Changing Genomics

How lichens' evolutionary history and environmental context can inform astrobiological habitability

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Acknowledgments

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Introduction

Lichens as extremophiles

Lichens are among the Earth's most hardy extremophiles. The symbiotic relationship formed between a fungus and a photosynthetic partner (as well as often bacteria) has enabled them to colonise almost every corner of the earth. This partnership provides them with adaptations such as UV protection, desiccation tolerance, and a protective structure, allowing lichen to survive otherwise inhospitable conditions.

The process of lichenisation (the formation of this symbiotic relationship) has occurred multiple times throughout lichens' history and evolution (Gargas et al., 1995), making it a particularly interesting case study of both evolutionary biology and astrobiology, and one whose potential has previously been understudied.

In fact, when subjected to outer space conditions for 18 months, two species of lichen, the *Rhizocarpon geographicum* and *Xanthoria elegans,* were able to survive the vacuum, extreme temperature variation, and extreme radiation conditions (de la Torre, 2010). They achieved this by shutting down metabolic processes and remaining dormant until reactivated by the presence of water, at which point they resumed normal metabolism as well as photosynthesis.

Research outline

In this project, I will focus on the Rhizocarpon genus and its evolutionary history to gain a deeper understanding of the distribution of some of these adapted traits, whether in response to its environment or through its phylogeny.

In doing so, I will try to answer the following questions:

- What is the evolutionary biology of the lichen traits that cause UV resistance, desiccation tolerance and structural adaptations, which allow for survival in extreme conditions?

- Are these traits, such as the presence of acids, pigmentation and desiccation tolerance, purely genetic adaptations and inherited conditions deriving from a common ancestor, or do they reflect the environment in which they are present, suggesting more localised environmental adaptation?
- How can understanding lichens' evolutionary biology inform astrobiological research, both in the context of our solar system's habitability and the detection of exoplanetary biosignatures?

Why Rhizocarpon?

Rhizocarpon is a suitable genus for research for several reasons; it is globally distributed across biomes, including deserts, tundra, and tropical mountain ranges. Its most prominent

member, *R. Geographicum*, is well studied concerning its ecological and astrobiological survivability (Consortium of Lichen Herbaria, 2025) (Sancho et al., 2007).

Figure 1 shows a random sample of 1000 of my initial individual Rhizocarpon *lichen samples. As you can see, they are spread geographically across much of the world and in a wide variety of biomes and conditions, including Siberia, the Andes, both polar regions and multiple deserts.*

Astrobiological relevance

A deeper understanding of the evolution of such extremophiles is important in constraining the bounds of habitability. Historically, we have categorised the habitable zone as the region where liquid water can exist stably on a rocky planet's surface, often a function of both stellar classification and atmospheric composition. Lichens and other extremophiles have the potential to redefine this range of habitability through biological adaptation to extreme conditions, as well as through their unique trait of surviving extreme desiccation, which allows them to reactivate in the presence of water. (Kranner, 2008) This process of hibernation and reactivation would hypothetically allow planets with extreme seasonal variation or orbital dynamics to potentially host this mode of life.

Furthermore, examining our own solar system, 'Lithopanspermia', the transfer of life between planets via comets or meteorites, becomes more viable with the hypothesis that life can survive on these bodies for extended periods, with lichen-like organisms a potential contender for surviving these transfer conditions. (Horneck, 2008)

Expanding on this is the hypothetical scenario that hibernation could end periodically, briefly reaching the warm and wet conditions necessary for photosynthesis and reproduction, before reverting to this hibernation state again.

Methodology

Selecting the genetic data

I have chosen to examine the evolutionary biology of the genus Rhizocarpon, which is distributed across much of the world. The aim at this stage was to build a robust database that would allow me to both generate successful phylogenetic trees and analyse traits against purely genetic mutations and those influenced by local environmental conditions.

I chose to examine as wide a range of Rhizocarpon species as possible for two reasons:

- The various species will share a close evolutionary history, so patterns of trait conservation/ divergence emerge clearly in a large sample size.
- The genus is geographically very diverse, and many can be found in extreme conditions, including astrobiological analogue sites for Mars.

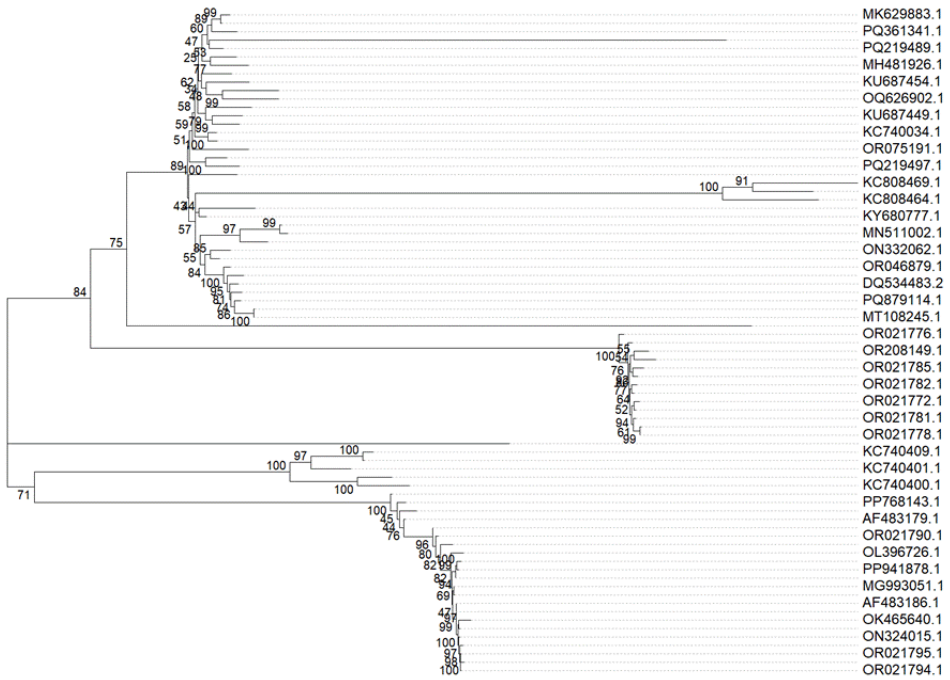

Figure 2 shows a phylogenetic tree of my largest sample of the Rhizocarpon genus (76 different species, 3 control duplicate tests), constructed using the Standard Bootstrap method with maximum likelihood and the Tamura-Nei model, with partial deletion at 90%. The various branches represent evolutionary changes in the genome.

To begin, I first collected the Rhizocarpon species genetic sequence data from the NCBI database, using the BLAST tool function to ensure that the same regions were compared across the species. I then aligned these samples using ‘MUSCLE’ on the MEGA software platform (Kumar et.al, 2024).

Initially, I constructed an exploratory phylogenetic tree using all the Rhizocarpon species I could access, as seen in Figure 2. The various branches represent inferred evolutionary relationships in the genome.

On a phylogenetic tree, a clade is a group of organisms that includes a common ancestor and all of its descendants, essentially representing a single, unbroken "branch" or "lineage" of evolutionary history.

‘Bootstrap values’ were high (>70) for most top-level clade branches. Higher bootstrap values indicate greater confidence in the observed branch, suggesting it's likely not an artefact of random data variation (Felsenstein, 1985).

However, the initial phylogenetic tree in Figure 2 did reveal some potential challenges. Sometimes what are labelled as identical species appear in different sections of the tree, and there appears to be clustering of species with similar accession numbers (as seen for the OR021… and KC740… branches in Figure 2). While at first glance this sounds potentially interesting - and suggestive of localised groups of lichen diverging so they are no longer clustered with their original species - closer inspection of the sources suggests that some of these divergences were more likely due to methodological differences, misidentified samples, or poorly aligned sequence data.

To address these issues, I pruned the dataset to make it more useful for phylogenetic analysis, attempting to standardise as best as possible the segments of the genetic code, while also balancing the published research and usable data available. To achieve this, I prioritised the inclusion of species that featured in an already-constructed timetree, which includes 7 Rhizocarpon species and their evolution mapped over the past 100 million years (Kumar, Sudhir, et al., 2022). A significant part of pruning down the dataset to find the most suitable data involved using BLAST to search for these specific genomes, allowing me to gather more information on relative timescales and branch separation.

Accession No	Species
ON324015.1	Rhizocarpon alpicola
AF483179.1	Rhizocarpon amphibium
KY680777.1	Rhizocarpon atroflavescens
PP941875.1	Rhizocarpon badioatrum
PQ219489.1	Rhizocarpon bolanderi
PP047689.1	Rhizocarpon chioneum
PP941878.1	Rhizocarpon cinereonigrum
MH481926.1	Rhizocarpon copelandii
KY680783.1	Rhizocarpon disporum
OK465640.1	Rhizocarpon distinctum
ON324016.1	Rhizocarpon effiguratum
OR021782.1	Rhizocarpon eupetraeoides
MT108256.1	Rhizocarpon furax
AY536838.1	Rhizocarpon geminatum
KC808469.1	Rhizocarpon geographicum
PQ219497.1	Rhizocarpon grande
KJ766788.1	Rhizocarpon hochstetteri
ON341127.1	Rhizocarpon inarense
OR021794.1	Rhizocarpon intermediellum
AF483178.1	Rhizocarpon lavatum
PQ871464.1	Rhizocarpon lecanorinum
KU687449.1	Rhizocarpon leptolepis
OR046879.1	Rhizocarpon macrosporum
AF483186.1	Rhizocarpon norvegicum
KJ766923.1	Rhizocarpon Oederi
MT108259.1	Rhizocarpon parvum
AF483177.1	Rhizocarpon petraeum
AF483184.1	Rhizocarpon polycarpum
OR021790.1	Rhizocarpon postumum
MW938040.1	Rhizocarpon pusillum
PP768143.1	Rhizocarpon reductum
ON332059.1	Rhizocarpon ridescens
KU687458.1	Rhizocarpon rittokense
PQ879114.1	Rhizocarpon saanaense
KU687454.1	Rhizocarpon santessonii
OR195104.1	Rhizocarpon sinense
AY853390.1	Rhizocarpon sphaerosporum
KU687452.1	Rhizocarpon subgeminatum
AF483181.1	Rhizocarpon suomiense
KC740400.1	Rhizocarpon superficiale
OR021795.1	Rhizocarpon tavaresii
OR021797.1	Rhizocarpon tinei
OQ626902.1	Rhizocarpon umbilicatum
KC740411.1	Rhizocarpon viridiatrum

Figure 3 shows the final selection of 45 Rhizocarpon's species used after carefully pruning and sanitising my initial genetic data bank. These come from a wide geographical region, encompassing both poles and 6 continents. But broadly cover the same segment of the genome when aligned. RevBayes provides an interactive environment for statistical computation in phylogenetics. It is primarily intended for modelling, simulation, and Bayesian inference in evolutionary biology, particularly phylogenetics.

Once my final selection of species was established, I was then able to model another phylogenetic tree. To achieve this, I employed the statistical Bayesian inference technique in RevBayes, with the model running for 10,000 generations on the CropDiversity HPC cluster, as *described by Percival-Alwyn et al. (2024)*, using the Jukes-Cantor substitution model. This tree provided me with a framework that I could use to run trait evolution tests. These timings were chosen to strike a balance between error and runtime, based on testing the duration of the cycles on the cluster.

Selecting the genetic traits

Once the dataset was selected, I had to choose which specific genetic traits I would analyse. My primary consideration for selecting the traits was those that would be most useful for the lichen to survive in extreme extraterrestrial conditions, and for which we can gather proxy data on Earth.

The following is a justification and exploration of the different traits that I chose to analyse against genomic & environmental data.

Acids (Rhizocarpic, Psoromic, Stictic, Norstictic)

Lichens are known to produce a variety of secondary metabolites, including acids, for many different applications. Some are used in symbiosis with the bacterial colonies within them to self-regulate the organism, while others help the lichen respond to external environmental stimuli (Goga et al. 2018).

Four acids appeared particularly commonly across the Rhizocarpon species: Rhizocarpic, Psoromic, Stictic, and Norstictic acids.

Rhizocarpic acid is unique to the genus, making it a suitable phylogenetic marker, whereas the others are found across a wide range of lichens and organisms. The acids are particularly interesting from a spectroscopic perspective due to their reported effect on UV shielding. (Hidalgo et al. 2002) Stictic acid also exhibits some anticancer properties, making it a potential candidate for medicinal purposes (Wassman et al., 2013).

While it is not directly monitored in this project, some further study would be interesting to assess the exact spectral effects of the acids produced by lichen, e.g. through reflection spectra. Understanding this better could potentially contribute to our understanding of hypothetical biosignatures detectable on other planets/ moons.

Thallus & Spore Colour

The main body of the lichen is known as the thallus, its colour is dependent on pigments present, such as parietin or chlorophylls. These pigments play a dual ecological role by both regulating light absorption for photosynthesis and also preventing extreme radiation signatures from penetrating to the photobiont. In practice, this often blocks UV radiation (Solhaug, 2003).

There is a considerable variety of lichen colours globally, with literature suggesting that they adapt as a function of light, due to varying levels of solar insolation, optimising different rates of absorption. (Färber, 2014) It will be interesting to test this hypothesis from both a phylogenetic and an environmental perspective. I am particularly interested in how the lichen thallus and spore colours will behave in the most extreme conditions, as it will help inform potential spectroscopy and expected responses on extreme rocky exoplanets or exomoons. The colour of the ascospore (spores of lichen fungi) is also of interest, as these pigments may act to shield spores during dispersal, which could provide us with a slight proxy for stress testing lichens' dispersal in extreme conditions.

KI Medulla Test, Areola Thickness, Thallus Thickness

The medulla is an internal layer of lichen tissue, just below the algal zone. A KI test applies Iodine-potassium iodide to detect the presence of polysaccharides, which relate strongly to both protecting against water stress and broadly deploy multiple methods to protect the lichen during these periods of extreme desiccation (Olafsdottir, 2001) (Ndhlovu, 2024), (Honegger, 2006). This is linked to the fact that lichens are poikilohydric, meaning they can survive periods of drying, hibernate, and then rehydrate when moisture is present (Lorenz, 2023), (Green, 2011). These are incredible traits for expanding habitability in terms of seasonal and orbital variation.

Furthermore, the thickness of both the areola (surface patches in lichen) and the thallus can also be used as proxies for water retention. With thicker tissues, the lichen can buffer against water loss, extreme temperatures, and dangerous radiation. (Armstrong, 2017)

Presence of chemicals K, C, KC, P tests

Spot tests are beneficial for determining the presence of certain lichen secondary metabolites. These work by applying a reagent (in this case, K - potassium hydroxide, C - Sodium Hydroxide, KC - K test followed by C, P - para-phenylenediamine). Depending on the compounds present, the lichen thallus or medulla may change colours in response, thus indicating the presence of a particular secondary compound. Ecologically, these compounds are beneficial as they often exhibit UV-resistive or antimicrobial properties, while astrobiologically, they provide a simple proxy to highlight adaptations to survival in extreme conditions. It is interesting to test these against both the environment and the phylogeny, as each represents a unique selection of secondary metabolites. Investigating their responses to the environment can help us gain a deeper understanding of the function of such metabolites.

Environmental Data

For my astrobiological interest, the most interesting variables to measure are the relative pressure, UV radiation, temperature, and sunlight to which each lichen is subject, ideally measured at each sample site. Unfortunately, while included in some studies, the specific data for all species are lacking; instead, this has forced me to use more prevalent proxies.

- Elevation is related to both temperature, and atmospheric pressure. (according to thermodynamic lapse rate laws)
- Latitudinal data, expressed as an absolute value. This serves as a generalised proxy for sunlight received over the long lifespans of lichen, but does not capture seasonal variation, purely the average.
- UV index values were found by averaging the species coordinate data with a global UV radiation dataset (Zippenfenig, 2023).

Initially, the database contained over 48,000 lichen samples. However, I then removed anomalous or poorly geolocated data, as well as restricting to only records collected after 1990, which, while reducing my sample size quite significantly, minimises the complication of comparing data conducted under different historical baselines, as lichen survive in some of the most climate-sensitive parts of the world.

These proxies have many limitations; none of them are quite able to capture microclimatic, localised variations such as geology, shade, or external variables. Nevertheless, globally, and for the concept of large-scale data analysis, they are useful for capturing generalised environmental gradients and provide a consistent framework for us to analyze the traits from. Another limitation appears to be some level of sampling bias present in my lichen samples. There is a significant underrepresentation of the Southern Hemisphere, and an overrepresentation of certain overstudied regions, including Norway, the Northeast United States, and the Rocky Mountains. While we can still obtain a general overview of the environmental conditions of all the lichens sampled, this is clearly a gap in research that would be beneficial to address by conducting further sampling. Despite this, it encompasses a broad range of extreme biomes, with a large sample taken in the Tibetan Plateau, alpine regions, and both polar regions. *(Alatan et. al, 2024).*

This trait information was carefully gathered using a variety of databases, and was the bulk of my research period, due to this being a relatively novel dataset and interpretation. (*Alatan et. al, 2024) (Consortium of Lichen Herbaria, 2025*) (*Friday et. al, 2024*)

Accession No	Species	Rhizocarpic	Psoromic	Stictic	Norstictic	ThColour	Areaola Thickness (cm)	Thalli Thickness (mm)	KL	SpColour	K	C	KC	P	Latitude	Elevation (m)	UV
ON324015.1	Rhizocarpon alpicola	1	1	0	0	0	1.5	20	0	1	0	0	NA	NA	68.06988961	820.8333333	2.131333333
AF483179.1	Rhizocarpon amphibium	0	0	0	0	1	0.5	5	0	0	NA	NA	NA	NA	59.47815624	307.6	4.098432
KY680777.1	Rhizocarpon atroflavescens	1	1	0	0	0	1.2	3	1	1	0	0	NA	NA	69.41243226	651.9333333	2.104309333
PP941875.1	Rhizocarpon badioatrum	0	0	0	0	1	2	10	0	1	0	0	0	0	44.84868867	794.6182796	6.381416774
PQ219489.1	Rhizocarpon bolanderi	0	0	1	0	0	1.2	10	0	1	NA	NA	NA	NA	41.74454624	1553.453608	6.745657732
PP047689.1	Rhizocarpon chioneum	0	0	1	0	0	1	1	0	0	NA	NA	NA	NA	63.97679542	458.5882353	2.073374118
PP941878.1	Rhizocarpon cinereonigrum	0	0	1	1	1	1	10	1	1	1	0	0	0	62.2647253	470	2.0752
MH481926.1	Rhizocarpon copelandii	0	0	1	1	1	1	10	0	1	NA	NA	NA	NA	69.25583936	523.0315789	2.083685053
KY680783.1	Rhizocarpon disporum	0	0	1	1	1	0.8	10	0	1	1	0	0	1	41.05038505	1599.942797	6.767972543
OK465640.1	Rhizocarpon distinctum	0	0	1	0	1	0.4	5	1	0	1	0	0	1	50.79257652	488.7777778	4.156408889
ON324016.1	Rhizocarpon effiguratum	1	1	1	0	0	0.7	2	1	1	0	0	0	1	47.086111	2642.163265	7.268238367
OR021782.1	Rhizocarpon eupetraeoides	1	0	1	1	1	1.5	10	1	1	NA	NA	NA	NA	62.21159417	417.972973	2.066875676
MT108256.1	Rhizocarpon furax	1	1	0	0	1	1	10	1	1	0	NA	NA	1	62.9474085	30	2.0048
AY536838.1	Rhizocarpon geminatum	1	0	1	1	1	0.8	10	0	0	1	0	0	1	37.85471329	1052.596226	8.673661585
KC808469.1	Rhizocarpon geographicum	1	1	0	0	0	2.5	15	1	0	0	1	NA	NA	42.51294049	1405.624625	6.67469982
PQ219497.1	Rhizocarpon grande	0	0	1	1	1	0.8	10	1	1	1	1	1	1	42.693904	843.2217899	6.404746459
KJ766788.1	Rhizocarpon hochstetteri	0	0	1	0	1	0.5	10	0	0	NA	NA	NA	NA	61.52175255	523.4647059	2.083754353
ON341127.1	Rhizocarpon inarense	1	0	0	1	1	1	15	1	1	NA	NA	NA	NA	65.9692678	717.0634921	2.114730159
OR021794.1	Rhizocarpon intermediellum	1	1	0	0	0	0.7	2	1	0	NA	0	NA	NA	41.8776815	1870.268293	6.897728781
AF483178.1	Rhizocarpon lavatum	0	0	0	0	1	0.5	10	0	1	NA	NA	NA	NA	43.0445	731.0172414	6.350888276
PQ871464.1	Rhizocarpon lecanorinum	1	0	1	1	0	1.2	10	1	1	NA	NA	NA	NA	49.24501748	660.5913978	6.317083871
KU687449.1	Rhizocarpon leptolepis	0	0	0	0	1	0.5	10	0	1	NA	NA	NA	NA	58.98671208	1024.090909	4.327709091
OR046879.1	Rhizocarpon macrosporum	1	1	0	0	0	1.5	15	0	0	0	0	0	1	39.2132818	2307.683333	9.476917333
AF483186.1	Rhizocarpon norvegicum	1	1	0	0	0	1	1	1	1	0	NA	NA	1	48.06071225	493	6.23664
KJ766923.1	Rhizocarpon Oederi	0	0	0	0	1	0.5	5	0	0	NA	NA	NA	NA	62.49489264	758.7192982	2.121395088
MT108259.1	Rhizocarpon parvum	0	0	0	0	1	0.2	1	1	1	NA	NA	NA	NA	68.34299898	735.8571429	2.117737143
AF483177.1	Rhizocarpon petraeum	0	0	1	0	0	0.5	10	0	0	NA	NA	NA	NA	62.58132296	242.5090909	2.038801455
AF483184.1	Rhizocarpon polycarpum	0	0	1	1	1	0.5	5	1	0	0	0	0	0	47.148611	670.2101449	6.32170087
OR021790.1	Rhizocarpon postumum	0	0	1	0	0	0.2	10	0	0	NA	NA	NA	NA	50.12788174	263.0909091	4.084189091
MW938040.1	Rhizocarpon pusillum	1	1	0	0	0	0.5	1	0	0	0	0	0	1	47.086111	2678.736842	7.285793684
PP768143.1	Rhizocarpon reductum	0	0	1	0	1	0.5	10	0	0	1	0	NA	NA	46.05122877	598.0361842	6.287057368
ON332059.1	Rhizocarpon ridescens	1	1	0	0	0	1	10	1	0	0	0	NA	NA	56.28157815	870.05	4.278416
KU687458.1	Rhizocarpon rittokense	0	0	0	0	1	1	10	0	1	0	0	0	0	65.82446916	658.4090909	2.105345455
PQ879114.1	Rhizocarpon saanaense	0	0	0	0	0	2	10	1	0	0	NA	NA	1	43.0209915	465	6.2232
KU687454.1	Rhizocarpon santessonii	0	0	0	0	0	0.5	5	0	0	NA	NA	NA	NA	63.30908	752.4	2.120384
OR195104.1	Rhizocarpon sinense	0	0	0	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	62.2842	910	2.1456
AY853390.1	Rhizocarpon sphaerosporum	0	0	0	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	43.888033	1742.4	6.836352
KU687452.1	Rhizocarpon subgeminatum	0	0	0	0	1	1	10	0	0	NA	NA	NA	NA	37.230817	1152.072464	8.737326377
AF483181.1	Rhizocarpon suomiense	0	0	0	1	1	1	10	0	0	NA	NA	NA	NA	61.6201675	677.7272727	2.108436364
KC740400.1	Rhizocarpon superficiale	1	0	1	0	1	1.5	10	0	1	NA	NA	NA	NA	44.02796214	1813	6.87024
OR021795.1	Rhizocarpon tavaresii	0	0	0	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	34.500863	800	8.512
OR021797.1	Rhizocarpon tinei	0	0	0	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	37.68375	310	8.1984
OQ626902.1	Rhizocarpon umbilicatum	0	0	0	0	0	1.5	5	0	0	NA	NA	NA	NA	47.402778	585.8405797	6.281203478
KC740411.1	Rhizocarpon viridiatrum	0	0	0	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	47.85384412	1445.888889	6.694026667

Figure 4 reflects the complete table of Rhizocarpon which I used for trait analysis, and the corresponding traits mapped for each of the species and accession numbers a)or each of the acids (Rhizocarpic, Psoromic, Stictic & Norstictic) 0 reflects the absence of an acid, and 1 the presence. b) Thallus Colour I used the (Alatan et. al, 2024) methodology to code pigmentation into a binary, attempting to apply this same methodology to Spore Colour, c) latitude reflects the net magnitude of the latitude (allowing me to combine both southern hemispheric with northern hemispheric data, while undoubtedly having different climates, combining the average latitude lets me compare the relative amounts of solar flux and insolation. d) For both KI and the other spot tests, a 0 represents a negative result, and 1 a positive result.

Statistical Tests

Once trait data for all species had been gathered, I conducted statistical tests to determine how the traits correlated with environmental conditions and which traits had evolved down the phylogenetic tree.

- For environmental tests, I used the Mann-Whitney U test, which compares the distributions of two groups. This approach worked well for my dataset, as many traits are coded into binary categories (light or dark, absent or present, positive or negative). I chose to visualize these using box and whisker plots to test trends because the binary data format lends itself to this type of output.
- For phylogenetic analysis, I applied Pagel's lambda test to assess the degree of phylogenetic signal and Brownian motion, which may also be impacting trait evolution. A lambda value closer to 1 suggests a phylogenetic signal consistent with Brownian motion, while a lambda value closer to 0 indicates trait distribution independent of phylogeny (Münkemüller, 2012)
- To further develop an understanding of how Rhizocarpon functions morphologically, I have also used Mann-Whitney U tests to compare the rates of co-occurrence between specific physiological traits.

Astrobiological modelling

The ESA experiment EXPOSE (de la Torre, 2020) aimed to test whether lichens and other organisms could survive in space, in relation to panspermia-based scenarios. One hypothetical is that the Earth could have been fertilised by life/organics from Mars, but EXPOSE did not explicitly examine this from a Martian perspective. Therefore, I am using the lichen traits and environmental conditions we have outlined above and overlayed them onto the ROCKE-3D NASA climate model (Tsigaridis et al, 2025) to simulate Martian environmental conditions throughout its history. Determining whether lichen similar to that found on Earth could survive. I have primarily focused on the Noachian period, which overlaps with the Late Heavy Bombardment (Kawaguchi, 2019), a time when the amount of debris leaving Mars is thought to have peaked. However, maintaining this method for the Hesperian, Amazonian, and present-day periods allows for an examination of how Earth-like lichens would have been able to survive. Using my results from previous statistical tests to influence boundary conditions within the model, I ran simulations for the varying planetary conditions of Mars throughout its history.

Results

Phylogenetic results

As outlined in Methodology section, Bayesian Inference using the RevBayes software provided the backbone of my phylogenetic tree of Rhizocarpon species, and trait evolution was tested using the phytools package in R (Revell, 2024).

The key finding, as shown in Figures 5 & 6, is that only the KI medulla test possessed a strong phylogenetic signature ($p < 0.05$), suggesting that this trait of desiccation tolerance is at least partially conserved along the phylogenetic tree. The other traits do not exhibit any significant phylogenetic signal; their distribution appears to be random and is more likely shaped by environmental context rather than inherited ancestry. Figure 6 shows how this trait carries throughout the tree visually. We find a fairly distinct clade with the trait present. We also see some independent offshoots throughout the tree, which suggests that this may have emerged multiple times throughout its evolutionary history.

Trait	Rhizocarpic	Psoromic	Stictic	Norstictic	ThColour	Spore.Colour	KL..medulla	K.test	C.Test	KC.test	P
p_{random}	0.139	0.187	0.505	0.676	0.462	0.459	**0.011**	0.159	0.230	0.714	0.061
$p_{brownian}$	**0.022**	**0.031**	**0.004**	**0.001**	**0.002**	**0.007**	0.144	0.171	0.521	0.092	0.503

Figure 5, a table of the different traits collected vs the phylogenetic p-tests of Brownian motion, and random motion throughout the tree.

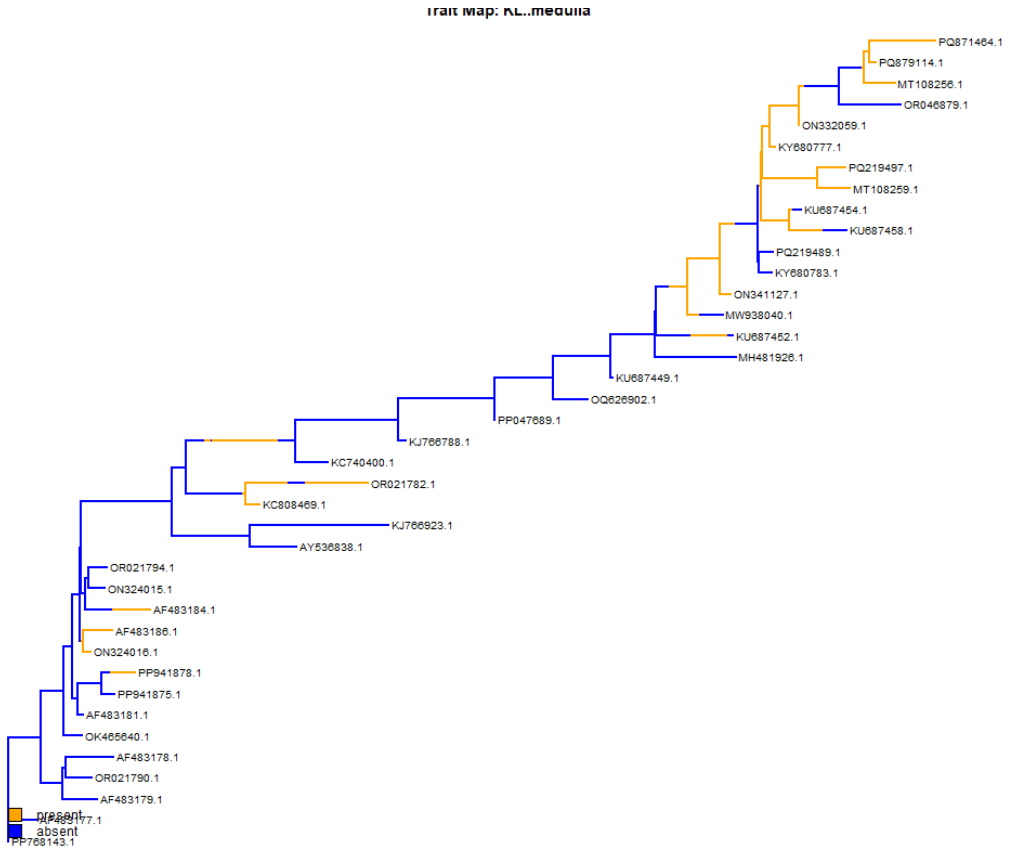

Figure 6: The phylogenetic tree of 45 Rhizocarpon species gathered as outlined in the methodology above, with the significant KI medulla test (p=0.011) mapped using the phytools package in R.

Environmental results

As discussed in the Methodology section, using box and whisker plots allowed me to compare the binary traits with environmental contexts and revealed several consistent patterns.

Elevation is the most significant indicator of acid presence, while UV appears to play a role as well. For Rhizocarpon & Psoromic acids, we see that the higher the elevation and the UV, the more likely it is to be present (significantly so for elevation). However, this is not the case for Norstictic and Stictic acids, which have negative relationships with elevation.

On the other hand, pigmentation traits suggest a clearer correlation with latitude, with darker thalli being closely related to high latitudes. This is consistent with adaptation to predicted light availability for higher latitudes. In fact, when running a Mann-Whitney U test for latitudes above 60 degrees, we reach significant results (P=0.0495) for an association between latitude and spore colour. In general, the UV index showed weaker associations; this is likely a reflection of local variability and microclimatological impacts that my methodology does not capture.

These results, as shown below in Figures 7 and 8, highlight how environmental contexts can exert pressure in shaping lichen traits, even in the absence of a phylogenetic signal.

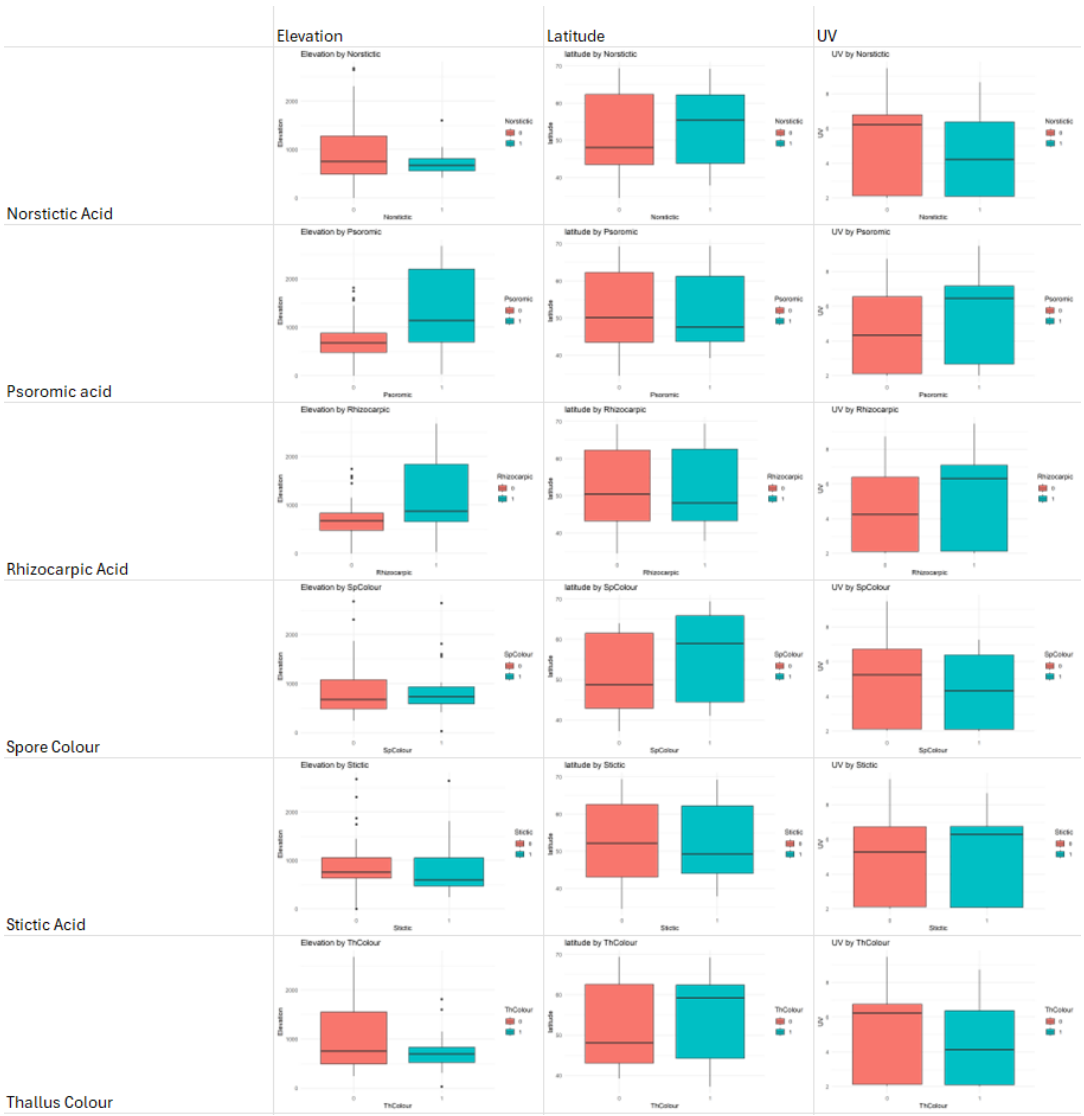

Figure 7 shows the various box and whisker plots of morphological and chemical traits against the environmental factors of UV, Elevation and Latitude. This process enables the visualisation of the relative distribution of many binary traits, allowing for the identification of potential correlations between them.

	Rhizocarpic	Psoromic	Stictic	Norstictic	Thallus Colour	Areaola thickness	Thalli Thickness	KL medulla	Spore Colour
Latitude	0.826	0.777	0.960	0.656	0.769	0.334	0.314	0.754	0.231
Minimum Elevation	**0.027**	**0.014**	0.160	0.481	0.639	0.425	0.537	0.654	0.511
UV index	0.191	0.156	0.365	0.307	0.481	0.490	0.803	0.788	0.609

Figure 8 shows a table of the p results from Mann-Whitney U statistical tests carried out between the different environmental factors and the traits. Significant results ($p<0.05$) are highlighted in bold.

Morphological results

	Rhizocarpic	Psoromic	Stictic	Norstictic	ThColour	KL	SpColour
Rhizocarpic	N/A	**5.81E-07**	6.78E-01	6.28E-01	**2.44E-02**	**1.16E-02**	2.79E-01
Psoromic	**5.81E-07**	N/A	**4.39E-02**	6.06E-02	**7.54E-04**	**3.46E-02**	9.41E-01
Stictic	6.78E-01	**4.39E-02**	N/A	**2.13E-03**	3.73E-01	1.00E+00	6.59E-01
Norstictic	6.28E-01	6.06E-02	**2.13E-03**	N/A	**1.50E-02**	1.68E-01	1.28E-01
ThColour	**2.44E-02**	**7.54E-04**	3.73E-01	**1.50E-02**	N/A	5.17E-01	1.50E-01
KL	**1.16E-02**	**3.46E-02**	1.00E+00	1.68E-01	5.17E-01	N/A	1.61E-01
SpColour	2.79E-01	9.41E-01	6.59E-01	1.28E-01	1.50E-01	1.61E-01	N/A

Figure 9, a table representing the p values of Mann Whitney U tests conducted between various morphological results against one another. The figures in bold are the statistically significant results with a p value <0.05.

Conducting Mann-Whitney U tests between the traits themselves has revealed several significant associations, suggesting a co-occurrence of certain traits.

- Rhizocarpic and Psoromic acids often co-occur, suggesting a shared ecological role, which is consistent with both their environmental and phylogenetic results.
- Furthermore, both relate significantly to the KI medulla and to the Thallus colour, with darker thalli being seen most commonly when Rhizocarpic acid and Psoromic acid are present.
- The relationship between the KI medulla suggests a potential link between acid production and the medulla structure.
- Stictic acid significantly co-occurs with Norstictic acid, and it also occurs in the opposite direction with Psoromic acid; again, this matches what we saw in their environmental roles earlier.
- Meanwhile, Norstictic acid has a negative relationship with thallus colour, with lichens that have higher rates of Norstictic acid often being lighter in colour

This suggests that many of the traits studied do not occur in isolation; instead, different ‘packages’ of chemical and morphological traits appear to be present, creating a complex defence and resilience strategy against varying environmental conditions and stresses.

Astrobiological Results

After inputting my criteria for both what Mars's climate is believed to have been during each time period (Wordsworth, 2016), and existing research on lichen stress tolerance and boundary information from my findings above, I have developed a map (using the ROCKE-3D NASA climate model outlined in the Methodology above) demonstrating the potential lichen habitability on Mars. This suggests that there are regions on Mars where Earth-like lichen could have survived, both during the Late Heavy Bombardment window and for longer into the Hesperian period. These regions appear to be geographically located close to the predicted river valleys in the Martian highlands, with further modelling on climate conditions suggesting that the limiting factor is most likely temperature, as this region of Mars is the only one able to reach sufficient temperatures year-round. However, desiccated survival adaptations suggest that lichens could remain in a dormant state across much of Mars, even though metabolic processes would be much more geographically limited. This not only allows localised pockets of habitability to occur within Mars, but also potentially allows for "survivable conditions" to be present to this very day, hypothetically allowing for the reactivation of lichens under wet conditions. Please note that this hypothesis is not saying that there is currently 'life on Mars' but that the conditions for lithopanspermia from Martian meteorites are technically viable using historical Martian conditions. Furthermore, this is purely speculative based on currently understood climate conditions on Mars, and the main focus was placed on atmospheric composition, water availability, energy, terrain, and minerals; therefore, it is a good model but does not incorporate all variables.

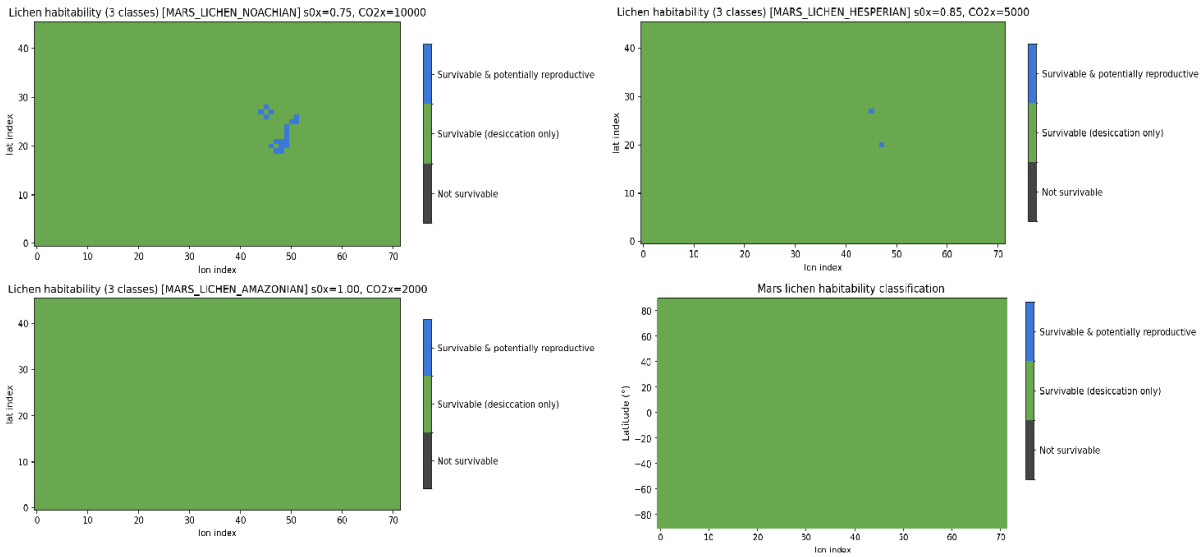

Figure 10 shows the various maps of Martian terrain, testing for habitability against the various conditions which Mars was estimated to have throughout 4 time periods in its history, the Noachian, Hesperian, Amazonian, and present day.

Discussion

To bring us back to our central questions, does this research suggest that the traits of Rhizocarpon lichens are predominantly determined by their shared genetic evolutionary history, or are they influenced by local environmental pressures?

In practice, both will have some influence on the underlying traits, but the proportion will differ, influencing our understanding of how stress tolerance has evolved.

Phylogenetic factors

As outlined above in the results section, my analysis has demonstrated a strong phylogenetic indication for the KI Medulla test trait in the lichen, which suggests that this trait of desiccation tolerance is at least partially conserved along the phylogenetic tree. In contrast, most of the other chosen lichen traits did not exhibit phylogenetic distribution, instead appearing more randomly scattered, suggesting environmentally driven adaptation.

Initial tests against the phylogenetic tree indicate that we can successfully reject random motion for the KI Medulla test, and we are approaching significance for the P spot test ($p = 0.061$). This suggests some level of phylogenetic influence on the presence of certain compounds reflected in the P test in methodology. Visually, Appendix A appears to support this however, a larger sample size for P would definitely be needed to investigate this trait further.

For the Rhizocarpic, Psoromic, Stictic, Norstictic acids and for thallus and spore colour, the Brownian motion model can be rejected. This suggests that these traits do not evolve along the tree, but are influenced more so by repeated independent origins or from environmental pressures.

Using the time tree (Kumar, 2022) already gathered from the Rhizocarpon genus, as shown in Figure 11, I estimate that the emergence of KI reactive medullary polysaccharides occurred roughly between 30 and 10 million years ago. This may well coincide with the global cooling temperatures of the late Eocene (Liu, 2019), which may favour the adaptation of water retention strategies.

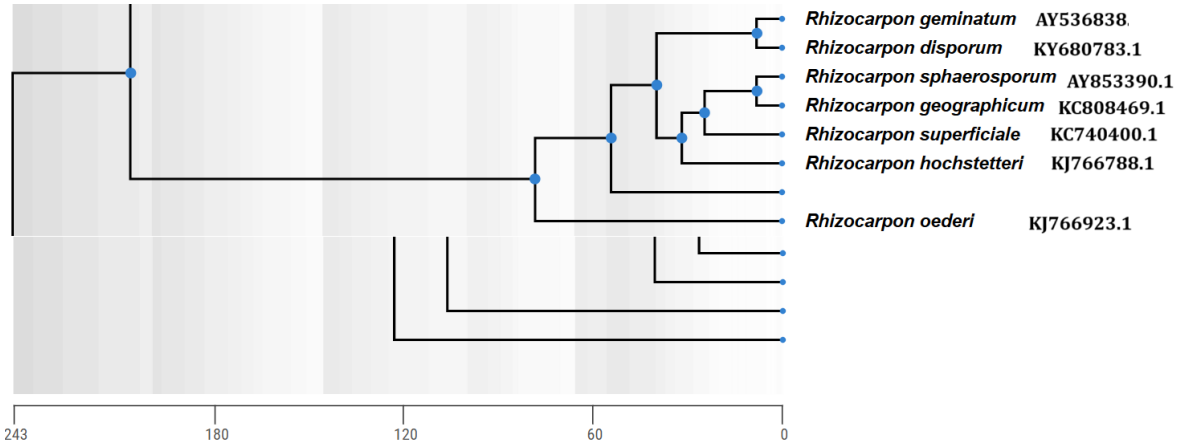

Figure 11, A time tree estimating various genetic deviations of the Rhizocarpon genus, with dates on the bottom representing millions of years BCE, the removed species on the diagram were not Rhizocarpon.

Overall, these findings show that some adaptations for stress tolerance are deeply embedded in Rhizocarpon's evolutionary history, meaning that not all of the survival traits are localised responses to stimuli, but rather part of a longer-term genetic mutation influencing the genus.

Environmental factors

As outlined above, with the exception of the KI Medulla trait, most other of the chosen lichen traits did not exhibit phylogenetic distribution, instead appearing more randomly scattered, suggesting environmentally-driven adaptation.

My analysis has found the following statistically significant correlations between environmental factors and lichen traits:

- **Elevation** has been found to be the most consistent predictor of trait distribution among the acids, with both Rhizocarpic and Psoromic acids significantly associated with higher elevations, higher UV levels, and lower atmospheric pressures and temperatures. In my opinion, this finding, compared to the lack of relationship between UV index and latitude, is most likely due to higher data quality; elevation data can integrate pressure, temperature, and radiation in a way that is less impacted by localised microclimates.
- **Latitude** was found to have closer association with pigmentation traits that develop, particularly at extreme latitudes (>60 degrees), where darker pigments are found to be significantly more common. Ecologically, this makes sense because the darker thalli can maximize heat absorption while also shielding against potentially damaging UV radiation.

Individual Trait Interpretations

Presence of Acids

Rhizocarpic and Psoromic acids are the strongest environmental correlators, with both increasing in frequency at high altitudes. This reinforces their roles in both stress-tolerance and UV-protecting metabolites. Norstictic acid, conversely, appears more common in the lowest of UV environments, suggesting ecological gradients between the two. On Earth, elevation affects the overall climate and temperature in several ways, including reducing the overall temperature, pressure, and relative abundance of certain pollutants/ biological agents, as well as UV radiation. Therefore, further research may be needed to investigate the direct causes of this relationship. From an astrobiological perspective, these acids are significant not only for protecting the lichen from radiation but also for modifying their reflectance spectra, which could make similar organisms detectable as biosignatures on other worlds.

Thallus & Spore Colour

For the thallus and spore colours, we observe positive correlations with latitude, with darker pigments more prevalent in polar regions. This supports the hypothesis that organisms aim to optimize the absorption rates of insolation in their environment; in fact, above latitudes of 60 degrees, a significant relationship emerges between latitude and spore colour. However, for lower latitudes, this relationship was less consistent, as diverse arrays of biomes complicate the picture. We can reject Brownian motion for both of these, and we do not have sufficient evidence to reject random motion. The correlation between thallus colour and acidity production suggests a co-occurrence of defences, both chemical and structural, to boost resistivity in high-stress environments. Pigmentation is also very important for astrobiology, as colour is a useful property for the remote detection of spectral signatures on exoplanets.

KI Medulla Test, Areola Thickness, Thallus Thickness

The KI Medulla was the only trait with robust phylogenetic signals. This marks it clearly as an inherited adaptation rather than a purely environmental one. Therefore, the water retention defence that it represents is related to the evolutionary history of certain clades. The areola and thallus thickness provide additional defences, by protecting against both desiccation and extreme temperatures. In our context, this is crucial for understanding survival in extremely arid conditions, such as the early Martian history, comets, or rocky exoplanets.

Spot Tests

Spot tests are helpful in revealing the presence of specific secondary metabolites through chemical reactions, with the P test being the most closely related to the phylogeny. This suggests that there may be some underlying phylogenetic influence, but other environmental and chemical factors are also likely to be at play. Many of the compounds detected by the tests relate to UV resistance or antimicrobial properties. Although the small sample size found limits the ability to achieve statistical significance, Appendix B shows that the other tests appear to indicate some environmental correlation, one that could be further investigated by future studies and tests conducted on more lichen samples. As spot tests highlight a chemical toolkit available to lichens to boost stress tolerance, they are incredibly useful basic tests for identifying relevant astrobiological traits.

Conclusion & Astrobiological Context

To conclude and try to discuss the original questions that we asked. We see a mixed picture for what has influenced the presence of certain stress-resistive traits in the lichen

Phylogenetic factors: We observe that for both the KI medulla and likely the P test, which are suggestive of desiccation resistance and UV-resisting metabolites, respectively, these traits are evolutionarily conserved, providing a stable framework for survival in extreme conditions. However, the evolutionary likelihood and rate of such mutations remains unclear.

Environmental factors: Lichen traits such as other UV-protective acids and pigmentation appear to be more environmentally flexible, allowing lichens to adjust physiologically and adapt to local conditions. This combination enables them to serve as strong analogues for survival in extreme extra-terrestrial conditions.

These findings would suggest that lichens that have inherited strong phylogenetic traits that support water retention adaptations, which suggest that lichens with similar adaptations could potentially maintain survive on extreme orbital or seasonal planets, such as Mars, or transiently on some comets. At the same time, lichens' other extremophile traits are more adaptable to environmental factors, with the UV-resistant acids produced in higher quantities at higher altitudes, and related pigments produced at higher latitudes. Lastly, my findings indicate an overlapping period of habitability between Mars and the Earth for the lichen currently in existence, indicating the potential viability of lithopanspermia between Mars and Earth.

Another finding of astrobiological significance is that the evolution of pigmentation on lichen is a relative function of solar insolation. This means that we can model what potential photosynthetic pigmentation would be and what reflected spectra would look like by comparing the stars' emitted radiation, planetary atmosphere, and orbital conditions, all of which can be detected with current exoplanetary methods.

Limitations & Further research

While this study has provided many new insights into explaining the evolutionary history of Rhizocarpon traits, there have also been some limitations in my overall methodology.

- A lack of global data for lichen meant that, although my dataset included over 48,000 records, many of these were clustered in the global north and in a few specific regions, leading to potential biases.
- To build a large and robust database, I needed to standardize many traits. Often, due to conflicting datasets, it was only possible to do this successfully by coding for presence or absence. While useful statistically, this approach overlooks more nuanced aspects of the data.
- The environmental proxies chosen were very broad scales and could not capture the individual microclimates that may exist (because all were constructed using coordinate data).
- Relying on numerous individual genetic data sources does have some risk associated with it, including the potential for misidentification of species, which could lead to the miscombination of trait data and reduce the reliability of our overall study.

However, I did my best to source these data from reliable institutions with robust methodologies.

These could all be improved by taking my own lichen samples, framed by astrobiological and environmental considerations from the beginning, so that I could gather a better array of usable proxy data.

Furthermore, there are several avenues of potential additional research around this topic that could be fruitfully explored:

- Testing Rhizocarpon lichens under laboratory stress tests (such as more explicit desiccation testing) to confirm that we can use the KI medulla as a proxy for water resilience, and similarly testing the presence of acids in the lichen under enhanced UV stress.
- Measuring the spectra of lichen with different acidic and pigment profiles to clarify how traits relate to optics. This would both improve our ecological interpretation and inform remote sensing potential, both for detecting life on other planets and to be able to detect lichen distribution on Earth remotely from space.
- Using more Rhizocarpon species in my dataset to improve statistical significance.
- Running more astrobiological simulations to test the 'punctuated habitability' hypothesis (hibernation and reactivation), to simulate both comet potential and Martian seasonal variation. This would be a fascinating area to explore further, to explore the potential for lichen to be a mechanism of lithopanspermia. This is supported by the sheer volume of comets and asteroids entering the inner solar system as they approach perihelion. The vast ice present would sublimate, releasing water, CO_2, and even volatiles such as iron and nickel into the coma. This remains untested and highly speculative

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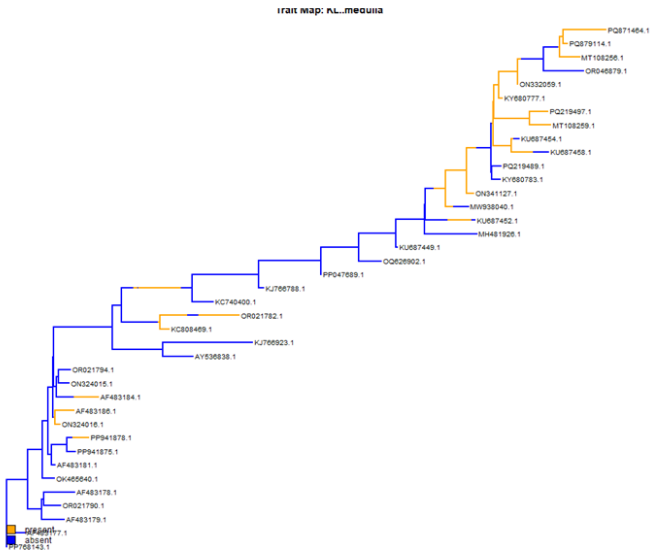
Appendix

Appendix A, phylogenetic trait maps across all species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ON332059.1
KY680777.1
PQ219497.1
MT108259.1
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KU687458.1
PQ219489.1
KY680783.1
ON341127.1
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KU687452.1
MH481926.1
KU687449.1
OQ626902.1
PP047689.1
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KC740400.1
OR021782.1
KC808469.1
KJ766923.1
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OR021794.1
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PP941875.1
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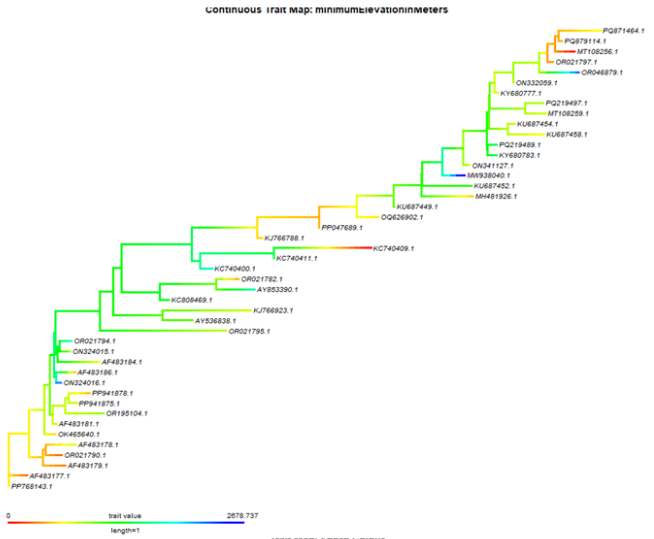
present
absent


Continuous Trait Map: MinimumElevationInMeters
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MT108256.1
OR021797.1
OR046879.1
ON332059.1
KY680777.1
PQ219497.1
MT108259.1
KU687454.1
KU687458.1
PQ219489.1
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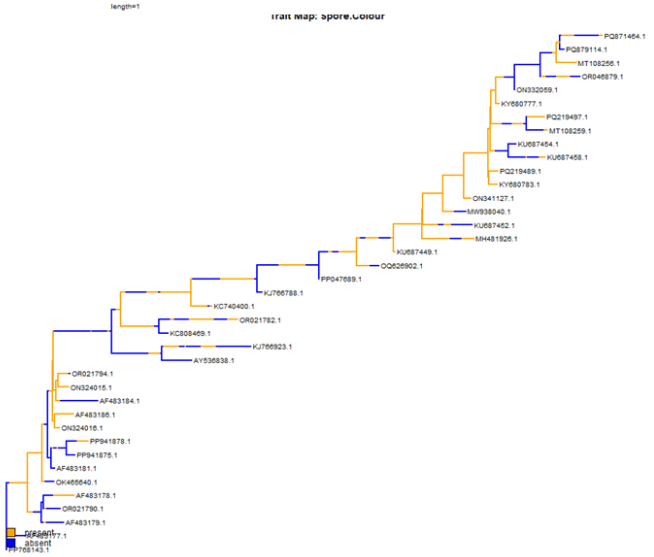
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MH481926.1
KU687449.1
OQ626902.1
PP047689.1
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KC740400.1
OR021782.1
KC808469.1
KJ766923.1
AY536838.1
OR021794.1
ON324015.1
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AF483186.1
ON324016.1
PP941878.1
PP941875.1
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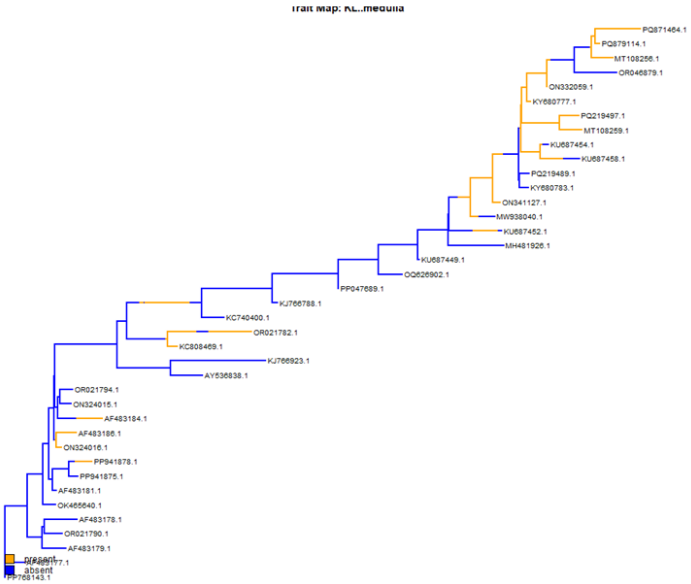
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KC808469.1
KJ766923.1
AY536838.1
OR021794.1
ON324015.1
AF483184.1
AF483186.1
ON324016.1
PP941878.1
PP941875.1
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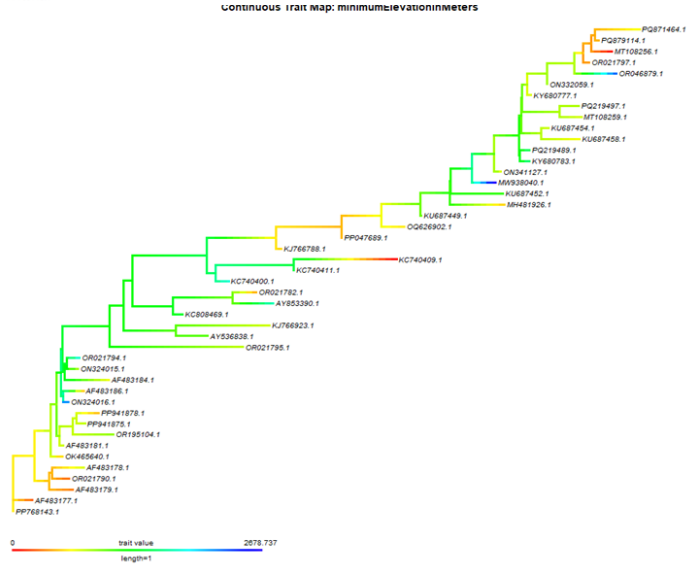
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KY680777.1
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MT108259.1
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PP047689.1
KJ766788.1
KC740409.1
KC740411.1
KC740400.1
OR021782.1
AY853390.1
KC808469.1
KJ766923.1
AY536838.1
OR021795.1
OR021794.1
ON324015.1
AF483184.1
AF483186.1
ON324016.1
PP941878.1
PP941875.1
OR195104.1
AF483181.1
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OR021790.1
AF483179.1
AF483177.1
PP768143.1
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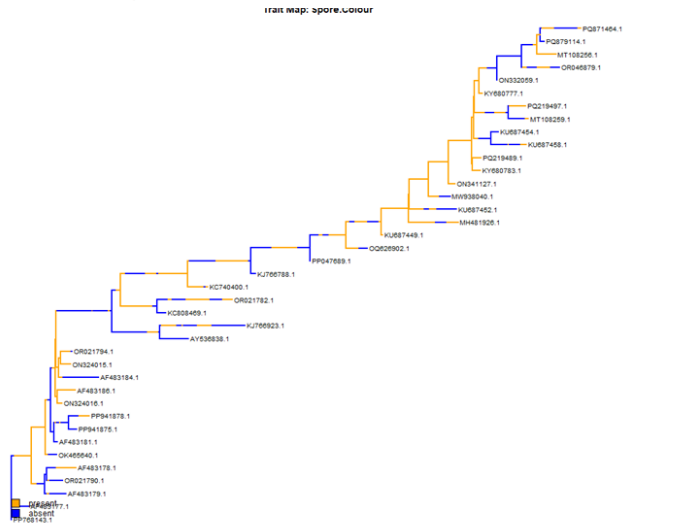
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OR046879.1
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MT108259.1
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AY536838.1
OR021794.1
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AF483186.1
ON324016.1
PP941878.1
PP941875.1
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AF483178.1
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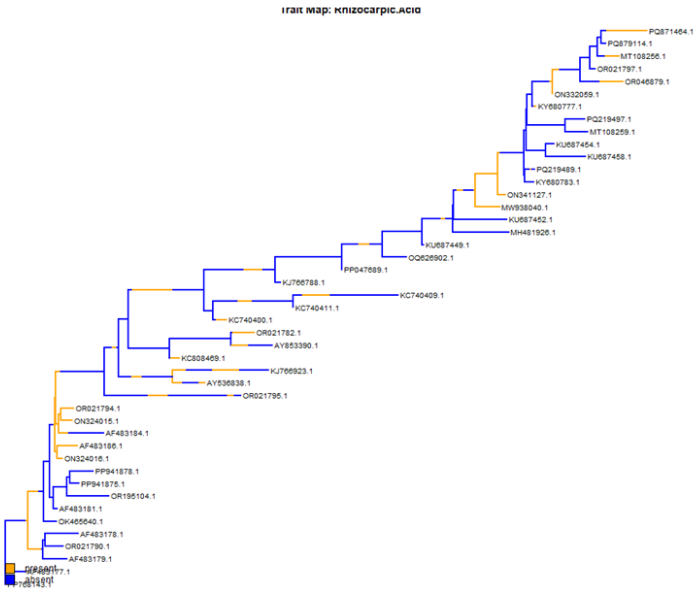
PP768143.1
present
absent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OR021797.1
OR046879.1
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MT108259.1
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KC808469.1
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AY536838.1
OR021795.1
OR021794.1
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AF483184.1
AF483186.1
ON324016.1
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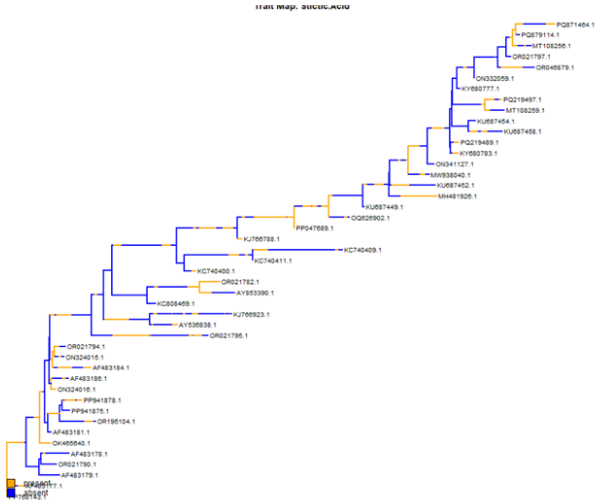
OR195104.1
AF483181.1
OK465640.1
AF483178.1
OR021790.1
AF483179.1


Trait Map: Sitellic.Acid
PQ871464.1
PQ879114.1
MT108256.1
OR021797.1
OR046879.1
ON332059.1
KY680777.1
PQ219497.1
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KC740409.1
KC740411.1
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OR021782.1
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KJ766923.1
AY536838.1
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ON324016.1
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OR195104.1
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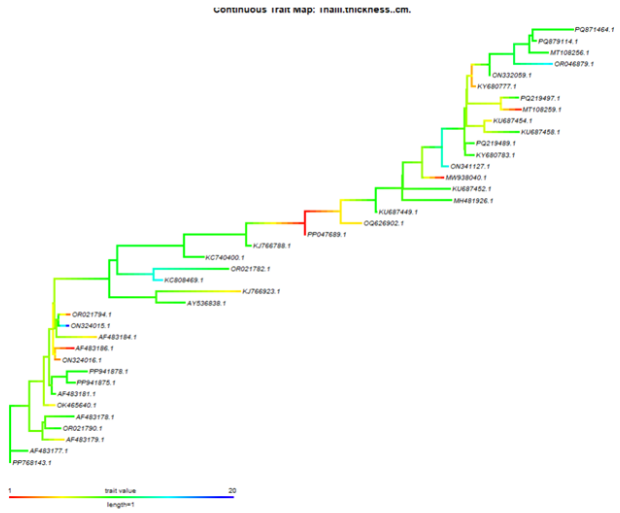
AF483179.1


Continuous Trait Map: Thalli.thickness..cm.
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ON332059.1
KY680777.1
PQ219497.1
MT108259.1
KU687454.1
KU687458.1
PQ219489.1
KY680783.1
ON341127.1
MW938040.1
KU687452.1
MH481926.1
KU687449.1
OQ626902.1
PP047689.1
KJ766788.1
KC740400.1
OR021782.1
KC808469.1
KJ766923.1
AY536838.1
OR021794.1
ON324015.1
AF483184.1
AF483186.1
ON324016.1
PP941878.1
PP941875.1
AF483181.1
OK465640.1
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OR021790.1
AF483179.1
AF483177.1
PP768143.1
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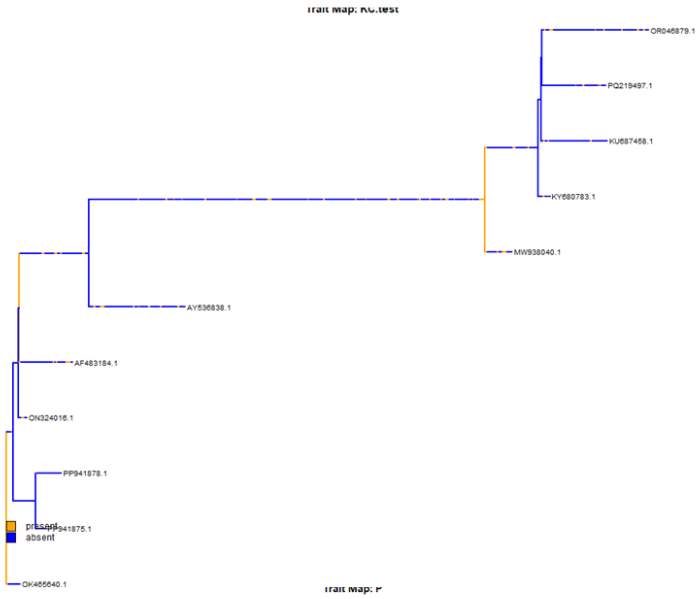
trait value
20
length=1


Trait Map: KC.test
OR046879.1
PQ219497.1
KU687458.1
KY680783.1
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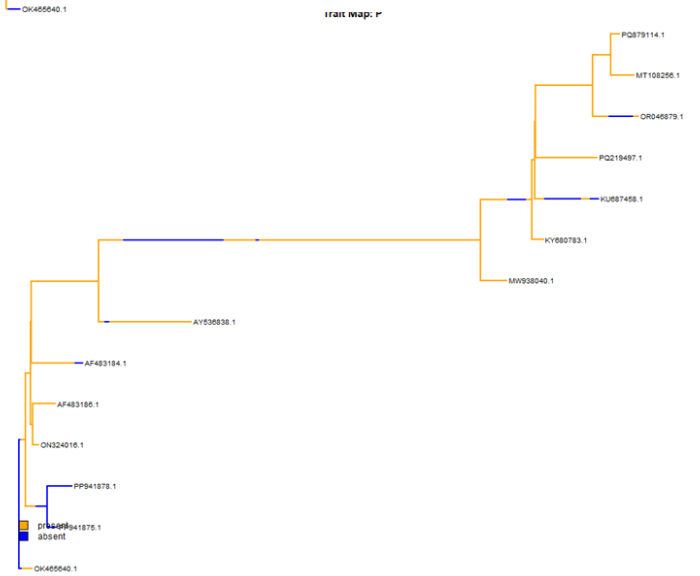
AF483184.1
ON324016.1
PP941878.1
PP941875.1
present
absent
OK465640.1


Trait Map: P
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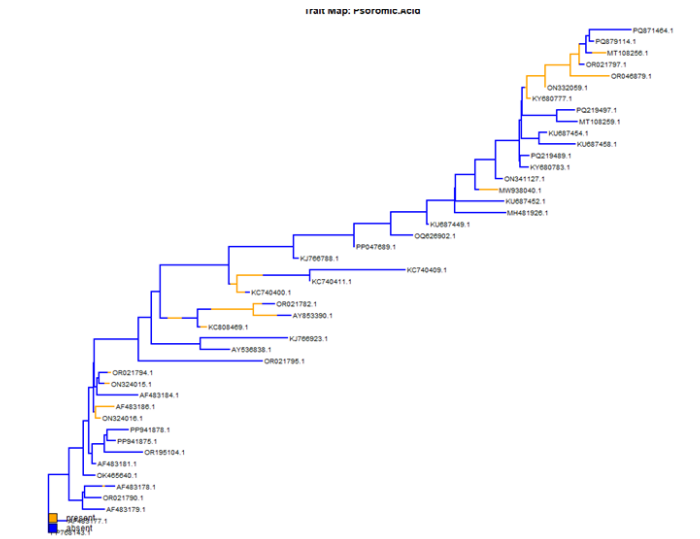
OR046879.1
PQ219497.1
KU687458.1
KY680783.1
MW938040.1
AY536838.1
AF483184.1
AF483186.1
ON324016.1
PP941878.1
PP941875.1
present
absent
OK465640.1


Trait Map: Psoromic.Acid
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OR046879.1
ON332059.1
KY680777.1
PQ219497.1
MT108269.1
KU687454.1
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PQ219489.1
KY680783.1
ON341127.1
MW938040.1
KU687452.1
MH481926.1
KU687449.1
OQ626902.1
PP047689.1
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KC740409.1
KC740411.1
KC740400.1
OR021782.1
AY853390.1
KC608469.1
KJ766923.1
AY536838.1
OR021795.1
OR021794.1
ON324015.1
AF483184.1
AF483186.1
ON324016.1
PP941878.1
PP941875.1
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AF483181.1
OK465640.1
AF483178.1
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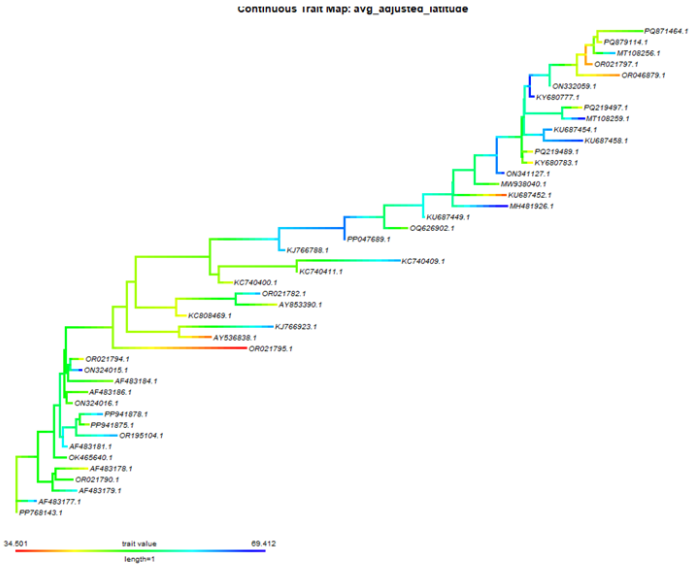
present
absent


Continuous Trait Map: avg_adjusted_latitude
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OR021797.1
OR046879.1
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KY680783.1
ON341127.1
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KC740409.1
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OR021794.1
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ON324016.1
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PP941875.1
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AF483181.1
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AF483177.1
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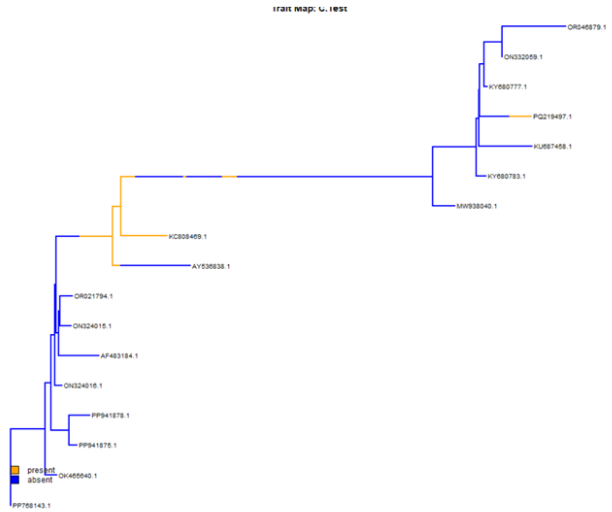
length=1


Trait Map: C.test
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ON332059.1
KY680777.1
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KY680783.1
MW938040.1
KC808469.1
AY536838.1
OR021794.1
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ON324016.1
PP941878.1
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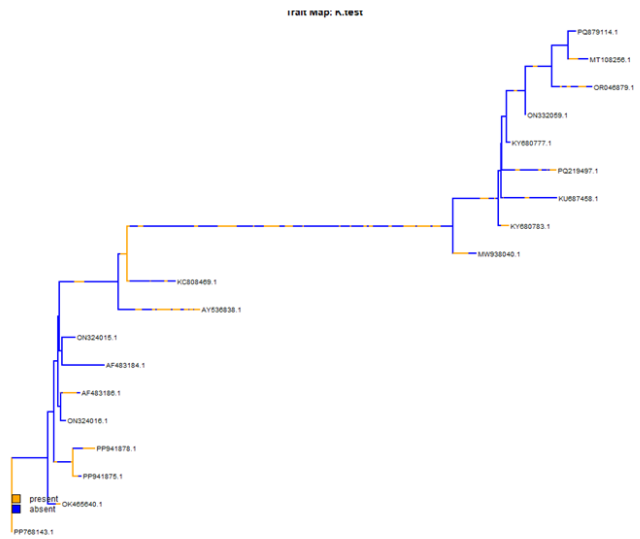
present
absent
OK465640.1
PP768143.1


Trait Map: R.test
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OR046879.1
ON332059.1
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PQ219497.1
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KY680783.1
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KC808469.1
AY536838.1
ON324015.1
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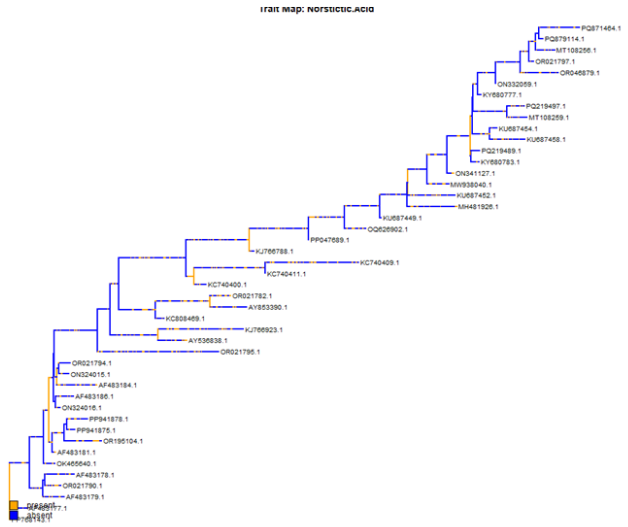
ON324016.1
PP941878.1
PP941875.1
present
absent
OK465640.1
PP768143.1


Trait Map: Norstictic.Acid
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MT108256.1
OR021797.1
OR046879.1
ON332059.1
KY680777.1
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MT108259.1
KU687454.1
KU687458.1
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ON341127.1
MW938040.1
KU687452.1
MH481926.1
KU687449.1
OQ626902.1
PP047689.1
KJ766788.1
KC740409.1
KC740411.1
KC740400.1
OR021782.1
AY853390.1
KC808469.1
KJ766923.1
AY536838.1
OR021795.1
OR021794.1
ON324015.1
AF483184.1
AF483186.1
ON324016.1
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OR195104.1
AF483181.1
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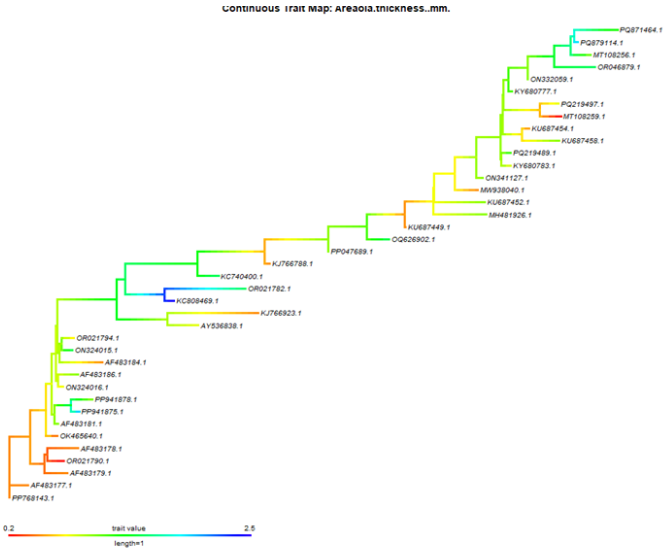
AF483178.1
OR021790.1
AF483179.1


Continuous Trait Map: Areaola.thickness..mm.
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OR046879.1
ON332059.1
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ON341127.1
MW938040.1
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KU687449.1
OQ626902.1
PP047689.1
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KC740400.1
OR021782.1
KC808469.1
KJ766923.1
AY536838.1
OR021794.1
ON324015.1
AF483184.1
AF483186.1
ON324016.1
PP941878.1
PP941875.1
AF483181.1
OK465640.1
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OR021790.1
AF483179.1
AF483177.1
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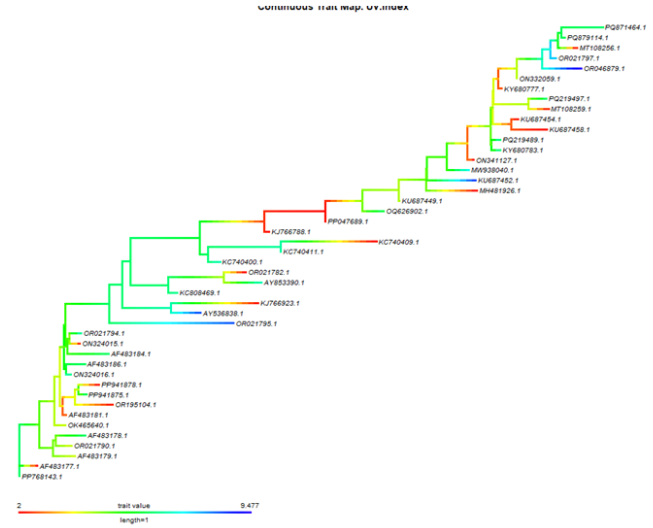
Continuous Trait Map: UV.Index
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MT108259.1
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KU687458.1
PQ219489.1
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MW938040.1
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MH481926.1
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KC740409.1
KC740411.1
KC740400.1
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KC808469.1
KJ766923.1
AY536838.1
OR021795.1
OR021794.1
ON324015.1
AF483184.1
AF483186.1
ON324016.1
PP941878.1
PP941875.1
OR195104.1
AF483181.1
OK465640.1
AF483178.1
OR021790.1
AF483179.1
AF483177.1
PP768143.1
2
trait value
9.477
length=1

Appendix B, a compilation of all the box and whisker plots comparing trait data vs environmental conditions