

Taxonomic complexity in eyebrights (*Euphrasia* L.,
Orobanchaceae) and the British flora

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For Molly

Declaration

I hereby declare that this thesis has been composed solely by myself and that it has not been submitted, in whole or in part, in any previous application for a degree. Except where stated otherwise in the acknowledgments or by reference, the work presented is entirely my own.

Max Brown

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“If, again, references were given to the parasitism of *Euphrasia*, etc., how likely it would be that some young man would go on with the investigation; and so with endless other facts...”

– Charles Darwin (letter to J.D. Hooker, December 2nd, 1868)

Cover image: A purple flowered variant of
Euphrasia foulensis on Fair Isle, August 2018

Lay Summary

Many plant groups have species that are difficult to distinguish based on their appearance. There are a number of biological factors that drive this complexity, for example asexuality and complex mating systems. Taxonomic complexity arises because of an interplay between these biological factors, and there are numerous plant genera that are recognised as taxonomically complex groups (TCGs). Plant parasitism is a potential driving force of taxonomic complexity that has been largely overlooked. In this thesis I use two main systems to explore these factors; the British flora and a parasitic genus of plants, eyebrights (*Euphrasia*). The British flora is an excellent system to study taxonomic complexity, due to the wealth of data available. *Euphrasia* is a useful experimental system, as multiple factors that contribute to taxonomic complexity are present, as well as *Euphrasia* being able to parasitise a wide range of host plant species.

The aim of this thesis is to understand the role of three main factors driving taxonomic complexity in *Euphrasia* and the British flora. The first factor is the cross mating between species (hybridisation). Second is the duplication of genetic material in every cell of an organism (polyploidy), and the last is the parasitic condition of some plant species which extract water and nutrients from host plants. I first review the frequency and importance of hybridisation between plants with different ploidy levels, and based on a literature review and survey of the British flora find it to be more common than usually appreciated. Next, I investigate how hybridisation is affected by how closely related species are across the British flora. I find that the probability of two species hybridising is impacted mainly by relatedness, ploidy level differences, and the extent of geographical overlap. Then, I investigate a contact zone between two *Euphrasia* species that differ in ploidy level and find little evidence of contemporary hybridisation, however there may have been low levels of historical hybridisation. In the second part of the thesis, I grow thousands of *Euphrasia* plants in a common environment to understand how plants differ in appearance depending on their host. I show that firstly, traits used to identify species in *Euphrasia* change depending on the host plant species used. I go on to show that different *Euphrasia* species respond similarly to most hosts, however there does appear to be some specialisation of *Euphrasia* on some host species. This thesis shows how integrated analyses incorporating genetic and ecological data can be used to explore the many and diverse factors underlying taxonomic complexity in plants.

Summary

Many plant groups are taxonomically complex with species that are difficult to distinguish. The main factors driving this complexity include apomixis, selfing, hybridisation, and polyploidy. Plant parasitism is a potential driving force of taxonomic complexity that has, however, been largely overlooked. In this thesis I use two main systems to explore these factors; the British flora and a hemiparasitic genus of plants, *Euphrasia*. The British flora is an excellent system with a wealth of large and comprehensive ecological and genetic data sets available, while *Euphrasia* is a tractable experimental system exhibiting rampant hybridisation, variation in ploidy level and mating system, and able to parasitise a wide range of plant species. The main aim of this thesis is to understand the role of hybridisation, polyploidy, and parasitism in driving taxonomic complexity in *Euphrasia* and the British flora. I first review the frequency and importance of cross ploidy hybridisation across plants, and based on a literature review and survey of the British flora find it to be more common than usually appreciated. Next, I investigate how hybridisation is affected by phylogenetic relationships and genetic distance between species across the British flora. I find that the probability of hybridisation is impacted mainly by parental genetic distance, ploidy level differences, and the extent of geographical overlap. Then, I investigate a single contact zone between a diploid and tetraploid species of *Euphrasia*, and find little evidence of contemporary hybridisation, however demographic modelling supports a model with low levels of gene flow. In the second part of the thesis, I use common garden experiments to understand the nature of species differences in the taxonomically complex, hemiparasitic genus *Euphrasia*. I show that firstly, traits used to identify species in *Euphrasia* are plastic, and change depending on the host plant species used. I go on to show that *Euphrasia* exhibit both conserved and host specific interactions across many different host species, which potentially reveals cryptic specialisation. This thesis shows how integrated analyses incorporating genetic and ecological data can be used to explore the many and diverse factors underlying taxonomic complexity in plants.