- *Cladonia* Symbiosis -
Pattern and Process

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> The Lichen Symbiosis

- The biodiversity of 'lichens' has focussed predominantly on the fungal partner. In general the lichenised-fungus controls lichen morphology, while each lichen definitely comprises a different fungal species - i.e. the scientific name of lichens is applied specifically to the fungus. However, the fungal partner is at most one-half of a symbiotic relationship, and lichens contain unquantified levels of algal biodiversity.

- The morphological characters of algae are insufficient to effectively resolve the diversity of lichen symbionts, and while lichenologists have proceeded to classify and study the diversity of lichenised-fungi, the diversity of their associated algae has remained neglected and is poorly understood.

- The development of molecular techniques has provided biologists with a tool to effectively quantify algal diversity. My research has used molecular tools to examine diversity in algal symbionts, addressing two fundamental themes:

  - First, how specific is the relationship between a lichen fungus and its algal partner(s)? Is a single fungal species associated with only one or several algal types? Answering these questions is essential to understanding cryptic levels of algal biodiversity associated with lichenised-fungi.

  - Second, what are the ecological and evolutionary drivers of algal selection (i.e. selection of a given algal-type) by a lichen fungus?

> The Study Habitat

- My study focussed initially on Florida rosemary scrub (Fig. 1). Within this habitat there is a predictable set of co-occurring *Cladonia* species, which occupy the bare ground between shrubs. The lichens form part of a dynamic fire-driven community. Periodic fire creates gaps within the developing shrub overstorey, providing a matrix of bare ground occupied by the lichens, though the lichens are themselves locally extirpated by fire events.

- Diverse *Cladonia* mats develop on the ground between shrubs (Fig. 2), comprising at least eight fungal species and including the rare *C. perforata* and *C. subsetacea*: but how many algal types are in these communities, and how are they distributed?

Figure 1: Florida rosemary scrub, a fire-driven ecosystem with diverse *Cladonia* communities.

> Algal Specificity

- I examined specificity of the symbiotic relationship between fungal species and phylogenetically distinct algal types. I sampled over 200 lichen thalli from six sites, including eight *Cladonia* species occurring in the Florida rosemary scrub habitat. Molecular sequence data were used to delimit phylogenetically related algal lineages. Three algal lineages were identified (Fig. 3), labelled Clade I, IIa and IIb. These algal clades occurred in equal abundance at the six sample sites.

- In Florida scrub six of the eight sampled *Cladonia* species were found to occur with only one of the three major algal clades, i.e. I, IIa and IIb only (Figs 3 & 4). These fungal species therefore showed greater specificity towards an algal symbiont, i.e. they associated with a narrow subset of available partners. Two fungal species were less specific and were found to occur with either two or three of the available algal symbionts (Fig. 4).

- The research highlights different levels of fungal specificity for algal symbionts. Moreover, phylogenetic relationships amongst lichen fungi did not predict which algae would be associated: i.e. the two sister species - *Cladonia dimorphoclada* and *C. pachycladodes* - formed symbiotic associations with different algal clades.

Figure 2: Mixed *Cladonia* mat growing in a gap between rosemary shrubs

> Algal Selection

- My study of algal selection focussed on a single lichen species, *Cladonia subtenuis*. I sampled *ca* 70 thalli from 11 sites across the North American range of *C. subtenuis*, and identified four distinct algal lineages associated as symbiotic partners, each of which was nested within algal 'Clade II'.

- There was predictable variation in the algal lineages associated with *C. subtenuis* based on both geographic locality and habitat, i.e. coastal plain *v.* inland (Fig. 5). For example, Clade IIa algae are only associated with *C. subtenuis* in the coastal plain, while Clade IIb algae are associated with *C. subtenuis* further inland. This is particularly interesting because Clade IIb algae also occur in coastal plain rosemary scrub, but are never associated with *C. subtenuis* in the rosemary scrub habitat.

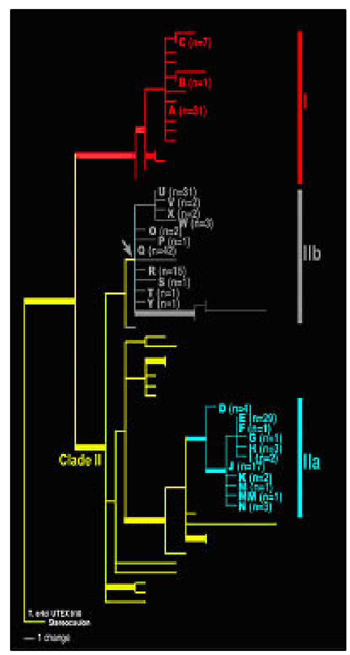


Figure 3: Three lineages of the algal genus *Asterochloris*, the green algal symbiont of *Cladonia*. Lineages are labelled as Clade I (red), and Clades IIa (grey) and IIb (blue).

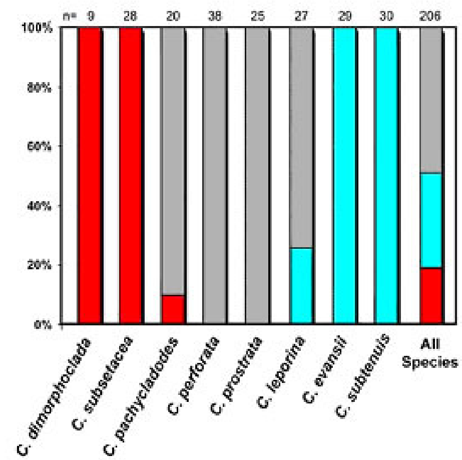
> KEY FINDINGS <

Evolutionary and ecological forces structuring the lichen symbiosis

- The results of my studies suggest selective pressure at the habitat scale leads to different levels of fitness among combinations of symbiotic partners. Thus, *C. subtenuis* appears to 'select' those algal lineages conferring greater fitness within a given habitat, from a pool of the multiple symbionts available (though not utilised) in a given geographic location.

- My studies have examined the pattern of algal diversity at contrasting scales, and the processes maintaining the diversity of algal partners associated with lichen fungi. I suggest that rather than being a passive component of the lichen symbiosis, algal partners and their diversity may play an important role in the adaptive response of the synthetic 'lichen' to evolutionary pressure within a habitat (i.e. niche response, competitive fitness etc). The importance of algal diversity in lichen symbioses has been largely ignored by lichenologists and in biodiversity conservation. In contrast, research into algal symbionts has much to contribute to the ecology under-pinning lichen conservation, as well as the wider evolutionary processes generating global biodiversity, i.e. the nature of symbiosis.

Figure 4: Percent frequency of occurrence examined between the eight different *Cladonia* species and the three algal clades (cf. Fig. 3).



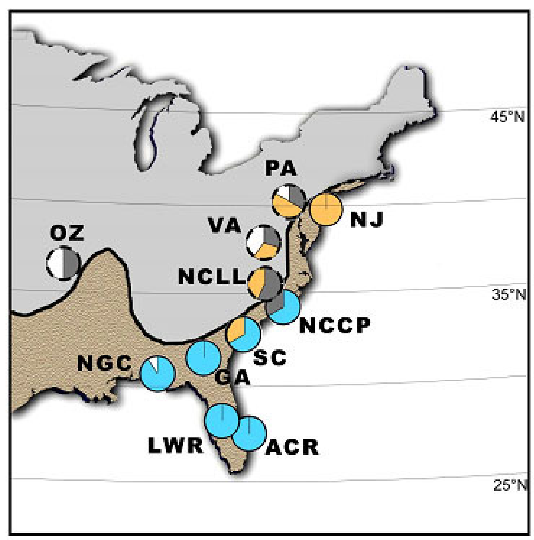


Figure 5: Geographic variation in the percent frequency of algal lineages associated with C. subtenuis, i.e. compare Clade IIa algae (blue) in the coastal plain (brown background), with Clade IIb algae (grey) occupying inland habitats (grey background).