



Introduction

Human-induced climate change is widely acknowledged as one of the greatest threats to the planet's biodiversity. Although the climate has changed throughout Earth's history, the current rate of climate change is unprecedented during the last 65 million years, and because of habitat fragmentation the species response may be weakened. The processes by which a species can respond to climate change include: migration, adaptation, and acclimation.

1. *Migration*: this involves a species shifting its distribution, in order to track changes in the spatial configuration of suitable climate space, e.g. in the northern hemisphere, more southerly distributed species may shift northwards as the climate warms. For this process to succeed, species must move relatively rapidly through the landscape between fragmented habitats to keep pace with their suitable climate and to counterbalance local extinctions in regions where the climate is becoming less suitable.
2. *Adaptation*: this involves species evolving *in situ*, through genetic change and modification in phenotype to survive and reproduce under a changing set of environmental conditions. The potential for evolutionary adaptation may - in general - be greater for larger populations, where there is more 'raw material' for evolutionary change, and for populations which have gene flow connecting them to other populations.
3. *Acclimation*: this involves species adjusting phenotypically (but not genetically) to new environmental conditions. Individual organisms may have a certain flexibility to undergo shifts in their structure, physiology and reproductive investment etc. that allows them to cope with and survive a changing environment.

Species Interactions – Rainforest Lichens as a Study System

Individuals, populations and species do not exist in isolation, and one of the major challenges in biodiversity science is explaining how interactions among species might affect the response to a changing climate. The EPACS project addressed the issue of climate change and species interactions using lichens as a study system. Lichens are a symbiotic association based on a fungus which builds the lichen structure (thallus; Figure 1) and which requires a source of carbohydrate for survival. The lichen-fungus protects within the thallus a photosynthetic partner (alga or cyanobacteria, called a photobiont), from which it harvests carbohydrate.

This study focussed particularly on lichen epiphytes which are restricted to and characterise Europe's oceanic temperate rainforests. Temperate rainforests are rare ecosystems, covering < 1% of global land area. Rainforest epiphytes are ecologically-important because they fix nitrogen from the atmosphere, making it biologically available; however, they are highly pollution sensitive, and where they occur outside optimum climatic conditions they are often restricted to pockets of ancient woodland. Consequently, temperate rainforest epiphytes are conservation priority species.



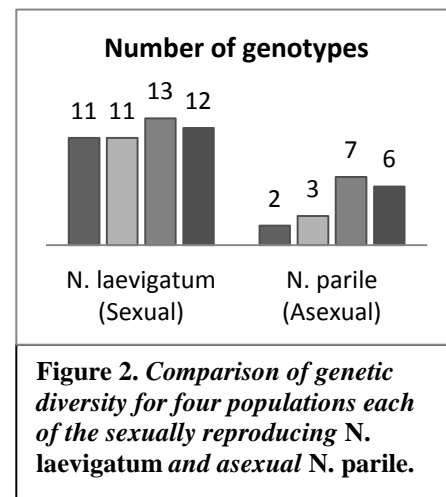
Figure 1. The lichen, *Nephroma parile*, showing its powdery lobe margins, which are made up of asexual propagules containing its symbiotic partner, *Nostoc*. Photo © Chris Jeffree, 2013.

Lichens, Climate Change and Interaction Processes

There are several hypothesised interactions involving the lichen-fungus and the photobiont, which are relevant to climate change effects on biodiversity more generally and which we tested for temperate rainforest epiphytes:

1. *Dispersal Mode and Genetic Diversity*. Some lichen-fungi reproduce sexually via spores that are small and easily dispersed, leading to high potential migration rates for tracking climate change. It is hypothesised that lichen-fungi reproducing via spores will tend to have higher genetic diversity because of genetic recombination during sex, and high gene flow among populations, increasing the opportunity for adaptation to cope with a changing climate. However, wherever a spore arrives, it must acquire a compatible photobiont to establish a new lichen thallus, grow and then reproduce. As an alternative, other lichen-fungi reproduce asexually; they are transported over smaller distances via a larger clonal propagule that include both the lichen-fungus and photobiont, so that

although the distances travelled are smaller, establishment is more reliable because the photobiont is carried along with the fungus. Lichen-fungi reproducing asexually are hypothesized to have lower genetic diversity because of lack of sex and more limited gene flow among populations. This would lower the opportunity for adaptation, increasing the risk presented by a changing climate.



The EPACS study successfully developed and tested novel fingerprinting markers (microsatellites) for two closely related lichens with very similar environmental requirements, but different reproduction, supporting the hypothesis of more genetic diversity in the sexual *Nephroma laevigatum* versus the asexual *N. parile* (Figure 2). The genetic markers are in publication, and will provide an improved study system for understanding the biology of threatened conservation-priority epiphytes.

2. *Acclimation via Photobiont Switching.* Each lichen-fungus can associate with a given range of photobionts, referred to as its 'specificity'. However, preliminary work by the EPACS research team suggests that within a local environmental setting a lichen-fungus might associate with a yet more limited suite of this broad specificity, to combine with photobiont types that optimise ecological fitness in a local environment, in a process referred to as 'selectivity'. The process of selectivity provides a potential opportunity for acclimation among lichens.

The EPACS study has tested a gene region that is variable among different strains of the photobiont (*Nostoc*) used by the *Nephroma* lichen-fungi (the *rbcLX* spacer). This was used to survey the diversity of *Nostoc* (i) within *Nephroma*, where a single *Nostoc* type was found with the asexual *N. parile*, compared with more than 20 types in the spore-producing *N. laevigatum*; (ii) in the wider community of *Nostoc* associated with other lichen-fungi, where only *N. laevigatum* shares sequence types with other co-occurring *Nostoc*-containing lichens, and, building on these results, (iii) on tree bark or mosses, where a novel pyrosequencing community approach is being used for the first time to understand *Nostoc* availability outside lichens. A portion of this work included a key training programme for an undergraduate to assist in the laboratory. Part (i) and (ii) results are now in preparation for publication, and the gene region is now being used to test whether *Nephroma* species show selectivity for particular *Nostoc* strains in different climates and habitats.

3. *Lichen Species Interactions.* Finally, different lichen species can interact among themselves to control distribution patterns in surprising ways. One important theoretical hypothesis challenged the assumption that spore-dispersed lichen-fungi can more easily migrate to track climate change. The 'core-fringe hypothesis' suggested that spore-dispersed lichen-fungi require the prior colonisation of a habitat by asexually-dispersed species with overlapping specificity, which seed a photobiont into the habitat. The spore-dispersed species can then scavenge this photobiont and become established, suggesting that migration rates would be limited by opportunities for establishment. Spore-dispersed lichen-fungi may migrate at a rate that is set by the lower-dispersal rate of asexual lichens, completely over-turning expectations under climate change.

The EPACS study confirmed a dependency of the spore-dispersed lichen-fungus (*N. laevigatum*) on the prior colonisation of asexual species which show overlapping specificity for the same types of photobiont. This stands in contrast to the ecologically similar though asexually dispersed lichen-fungus (*N. parile*), which showed no such dependency. This provides a compelling example of how species interactions might fundamentally alter expectations under climate change, focussing on two-scales: (i) the interaction of fungus and photobiont to create a lichen, and (ii) the interaction among lichens within an epiphyte community.

Policy Implications

The project was carried out in Scotland, which has among the best remaining examples of epiphyte-rich European temperate rainforest. At this early stage of completion the results are being disseminated through peer-reviewed publication and conference proceedings, and they are being used directly by the national conservation agency (Scottish Natural Heritage) to develop improved management plans for key temperate rainforest sites within the European conservation site network, e.g. NATURA Special Areas of Conservation.

Contact: For further project information please contact Dr Christopher Ellis (c.ellis@rbge.org.uk)