Do saxicolous lichen communities represent photobiont-mediated guilds?

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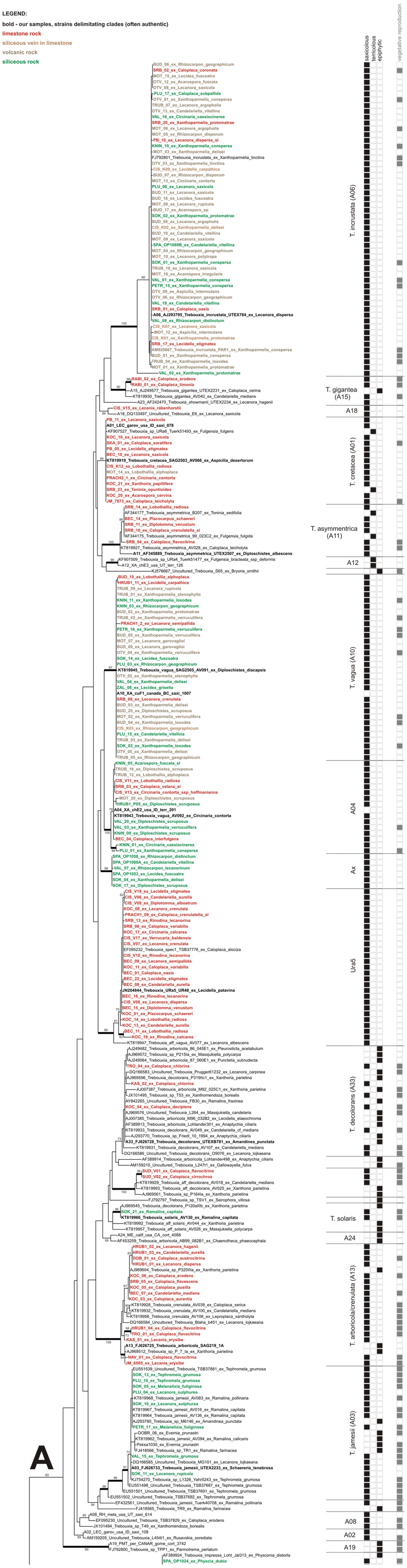


Introduction

More then 15 000 lichen (fungal) species have been described to date, occurring in almost all terrestrial ecosystems, colonizing a wide range of habitats. In a certain geographical space, particular habitats can host more or less unvarying **lichen communities**. Their composition is usually a good indicator of specific local conditions (e.g. heavy-metal content in siliceous rock). Many of lichen communities were described based on the composition of lichen (fungal) species, however, we know almost nothing about the composition of their photobionts...

Some recent studies have found lichen-forming algae or cyanobacteria from different environments clustered in distinct lineages. Such environmental preferences of autotrophic partners may limit ecological niches available to lichens. Together with requirements of mycobionts they result in the existence of **lichen guilds**.

Hypothesis: Lichen communities function as lichen guilds, i.e. each lichen (fungal) community growing in specific environmental conditions associates with a distinct pool of photobionts.
Object: saxicolous lichen communities of central Europe...
… growing in similar climatic conditions (low altitudes) on different rock types
… sharing *Trebouxia* photobionts

Results

Photobiont diversity

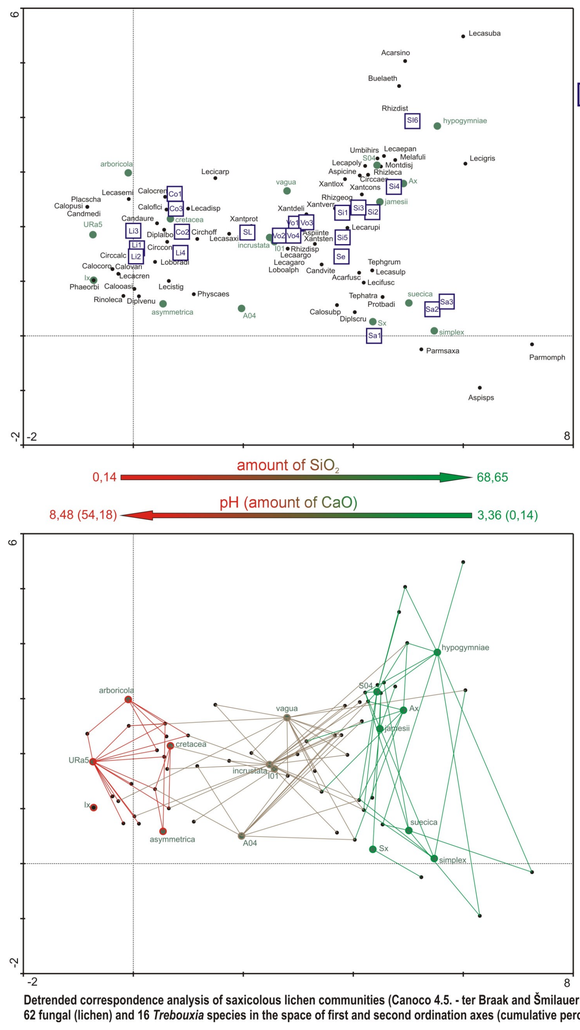
- In 89 lichen taxa of saxicolous communities, 24 *Trebouxia* lineages were found, including eight authentic *Trebouxia* species (additional sequences used in the analysis represent further 25 clades).
- Photobionts of saxicolous lichens of central Europe belong to three of four *Trebouxia* major clades – A, I, and S (see phylogenetic tree on the left).

Lichen guilds

- All individual *Trebouxia* lineages were shared by several fungal species (3–34); the selectivity of fungi varied from low to high.
- The photobionts exhibited rather clear habitat/community preferences – each lichen community shared a specific pool of distinct algal lineages.

→ **The lichen fungi and their photobionts formed obvious ecological assemblages – limestone (calcareous), volcanic and siliceous rock guilds.**

- Each guild had its „core“ comprising species with narrow ecology, but the boundaries among guilds were not strictly defined – ecologically closer communities partly shared their photobionts.
- Volcanic guild formed a natural link between limestone and siliceous guild.
- Euryecious lichen taxa often represent the intermediates between „neighbouring“ guilds (e.g. *Lecanora saxicola* between limestone and volcanic guild, *Candelariella vitellina* between volcanic and siliceous guild – see figs on the right).



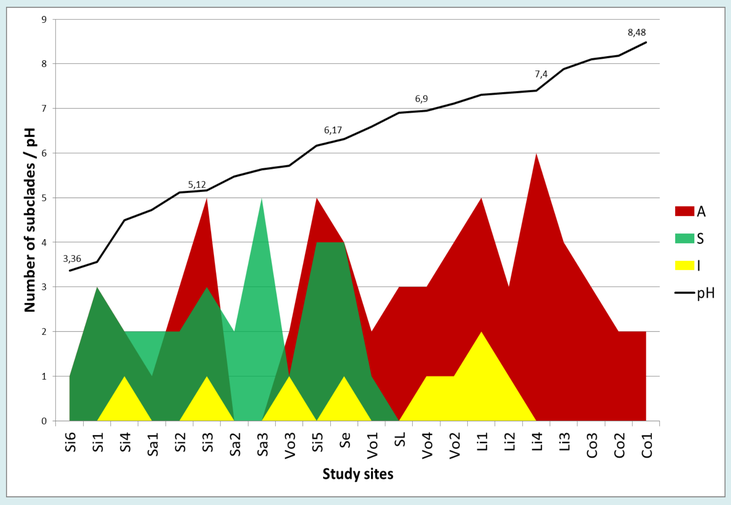
Biplot showing the position of study sites, *Trebouxia* species and lichen taxa in ordination space.

The same biplot (without localities) with links among associated mycobionts and photobionts.

Colours highlight the separation of three photobiont-mediated guilds:
limestone guild
volcanic guild
siliceous guild

The interconnections between ecologically close guilds through several (ecological plastic) lichen taxa are apparent.

Detrended correspondence analysis of saxicolous lichen communities (Canoco 4.5. - ter Braak and Šmilauer 1995): distribution of 22 samples, 62 fungal (lichen) and 16 *Trebouxia* species in the space of first and second ordination axes (cumulative percentage variance of species data 25.5 %).

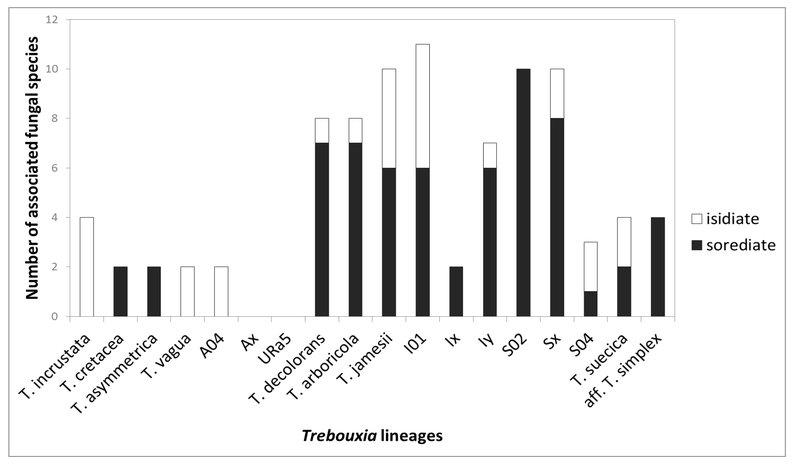


Ecology of photobionts

- The adaptation to different chemical composition and pH of substrate seems to have an origin in the evolution of *Trebouxia* – the preferences were obvious already on the level of major clades:
  - clade A is rather basiphilous (but including acidophilous subclades as well, e.g. *T. jamesii*, clade *Ax*)
  - clade S is strictly acidophilous
  - clade I does not prefer distinct pH, but their members were mainly found in lichens typical for eutrophicated environments.
- It may have a consequence in algal preferences to main substrate types: rock, soil and tree bark – *T. incrustata* and its close relatives from clade A were exclusively associated with saxicolous and terricolous lichens, on the other hand, the members of clades I and S represented mainly substrate generalists or prefered epiphytic lichens (see tree on the left).

Core species wanted!

- In a system of lichen guilds, vegetatively reproducing lichens (*core species* sensu Rikkinen et al.) may serve as propagators of photobionts within their soredia or isidia.
- We detect an interesting disproportion in numbers of vegetatively and sexually reproducing lichens associated with individual photobionts – some algae were never found in a core species (especially rock specialists from clade A), other seemed to predominantly associate with asexual, often epiphytic lichens.
- We can speculate about the role of symbiotic propagules as a common source of photobionts. The „photobiont rain“ probably includes relatively high portion of free-living forms of symbiotic algae (at least of some algal lineages).



The plot based on complete dataset of *Trebouxia* sequences of vegetatively reproducing lichens from Europe. Numbers of strictly sexual lichens are not shown (dataset incomplete, yet). Lineages with at least five sequences were included.

Conclusions

- We found photobiont-mediated guilds in saxicolous lichen communities in central Europe.
- More then 24 photobiont species occured in studied lichens. Four to five distinct *Trebouxia* lineages formed a core of each lichen guild.
- Some photobionts exhibit clear environmental preferences and participate only in one specific guild, several algae represent euryecious taxa participating in various guilds (mainly *Trebouxia* species of volcanic guild).
- The most of *Trebouxia* species „read“ chemical characters and pH of substrate rather than its „type“ – they are able to associate with saxicolous, terricolous as well as epiphytic lichens within similar range of pH.
- *Trebouxia*-mediated guilds have commonly a low proportion of vegetatively reproducing lichens. Moreover, some algal lineages are associated with very low number of sorediate or isidiate species. Therefore, we suppose they spend considerable part of their existence, including dispersal, as free-living algae.

Phylogenetic tree: nrITS phylogeny, maximum likelihood analysis using GARLI v. 2.0 (Zwickl 2006), GTR+G+I model, ML bootstraps ≥60% are shown, branches with boostrap ≥90% are in bold. Sequences included: own (256) – *Trebouxia* seq. of saxicolous lichen communities + some seq. of additional sorediate saxicolous lichens from other localities; GenBank (177) – seq. of authentic strains and *Trebouxia* OTUs sensu Leavitt et al. (2015), all unicate *Trebouxia* seq. of terricolous, epiphytic and sorediate saxicolous lichens photobionts from Europe. The provisional names of *Trebouxia* clades and OTUs follow Beck (2002), Hauck (2007), Ruprecht et al. (2014), Leavitt et al. (2015) . Ax, Ix, Iy, Sx: own provisional codes.
Sampling: At each sampling site (see map and legend to DCA plot above), all lichen taxa belonging to a local community were collected and analyzed. DNA was extracted from one thallus of each lichen taxa.

Acknowledgments
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