

## Communities Adjust their Temperature Optima by Shifting Producer-to-Consumer Ratio, Shown in Lichens as Models: I. Hypothesis

E. Imre Friedmann<sup>1</sup>, Henry J. Sun<sup>2</sup>

(1) NASA Ames Research Center, Mail Stop 245-3, Moffett Field, CA 94035-1000, USA

(2) Desert Research Institute, 755 East Flamingo Rd., Las Vegas, NV 89119-7363, USA

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### Abstract

An apparent paradox exists in the ecology of Antarctic lichens: their net photosynthetic temperature optimum (around 0°C) lies far below the temperature optima of their constituent algae and fungi (around 20°C). To address this paradox, we consider lichens as microbial communities and propose the “community adaptation” hypothesis, which posits that in each thermal regime there is an equilibrium between photosynthetic primary producers (photobionts), and heterotrophic consumers (mycobiont and parasymbiont fungi). This equilibrium, expressed as the producer/consumer ratio ( $R_{p/c}$ ), maximizes the fitness of the community. As respiration increases with temperature, more rapidly than does photosynthesis,  $R_{p/c}$  will shift accordingly in warm habitats, resulting in a high-growth temperature optimum for the community (the lichen). This lends lichens an adaptive flexibility that enables them to function optimally at any thermal regime within the tolerance limits of the constituent organisms. The variable equilibrium of producers and consumers may have a similar role in thermal adaptation of more complex communities and ecosystems.

### Introduction

What determines the optimal temperature of a microbial community? Are communities capable of adapting to their physical environment? These two, seemingly unrelated questions came into sharp focus while attempting to analyze the paradoxical behavior of Antarctic lichens. These lichens have net photosynthetic temperature opti-

ma around 0°C, yet the algal and fungal components of the same lichens, when isolated in pure culture and grown separately in the laboratory have temperature growth optima around 20°C. Two explanations are possible for this phenomenon. First, adaptation occurs at the species level by both alga and fungus modifying their temperature responses to the Antarctic environment; or second, the lichen as a unit is able to adapt at the community level by controlling the ratio of photobionts (i.e. producers) to mycobionts and parasymbiont fungi (i.e. consumers) in the thallus. We propose that the latter is the case and that lichens are able to adjust their photosynthetic optima to a wide range of temperature conditions by the mechanism of community adaptation. While the role of optimal growth temperatures of constituent organisms seems to be obvious, the mechanism by which a community temperature optimum established is not. We suggest that it is possible to get a glimpse into this process by considering lichens as simple microbial communities.

The composite structure of lichens is known since Simon Schwendener's revolutionary finding in 1868 [33], although the idea was not easily accepted: the last paper contesting the symbiotic nature of lichens was published as late as 1931 [21]. Even today, lichens are treated, out of practical necessity, as species (although the name belongs only to the mycobiont fungus). We now know that lichens often contain two or more fungi and upto two or three algae or cyanobacteria [11, 31, 39]. Farrar [4] pointed out that lichens are small ecosystems, and Kappen [15] emphasized that they are “mutualistic systems,” facts often forgotten when considering the physiological responses of a lichen “species.”

In the first paper of the present series we discuss the theory of community adaptation which offers an explanation of the seemingly contradictory facts in the ecology of Antarctic lichens. In the second paper [38], we present experimental evidence to validate the hypothesis and

Correspondence to: E. Imre Friedmann; E-mail: ifriedmann@mail.arc.nasa.gov

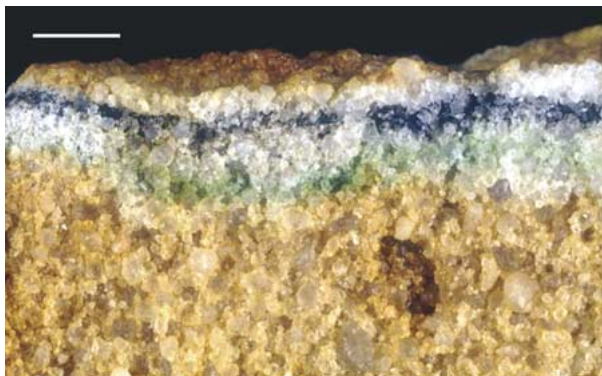
compare the range of community adaptations with those of adaptive mechanisms active at the species level.

### Antarctic Cryptoendolithic Lichens

Lichens are dominant in the cryptoendolithic microbial communities of the Ross Desert, the high mountainous area of the McMurdo Dry Valleys in Antarctica. This rocky desert is the coldest and among the harshest environments on Earth [5, 6, 24]. The rock surface is practically abiotic. The only life forms are microorganisms that live under the surface of porous rocks (cryptoendoliths, “living hidden in the rock”) by colonizing microscopic airspaces periodically warmed by solar radiation to above-ambient temperatures [23, 28]. The most commonly occurring community consists of fungi, algae, and bacteria and has been described as “lichen-dominated microbial community” [7]. The cryptoendolithic growth form is a morphological adaptation of thallose lichens (*Buellia grisea* Dodge et Baker, *Buellia pallida* Dodge et Baker, *Carbonea capsulata* (Dodge et Baker) Hale, *Lecanora fuscobrunnea* Dodge et Baker, *Lecidea cancriformis* Dodge et Baker, and *L. siplei* Dodge et Baker ([10], for recent nomenclatural changes cf. [30]). Under such extreme environmental conditions of the Ross Desert, the lichens “give up” their macroscopic thallus morphology to grow into the sandstone rock for protection against the hostile environment [5, 14, 26, 27]. Antarctic cryptoendolithic lichens, having no morphologically distinct thallus, do not look like plants but like a layered microbial community (Fig. 1).

Metabolic activity of the Antarctic cryptoendolithic lichens has been measured in the laboratory [8, 16], and the optimal temperature for net photosynthesis under saturated light conditions is  $+2^{\circ}\text{C}$  (Fig. 2). Although Antarctic lichens can photosynthesize at temperatures as low as  $-20^{\circ}\text{C}$  [14], nearly all photosynthetic activity in nature takes place between about  $-10^{\circ}\text{C}$ , the lowest temperature at which water can remain liquid in the rock, and  $5^{\circ}\text{C}$ , about the highest temperature reached by horizontal rock surfaces [8]. The range of commonly occurring summer temperatures of the natural habitat [6, 24] is indicated in Fig. 2 by horizontal hatching. Optima of net photosynthetic activity [8] are within this range, evidence that cryptoendolithic lichens are well adapted to their environment. This situation is not unique to the cryptoendolithic growth form: thallose lichens in continental Antarctica have a similarly cold temperature response, with photosynthetic temperature optima between  $0^{\circ}\text{C}$  and  $5^{\circ}\text{C}$ .

According to the generally accepted definition of Morita [25], microorganisms with optimal temperatures below  $15^{\circ}\text{C}$  and temperature maxima below  $20^{\circ}\text{C}$  are psychrophiles. While most marine microorganisms living

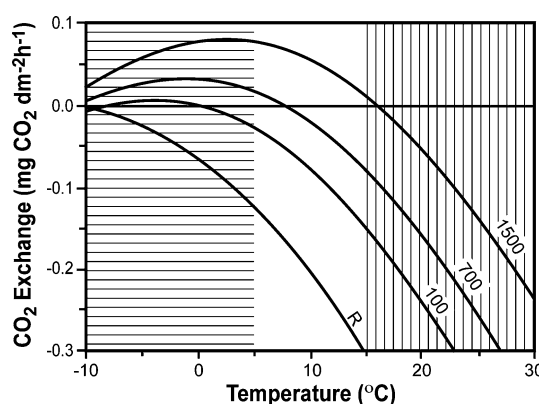


**Figure 1.** Cryptoendolithic lichen (“lichen dominated microbial community”) in the Antarctic desert (from [5]). Scale bar: 5mm.

in the thermally stable cold environments of polar seas are psychrophiles [2, 17], terrestrial microorganisms on the Antarctic continent are, with few exceptions, cold-tolerant mesophiles (psychrotrophs) with temperature optima around  $20^{\circ}\text{C}$  or above. This seems to be true for bacteria [1, 12, 22, 35, 36, 42] and for terrestrial or freshwater algae and cyanobacteria [3, 29, 32, 34, 40], as well as for fungi isolated from Antarctic terrestrial habitats [41, 44]. The reason for this is that most terrestrial habitats are thermally unstable with occasional warm periods [6] that apparently are not tolerated by obligate psychrophiles.

The thermal response of terrestrial Antarctic lichens [14] growing on thermally highly unstable rock and soil surfaces yet with optima mostly around  $0^{\circ}\text{C}$  and upper compensation points mostly below  $20^{\circ}\text{C}$  stands in conspicuous contrast to that of microorganisms. By Morita’s definition, these lichens would qualify as extreme psychrophiles.

What are the temperature requirements of the algal and fungal components of these “extreme psychro-



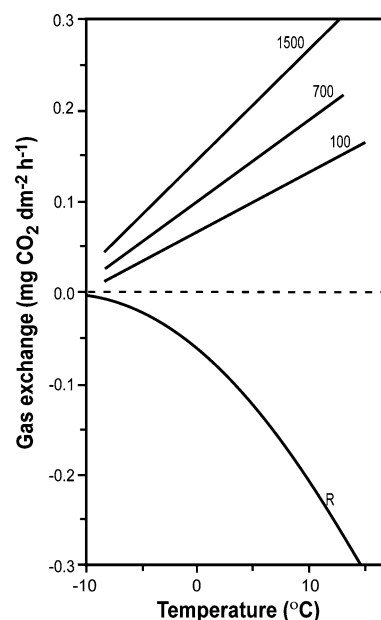
**Figure 2.** Temperature dependence of apparent photosynthetic gas exchange rates of Antarctic cryptoendolithic lichens at irradiance levels of 100, 700, and  $1500 \mu\text{mol photons m}^{-2} \text{s}^{-1}$  and in the dark ( $R$ ). The range of habitat temperatures is indicated by horizontal hatching, and the range of temperature optima of algae and fungi of the community is indicated by vertical hatching. Based on data from ([3, 8, 29, 40]; R. Ocampo-Friedmann, pers. com.).

philic" lichens? Two *Trebouxia* strains isolated from Ross Desert cryptoendolithic lichens have growth optima around 17°C and maxima around 20°C [29]. Similarly, five of six *Trebouxia* strains isolated from thallose Antarctic lichens [32] probably have growth optima above 15°C, and one is between 10°C and 15°C (Schofield and Ahmadjian report growth response only at 5, 10, and 15°C and need some interpretation based on the generally asymmetric shape of the temperature growth curve of microorganisms). As shown by Zucconi et al. [44], determination of exact temperature optima of mycelium-forming fungi is notoriously difficult. Temperature optima of extremely slow growing mycobionts could not be determined in the laboratory, but the faster growing parasymbiont fungi (dark pigmented "black yeasts") could. These latter organisms are nearly always present in Antarctic cryptoendolithic lichens and usually constitute a significant portion of fungal biomass. Parasymbiont fungi isolated from the cryptoendolithic community have growth optima between 17.5°C and 22.5°C and maxima between 22.5°C and 27.5°C (R. Ocampo-Friedmann, pers. com.). Thus, the constituent organisms of the "extreme psychrophilic" cryptoendolithic lichens are, like most Antarctic terrestrial microorganisms, psychrotrophic mesophiles. The temperature range of their growth optima is shown in Fig. 2 by the vertically hatched area.

In the present study we compare growth optima of algae and fungi with net photosynthetic optima of lichens. This requires justification. No experimental data on growth temperature optima of lichens exist in literature because, at least at this time, lichens cannot be grown under controlled laboratory conditions. However, the measured net photosynthesis in lichens, which is the net photosynthetic activity of the photobiont less the respiration of the mycobiont, is a fair indicator of carbon available for growth. The optimal temperature for net photosynthesis is most probably very close to the actual growth temperature optimum of the lichen thallus. In lichenological literature the temperature response of net photosynthesis is commonly used as a measure of fitness of lichens [19].

### Community Adaptation

The difference between the temperature optimum of lichen photosynthetic activity and optimal growth temperatures of isolated components appears puzzling at first. Temperatures in the natural habitat never even remotely approach the range of physiological optima of lichen-forming microorganisms. In fact, the temperature range optimal for growth of the organisms lies beyond the upper photosynthetic compensation point and would be lethal for the lichen in the long term (Fig. 2).



**Figure 3.** Gross photosynthesis (carboxylation rate) at irradiance levels of 100, 700, and 1500  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  and total community respiration (*R*) in the Antarctic cryptoendolithic lichen community based on data from [8].

Explanation of this phenomenon lies in the fact that a lichen is a community of different organisms with physiological responses of their own. The temperature curve of net photosynthesis of the alga (i.e. the producer of nutrients used by the fungus) does not necessarily parallel the temperature curve of fungal respiration, which is the measure of consumption by the fungi. Although it would be practically impossible to independently measure net production by the alga and consumption by the fungi within the lichen thallus, it is possible to compare the temperature dependence of total production with that of total consumption based on values of gross photosynthesis (carboxylation rate) of the alga and total dark respiration (of alga and fungi), both of which have been experimentally determined ([8]; Fig. 3). While the rate of increase of gross photosynthesis (total production) with temperature is linear (at least in the middle range where most production takes place), total respiration (total consumption) increases exponentially. This is consistent with a well-documented principle in physiology that the temperature quotient ( $Q_{10}$ ) for respiration is higher than that for photosynthesis. It follows that at lower temperatures, the same number of algae would be able to "provide" for more fungi than at higher temperatures. Evidently, for any given temperature there is an optimal ratio of producers and consumers (algae and fungi) where production matches consumption. This producer/consumer ratio ( $R_{p/c}$ ) represents the state of equilibrium at the temperature of the environment where net photosynthesis (as

discussed above, a measure of growth in lichens) reaches its maximum value in relation to temperature.

Thus, the temperature optimum of a community may lie outside the range of the optima of its members. This may appear counterintuitive as one would expect that the temperature optimum of a community would be close to the mean, or the median, of the optima of its members. As shown in the rather extreme case of Antarctic cryptoendolithic lichens, this is not so, and the variability in the values of  $R_{p/c}$  expresses the adaptation of the community as a whole to various temperature regimes. In other words, the lichen as a microbial community adapts to a wide range of temperatures by optimizing its  $R_{p/c}$ .

Many examples have been reported of the remarkable temperature adaptation of lichens to environmental conditions. Lechowicz [19] compiled an impressive data set from the literature and found a significant correlation between optimal temperature for net photosynthesis and mean July air temperature of the habitat or geographic latitude for 42 fruticose and foliose lichen species from below 30°N to above 70°N. In a second study based on measurements in 78 lichens, a similarly high correlation was found between maximum photosynthetic rates and mean summer temperatures [20].

It seems reasonable to assume that  $R_{p/c}$  is determined by the cell division rates of lichen components. Rates for each component are, in turn, regulated by the activity of the *other* component—for the mycobiont, by the supply of nutrients produced by the photobiont and for the photobiont, by the supply of provisions from the mycobiont (ranging from growth substances to physical space and protection by thallus architecture). These processes take place mostly, if not entirely, during formation of the thallus, and thus lichens grow “into” their thermal environment with the correct  $R_{p/c}$ . The six lichen species known to form cryptoendolithic communities in the Ross Desert commonly occur as epilithic thallose lichens in substantially warmer thermal environments in the maritime regions of Antarctica and on the Antarctic islands, but as epilithic thallose lichens [30].

Limits to the range of community adaptation are set by the absolute physiological temperature limits of lichen constituents. Further, community adaptation limits are different toward the lower and higher temperature limits. As temperature optima of organisms are generally closer to the maximum than to the minimum temperature limits, there is more flexibility in community adaptation toward low, than toward high temperatures. In other words, the potential difference between temperature optima of communities and their constituent species—and hence the evolutionary significance of thermal community adaptation—increases in colder environments.

Does community adaptation enable lichens to make short-term adaptations (e.g. to seasonal change in temperatures)? The answer to this question may depend on

the growth rate of lichen components in relation to the rate of change in the thermal environment. Seasonal changes in photosynthetic temperature optima of some lichens have been reported [13]; but in many, or perhaps most, growth rate of lichens of both photobionts and mycobionts seem to be too slow to permit shifting of the  $R_{p/c}$  in response to seasonal changes in temperature. Thus community adaptation, while conferring on lichens an extraordinary range of adaptive flexibility, also imposes limitations, especially for the extremely slow growing polar and alpine lichens. The estimated age of Antarctic cryptoendolithic lichen communities is around  $10^4$  years [26, 37], and climate changes may occur at a shorter timescale. Once formed, these lichens are unable to shift their  $R_{p/c}$ ; and changes in climate may lead to death and extinction, as witnessed by the widespread occurrence of dead and fossilized populations of cryptoendolithic lichens in the Antarctic Ross Desert [9, 43].

Community adaptation may be the mechanism behind the high degree of thermal adaptability in lichens and thus may account for their well-known ability to tolerate temperature extremes, a faculty that has been recognized as one of the important reasons for their ecological success [13]. Another and perhaps equally important factor is the capability of lichens to fine-tune their temperature optima within the range of the photosynthetically active temperature regime [13, 18–20]. Thus the composite nature of lichens may lend themselves a level of adaptive flexibility beyond that of a single species with more rigid, genetically determined characters.

It stands to reason that the principle of community adaptation, the variable equilibrium of producers and consumers as an instrument of adaptation, also may be applicable for more complex communities and even ecosystems. Analysis of interrelationships in such systems may prove to be more difficult than the present one proposed for lichens.

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