

Arachnid lineages

While biodiversity research is a hot topic in the environmental sciences, sound understanding of the evolutionary mechanisms that drive heterogeneity amongst species is still lacking. **Drs Ingi Agnarsson** and **Greta Binford** lead a collaborative project that analyses diversity patterns within arachnid lineages in the Caribbean

Could you begin by explaining the context from which this project on biodiversity in the Caribbean region emerged? How does island biogeography help researchers to understand the evolutionary mechanisms involved in generating biodiversity?

The project emerges from our shared interest in biodiversity and the processes that have generated the diversity of life on earth. At a scientific congress of arachnologists a group of us were discussing how dispersal ability of organisms might relate to their diversification. We had some preliminary data for a couple of arachnid lineages and realised the power of simultaneously analysing the various different groups we each study, and bringing in a time axis by including fossils available in Dominican Amber through collaboration with Paleoarachnologist Paul Selden.

The Caribbean seemed like an ideal place as a conveniently located island archipelago. The attractiveness of islands for this kind of research is their discreteness and the obvious role of stretches of ocean in reducing dispersal and thus the exchange of genes among terrestrial populations on different islands.

Could you briefly outline your research background and what drew you towards the topics addressed in this NSF-funded work?

We both study diversity and evolution of spiders; Ingi researches spider sociality and spider silk, while Greta focuses on their venoms. So, our joint interest in diversity and evolution reaches across scales of taxonomy and biogeography to phenotypic and molecular diversity within organisms. We also both love fieldwork and the opportunities it brings to us and our students to better understand the organism in their natural context. The Caribbean is a great opportunity to understand broader-



scale influences of species diversity that will keep us busy for a long time, asking questions about the more subtle scale of diversity of the phenotypes of silks, venoms and behaviours.

You utilise a phylogenetic approach to analysing the arachnid lineages. What does this approach entail and what are its strengths?

Phylogenetic analyses are used to reveal the relationships among species. When we then examine these species' relationships in the context of their geographical distribution we can determine broad patterns, such as the number of times an island has been colonised by a given group and where the colonisers may have come from. Phylogenies combined with taxonomy, in turn, help us understand species richness, and if there has been diversification within or among islands. Another strength of phylogenetic analyses, when combined with fossil data, is that we can get an idea of the timing of events. This is crucial information. For example some of the Caribbean islands were once connected to the continents, and dating the phylogenies allows us to determine if a group of arachnids was present on the island before it fragmented away from the continent, or if it dispersed to the island after the fragmentation.

What challenges have you faced in putting together the groundwork for this project

given the scale and scope of the research effort?

It is logistically complex, as we are organising numerous expeditions that involve people from three continents, planning to visit over 50 islands belonging to some 30 nations, and thus over 30 different procedures to secure the necessary permits to conduct the work. The numbers of specimens is also very large, many tens of thousands, and requires a massive collaborative effort to sort through, identify, organise, and process for molecular and morphological data sampling.

Finally, even with heavy investment in fieldwork, we find it very likely that we will not encounter all the species that are present. Despite these challenges this project has already in its first year contributed to our understanding of the distribution of arachnid diversity in the Caribbean.

Could you outline some of the dissemination and outreach strategies you will employ over the course of the project's duration?

We aim to strike a balance between dissemination of our findings in scientific literature, and in outlets more accessible to the public. We have, for example, launched a website for the project (www.islandbiogeography.org) aimed primarily at the general public. It will soon contain a photographic catalogue of Caribbean arachnids so that scientists and laymen alike can access information to identify species. We are also planning a spider biodiversity camp (June, 2012) in collaboration with Dominican Outreach giving children the opportunity to learn about nature, the diversity and value of their local arachnids, and to work side-by-side with professional biologists.

A biodiversity hotspot

The Caribbean archipelago is home to very diverse fauna yet little is known about the mechanisms that brought about this diversity. New research exploring arachnids promises to enhance understanding of how biodiversity on the islands was generated by evolution and how that relates to dispersal abilities of different lineages

SINCE DARWIN'S WORK on the Galapagos and Wallace's findings on the Malay Archipelago, island biogeography has played an important role in revealing evolutionary processes. Following their research, studies in archipelagos such as Hawaii and the Galapagos have provided examples where cycles of evolutionary radiation have produced replicated patterns of endemic forms.

A Conservation International hotspot, the Caribbean, is one such example of biological diversity. With over 7,000 islands and islets, the region supports exceptionally diverse ecosystems ranging from cactus deserts to rainforests. The islands can be classified according to their history as 'Darwinian' islands (that form *de novo* and have always been surrounded by sea); fragment islands (produced via fragmentation of continental crust); or

platform islands (low elevation islands that have regularly been submerged with changing sea-level). Due to their different geological histories, species diversification patterns differ among the island types. The Caribbean is also an important source of fossil data allowing understanding of when diversification occurred in the region.

EXPLORING THE UNKNOWN

Even though the Caribbean is a designated hotspot of diversity, detailed processes that generate species diversity across the archipelago are complex and poorly understood, and there is much to be discovered about the diversity of smaller animals within the region. Since February 2011, new research undertaken in the region seeks to examine how the age and dispersal ability of lineages and the geological history of the islands interplay. The research aims to contribute to theoretical development of fundamental principles in biogeography and bring new insight into the role of dispersal and dispersal ability, as well as providing information and education to students about island biogeography in general.

Ingi Agnarsson, Assistant Professor and Director of Zoology Museum at the University of Puerto Rico, and Greta Binford, Lewis & Clark's Associate Professor of Biology, are at the forefront of this NSF-funded research, using arachnids to understand speciation within the islands.

For nearly 20 years, Agnarsson has worked in arachnology and received numerous grants and awards for his contribution to this field, including the Smithsonian Small Grants Program in 2005 for fieldwork in French Guiana, Killam Postdoctoral Fellowship at the University of British Columbia in 2004 and a research fellowship at the Slovenian Research Agency in 2007. Binford also boasts a long list of achievements and in 2011 was named Oregon Professor of the Year.

Binford and Agnarsson collaborate with taxonomic experts, a postdoc, undergraduate and graduate students, and local collaborators to undertake the project. Many of the collaborators have unique taxonomic expertise that is crucial to understanding the diversity of the various groups of arachnids, including expertise of fossil arachnids. The local Caribbean arachnologists provide expert knowledge on local faunas, habitats and geology whilst other collaborators are theoretical biologists that contribute to the conceptual framework of the project. The combined expertise of the team provides a multidisciplinary approach, merging taxonomy, morphological and molecular phylogenetics, ethology, geology, paleontology and theoretical evolutionary biology.

FIRST STEPS

Agnarsson and Binford started the research by leading a workshop in July 2011 to educate students on the project, arachnids and collection methods. Additionally, collaborators provided overview presentations on the key objectives of the project and the history and diversity of the Caribbean, as well as the theory and logistics of collecting, curating, processing specimens and data analyses.

In total, nearly 800 arachnid specimens, representing all focal lineages, and an estimated 50+ species were processed for initial inclusion in the project

Following this, the team began sampling in Puerto Rico, with a focus on 30-40 arachnid lineages. As a group, arachnids represent multiple lineages that have independent biogeographical histories, but that resemble each other in life histories and ecologies (all are arthropod predators, and most rely heavily on silk). Yet, they differ dramatically in dispersal ability, such that arachnids provide an ideal study system to understand the role of dispersal and dispersal ability in the formation of biodiversity. Furthermore, as small animals, arachnids have relatively large population sizes so that even intense sampling will not hurt populations.



The team focussed on collecting in different habitats, aiming to maximise the collection of focal lineages. They collected 15,000 arachnid specimens and over 7,000 specimens of Diptera from five different localities across Puerto Rico. All specimens were sorted to families, within families to focal groups, and within focal groups to morphospecies. In total, nearly 800 arachnid specimens, representing all focal lineages, and an estimated 50+ species were processed for initial inclusion in the project.

SWIFT PROGRESS

In October and November 2011, Agnarsson and Binford delivered the first 1,600 tissue samples to the Smithsonian Global Genome Initiative Laboratory for Analytical Biology, a collaborating institute on the project. Half of the 1,600 samples were sent for long-term storage in deep freeze, whilst DNA will be extracted from the remaining samples for gene sequencing.

Specimens have also been shipped to taxonomic experts for identification and descriptions whilst Agnarsson and Binford are further identifying specimens within their own labs. For example, specimens of Pholcidae were sent to pholcid expert Dr Bernhard Huber, who found that the team had collected all the described species of pholcids in Puerto Rico, but also many species hitherto unknown to science.

In fall 2011, Lewis & Clark undergraduate student Trevor Bloom completed taxonomic illustrations and DNA extraction, PCR and phylogenetic analyses of four loci for all species of Amblypygids encountered to date. UC Berkley postdoc Lauren Esposito is also finishing a portion of her scorpion work in the Caribbean as part of her postdoctoral research. Her work is resulting in some of the clearest geographically-related patterns seen for any organisms and thus brings novel understanding to Caribbean biogeography.

Graduate students within the team are also making discoveries. University of Puerto Rico graduate student Heine Kiesbuay continues collecting argyrodine spiders throughout Puerto Rico. These spiders are kleptoparasites in the webs of other spider groups. As with pholcids, to date, more species have been discovered than were previously known to exist on the island.

The project also feeds into coursework in courses taught by Agnarsson and Binford (Phylogenetic Systematics, Evolution) at their respective

institutions. The project has been the subject of two conference talks delivered by Agnarsson in the U.S. and Israel.

FUTURE STAGES

Following the fieldwork in Puerto Rico, the team is currently executing two major expeditions to Cuba and the Dominican Republic. As the largest and most biodiverse islands in the Caribbean, sampling in these regions will allow the team to begin addressing their broader research question. Agnarsson, Binford and postdoc Esposito continue devising and adapting strategies to thoroughly sample the large number of islands in the Caribbean, collecting both molecular and morphological data from over 40 different arachnid groups.

Agnarsson has great hopes that the project will provide new insight into the role of dispersal and dispersal ability in the generation of biodiversity, as well as inspiring students, particularly underrepresented minorities in the region with an interest in pursuing science: "We expect that our research will allow a more detailed knowledge of Caribbean biogeography than prior studies, and what have been the key factors in shaping both the distribution and diversity of species in the biodiversity hotspot. We hope that our project contributes to theoretical development of fundamental principles in biogeography".



INTELLIGENCE

THE GENERATION OF A BIODIVERSITY HOTSPOT

PALEOBIOGEOGRAPHY OF THE CARIBBEAN INFERRED FROM MULTIPLE ARACHNID LINEAGES WITH DIFFERING DISPERSAL ABILITIES

OBJECTIVES

To test hypotheses about how the age and dispersal ability of various species, and the geological history of islands, interplay to generate biodiversity hotspots. The research will also test the importance of islands as sources of continental colonisation, and the role of dispersal versus geological land-bridges in island colonisation.

KEY COLLABORATORS

Dr Paul Selden, University of Kansas

Dr Lauren Esposito, University of California, Berkeley

Dr Nadine Dupérré

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CONTACT

Department of Biology

University of Puerto Rico
Rio Piedras
Po Box 23360, San Juan
Puerto Rico, 00931-3360
USA

T +1 787 7640000
E iagnarsson@gmail.com

www.islandbiogeography.org
www.theridiidae.com

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DR INGI AGNARSSON has just accepted an Assistant Professor position in Biology at the University of Vermont. He has discovered and described many new species, and co-discovered the largest spider orb web and the toughest biological material.

DR GRETA BINFORD is an Associate Professor of Biology at Lewis & Clark College. She studies diversity and evolution of spiders and their venoms. She is a recipient of a NSF CAREER award, has featured in the New Yorker and NOVA, and was 2011 Oregon Professor of the Year.

