused



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colleagues. In addition to traditional modeling, I also employ data-driven, computational approaches to test existing theories and gain inspiration for new ones (I have a major in statistics).

I have published seven first-author theory papers in the last seven years and presented my interdisciplinary research at >10 academic conferences across physics, ecology, evolution and genetics. I funded my graduate training in both physics and theoretical ecology entirely with merit-based fellowships (AUS\$125000). Recently, I was awarded an independent research fellowship at Indiana University. I have developed collaborations with colleagues from around the world working in a wide variety of disciplines.

In my teaching I strive to make the power and insight of mathematical modeling accessible to students. I have co-developed a modeling course for evolution and ecology students at the University of Arizona. I have supervised three undergraduates, and currently co-advise a graduate student working on models of asexual trait evolution. I enjoy teaching theoretical evolutionary biology and ecology, population genetics, statistics, mathematical modeling, and scientific programming.

Thank you for your consideration.

Sincerely,

A handwritten signature in black ink, appearing to read "Jason Bertram".

Dr. Jason Bertram

Personal data

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Education and Academic Positions

2018-present **Assistant Research Scientist** Environmental Resilience Institute, Indiana University
 2015-2018 **Postdoctoral Researcher** Department of Ecology and Evolutionary Biology, University of Arizona. Advisor: Joanna Masel.
 2012-2014 **PhD** Statistical mechanics, population ecology, turbulence theory (Australian National University). Advisors: Roderick Dewar, Graham Farquhar, Michael Roderick.
 2009-2011 **MPhil** Theoretical plasma physics (Australian National University)
 2008 **BSc (Hons)** Applied Mathematics (University of Cape Town, South Africa)
 2005-2007 **BSc** Pure Mathematics, Applied Mathematics, Statistics

Peer-reviewed Publications

1. S Foy, B Wilson, **J Bertram**, M Cordes, J Masel (2018) A shift in aggregation avoidance strategy marks a long-term direction to protein evolution (in revision at *Genetics*) <https://doi.org/10.1101/176867> (older preprint)
2. K Gomez, **J Bertram**, J Masel (2018) In rapidly adapting asexuals, the orientation of G can reflect selection rather than functional constraints (in revision at *Genetics*) <https://doi.org/10.1101/351171> (preprint)
3. **J Bertram**, J Masel (2018) Different mechanisms drive the maintenance of polymorphism at loci subject to strong versus weak fluctuating selection. (in revision at *Evolution*) <https://doi.org/10.1101/164723>
4. **J Bertram**, J Masel (2018) Density-dependent selection and the limits of relative fitness. (in revision at *Theoretical Population Biology*) <https://doi.org/10.1101/102087> (preprint)
5. **J Bertram**, K Gomez, J Masel (2016) Predicting patterns of long-term adaptation and extinction with population genetics. *Evolution* **71** 204 <https://doi.org/10.1111/evo.13116>
6. S Haskey, B D Blackwell, C Nuehrenberg, A Koenies, **J Bertram**, C Michael, M Hole, J Howard (2015) Experiment-theory comparison for low frequency BAE modes in the strongly shaped H-1NF stellarator. *Plasma Phys. Control. Fusion* **57** 095011
7. **J Bertram** (2014) Maximum kinetic energy dissipation and the stability of turbulent Poiseuille flow. *J. Fluid Mech.* **767** 342 <https://doi.org/10.1017/jfm.2015.65>
8. **J Bertram** (2014) Maximum entropy models of ecosystem functioning. *AIP Proceedings MaxEnt 2013* <https://doi.org/10.1063/1.4903722>
9. **J Bertram** and R C Dewar (2014) Combining mechanism and drift in community ecology: a novel statistical mechanics approach *Theor. Ecol.* **8** 419 <https://doi.org/10.1007/s12080-015-0259-7>
10. **J Bertram** and R C Dewar (2013) Statistical patterns in tropical tree cover explained by the different water demand of individual trees and grasses. *Ecology* **94** 2138. <https://doi.org/10.1890/13-0379.1>
11. **J Bertram**, B D Blackwell and M J Hole (2012) Ideal-magnetohydrodynamic theory of low-frequency Alfvén waves in the H-1 Helic. *Plasma Phys. Control. Fusion* **54** 055009 <https://doi.org/10.1088/0741-3335/54/5/055009>
12. **J Bertram**, M J Hole, D G Pretty, B D Blackwell and R L Dewar (2011) A reduced global Alfvén

eigenmodes model for Mirnov array data on the H-1 NF Helic. *Plasma Phys. Control. Fusion* **53** 085023 <https://doi.org/10.1088/0741-3335/53/8/085023>

- 13.** M J Hole, G von Nessi, **J Bertram**, J. Svensson, L. C. Appel, B. D. Blackwell, R. L. Dewar and J. Howard (2010) Model Data Fusion: developing Bayesian inversion to constrain equilibrium and mode structure. *J. Plasma Fusion Res.* **9** 479

Conferences and Workshops

1. "Density-dependent selection and limits of relative fitness" (Talk) *Evolution* (Montpellier, 2018)
2. "Reversal of dominance is a powerful stabilizer of polymorphism in fluctuating environments, but boom-bust cycles and storage are more likely to stabilize many loci of large effect" *Population and Quantitative Genetics* (Madison, 2018)
3. "Density-dependent selection and limits of relative fitness" (Talk) Arizona Population Genetic Group (Tucson, 2018)
4. "Feedbacks can drive large fluctuations in adaptation rates when sex is optional" (Talk) *Mathematical Modeling and Analysis of Populations in Biological Systems* (Tucson, 2017)
5. "Contrast between selection on fecundity versus interference" (Talk) *Evolution 2016* (Austin, 2016)
6. "Modelling long-term adaptation and extinction" Microbial Population Biology Gordon Conference (2015)
7. "A population-genetic model of long-term adaptation and extinction" (Talk) *Mathematical Models in Ecology and Evolution 2015* (Paris, 2015)
8. "Statistical stability arguments for maximum kinetic energy dissipation" (Talk) *Mathematics of the Fluid Earth* (Newton Institute, Cambridge, UK, November 2013)
9. "Maximum Entropy Models of Ecosystem Functioning" *MaxEnt 2013* (Canberra, December 2013)
10. *Frontiers in Macroecology Workshop* (UC, Berkeley, January 2013)
11. "A reduced global Alfvén eigenmodes model for Mirnov array data on the H-1 NF Helic." EPS Plasma Physics (Dublin 2010)

Research supervision

Undergraduate research students:

- Austin Fritzke (Primary supervisor, Spring 2015)
- Jasmin Templin (Primary supervisor, Spring 2015 – Spring 2017)
- Madison Delmoe (Primary supervisor, Fall 2017 – Spring 2018)

PhD students:

- Kevin Gomez (Co-supervisor, Fall 2015 – present)

Teaching

- | | |
|------|--|
| 2016 | Co-developer and instructor of an active-learning-based mathematical modelling course to teach critical model "usership" (University of Arizona) |
| 2012 | Teaching assistant, introductory physics, Australian National University |
| 2010 | Teaching assistant, mathematics (linear algebra, calculus), Australian National University |

Awards

- Cambridge Philosophical Society Bursary to visit the Newton Institute, Cambridge University (2013)
- Australian National University Graduate Scholarship (Australian National University 2009-2014)
- Crompton Travel Scholarship Award (Australian National University, 2010)

Service

1. Regular editor of scientific Wikipedia pages to add content and improve scientific accuracy
<https://en.wikipedia.org/wiki/Special:Contributions/Jasonbertram>.
2. Organizer of annual Wikipedia Edit-a-thons in the Department of Ecology and Evolution at the University of Arizona. Significant improvement to many pages across evolution and ecology.
3. Contributing author to University of Arizona postdoctoral guide
4. Reviewer for *Evolution*, *Genetics*, *BioScience*, *Phil. Trans. B*

References

1. Prof. Joanna Masel
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3. Prof. Joachim Hermisson
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Overview: eco-evolutionary dynamics under genetic constraint

Adaptive evolution and ecology are closely intertwined. The density of a population influences which traits are favored by selection, as do the densities of other species in the same environment. Trait evolution changes ecological interactions and population densities. The resulting eco-evolutionary dynamics can be complex, and have so far largely been studied at the level of phenotypic traits.

Yet evolution is fundamentally a genetic process, and genetic factors can profoundly constrain trait evolution. Arguably the central constraint of the genetic architecture is the physical link between genes in DNA (“linkage”). Linkage makes it harder for evolution to simultaneously address multiple environmental challenges, and causes adaptive mutations to compete with – and potentially eliminate – each other (Fig. 1).

Infectious diseases, cancer and many evolution experiments all involve the evolution of large cellular/viral populations in which linkage has a pervasive influence and adaptation occurs at a similar rate as ecological processes. Similar circumstances can occur in the presence of strong environmental pressures such as host-parasite co-evolution, seasonal cycles (e.g. in wild fruit flies) or human-induced disturbances.

At this critical intersection of ecology and genetic evolution, I develop mathematical models to understand how populations overcome – or fail to overcome – the challenges of their environment, and what genetic patterns to expect as a result.

Research Theme 1: The interplay between ecology and evolution

Current research: stable polymorphism maintained across many loci

Theoreticians have long been argued that selection which fluctuates over time is not likely to be a major source of balanced polymorphism. It has therefore been a great surprise to discover in wild fruit flies a large number of apparently balanced polymorphisms oscillating seasonally in frequency. I have analyzed³ a variety of genetic and ecological mechanisms for stabilizing polymorphism under temporal fluctuations, including the interactions between mechanisms (Fig. 2 shows polymorphism stabilized by the repeated growth and collapse in population density). I have found, contrary to previous work, that temporally fluctuating selection could in principle stabilize polymorphisms across a large number of loci, provided that multiple of these stabilizing mechanisms are present at the same time. This work offers a plausible theoretical explanation for how such pervasive balancing selection is even possible, and underscores the importance of accounting for ecological processes in evolutionary genetics.

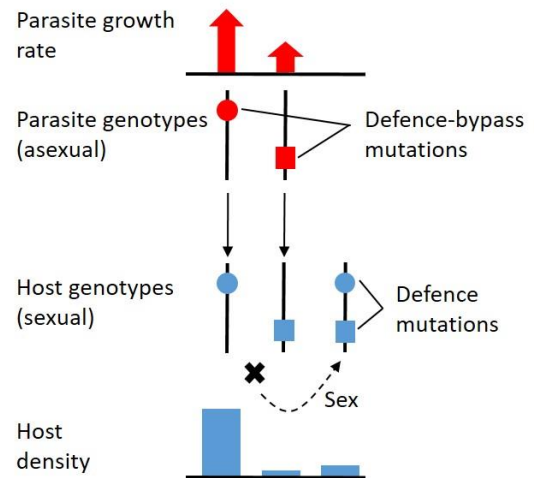


Figure 1: Adaptive evolution constrained by linkage, illustrated in a host-parasite system. Parasites attacking the most abundant host genotype reproduce fastest (vertical red arrows). In the absence of sex, the appearance of parasite double-mutants is delayed (in a finite population).

Current research: selection versus demography

One of my major ongoing projects is to develop general-purpose models of selection that are grounded in the births and deaths of individuals rather than viewing selection as simply changing the proportions of different genotypes (as in the norm in evolutionary genetics). This is essential for modeling evolution in ecologically realistic contexts where reproduction and death are ecologically distinct processes which together drive changes in population density.

With this aim in mind, I have developed⁴ an extension of the famous Wright-Fisher model of population genetics to allow population density to vary depending on the demographic rates of the population (Fig. 3). The interaction between selection and population density in this model differs from that found in standard models of density-dependent selection in interesting ways; for instance, selection can occur in crowded populations without affecting total population density.

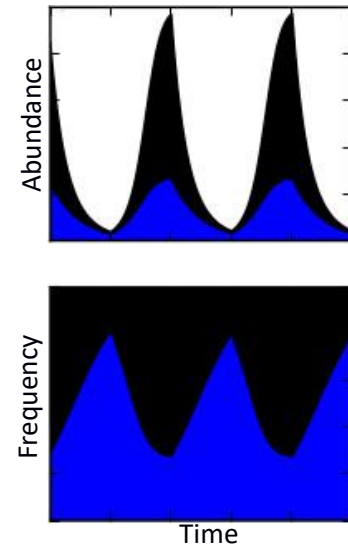


Figure 2: Co-existence of “summer growers” and “winter survivors” with boom-bust demography².

Current work: extinction and evolutionary rescue

Over long periods of time, a population’s environment deteriorates due to changes in the abiotic environment and the evolution of competitors/parasites/predators, and its average abundance will gradually decline. Adaptive evolution counteracts this deterioration, as though the population is running on an evolutionary treadmill. I have shown, using a novel population-genetic model of the evolution of birth and death rates, that this tug-of-war (1) reproduces van Valen’s famous exponential survivorship law for fossil species, and (2) predicts stable persistence followed by sudden extinction⁵.

Future directions: evolutionary genetic inference

Building on the developments above, my lab will develop an inference framework that explicitly accounts for the interdependence of population density, selection and drift. The essence of this framework will be to infer the contribution of individual alleles to demographic rates, rather than changes in allele frequencies tied to a separate demographic model as currently done. The initial testing ground for this framework could be the wild fruit fly system mentioned above, or another system with direct measurement of population density.

Research Theme 2: Linkage, facultative sex and saltation**Current research: the benefits of linkage and saltation**

Recombination counteracts linkage by shuffling alleles between genetic backgrounds, potentially bringing adaptive alleles together in the same genotype (Fig. 1). Even weak recombination is effective at creating adaptive allele combinations (“a little bit of sex goes a long way”). This argument, widely cited to explain the ubiquity of sex, has a lesser-known flip-side. Linkage also *facilitates* adaptation by preventing adaptive alleles on the same background from being separated. The case of weak recombination (e.g. due to facultative sex) is particularly interesting, because highly adaptive genotypes created by recombination can expand without further disruption from recombination.

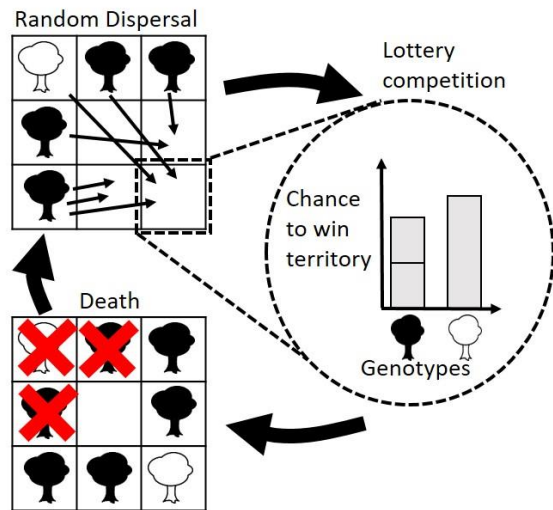


Figure 3: Density-dependent selection mediated by territorial contests².

challenges posed by linkage must be confronted head on. A mathematical understanding of the weak recombination regime would thus give precious insight into the broader evolutionary role of linkage. My lab will develop such an understanding, building on my current simulations, but also with analytical “pen and paper” approaches.

References: numerical citations refer to my CV.

In my current work, I am exploring these novel aspects of weak recombination. A striking feature of the resulting adaptive process is the prevalence of evolutionary leaps or “saltations”. It is intriguing that saltations could be an important part of the explanation for why weak recombination is so common.

Future directions: confronting the linkage problem

When recombination is strong, genes are effectively unlinked from their genetic background and the complications of linkage disappear. In the opposite case of no recombination, adaptation can be analyzed at the phenotypic level, bypassing the complications of predicting the underlying decomposition of phenotypic effects among distinct genes. When recombination is weak, neither of the above simplifications hold, and the

I enjoy teaching theoretical evolutionary biology and ecology, population genetics, statistics, mathematical modeling, and scientific programming. I particularly enjoy teaching the principles of modeling, including the unique challenges of modeling in the life sciences.

Teaching for the whole class through active learning: At the University of Arizona, I developed and led active learning classes with mentoring from faculty. I was struck by the importance of constantly evaluating student understanding and adjusting the classroom around that in real time. I was surprised at how ineffective it is, by comparison, to simply ask students what they are struggling with. Students are often not aware of their own misunderstandings, and struggling students are the least likely to speak out. This is a challenge in any classroom, but it can be acute in quantitative biology, where there can be dramatic differences in mathematical ability and training, and previous disadvantage can have a severe impact. I aim to create a classroom environment in which open inquiry is encouraged for all. An important aspect of achieving this is to emphasize that grappling with uncertainty is central to the scientific method. I also aim to discuss difficulties without a sense of judgment about what “should be known”, and to retain a sense of enthusiasm and discovery even when discussing “well-known” facts or concepts.

Bridging the gap between theory and experiment in the classroom: Critical evaluation and use of mathematical models is essential for empiricists and theoreticians alike. By contrast, technical mathematical skills or the details of well-known models - material commonly covered when models are taught - is primarily useful for model development. The latter can intimidate or bore empirical students, and contribute to a disconnect between theory and experiment. For most science students, models should be taught from the perspective of how they are used, including the critical evaluation of modeling studies. At the University of Arizona, I co-developed and instructed a mixed undergraduate-graduate course on biological model “usership”. Students read modeling papers, and are given classroom exercises to identify and evaluate key assumptions, and devise their own critiques. Technical details are avoided. Student comprehension of modeling studies improves markedly over the course.

Mentoring: I have been the primary advisor for three undergraduates, and am co-advisor for a graduate student, all in mathematical biology. The graduate student and one of the undergraduates are Hispanic and among the first members of their extended families to pursue higher education. As a result of these mentoring experiences, I believe that research mentoring should be a “guided collaboration”. Research mentees can easily become occupied with accumulating knowledge, while the mentor makes all higher-level decisions. I have found that students benefit enormously from being encouraged to take intellectual ownership of their work. I continually return to the questions: Why are we exploring this avenue? Where will we end up? Is there a better approach? Apart from developing valuable analytical skills, I have found that as these questions are internalized, students become far more invested in their research.

Making Wikipedia a high quality, free resource for scientific learning: Many students use Wikipedia to supplement classroom learning, or even as a primary source. Unfortunately, many biology pages are in relatively poor shape. During my postdoc at the University of Arizona, I organized three annual Wikipedia “editathons” focused on biology, which included training, moral support and prizes. As teachers and experts, faculty and postdocs are able to transform scientific Wikipedia pages. The best pages are better written, more up-to-date and better connected to related topics than expensive textbooks. This can be an incredibly valuable resource for all students, particularly those with limited access to textbooks in poorer regions of the world. I intend to develop an ongoing program for increasing the Wikipedia participation of faculty, postdocs and graduate students.