Global patterns in the evolution of oak gallwasps

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Project Background
Gall inducers are highly specialized herbivores that hijack the development of their host plant, causing it to produce a novel growth - a gall. Internal gall tissues provide the inducer with all its food, while outer tissues protect it from external environments and natural enemies. Because gall structures are diagnostic of the gall-inducer, they are thought to be under inducer control, and can be seen as the ‘extended phenotypes’ of inducer genes. Galls come in all shapes and sizes (Figure 1), with a wide diversity of internal and external structures and locations on the host plant. Recent years have seen concerted efforts to understand the adaptive significance of individual gall traits and the processes that might drive the evolution of trait diversity. This project will focus on a group of insects – oak gall wasps – that induce some of the most diverse structurally complex galls on oaks and related trees in the family Fagaceae. Most species have one sexual and one asexual generation each year, and these always have different gall structures. Around 1000 oak gallwasp species have been described, primarily from temperate areas of North America and Eurasia, but recent work has revealed dramatic new diversity on tropical oaks and their relatives in Southeast Asia. These new species show that host plant associations of oak gall wasps are wider than previously thought, and represent novel and deeply diverging lineages within the gallwasp family tree. Over the last 10 years, we have collected and sequenced 200 gallwasp species – including most Palaearctic species and a comprehensive sampling of North America groups – for a set of 6 phylogenetically informative genes. This project will use this phylogeny to explore pattern and process in the diversification of this group, focusing on the evolution of gall traits, host plant associations, and global biogeographic patterns. There will be opportunities for fieldwork in China.

Key Research Questions:

1. How do gall traits evolve? Have traits with apparent adaptive value evolved repeatedly in independently evolving gallwasp lineages? Do the traits of sexual and asexual generation galls evolve independently, or in concert?

2. How often do gallwasp lineages switch between alternative host plant lineages through evolutionary time?

3. Do patterns in the diversification of gallwasps depend on which group of host plants they are associated with?

Figure 1. A selection of oak gall morphologies induced by different European species of the gallwasp genus *Andricus*. For an exploration of the forces that may drive the evolution of diverse gall shapes, see the recommended reading paper by Stone and Schönrogge (2003).
Methodology
The studentship will extend an existing six–gene phylogenetic dataset for oak gall wasps and apply a range of analytical techniques to infer patterns of character state evolution and models of lineage diversification. The current dataset includes almost all oak gall wasps in the palaearctic, including Asia, and a substantial and carefully selected subset of North American species. In Year 1 the student will extend this sampling by collaborative fieldwork in Taiwan and China to extend what is known of gall wasp diversity associated with tropical and subtropical Fagaceae. Work in China will take place within an existing collaboration between the University of Edinburgh, Emeishan Biological Resources Research Station in Sichuan, and Zhejiang University, which includes provision for sequencing of new species in China. There is also potential for extension of sampling of North American species. In Year 2 the student will generate a phylogeny for the sampled taxa, compile a matrix of the gall and host plant character states for each species, and use a range of methods (primarily in R) to examine patterns in their evolution. The student will be expected to generate a research manuscript by the end of this year. In Year 3 the project will focus on analysis of relative rates of diversification of different gall wasp lineages, and ask whether patterns in the diversification of gall structures vary across different host plant groups and geographic regions.

Training
A comprehensive training program will be provided comprising both specialist scientific training and generic transferable and professional skills. Specialist training will be provided in field sampling design and methodology, lab skills associated with DNA extraction and Sanger sequencing of gene sequences, phylogeny reconstruction from sequence data, and R-based analyses of phylogenetic dynamics and character state evolution.

Requirements:
1. A first class undergraduate degree or MSc in ecology or evolution is desirable.  
2. Demonstrated strength in statistics is a key requirement for the project.  
3. Experience of phylogenetic analysis and lab-based Sanger sequencing of DNA are both desirable.  
4. Enthusiasm for overseas fieldwork and willingness to work long hours in a team when required are desirable.  

Candidates are expected to contact the supervisors to discuss the project, and we would be happy to forward .pdf copies of the papers below on request.

References

The following are some specific examples of evolutionary analyses in gall wasps:
This paper links gall traits to enemy-imposed selection:
These two papers cover processes that the studentship could explore in oak gall wasps:

Project Summary
The project will use phylogenetic approaches to understand the patterns and processes underlying the diversification of gall traits, host plant associations, and geographic distribution of oak gall wasps.