

Article

Greenhouse Gas Fluxes from the Epiphytic Lichens: Incubation Experiments

Anastasia I. Matvienko ^{1,*}, Svetlana Y. Evgrafova ^{1,2}, Natalia M. Kovaleva ¹, Elizaveta V. Sideleva ², Maria V. Sitnikova ², Oleg V. Menyailo ³ and Oxana V. Masyagina ¹

¹ Sukachev Institute of Forest SB RAS, Federal Research Center “Krasnoyarsk Science Center SB RAS”, 660036 Krasnoyarsk, Russia; esj@yandex.ru (S.Y.E.); nk-75@mail.ru (N.M.K.); oxanamas@ksc.krasn.ru (O.V.M.)

² School of Fundamental Biology and Biotechnology, Siberian Federal University, 660041 Krasnoyarsk, Russia; ms.cd.eva@mail.ru (E.V.S.); marias0205@list.ru (M.V.S.)

³ Joint FAO/IAEA Centre of Nuclear Techniques in Food and Agriculture, P.O. Box 100, 1400 Vienna, Austria; menyailo@hotmail.com

* Correspondence: matvienko.ai@ksc.krasn.ru; Tel.: +7-908-012-0792

Abstract: Because they are widespread and evolutionarily old, epiphytic lichens (ELs) play an important role in global forest ecosystems. ELs are abundant in Siberian forest ecosystems, which are highly vulnerable to climate change; thus, ELs can be important contributors to the carbon (C) cycle. This study aims to address the unknown role of tree-inhabiting ELs in the C cycle of forest ecosystems in Central Siberia, where the EL biomass ranges from 492 to 3200 kg per ha. The main finding of this study is that ELs in a hydrated state can generate CH₄ for an extended period (at least two weeks), as determined by an incubation method. At the same EL moisture level, EL CO₂ fluxes are species-specific. The pattern of the release or uptake of GHGs by ELs may also alter due to climate change, e.g., changes in precipitation regimes (such as more frequent extreme rainfalls and droughts). Therefore, the EL contribution to the C cycle in forest ecosystems should be assessed, e.g., via the modeling of C cycling. Furthermore, specific factors, such as the EL exposure on the phorophyte stem, the EL biodiversity, and the day/night GHG fluxes, should be considered for a more concise assessment of ELs' contribution to the C cycle of forest ecosystems and their response to ongoing and projected climate change.

Keywords: biocrusts; birch; boreal; carbon; carbon dioxide; climate change; cryptogamic communities; Cyanobacteria; methane; Siberia



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1. Introduction

Epiphytic lichens (ELs), or lichenized fungi, play a crucial role in the development of forest communities and are widely distributed in forest ecosystems at middle and high latitudes. They dominate 8% of the world's land surface, mainly in high-latitude and high-mountain regions [1,2]. Lichens are the first organisms to colonize substrates because they are a symbiotrophic (autoheterotrophic) component of biogeocenoses. Owing to that, they can simultaneously perform photosynthesis, synthesize and accumulate organic materials, and decompose mineral compounds. Numerous studies are currently focusing on the characteristics of the EL distribution in various phytocoenoses [3–9]. ELs settle on the stems and branches of phorophytes and, in biocenosis, form distinct groups (synusia) that are distinguished by the EL-specific species composition and morphological type. ELs have a high ecological value, and their specific biological characteristics play an important role in environmental improvement, biological diversity, water conservation, and soil formation via nitrogen fixation by the ELs [10]. ELs have valuable ecosystem functions, acting as a food source for mammals and invertebrates and as a habitat for many species [11,12]. They are also highly effective at absorbing pollutants and contributing to nutrient and

water cycling by intercepting and holding moisture and nutrients [13]. Furthermore, they can act as environmental indicators for air and water quality and forest continuity [14], as indicators of climate change [15], and have importance to human everyday life and culture (food, clothing, and pharmaceuticals) [16,17]. In addition to its crucial role in ecosystem services, the EL may have a definite but not yet determined impact on the carbon (C) cycle. Considering their distribution and biomass in the Arctic (from 492 to ~3200 kg per ha), ELs may contribute significantly to the C cycle of high-latitude permafrost ecosystems [13,18]. World cryptogamic communities (algae, mosses, and lichens), which also include ELs, take up around 0.05 Pg of N and 3.9 Pg of C per year, which corresponds to 7% of the net ecosystem exchange (NEE) by terrestrial vegetation [19]. In addition to the greenhouse gas (GHG) uptake, cryptogamic communities can emit them, e.g., carbon dioxide (CO₂), nitrous oxide (N₂O), and methane (CH₄) [19–25]. Emissions of N₂O and CH₄ by cryptogamous organisms are found to increase at temperatures above 20 °C; therefore, climate change (warming) will provoke higher emissions of GHGs by lichens, Cyanobacteria, and mosses. That is important for temperate latitudes, where cryptogamous organisms are one of the critical sources of N₂O [24].

Climate change in high latitudes, including Siberian forest ecosystems, is of great concern, and ELs are essential components of forests. In a recent review, we showed the existing positive trends for soil CO₂ and CH₄ fluxes in the permafrost ecosystems of Central Siberia [26]. The ability to be highly tolerant to abiotic stresses, such as desiccation, temperature extremes, and UV-light intensities, will be favorable for lichens in the future, since climate models indicate uneven precipitation, temperature increase, and gradually changing levels of UV-B radiation exposure (resulting from depleting ozone) [27–29].

ELs associated with boreal tree species are both phototrophs (CO₂-assimilating organisms, like green algae and/or Cyanobacteria) and heterotrophs (e.g., bacteria, fungi, Archaea, and fungus yeast) [30,31]. Photobionts participate in C fixation and its transformation into sugar alcohols; later, photosynthetic products are used by the mycobiont [32]. Meanwhile, there have been relatively few studies on how ELs contribute to the C cycle. Numerous studies have demonstrated that components of ELs (fungi, Cyanobacteria, Archaea, bacteria, etc.) actively contribute to the C cycle via GHG emission/uptake. Thus, ELs can fix atmospheric C via photosynthesis and store it in their biomass. Additionally, the components of lichens (such as Cyanobacteria, fungi, Archaea, and bacteria) are known for their ability to emit CH₄, which is a more potent greenhouse gas than CO₂ in the context of climate change [33,34].

We hypothesize that ELs may have an impact on the C cycle of an ecosystem via their associated Cyanobacteria, fungi, green algae, bacteria, and Archaea, which are known for their capability to emit GHGs (CO₂ and CH₄). Therefore, to understand the potential impact of ELs on C fluxes in forest ecosystems, we carried out a series of laboratory incubation experiments. To fulfill this aim, we settle the following tasks: (1) to evaluate the projecting cover and the occurrence of ELs in a birch forest (Siberia); (2) to assess the diel dynamics of EL CO₂-photoassimilation and respiration; (3) to estimate the capacity to evolve CH₄ by the most widespread EL species inhabiting the birch trees in the study sites.

2. Materials and Methods

2.1. The Study Site

The study sites are located in the Gremyachaya Griva Eco-Park in Krasnoyarsk (Siberia, Russia) (Figure 1). Krasnoyarsk lies in the zone of the continental climate. The region is characterized by a long winter with little snow, with persistent severe frosts, a short warm summer, a short dry spring with late returns of cold weather (frosts), and a short autumn with early frosts and frequent returns of heat. The mean air temperature in January is −18.3 °C, and in July it is +19.4 °C. Annual air temperature amplitude (based on monthly averaged values) is 38 °C. The sum of active air temperatures ($\Sigma T > 10$ °C) during the nonfrost period (ca. 120 days) accounts for 1600–1875 °C [35–37]. The annual sum of precipitation is 316 mm, and the maximum amount occurs in the summer. Precipitation in

summer is predominantly rainfall. From the end of May to the beginning of June, droughts are frequent. The snow period lasts from November to mid-April. Southwestern winds prevail in the autumn–winter period, and western winds dominate in the summer–autumn period [35,38].



Figure 1. Map of the sampling plot (A, B, and C) locations near Krasnoyarsk (55.9 N, 92.7 E; <https://maps.google.com/>, accessed on 11 October 2023). The numbers indicate the number of the trees (from the first to the twelfth tree).

2.2. Study Objects

The study focused on three EL species: *Parmelia sulcata* Taylor, *Hypogymnia physodes* (L.) Nyl., and *Evernia mesomorpha* Nyl., growing in a birch forest mixed with pine in the Gremyachaya Griva Eco-Park in Krasnoyarsk (Figure S1). These species prevail at a height of 1–1.5 m of the birch stem (up to 14% of the total projecting cover of the ELs), and are the most common species (up to 90%) in the study area (Table 1).

Table 1. Description of the model trees.

| Plot | Tree | Tree Height, m | DBH, cm | Canopy Cover, % | Age, Years |
|------|------|----------------|---------|-----------------|------------|
| A | A1 | 25.3 | 67.7 | 54 | 111 |
| | A2 | 28.0 | 47.8 | 58 | 106 |
| | A3 | 25.5 | 42.9 | 75 | 94 |
| | A4 | 28.5 | 42.5 | 68 | 100 |
| B | B5 | 25.9 | 37.3 | 64 | 118 |
| | B6 | 26.0 | 47.7 | 70 | 117 |
| | B7 | 32.9 | 47.1 | 86 | 115 |
| | B8 | 27.9 | 58.6 | 72 | 101 |
| C | C9 | 29.3 | 35.4 | 65 | 95 |
| | C10 | 33.8 | 38.2 | 70 | 102 |
| | C11 | 32.0 | 36.8 | 49 | 98 |
| | C12 | 24.2 | 41.9 | 60 | 115 |

Species Characteristics

Hypogymnia physodes is a foliose lichen in the family Parmeliaceae. The upper surface of its thallus is smooth, gray, or gray–green with brownish lobe ends, while the lower, dark part, becoming pale brown towards the margin, is strongly wrinkled. The diameter of the thallus reaches 10 cm. The photobiont is the green algae *Trebouxia* [39]. *Hypogymnia* does not have rhizines and attaches to the substrate by wrinkles. Hollow lobes are 2–3 mm wide. The bottom is often coated with white, powdery soredia and the outer edge curves upward. The lower surface of the lobes is black and folded, with a lighter color near the lobe edges.

The pycnidia are black and abundant and, if present, create a pepper-like effect across the upper surface. Because of its abundance and its moderate sensitivity to sulfur dioxide and heavy metals, *Hypogymnia physodes* is often used in bioindicator and biomonitoring studies that enable the assessment of air pollution and other environmental conditions. This species is common in boreal and temperate ecosystems in the Northern Hemisphere.

Parmelia sulcata is a foliose lichen in the taxon Parmeliaceae and one of the most prevalent lichens due to its high pollution tolerance and global distribution. It harbors a unicellular *Trebouxia* green algal symbiont [39]. It is defined by a thallus that is typically circular and has a black lower surface. An upper cortex can vary in color from glaucous white to gray. The thallus is broadly lobed. Each lobe width is varied from 2 to 5 mm, and the lobes are overlapping. In temperate to cold regions in both the Northern and Southern Hemispheres, *Parmelia sulcata* is a widespread species.

Evernia mesomorpha is a fruticose lichen in the family Parmeliaceae. The thallus is bushy and upright, in the form of hanging or protruding bushes (2.5–10.0 cm in length), and attached to the substrate using a pseudogomph. The lobes are 1.0–2.5 mm in width, dichotomously branched, more or less flattened, sometimes slightly rounded, radial in structure, and equally colored on both sides. The photobiont is the green alga *Trebouxia* [40]. Soredia are point-shaped, whitish or grayish, often numerous, and covering the entire surface of the lobes. Isidia are short, occasionally up to 2 mm in length, rod-shaped, simple or branched, and grayish. They can also infrequently arise in an abundance. Apothecia develop quite rarely, up to 3 mm, located at the edges of the thallus lobes, saucer-shaped, with a dark-brown disk surrounded by a thin edge, which is the same color as the thallus. It can be found in the temperate and tropical zones of Asia, Europe, and North America, including Mexico and the Arctic zone; in Russia, it is distributed throughout the entire territory.

2.3. EL Sampling and Probe Preparation

The EL collection sites were chosen following the European standard method outlined by Rocha et al. [41]. Every plot (A, B, and C) represented a centroid with a diameter of 50 m in a homogenous vegetation patch dominated by *Betula pubescens* Ehrh. in the canopy. At the three replicate plots (A, B, and C) along the 3 km transect, twelve model trees of *Betula pubescens* with four trees in each of the three plots were selected to assess the EL biodiversity and GHG fluxes from the prevailing EL species to understand the potential contribution of the ELs in the area with the certain EL biodiversity (Figure 1, Table 1). Model trees were selected to be erect, not oppressed, without signs of pathology, and the most uniform in morphology. For each tree, we determined the tree age (from cores taken with an age drill at a height of 130 cm), tree height (using TruePulse 200b Laser Rangefinder, Laser Technology, Inc., Centennial, CO, USA), and stem diameter (DBH; at a height of 130 cm using the Hultafors Talmeter 3 m) (Table 1). In June–August 2023, EL thalli were carefully sampled at a height above 1 m (within the band from 1 to 1.5 m) from the northern, western, or southern sections of the stem of the model trees where they were found in sufficient abundance. The samples were packed in zip packages, transferred to the laboratory, and immediately weighed to obtain the weight of the fresh ELs. After that, they were air-dried and stored until the incubation experiments. On the same trees where the ELs were sampled, the epiphytic cover was described (see Section 2.4, Table 2).

2.4. Methods for the Assessment of EL Diversity

Before taking the EL samples for the subsequent incubation experiments, the epiphytic cover was assessed using the same twelve model trees of *Betula pubescens* at a stem height of 1–1.5 m (Figure 1). The projecting cover of the ELs was assessed using frames of 10 × 62 cm² consisting of five 10 × 10 cm² square slots. For that, the frames were fixed on the stem of the model tree at every exposure (northern, western, eastern, and southern) at a height of 1 m (a total of 20 slots per model tree). The species composition and projecting cover were assessed at each slot (a total of 240 slot descriptions). The occurrence of the studied EL

species (%) on the stem height of 1–1.5 m of the birch trees was determined by the ratio of the number of trees on which the lichen was found to the total number of trees.

Table 2. Characteristics of the ELs at a height of 1–1.5 m, where the thalli were collected.

| Plot | Projecting Cover (Mean ± SE), % | | | Occurrence, % | | | Total EL Projecting Cover (as an Average Value of 20 Slots ± SE) at a Height of 1–1.5 m, % |
|------|---------------------------------|-----------|-----------|---------------|----|----|--|
| | P | H | Ev | P | H | Ev | |
| A1 | 13.5 ± 3.8 | 2.5 ± 1.2 | 0.5 ± 0.3 | 50 | 25 | 10 | 33.5 ± 4.1 |
| A2 | 5.2 ± 1.6 | 3.0 ± 1.6 | 3.0 ± 1.1 | 45 | 20 | 40 | 28.9 ± 3.8 |
| A3 | 6.5 ± 1.3 | 0.5 ± 0.5 | 1.0 ± 0.5 | 65 | 5 | 20 | 48.3 ± 3.5 |
| A4 | 11.8 ± 3.0 | 1.5 ± 0.6 | 8.5 ± 2.3 | 60 | 25 | 75 | 40.1 ± 5.5 |
| B5 | 6.2 ± 1.8 | 1.5 ± 0.6 | 1.3 ± 1.0 | 50 | 25 | 10 | 38.5 ± 5.7 |
| B6 | 5.5 ± 1.5 | 0 ± 0 | 1.4 ± 0.5 | 45 | 0 | 30 | 36.2 ± 5.5 |
| B7 | 2.9 ± 1.2 | 4.0 ± 1.7 | 1.0 ± 0.4 | 30 | 25 | 25 | 24.1 ± 5.3 |
| B8 | 8.2 ± 1.9 | 1.5 ± 1.1 | 0.3 ± 0.3 | 65 | 10 | 5 | 29.4 ± 4.7 |
| C9 | 5.8 ± 1.8 | 2.7 ± 0.8 | 3.9 ± 1.0 | 45 | 45 | 55 | 22.4 ± 5.2 |
| C10 | 1.9 ± 0.4 | 3.0 ± 0.6 | 1.4 ± 0.4 | 65 | 80 | 60 | 27.8 ± 6.1 |
| C11 | 6.5 ± 1.7 | 1.4 ± 0.5 | 2.7 ± 0.6 | 90 | 55 | 85 | 15.8 ± 2.3 |
| C12 | 7.3 ± 1.9 | 3.3 ± 0.6 | 2.7 ± 0.9 | 60 | 70 | 45 | 26.6 ± 3.2 |

Note: P—*Parmelia sulcata*; H—*Hypogymnia physodes*; Ev—*Evernia mesomorpha*.

To assess the potential impact of the EL species diversity on the EL C fluxes, the Shannon index, species richness, and poleotolerance index were calculated. The Shannon index is based on the relative abundance of species and determines the EL species richness. This index refers to heterogeneity indices, since it takes into account both the evenness and species richness. This index adds more detail to biodiversity assessments than species richness indices that rely on a single parameter. The Shannon index usually varies from 1.5 to 3.5, rarely exceeding 4.5 [42]. The higher the Shannon index value, the higher the species diversity in a particular community. A Shannon index = 0 indicates a community consisting of only one species. The poleotolerance index reflected the air pollution level in the area [43–46] and was assessed according to Truss [43].

2.5. EL Incubations

In the laboratory, air-dried EL samples were separated from the substrate (bark, mosses, etc.) after they were soaked in artificial rainwater [47] for 10–20 min. Then, the hydrated EL samples were air-dried again until the incubation experiments.

Two incubation experiments were carried out to measure the EL gas exchange. This approach enables the determination of key parameters, such as the net CO₂ photoassimilation rates and the CO₂ losses associated with dark respiration and photorespiration, which are fundamental processes that characterize lichen growth and their ability to adapt to changing environmental conditions, such as humidity, temperature, and anthropogenic pollution [48–50]. A one-day aerobic preincubation was conducted at room temperature, during which the incubation jars were covered with lids to maintain a controlled environment. The first experiment was conducted to assess the diel CO₂ fluxes by two EL species—foliose *Parmelia* and fruticose *Evernia*—of northern and western exposure on the birch stem. The second experiment encountered the CO₂ and CH₄ fluxes by the ELs during the two-week incubation.

In the first incubation experiment, the air-dried 3 g samples of the ELs (*Evernia* and *Parmelia* collected from the northern and western exposures of the birch trees at plot A) were placed in 500 mL incubation jars (a total of 14 jars). The jars with the EL thalli, after they were hydrated to ca. 800% of water content by spraying the ELs with artificial rainwater, were placed in a Peltier-cooled incubator with a programmable temperature-control system (Memmert, Schwabach, Germany) and a built-in illumination system, comprised of four LED lamps (Camelion LED13-A60/830/E27, Moscow, Russia), providing a cumulative photosynthetically active radiation (PAR) range of 160–220 μmol m⁻² s⁻¹ (Figure S2B).

Throughout the three 24 h long incubation series, the controlled photoperiod with the different light and temperature conditions was applied: 18 h of illumination at a temperature of +18 °C during the period from 6 a.m. to 24 p.m., and then 6 h without illumination at a temperature of +14 °C during the night (0–6 a.m.). The achieved level of EL water content was controlled by a weight method. To monitor the CO₂ flux rates, measurements were taken every two hours using an infrared CO₂ analyzer (Li-Cor 8100A) and a 16-port Li-Cor 8150 multiplexer (Li-Cor Incorporated, Lincoln, NE, USA) specifically designed for this purpose. The results of three diel series of CO₂ flux measurements were averaged for every 2 h. The CO₂ flux rates were expressed as µg C-CO₂ g⁻¹ of the dry weight of EL h⁻¹. These measurements enabled the evaluation of the CO₂ flux rates throughout the entire incubation period, capturing any variations under the specified experimental conditions.

The second experiment was designed as a 14-day aerobic incubation with the ELs, with five variants, each being 3-replicated. The variants were as follows: EvCN is *Evernia* of a northern exposure from the C plot; HypCN is *Hypogimnia* of a northern exposure from the C plot; ParAN is *Parmelia* of a northern exposure from the A plot; ParBW is *Parmelia* of a western exposure from the B plot; ParCN is *Parmelia* of a northern exposure from the C plot. For the incubation, 1 g samples of air-dried ELs were placed in 125 mL incubation jars, SIMAX 2070/M/100 mL (Kavalierglass, Sázava, Czech Republic). The ELs were then hydrated using artificial rainwater to achieve a humidity level of 400%. The EL samples were incubated under controlled conditions, with a photoperiod of 18 h of light and an air temperature at +18 °C, followed by 6 h without illumination at an air temperature of +14 °C in a Peltier-cooled incubator with a programmable temperature-control system (Memmert, Germany) and a built-in illumination system (Figure S2C). The illumination facility consisted of two types of lamps to provide an optimal EL PAR level of 160–220 µmol m⁻² s⁻¹: three lamps of Camelion LED13-A60/830/E27 with visual spectrum and one lamp of REPTILE UVB200 PT2341 with a UVB spectrum of a high intensity. The achieved level of the EL water content was controlled by a weight method. Gas sampling was performed on days 0, 1, 3, 7, 10, and 14 of the incubation period. During these sampling dates, the ELs were incubated in closed vessels for 2 h under illumination at 18 °C; then, the gasses were collected using 60 mL Luer Lock syringes via the septa in the jar lead for the subsequent analysis of the CO₂ and CH₄ concentrations using the Cavity Ringdown Spectrometer Picarro G2201-*i* analyzer. The GHG fluxes were calculated using Formula (1):

$$F = \frac{(C_2 - C_1) \times V \times M}{24.5 \times m \times t} \quad (1)$$

where F is the CH₄ or CO₂ flux (µg CH₄ or CO₂ g⁻¹ of the dry weight of EL h⁻¹); C_1 is the concentration of gas (CH₄ or CO₂) before the 2 h incubation (ppm); C_2 is the concentration of gas (CH₄ or CO₂) after the 2 h incubation (ppm); V is incubation jar volume (liter); M is molar mass of the CH₄ or CO₂ (16.043 or 44.01 g mol⁻¹); 24.5 is one mol of air (liter per mol); m is the EL sample dry weight in the incubation jar (g); t is the incubation period of 2 h (h). The flux rates of the gasses were then expressed per C (µg C-CH₄ or C-CO₂ g⁻¹ of the dry weight of the EL h⁻¹), where the negative fluxes reflected the CO₂ photoassimilation, because we analyzed the difference in the CO₂ concentration before and after the 2 h incubation of the ELs in the closed vessel; therefore, this was the result of both processes (photosynthesis and photorespiration) [51,52]. The negative fluxes of the CH₄ represent the consumption. The positive values reflect the respiration or the CH₄ production.

2.6. Data Examination

The differences in the Shannon index, species richness, and poleotolerance index of the ELs in different plots (A, B, and C) were assessed using Kruskal–Wallis comparisons of the means analysis, and pairwise comparisons using the Wilcoxon rank sum test. We applied a bootstrapping technique and produced 50 bootstrap replicates for every variant per sampling date using the ‘boot’ R package to reduce the variability in the GHG fluxes [53]. Differences between variants were assessed by pairwise comparisons using the Wilcoxon

rank sum exact test. The EL GHG (CO₂ and CH₄) fluxes were assessed regarding the effects of the EL species, the photoperiod conditions, the EL exposure on the tree stem, and the incubation time using ANOVA in the STATISTICA 10 package (StatSoft, Tulsa, OK, USA). All statistical analyses and visualizations were performed in R software (ver. 4.2.3, 15 March 2023—“Shortstop Beagle”) using the following R-packages: “ggplot2”, “ggpubr”, etc.

3. Results

3.1. Assessment of the EL Biodiversity

The studies showed that, at a stem height of 1–1.5 m, the EL species richness varied from four to eight species. The northern and western sides of the *Betula pubescens* stems had the largest projective cover of ELs. The smallest lichen projective cover was found on the stem’s eastern side. On the northern side of the stem, *Parmelia sulcata* was dominated with a projecting cover ca. 11%. On the western sides of the stems, *Parmelia sulcata* also prevailed, with a projecting cover ca. 10%. *Evernia mesomorpha* and *Parmelia sulcata* were found in all model trees (Table 2). Among the studied ELs, *Parmelia sulcata* was characterized by the maximum occurrence (30–90%). The occurrence of *Evernia mesomorpha* and *Hypogymnia physodes* varied widely from 5% to 85%. Variations in the quantitative indicators (occurrence, projective cover) showed that the ELs were highly sensitive to a variety of environmental factors that contributed to the uniqueness of the habitats on the birch stems.

According to the evaluation using the Shannon index and species richness index, the biodiversity of the ELs on the birch trees was low and rather consistent across the three examined plots (Figure 2). Interesting to note that the Shannon index was significantly lower, and the species richness at plot B was visually lower, possibly due to the high heterogeneity of the studied parameters at this plot (Figure 2A,B). The poleotolerance index (C) showed a similar pollution load among the study plots (Figure 2C).

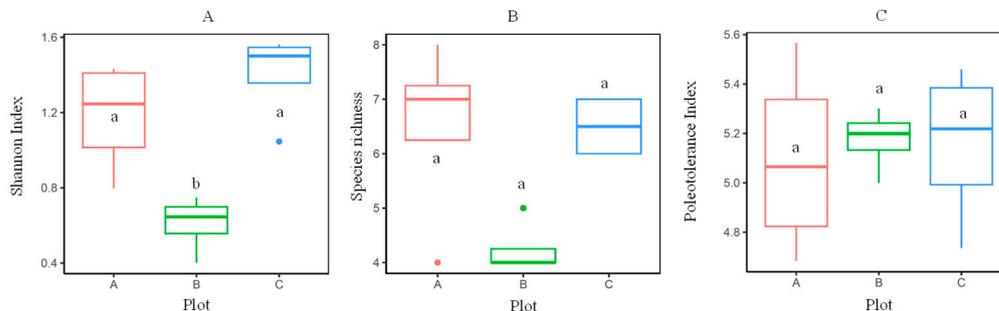


Figure 2. Shannon index (A), species richness (B), and poleotolerance index (C) of the ELs in study plots. Letters represent a significant difference among the plots (A, B, and C) at $p < 0.05$ according to the Kruskal–Wallis comparisons of the means analysis and the pairwise comparisons using the Wilcoxon rank sum test.

3.2. Diel Dynamics of CO₂ Fluxes by the ELs

In the first incubation experiment, the factorial ANOVA showed that all studied parameters (the EL species, photoperiod conditions, and the exposure of the EL on a tree stem) had an effect on the CO₂ fluxes as individual factors and in the combination of factors (Table 3). For example, the EL exposure on a tree stem significantly affected the rate of the CO₂ flux (Figure 3). Both *Evernia* and *Parmelia* of the northern exposure showed significantly lower respiration ($p < 0.001$) than those of the western exposure both in illuminated and nonilluminated conditions; the CO₂-photoassimilation was higher in the north-exposed ELs. Moreover, the west-exposed *Evernia* did not display photoassimilation at all. North- and west-exposed *Parmelia* generally repeated the patterns on the CO₂ fluxes during the 24 h period, with one exception: both west- and north-exposed *Parmelia* demonstrated similar rates of CO₂-photoassimilation in the daytime. In both species of the northern

exposure, an intensive process of photoassimilation was confirmed (up to 121.6 $\mu\text{g C-CO}_2 \text{ g}^{-1}$ of the dry weight of ELs per hour) during the illuminated period.

Table 3. The results of a factorial ANOVA analysis of the effects of EL species, photoperiod conditions, and the exposure of the EL on a tree stem on the CO_2 fluxes by the ELs in the first experiment.

| Factors and Their Interactions | CO_2 Fluxes | |
|--|----------------------|---------|
| | F | p |
| EL species | 10.1 | <0.001 |
| Photoperiod | 20.3 | <0.0001 |
| Exposure on the tree stem | 100.9 | <0.0001 |
| EL species \times Photoperiod | 13.4 | <0.0001 |
| EL species \times Exposure on the tree stem | 20.0 | <0.0001 |
| Photoperiod \times Exposure on the tree stem | 10.5 | <0.001 |
| EL species \times Photoperiod \times Exposure on the tree stem | 3.1 | 0.76 |

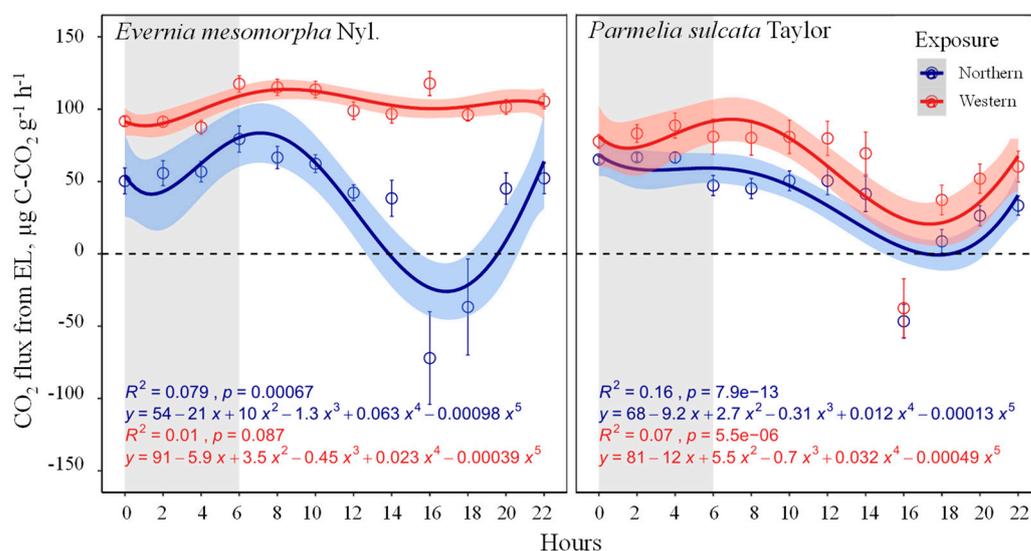


Figure 3. Diel CO_2 fluxes (the average of three biological replicates during three diel series of measurements \pm SE) by the ELs of two species (*Evernia mesomorpha* Nyl. and *Parmelia sulcata* Taylor) of various exposures on the tree stems incubated at a controlled photoperiod and thermal regime. The negative values reflect CO_2 -photoassimilation; the positive values reflect dark respiration. The gray-shaded rectangular area shows the night period without illumination. Shaded areas represent the 95% confidence interval associated with each polynomial curve.

3.3. Assessment of CH_4 and CO_2 Fluxes by the ELs

In the second incubation experiment, the rANOVA showed that the studied factors (the EL species and the time of incubation) had different effects on the CO_2 and CH_4 fluxes by the ELs (Table 4). For example, the CH_4 fluxes by the ELs were not species-specific (they did not differ significantly among EL species), though the CO_2 fluxes (both dark respiration and CO_2 -photoassimilation) significantly differed among the EL species.

During the second experiment, the CH_4 release was recorded in all studied EL species: *Evernia* (0.06–4.3 $\text{ng C-CH}_4 \text{ g}^{-1}$ of the dry weight of ELs per hour), *Hypogymnia* (0.2–3.1 $\text{ng C-CH}_4 \text{ g}^{-1}$ of the dry weight of ELs per hour), and *Parmelia* (0.06–6.1 $\text{ng C-CH}_4 \text{ g}^{-1}$ of the dry weight of ELs per hour) (Figure 4).

Table 4. The results of a repeated-measures analysis of variance (rANOVA) of the effect of EL species and the time of incubation on the mean rate of CO₂ and CH₄ fluxes by the ELs in the second incubation experiment.

| Factors and Their Interactions | CH ₄ | | CO ₂ | |
|--------------------------------|-----------------|-------|-----------------|---------|
| | F | p | F | p |
| EL species | 0.698 | 0.610 | 13.77 | <0.0001 |
| Time | 5.158 | <0.01 | 21.06 | <0.0001 |
| EL species × Time | 0.903 | 0.585 | 2.25 | <0.0001 |

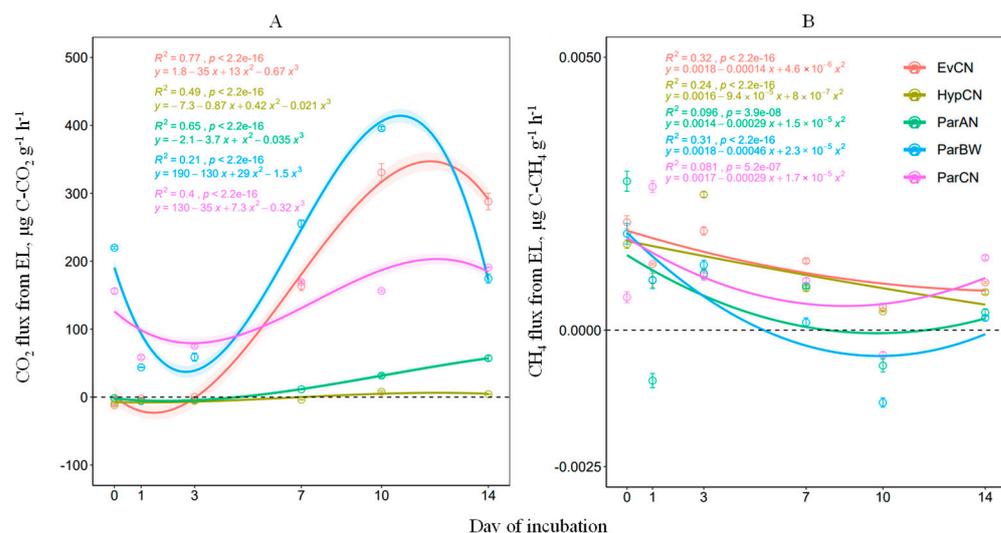


Figure 4. Daytime CO₂ (A) and CH₄ (B) fluxes (mean ± SE) by the EL species (*Evernia mesomorpha* Nyl., *Parmelia sulcata* Taylor, and *Hypogymnia physodes* (L.) Nyl.) of various exposures on the tree stems incubated at a controlled photoperiod and thermal regime. The negative values reflect photoassimilation and the positive values reflect respiration. EvCN is *Evernia* of a northern exposure from the C plot; HypCN is *Hypogymnia* of a northern exposure from the C plot; ParAN is *Parmelia* of a northern exposure from the A plot; ParBW is *Parmelia* of a western exposure from the B plot; ParCN is *Parmelia* of a northern exposure from the C plot. Shaded areas represent the 95% confidence interval associated with each polynomial curve.

During the entire course of the experiment (14 days), the CO₂-photoassimilation of the EL in a permanently hydrated condition within the 2 h illuminated period of incubation was found only in *Hypogymnia* (Figure 4). Its mean values varied from -1 to -11 $\mu\text{g C-CO}_2 \text{ g}^{-1}$ dry weight of ELs per hour. *Evernia* (collected from the north-exposed stem side in plot C) and *Parmelia* (collected from the north-exposed stem side in plot A) in the hydrated condition demonstrated CO₂-photoassimilation during the first three days of the experiment; after that, the ELs switched to the CO₂ emission up to the end of the incubation. The other two *Parmelia* variants (collected from the north-exposed stem side in plot C and the west-exposed stem side in plot B) sustained high levels of CO₂ emissions during the entire incubation experiment (2 weeks) (Figure 4).

4. Discussion

To this day, little is known about the ELs of Krasnoyarsk and their surroundings. The studies were mainly carried out in the Stolby State Nature Reserve in the southern part of Krasnoyarsk. In his work, Dubrovsky [54] documented 68 EL taxa belonging to 66 species. An inventory of ELs by Perova [55] included 82 species. Otnyukova [56–58] provided data on 69 species for the Stolby State Nature Reserve. As revealed by our study, the Shannon index, which, in our case, ranged from 0.4 to 1.56, with an average value for all study sites of 1.1, indicated that the ELs at the study location had a relatively low

diversity. According to published sources, this variation range lies at the lower limit of the Shannon index range (from 1.5 to 3.5) [42]. Despite that, in this biogeocenosis, the studied ELs (*Parmelia sulcata* Taylor, *Hypogymnia physodes* (L.) Nyl., and *Evernia mesomorpha* Nyl.) appeared to contribute to the C cycle due to their high occurrence and projective cover (Table 2). Numerous variables, including the physical and chemical characteristics of the substrate (i.e., phorophyte's bark or cortex), such as the pH, structure, division, rigidity, and frequency of peeling, can affect the distribution of ELs, as well as the CO₂ exchange (CO₂-photoassimilation and respiration) of the ELs [59–61]. For example, crustose lichens with an endophleoid thallus typically grow on young deciduous trees with smooth bark. The bark's qualities alter as it ages: it becomes rougher, with fissures and roughness. That causes a change in the composition of the ELs living on it. Foliose and fruticose ELs develop on this bark. In addition, the age parameters of phorophytes influence the species composition, abundance, and quantitative properties of the ELs [6,60,62–67]. It was found that ELs are dependent on the DBH of the tree [5,66,68–72]. Furthermore, the composition of the EL synusia on the same tree stem varies with height above the ground; in this case, the distribution of the ELs is determined not only by the physical features of the bark, but also by the environmental factors, such as light, humidity, etc. Our findings show that EL exposure on the stem visually affects the projective cover and Shannon index of the ELs (Figure S3). Moreover, it influences the EL CO₂ exchange, i.e., the presence or lack of photosynthetic activities and respiration rates. In contrast to the north-exposed *Evernia*, CO₂-photoassimilation did not occur in the daily photoperiod incubations in the west-exposed *Evernia* (Figure 3). One of the components of ELs is the photobiont, which is represented by autotrophic organisms, such as green algae, that are susceptible to toxicological pressure. We hypothesize that the lack of photosynthetic activity can be related to the aerotechnogenic load that is a characteristic of Krasnoyarsk, which is an industrial center and employs coal burning for central heating, and that the most prevalent westward winds can transfer pollutants via air streams. On the one hand, ELs are known for their potential to accumulate numerous aerogenic pollutants in the phycobiont thallus, including hazardous ones, such as heavy metals. Additionally, they can tolerate extended cycles of hydration and dehydration, during which contaminants accumulate in the phycobiont thallus. Kryuchkova [38] demonstrated that the study sites, according to the poleotolerance index, belong to the zone of initial pollution. According to our data, collected almost 20 years later (based on our data, the poleotolerance index varied from 4.7 to 5.6; Figure 2), the situation with the pollution status of the studied birch forests worsened; now, we identify these forests as areas of light or moderate pollution, with no differences in the aerotechnogenic influence among the study plots (Figure 2). Such a state of biocenosis can affect both the biodiversity and the physiological characteristics of the ELs. Under the primary southern and western wind direction, the ELs located at the western and southern parts of the stem will encounter an elevated aerotechnogenic burden in the form of harmful chemical accumulation (likely heavy metals and coal combustion products) [73–75]. This is supported by the pH data measured at the birch bark (Figure S4) [76] where the ELs were collected. The pH and TDS values of the south-exposed bark were higher than those measured at the north-exposed bark. Southern areas of Krasnoyarsk are a cluster of industrial and energy facilities; for example, thermal power plants using coal, and in the western area, there is a private sector where households have been using coal for heating for decades. In contrast to the ELs with a northern exposure, such ELs (Figure 3) lacked CO₂-photoassimilation in light and were more vulnerable to long-term hydration. During this time, it is likely that excessively accumulated toxic substances in the thallus impeded the physiological activities in the photobiont, including CO₂-photoassimilation. In addition to the suppression of CO₂-photoassimilation, the formation of brown patches in the west-exposed ELs in our incubation studies confirmed this. The melanization of the thalli due to UVB exposure can occur as a result of melanin formation in the phycobiont, which is one of the secondary metabolites that provide a variety of survival purposes in the natural environment [77,78]. In our study, brown spots cannot be the consequence of

phycobiont thallus melanization during incubation under UVB radiation conditions (as in our second experiment with a UVB lamp, Figure 4), because thallus melanization does not impede photosynthetic processes in the photobiont due to the photoprotective capacity of melanin [79–81]. Furthermore, in the first incubation experiment (Figure 3), we solely employed LED lamps, which do not emit UVB light. Accordingly, high aerotechnogenic pressure, which is reflected in the buildup of pollutants in the phycobiont thallus, is the most likely cause of the lack of CO₂-photoassimilation in the ELs exposed to the west. This finding is further supported by the visual reduction in the projective cover of the ELs found on the western side of the stem (Figure S3).

We demonstrated the species-specificity of the CO₂ release mechanisms in connection to the ELs and the lack of such regarding the ELs' CH₄ fluxes (Figures 3 and 4, Tables 3 and 4). For example, in illuminated conditions, *Hypogymnia* photosynthesized in a hydrated state for two weeks, whereas the other species (*Evernia*, *Parmelia*) converted under the light to respiration after three days. Consequently, under a phytocoenosis environment, the contribution of different types of ELs may differ, not only in seasonal dynamics, but also in daily dynamics, and the influence of external variables on the components of the C cycle may also be species-specific.

The ELs studied are characterized by relatively low levels of photoassimilation, according to a comparison of CO₂ emissions or uptake with the literature data (Table 5). In contrast, the values of CO₂ emissions correspond to those found in the taiga zone of the European northeast of Russia [80,82], Canada [83], and Italy [84], while exceeding the CO₂ emissions of the ELs in Portugal [85].

Finally, we showed here, for the first time, that ELs are capable of emitting CH₄. We found no studies on EL CH₄ emissions among the works studying EL GHG fluxes published from 1950 to the present. Using incubation experiments, we showed that ELs in a hydrated state could emit CH₄ during prolonged periods (ca. two weeks; Figure 4). This suggests that, with changes in precipitation regimes and a consequent rise in the duration of ELs being in a hydrated condition, they would have quite a large potential contribution to GHG exchange in Siberian forest ecosystems. Unfortunately, there is no clear answer yet which component of the EL is responsible for the release of CH₄. Two major components of the EL are the photobiont (autotrophic organisms, such as green algae or Cyanobacteria) and mycobiont (the heterotrophic organism, represented by lichenized fungi) [17]. Both archaea and bacteria can function as minor associates of ELs. All these coexisting species in a single EL organism are known for their ability to emit CH₄ [23,33,34,86,87]. Therefore, the next step will be to determine which component is responsible for the emission of CH₄. We encourage researchers specializing in the C cycle in natural ecosystems to study GHG fluxes (CO₂, CH₄, and N₂O) to fill the current knowledge gap that currently exists. In addition, the contribution of ELs must be accounted for in the models estimating the response of the C cycle in natural ecosystems to climate change.

Table 5. The EL CO₂ and CH₄ fluxes according to the literature sources.

| EL Species | Phorophyte | Geographical Location | GHG Fluxes in Author Units | GHG Fluxes in Our Units, $\mu\text{g C-CO}_2$ or $\mu\text{g C-CH}_4$ per g of EL Dry Weight h^{-1} | Source |
|--|--|---|---|--|------------|
| CO₂ | | | | | |
| <i>Parmelia sulcata</i> Taylor, <i>Hypogymnia physodes</i> (L.) Nyl., <i>Evernia mesomorpha</i> Nyl. | <i>Betula pubescens</i> Ehrh. | Krasnoyarsk, Russia | | from +0.1 to +510.8; from −1.0 to −23.4 | This study |
| <i>Lobaria pulmonaria</i> | | Taiga zone of the European northeast of Russia | from +0.2 † to +4.9; from −0.1 ‡ to −5.5 mg CO ₂ g ^{−1} of the dry weight of EL h ^{−1} | from +54.5 to +1336.4; from −27.3 to −1500 | [80,82] |
| <i>Lobaria pulmonaria</i> | Aspen forest mixed with spruce and fir | Syktyvkar, Russia, 61.57 N, 50.55 E | from −1.7 to −5 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ | | [79,88] |
| <i>Parmelia sulcata</i> | <i>Castanea sativa</i> Miller | Abbadia San Salvatore, Tuscany, Italy, 42.90 N, 11.65 E | from +0.36 to +1.91; from −4.5 to −8.7 mg CO ₂ g ^{−1} h ^{−1} * | from +98.2 to +520.9; from −1227.3 to −2372.7 | [84] |

Table 5. Cont.

| EL Species | Phorophyte | Geographical Location | GHG Fluxes in Author Units | GHG Fluxes in Our Units, $\mu\text{g C-CO}_2$ or $\mu\text{g C-CH}_4$ per g of EL Dry Weight h^{-1} | Source |
|--|---|--|--|--|------------|
| CO₂ | | | | | |
| <i>Peltigera canina</i> , <i>Stereocaulon paschale</i> | Spruce–lichen forest | Southern Ontario, Canada, 44 N, 80 E | from +1.25 to +2.75 $\text{mg CO}_2 \text{ g dry wt}^{-1} \text{ h}^{-1}$ | from +341 to +477 | [83] |
| <i>Lobaria pulmonaria</i> , <i>Evernia prunastri</i> , <i>Lobaria scrobiculata</i> , <i>Peltigera canina</i> | Deciduous sub-med. forest; temperate forest | Portugal (Continental and Madeira Island) | from +0.25 to +0.36; from −4.50 to −4.80 $\text{nmol CO}_2 \text{ g dry wt}^{-1} \text{ s}^{-1}$ | from +39.6 to +57.02; from −712.8 to −760.3 | [85] |
| <i>Ramalina maciformis</i> | | Negev desert, Israel | from −0.2 to +10 $\text{mg CO}_2 \text{ g}^{-1} \text{ h}^{-1}$ ** | from −54.5 to +2727.3 | [89] |
| <i>Ramalina menziesii</i> | | Central California, USA | −15 $\text{mg CO}_2 \text{ g}^{-1} \text{ dry wt d}^{-1}$ * | −170.5 | [90] |
| <i>Sticta filix</i> , <i>Pseudocyphellaria faveolata</i> | <i>Nothofagus menziesii</i> , <i>Ixerba brexioides</i> , <i>Dacrydium cupressinum</i> | Aniwaniwa river valley, New Zealand, 38.75 S, 177.15 E | from −12.41 to −14.97 $\text{nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$ | from −536.1 to −646.7 | [91] |
| <i>Erioderma pedicellatum</i> | <i>Picea abies</i> | Rendalen, Norway, 61.87 N, 10.85 E | from +1.14 to +1.49; from −2.5 to −6.1 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ | | [92] |
| <i>Evernia mesomorpha</i> , <i>Bryoria nadoornikiana</i> | <i>Picea mariana</i> | Northern Clay Belt, Canada, 50 N, 77–78 W | from −0.628 to −0.704 ** ***; from +0.359 to +0.456 *** | | [50] |
| <i>Lobaria crenulata</i> , <i>Pseudocyphellaria aurata</i> , <i>P. intricata</i> , <i>Sticta sublimbata</i> , <i>S. weigelii</i> | Premontane tropical rainforest | Republic of Panama, 8.75 N, 82.25 W | From −2.90 to −12.96 **; from 2.72 to 7.66 $\text{mg C (g C)}^{-1} \text{ d}^{-1}$ | | [93] |
| CH₄ | | | | | |
| <i>Parmelia sulcata</i> Taylor, <i>Hypogymnia physodes</i> (L.) Nyl., <i>Evernia mesomorpha</i> Nyl. | <i>Betula pubescens</i> Ehrh. | Krasnoyarsk, Russia | | from +0.00006 to +0.0061; from −0.00004 to −0.003 | This study |

[†] positive values (with a plus) reflect the amount of carbon released during respiration (or CH₄ emissions);

[‡] negative values (with a minus) reflect the carbon uptake during CO₂-photoassimilation (or CH₄ consumption);

* gross photoassimilation; ** net photoassimilation; *** no units provided.

5. Conclusions

Our study showed the potential for CH₄ emissions by ELs if they are in the hydrated condition, which occurs after precipitation events throughout the year. The exposure of the EL on the host-tree stem is essential, since the GHG fluxes can be significantly different (up to two-fold), e.g., by north- and west-exposed ELs. CO₂ fluxes are EL species-specific at the same EL humidity. This shows the significance and the need to consider ELs when evaluating their contribution to the C cycle in forest ecosystems, and how they respond to recent and future climate change. However, when including the EL GHG flux data to the models, the GHG fluxes by the dominant ELs, the EL exposure on the phorophyte stem, and the day/night GHG fluxes should be accounted for in a more concise evaluation of ELs in the C cycle of forest ecosystems and their response to ongoing and projected climate change. The pattern of the release or uptake of GHGs by ELs may also alter due to climate change, e.g., changes in the precipitation regime (such as more frequent extreme rainfalls and droughts). CH₄ will escape faster into the atmosphere during wetter periods.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f15010107/s1>, Figure S1: Examples of the studied ELs—*Parmelia sulcata*, *Hypogymnia physodes*, and *Evernia mesomorpha*; Figure S2: The EL sample prepared for incubation (A) and the setup of the first (B) and the second (C) incubation experiments; Figure S3: Shannon index (A) and projecting cover (B) of ELs depending on the EL exposure on the phorophyte at various study plots (A, B, and C); Figure S4: The pH and TDS in birch bark depending on the exposure in the phorophyte stems at various study plots (A, B, and C).

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