Article

Heterocysts of *Rivularia* Type for Interpreting a Palaeoenvironmental Context of the Late Quaternary in Northern Italy

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Abstract: This paper presents new results on a quali-quantitative analysis of the heterocysts of the *Rivularia* type as a key bioindicator informative on local eutrophic conditions. The *Rivularia* type is usually reported in palynological analyses due to the thick, multilayered envelope that ensures the preservation of heterocysts in sediments. Samples come from two continuous terrestrial cores (N-S3: 77 samples, C-S1: 20 samples) drilled in the area surrounding the Bronze Age site of the Terramara S. Rosa di Poviglio (Po Plain; N Italy) and spanning at least over the last 15 ka years. Concentrations and percentages of the *Rivularia* type, combined with pollen curves of wet environments, describe local variability and rapid changes in ecological conditions over the millennia of deposition. Given the abundance and diversity of heterocysts of the *Rivularia* type in the studied samples, this paper attempts to group these cells based on morphology (ellipsoidal or elongated) and the state of preservation of the sheaths (presence or absence). Actually, it is difficult to confirm a relationship between heterocyst morphologies and the presence of different cyanobacteria species. Increasingly accurate identification of heterocysts from biostratigraphical archives may improve the data available on these bioindicators for achieving more detailed decoding of wetland (and terrestrial) transformations. Since the Bronze Age and at the most recent levels, the *Rivularia* type may be a good indicator of the local presence of agriculture and livestock, which lead to trophic and water changes in the soil.

Keywords: cyanobacteria; non-pollen palynomorphs; pollen; Po Plain; human impact; climate change

1. Introduction

The knowledge of Non-Pollen Palynomorphs (NPPs), a large group of biological objects including organic-walled microfossils, such as remains of cyanobacteria, algae, vascular plants, invertebrates, and fungi [1–3], is increasingly complementary to pollen analysis because these remains can be observed in the same palynological preparations [4–6]. NPPs provide ecological information on a more local scale than pollen does and adds detail by associating the environmental transformations with certain natural events or human activities [1,7].

Recent studies have confirmed the importance of these microfossils [8] as useful elements for interpreting changes in ecological parameters at a local scale in stratigraphical archives. Data have been provided on land use [9,10], herbivore presence and possible grazing activities [11–14], natural and human-induced fires [15], erosion processes [16], trophic levels, and water quality [17,18] for different environmental and cultural contexts.

Freshwater algal palynomorphs are usually well preserved in sediments and are identifiable due to the sporopollenin-like composition of their outer wall layers [19,20]. Cyanobacteria, formerly called "blue-green algae", are one of the major constituents of NPP, especially in Quaternary deposits. Hormogonia, heterocysts, and akinetes (the adaptive

traits of filamentous cyanobacteria in changing environmental conditions) are comparatively more resistant than their vegetative cells in palynological preparations [21]. Among them, *Rivularia* heterocysts are the most reported in palynological analyses.

1.1. Cyanobacteria: An Ecologically Important Group of Phototrophic Bacteria

Cyanobacteria comprise a wide group of organisms in terms of abundance, diversity, and ecological features. As photosynthetic prokaryotes with approximately 3500 million years of evolution on Earth, they live in various environments, from fresh and marine waters to terrestrial ecosystems. They can tolerate extreme conditions, including geothermal habitats, frozen systems, and hypersaline environments [22] and references therein.

Cyanobacteria are usually unicellular, and they often grow in colonies large enough to be easily visible to the naked eye. Although the life cycle is still poorly understood, their occurrence allows us to interpret the ecology of freshwater environments. Available information comes from cyanobacterial studies on blooms with rapid proliferation and visible colonies in freshwater or marine systems [23], and on genera toxic or harmful to ecosystems [24]. Processes of cell division or differentiation occur in response to environmental changes, such as the presence and quantity of nutrients and light irradiation, or to internal factors related to catabolism and anabolism. Optimal conditions for blooming occur in spring and summer with increased nutrient supply, high irradiation, and optimal temperatures of at least about 25 °C (77 °F) [25]. When excessive inputs of phosphorus (P) relative to nitrogen (N) or low N:P ratios occur, cyanobacteria tend to spread and dominate phytoplankton communities [26] and references therein. The first limitation to vegetative cell growth is the lack of nutrients as a result of rapid colony proliferation, which requires and consumes a large number of substances. Most species that form blooms can fix atmospheric N_2 into biologically available NH_3 and thus contributing new nitrogen to nitrogen-limited systems [27,28]. In the absence of combined nitrogen, N fixation takes place in heterocysts that differentiate through a highly regulated process [29]. These cells are involved in the fixation of atmospheric N_2 in oxic environments for the proper functioning of nitrogenase and other proteins during the process [30]. The fixed N is then transferred to the vegetative cells of the trichome, while the heterocyst receives photosynthates from the adjacent cells for its metabolism [25]. Heterocysts form as responses to rapid environmental or internal colony changes, as well as in habitats rich in combined N (such as nitrate, ammonium, or other organic compounds) for prolonged periods that may affect heterocyst efficiency [31]. Other elements that could influence their differentiation are potassium, molybdenum, magnesium, calcium, and iron, which are essential to the functioning of these cells [32]. For this reason, colonies grown for several years show residual heterocysts below the terminal and functioning heterocysts. In rare cases, intercalary heterocysts may also develop and achieve higher levels of N fixation [33].

Heterocysts, visible under the light microscope, are large, round-shaped cells featuring by a thicker, multilayered envelope with diminished pigmentation than vegetative cells, and usually contain cyanophycin granules [34].

1.2. Rivularia as a Palaeoecological Indicator and Aim of the Paper

Rivularia heterocysts are usually the best preserved morphotypes of cyanobacteria in almost all the studied biostratigraphic profiles. In particular, their abundance increased toward Early to Middle Holocene, influenced by heavy precipitations and wet climate conditions during the Holocene Climate Optimum (HCO) [21]. Rivulariaceae have been documented in sediments since the Pliocene (5.332–2.588 million years ago). Many Pleistocene deposits (between 2.58 million years and 11,500 years ago) show cyanobacteria-like structures [31]. Data on *Rivularia* in Quaternary sediments, combined with information on vegetation, allow assessment of hydrogeological transformations, trophic conditions, and changes in ecosystems caused by natural and anthropogenic factors [35].

Even though thalloid forms of *Rivularia* colonies have been sometimes observed within more conservative sediments [36], *Rivularia* heterocysts are the most recurring remains

in palynological analyses. Van Geel et al. [37] first identified these structures preserved in the Hugo de Vries Laboratory's reference collection of blue-green algae. However, not only *Rivularia* but also other genera may have similar heterocysts. Therefore, it has been assigned the provisionally, but not formally, named form-species [38] (p. 47) "Type 170" (currently classified as "*Rivularia* type" [1]). These structures appear hyaline under a light microscope, ellipsoid to almond-shaped ($9.7 - 18.4 \times 6.0 - 13.3$ μm), and their walls are about 1 μm thick. A pore, known as a "neck" [39], about 1 μm wide, is present at the cell margin for the connection with the trichome. Remnants of the proximal part of the gelatinous sheath often remain, still connecting with the heterocyst [37].

This paper reports on a quali-quantitative analysis of heterocysts of the *Rivularia* type in a palaeoenvironmental context to verify their role as bioindicators in ecosystem dynamics. Floodplains are complex human-water systems whose dynamic behaviors are determined by both natural and human pressure over time [40]. The case study of the archaeological site of the Terramara Santa Rosa di Poviglio in the central Po Plain fits into this type of context. The record of *Rivularia* heterocysts emerging from the palynological analysis of two near-site terrestrial cores [41] is presented here.

2. Materials and Methods

2.1. Palaeoenvironmental and Archaeological Context

The study area is located in the Po Plain, the largest plain in Italy, south of the Po River, Reggio Emilia Province (northern Italy).

This territory has been under investigation for about 40 years since the archaeological excavation of the Terramara S. Rosa di Poviglio-PVG started in 1984 (excavation directors: Maria Bernabò Brea, Mauro Cremaschi, and, in recent years, Andrea Zerboni). The archaeological site of S. Rosa di Poviglio (Lat. 44°52′21″ N; Long. 10°34′31″ E) is a Middle-Recent Bronze Age settlement belonging to the Terramare civilization [42]. A detailed investigation is extended over a large portion of the settlement and its surroundings [43–46].

Geomorphological records suggest that this site was located near a palaeo-channel of the Po River active during the Bronze Age [44].

The settlement consists of two agglomerations and a complex and structured hydraulic system with a peripheral moat, large water wells, and interconnecting ditches for the collection and redistribution of water. The small village ("Villaggio Piccolo" in Italian—VP) extends for 1 ha in area and is the oldest settlement dating back to the Middle Bronze Age; the large village ("Villaggio Grande"—VG), dated to the Recent Bronze Age, flanks the oldest one, and covers an area of 7 ha (Figure 1a).

The effects of climate change and human impact on past vegetation are well described based on a considerable amount of palynological analyses [47–51], studies on seeds and fruits [52], as well as anthracological and xylotomic records [53]. The Terramara was mainly surrounded by riparian communities and oak woods. However, the open landscape was widespread, with an important role for synanthropic plants, crop fields, and pastures. A continuous transformation of the vegetation cover and biodiversity of the area is assessed by pollen analyses, which show the increasing trend of human activities [47–51]. In the context of over-exploitation of natural resources, changes in land use (toward the spread of dry pastures and the cultivation of cereals of drought-tolerant varieties) are considered adaptations to drier climatic conditions and the decline in soil fertility that occurred in the Recent Bronze Age [49].
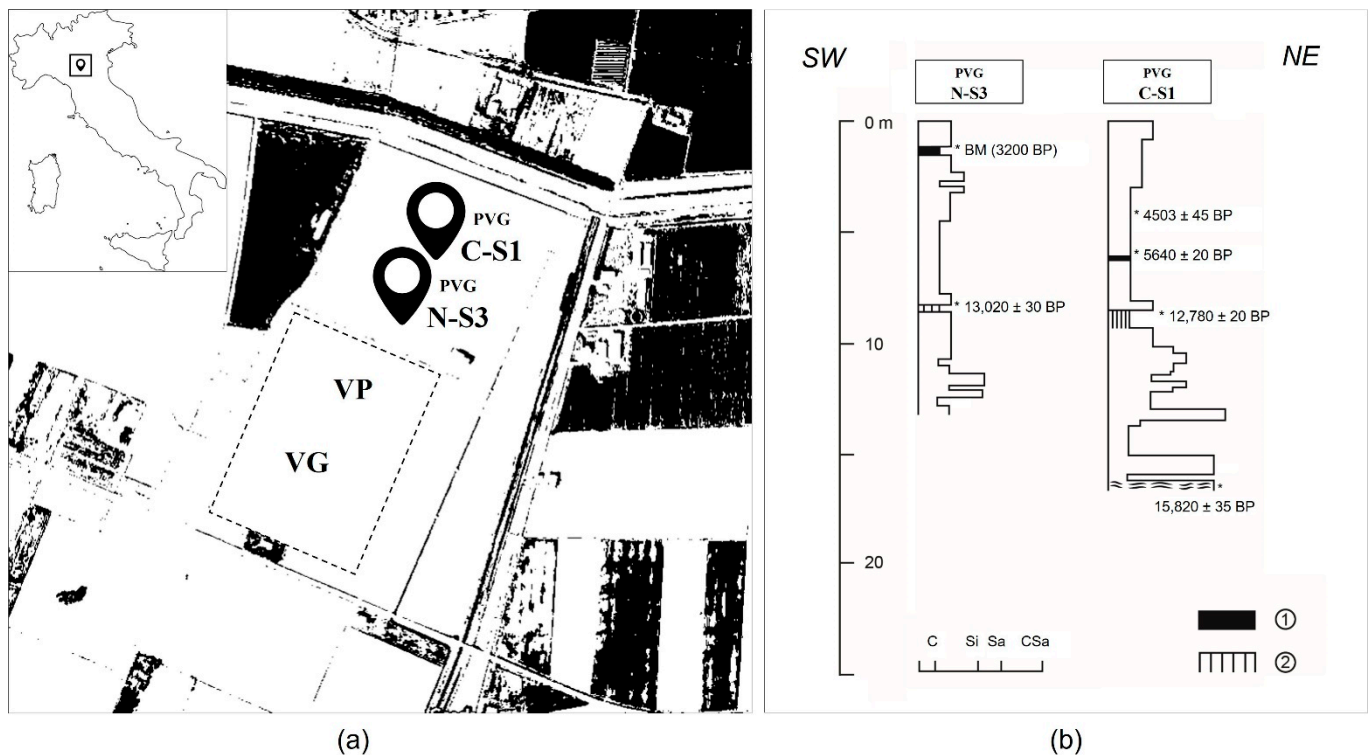
(a)

(b)

Figure 1. (**a**) Location of the N-S3 and C-S1 cores in the area N of the Terramara S. Rosa di Poviglio (PVG), which is highlighted by the dashed rectangle (VP-Villaggio Piccolo and VG-Villaggio Grande). The basemap is a modified satellite image provided by GoogleEarth™; (**b**) The Stratigraphy and uncalibrated age BP (marked by asterisks *) of the N-S3 and C-S1 cores, drilled in a SW-NE direction from the Terramara [C = clay, Si = silt, Sa = sand, CSa = coarse sand, 1 = organic sediments, 2 = buried organic soils]. The main element of the deposits is their texture, consisting of alluvial sediments ranging from coarse sand to silt and clay, including levels of organic soils. The uppermost part of the N-S3 sequence preserves an archaeological buried soil dating to the Bronze Age (marked by asterisk *).

2.2. Coring and Pollen Sampling

Palaeoenvironmental samples came from two continuous terrestrial cores (N-S3 and C-S1) drilled in 2018. The cores were collected in a SW-NE direction about 150 (N-S3) and 320 (C-S1) meters from the archaeological site. The drilling sites (N-S3: Lat. 44°52′27″ N, Long. 10°34′38″ E; C-S1: Lat. 44°52′32″ N, Long. 10°34′42″ E; Figure 1a) were selected according to geophysical surveys on lithological differences in the sedimentary context of the alluvial plain [45,54]. Stratigraphic logs of the N-S3 e C-S1 cores illustrating the different grain size of stratigraphic units are shown in Figure 1b. The deposits consist of alluvial sediments of different grain sizes, from coarse sand to silt and clay, interlayered by buried soil horizons bearing archaeological materials dating to the Bronze Age, and clayey layers enriched in organics formed after decantation in water. From the lithological point of view, deposits mostly consist of siliciclastic sediments with a limited amount of limestone and marl fragments [55]. The chronology of the sequences, consistent with the core stratigraphy and palaeobotanical reconstruction [41], relies on two types of evidence: (i) radiocarbon dates (four dates are published in [54], where the cores are named "S.R. Carotaggio 3" and "S.R. Carotaggio 1"); a new dating for the C-S1 core is published here (Table 1); (ii) ceramic fragments found at 110–130 cm depth into the N-S3 core that have been attributed to the Middle Bronze Age (3200 yr BP) based on typological features. Correlations between the accepted dates were made by stratigraphic and sedimentary trends and the pollen assemblage of the sequences [41].

Table 1. AMS-14C age for the C-S1 core.

CeDaD Laboratory Code	Uncal14C Age (Years BP)	δ 13C‰	Site/Depth	Dated Material
LTL21118	4503 ± 45	-22.1 ± 0.5	PVG C-S1 $-407/412$ cm	Organic soil

Pollen samples were collected throughout the cores (excluding the top levels of arable land) at about 10–30 cm intervals based on the stratigraphy and archaeological phases. The N-S3 core was analyzed entirely for pollen and *Rivularia* type (77 samples) to obtain a complete and long-term reconstruction. According to the detection of vegetation and ecological changes in the most recent phases of the Holocene, heterocysts of the *Rivularia* type were analyzed qualitatively and quantitatively only in the upper part of the C-S1 (20 samples).

2.3. Pollen and Non-Pollen Palynomorphs Extraction

Samples were treated using the routine method of the Laboratory of Palynology and Palaeobotany (LPP) of Modena, which led to the concentration of palynomorphs after the elimination of the organic and mineral parts of the sediment (see [6] for the methodological protocol imported and adapted from the Institute of Earth Sciences, Vrije Universiteit Amsterdam: PALICLAS project [56,57]). About 1–2 g of sediment per sample was prepared with the addition of *Lycopodium* spore tablets to calculate pollen and heterocyst concentrations (expressed in p/g and h/g [58]). Nylon filtering (7 μm sieve) and the use of heavy liquid allow palynomorphs to be concentrated even in poorly preserved contexts. The final residues were mounted on permanent glycerol jelly slides for long-term storage within the Pollen Reference Collection of the LPP of Modena.

2.4. Identification of Heterocysts of the Rivularia Type and Data Elaboration

This work is based on the significant and fairly recurring presence of *Rivularia* heterocysts (*Rivularia* type: [37]; HdV-170: [1]) in the samples.

Due to the morphological diversity of the *Rivularia* type, a systematic quali-quantitative analysis of these structures was carried out on an entire slide for each sample of the N-S3 and the C-S1 cores. Heterocysts were divided into categories (Figure 2; [59]) based on morphology (ellipsoidal or elongated) and the state of preservation of the sheaths surrounding the trichome (presence or absence).
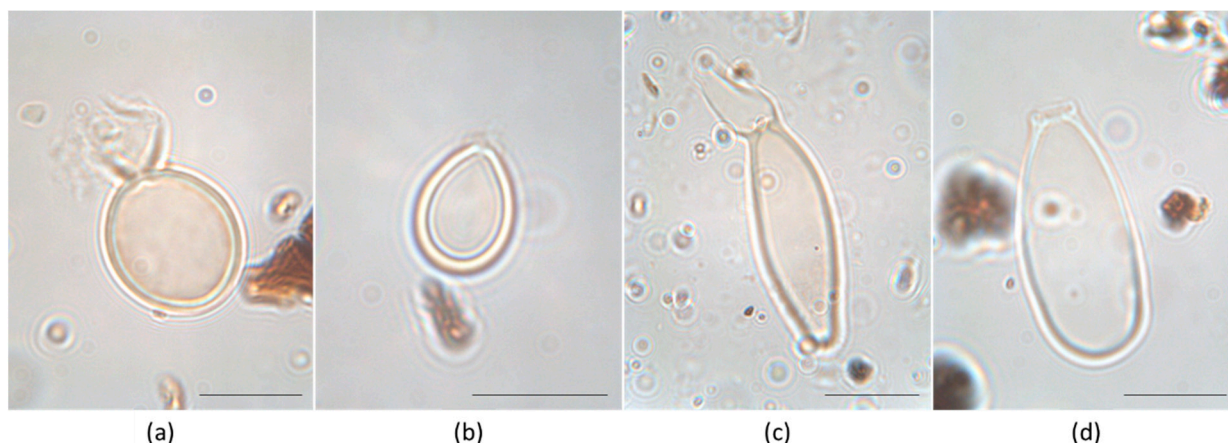

(a) (b) (c) (d)

Figure 2. Categories of the *Rivularia* type based on morphology and presence/absence of sheats: (**a**) Ellipsoidal with sheaths (15 × 14 μm); (**b**) Ellipsoidal without sheaths (10 × 8 μm); (**c**) Elongated with sheaths (27 × 11 μm); (**d**) Elongated without sheaths (24 × 11 μm). The scale is 10 μm.

The morphological subdivision of the structures is based on the ratio between the major and minor diameters (Md/md) of the heterocyst body. The ellipsoidal shape includes

heterocysts of nearly-spherical or spherical shape, while the elongated shape has a greater difference between the sizes of Md and md. Based on the measurements that characterize the elongated and flattened cells, the ratio between the diameters useful for identifying the two morphologies was set at 1.6:

- $\frac{\text{Major diameter (Md)}}{\text{minor diameter (md)}}$ from 1 to <1.6 = ellipsoidal heterocysts
- $\frac{\text{Major diameter (Md)}}{\text{minor diameter (md)}}$ from ≥1.6 to higher values = elongated heterocysts

Data on *Rivularia* heterocysts were also analyzed by comparison with pollen assemblages. The selected pollen sums were considered for the interpretation: (i) hygrophilous trees; (ii) hygrophilous herbs; (iii) hydrophytes. Pollen diagrams were drawn with Tilia [60].

3. Results

The general results of the N-S3 and C-S1 cores are shown below.

3.1. The Rivularia Type in the N-S3 Core

The presence of the *Rivularia* type is highly variable throughout the core, from the complete absence of these structures at some levels to the maximum value of 94 heterocysts in sample 58. Heterocyst concentrations reflect these fluctuations (min.: 18 h/g in sample 27—not including samples in which these structures are absent; max.: 4115 h/g in sample 58; on average: 266 h/g). Additionally, the percentages of the *Rivularia* type, which is closely dependent on and related to local vegetation, have different values throughout the core (min.: 0.1% in sample 53; max.: 13.6% in sample 58; on average: 1.6%).

Heterocysts are usually characterized by an excellent state of preservation of the cell body, intact cell walls, and a well-defined morphology, which have always ensured the identification of these structures. A highly variable feature is the presence or absence of sheaths surrounding the trichome (see Figure 3a for sample details).

The *Rivularia* type morphology and size also show variability (Figure 4). Elongated and ellipsoidal heterocysts are present in almost equal amounts throughout the sequence (315 and 321 heterocysts, respectively). However, some samples are characterized by the prevalence of one morphology (see Figure 3b).

3.2. The Rivularia Type in the C-S1 Core

In C-S1, the presence of the *Rivularia* type is variable and mostly in low amounts (up to eight heterocysts in sample 6). Except for the samples in which no heterocysts were observed, concentrations range from 17 h/g (sample 4) to 178 h/g (sample 2), with an average value of 80 h/g.

Rivularia-type percentages range from 0.1% (samples 4, 8, and 10) to 1.7% (sample 18); the average value is 0.6%.

The state of preservation of the heterocysts is good and homogeneous, with a higher abundance of heterocysts with sheaths (Figure 5a) and ellipsoidal in shape (Figure 5b).
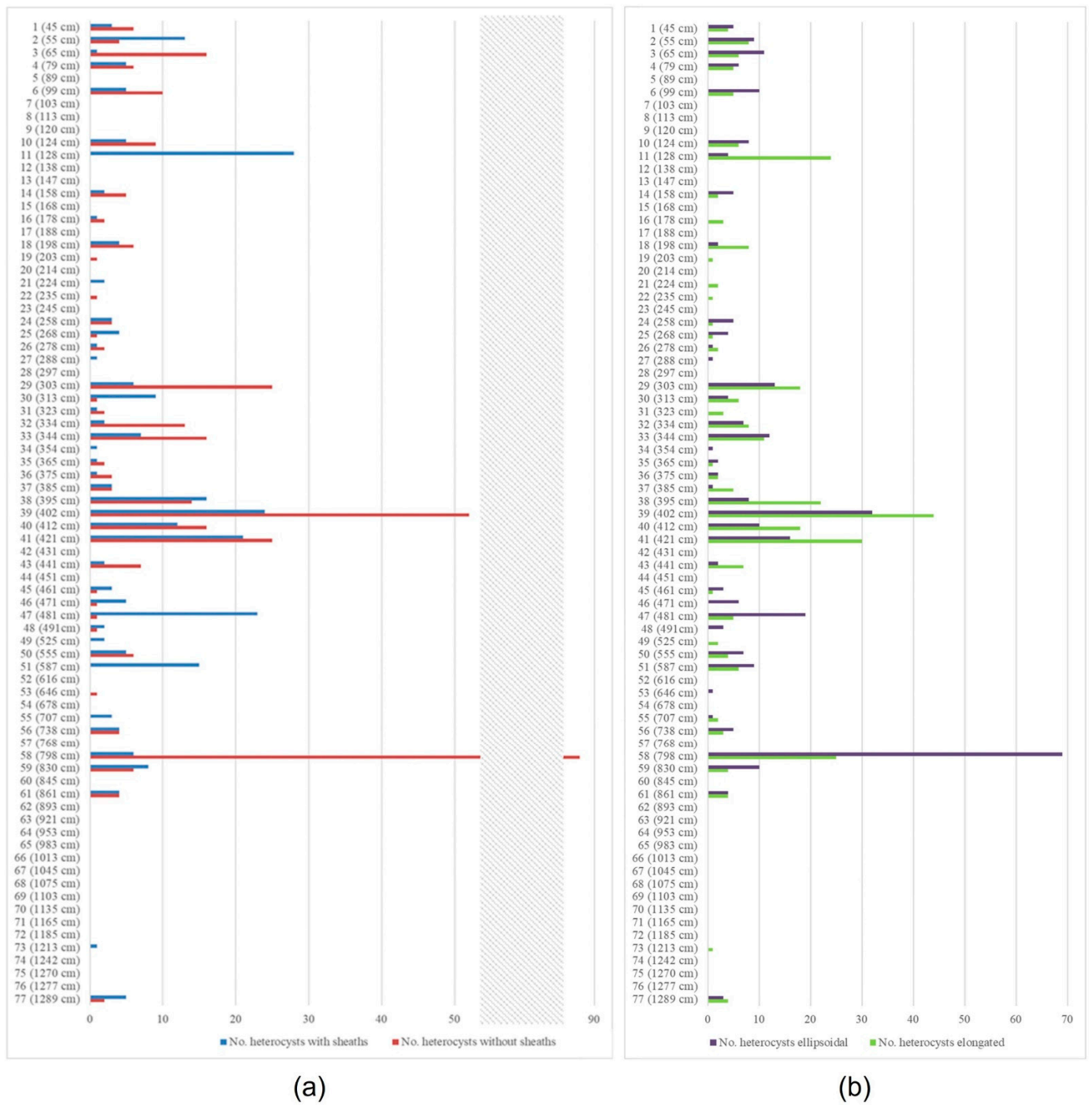
Figure 3. The *Rivularia* type in the N-S3 core: (**a**) Heterocysts with (blue bars) and without (red) sheaths; (**b**) Ellipsoidal (purple) and elongated (green) heterocysts. The grey rectangle marks the graphical short for the maximum value of heterocysts.
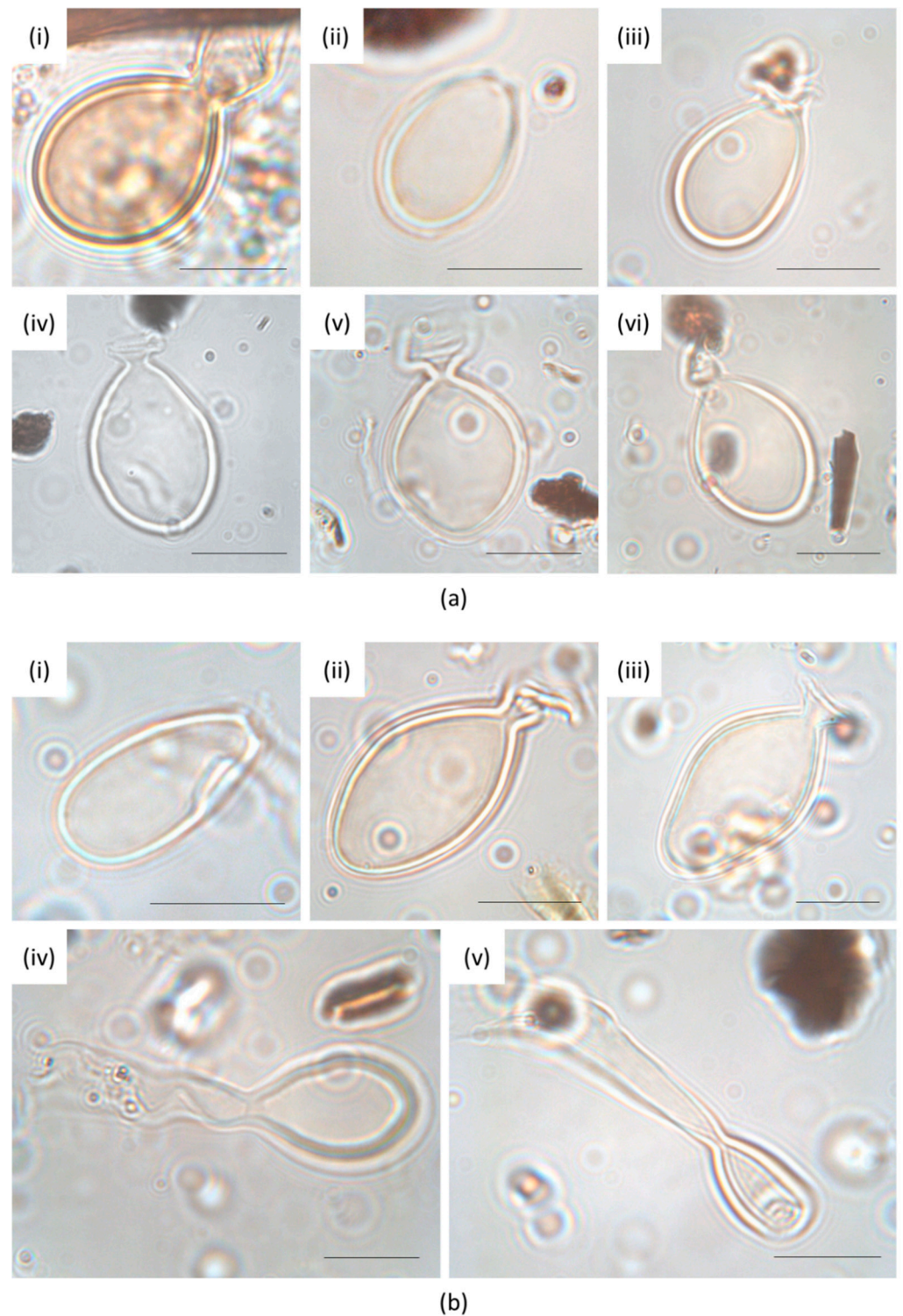
Figure 4. Morphological variability of the *Rivularia* type in the N-S3 core: (**a**) Ellipsoidal heterocysts—(**i**) 16 × 14 μm, (**ii**) 12 × 8 μm, (**iii**) 17 × 14 μm, (**iv**) 20 × 15 μm, (**v**) 20 × 17 μm, (**vi**) 21 × 15 μm; (**b**) Elongated heterocysts—(**i**) 17 × 8 μm, (**ii**) 25 × 15 μm, (**iii**) 25 × 16 μm, (**iv**) 20 × 12 μm, (**v**) 11 × 6 μm. The scale is 10 μm.
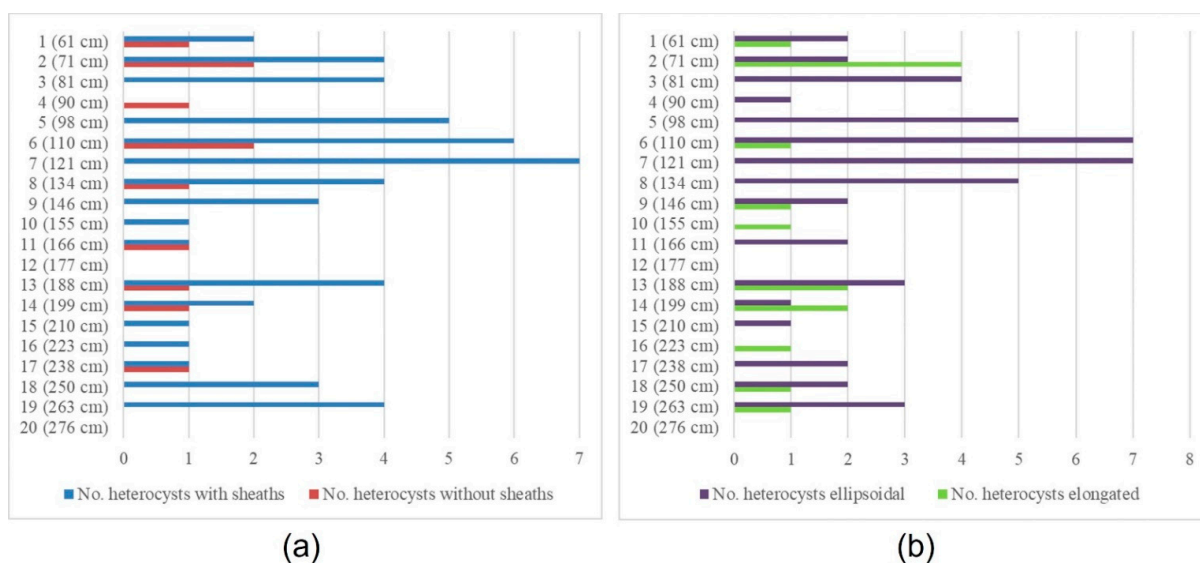
Figure 5. The *Rivularia* type in the C-S1 core: (**a**) Heterocysts with (blue bars) and without (red) sheaths; (**b**) Ellipsoidal (purple) and elongated (green) heterocysts.

4. Discussion

Data on the concentrations and percentages of the *Rivularia* heterocysts from the N-S3 and C-S1 cores describe a non-constant trend, reflecting different, and sometimes rapid, changes in ecological conditions over millennia of deposition.

Recent studies have shown the possible effect of several factors (including total nitrogen-TN, total phosphorus-TP, TN:TP ratio, temperature, pH, and trophic state) on the relative abundance of heterocystous cyanobacteria [61,62]. Basically, high concentrations of phosphorous in eutrophic systems produce an increase in biological productivity and algal blooms of N-fixing cyanobacteria [63]. The almost constant presence of the *Rivularia* type in the upper part of the cores indicates phosphate eutrophication [19], which is strongly dependent on mild temperatures, humidity, or the direct presence of water. The high quantity of these remains may suggest a high concentration of nutrients (organic P and combined N) that favored colony proliferation. The decrease in availability of nitrogen, the nutrient most consumed during flowering, stimulates the development of new heterocysts, enabling colonies to survive. Therefore, the diverse presence of the *Rivularia* type is an indicator of a decrease in nitrogen concentration following a condition of eutrophication that allowed the blooming of colonies. Conversely, phases of absence or limited abundance in heterocysts, may be influenced by the reduced concentration of nutrients, especially phosphorus.

Concerning the qualitative analysis of the *Rivularia* type, the great variability in the presence/absence of sheaths denotes a different state of preservation of the remains. Postdepositional disturbances and soil compaction may have favored the loss of the sheaths as the less resistant structural part due to their mucilaginous composition. Phases characterized by a high presence of heterocysts with sheaths are attributable to prevailing low-energy conditions, in which most biological organisms have a better preservation potential. In contrast, no preservation issues were observed on the bodies of heterocysts due to their wall structure containing an extra cell envelope compared to vegetative cells. Two chemically different layers cover the outer membrane of the heterocyst cell envelope: one made of glycolipids (heterocyst glycolipid; Hgl) and the other high in polysaccharides (heterocyst envelope polysaccharide; Hep) [64] and references therein. Thanks to these glycolipids (consisting of long-chain diols, triols, keto-ols, and keto-diols that are glycosidically bound to hexose molecules), the heterocysts are well preserved in sediments, unequivocally indicating the presence of N_2-fixing heterocystous cyanobacteria [65].

Heterocysts of different morphology, which cannot be attributed to various species according to current knowledge, are observed in all samples.

This investigation leads to the formulation of two questions underlying the interpretation of the data: (i) Could the presence of different morphologies of heterocysts be an indication of the simultaneous presence of various cyanobacteria species? (ii) Could the presence of different species be linked to rapid changes in environmental conditions?

Further studies on heterocysts in a modern context and in-depth morphological analyses would be needed to unravel these issues.

4.1. Trend of the Rivularia Type in the Cores

Observing the *Rivularia* type trend along the N-S3 core (Figure 6), an almost total absence of these structures characterizes the deepest levels, between 1289 cm (sample 77, N-S3) and 830 cm (sample 59, N-S3). These data, together with the palaeoenvironmental reconstruction obtained from pollen spectra, reflect the low presence of *Rivularia* colonies during the transition from the Late Pleniglacial and Lateglacial climatic conditions. In this case, the limiting factor is probably the temperature, which, even in spring and summer, does not reach conditions suitable for the development of cyanobacteria colonies. However, the *Rivularia* type in some samples (e.g., 0.4%—sample 61, N-S3) may suggest the occurrence of different conditions, such as higher temperatures during warmer phases. Similar observations were also made by Stivrins et al. [66] with information from algal pigments and higher taxonomical resolution from sedaDNA, demonstrating insignificant accumulation rates of cyanobacteria and few shifts in composition during the Lateglacial (14,500–11,700 cal. BP). At 708 cm (sample 58, N-S3), there is the highest concentration and percentage of the *Rivularia* type (4115 h/g and 13.6%). This level probably intercepts the transition from the Pleistocene to the Holocene, when rising temperatures and increasing moisture concentration reached conditions favorable to colony development. Again, the data agree with those described by Stivrins et al. [66,67] at the end of the Pleistocene, when a clear algal turnover indicates a stable aquatic and terrestrial environment. According to Tappan [68], N-fixing forms also find optimal conditions with very low nutrient concentrations, and they require only light, water, and a few other minor elements. Their nutritional requirements are the most basic of any organism, making them important early colonizers in degraded soils both on and below the surface [69].

Then, the percentages of the *Rivularia* type fluctuate to recent levels, reflecting different nutrient (and water) inputs resulting from both environmental and anthropic factors. Specifically, the flooding of the nearby Po River and anthropic activities related to grazing and cultivation, changed soil trophic conditions and water regulation. The trend of the *Rivularia* type up to 303 cm (sample 29, N-S3) reflects a chronological interval mainly characterized by mild temperatures and high humidity levels. However, fluctuations are present, reflecting the cooler Early Holocene (e.g., the 8.2 ka cooling event described by Stivrins et al. [67] with algal composition stable in time) and the wetter Middle Holocene. During this wide chronological interval, high values of heterocysts testify the proliferation of cyanobacteria related to the freshwater influx of the rainfall as well as the local hydrological regimes [21]. The often high, though fluctuating, values of the *Rivularia* type suggest high level of water table favoring the blooming of blue-green algae colonies.

Only the deepest samples analyzed for C-S1 intercept this phase, in which higher values of the *Rivularia* type are observed (Figure 7). This wetter phase is followed by levels characterized by reduced water availability (Figures 6 and 7). Particular attention was given to the levels intercepting the Terramare settlement (130–110 cm: samples 11-8, N-S3). The *Rivularia* type trend reflects an initial high nutrient availability compatible with a local eutrophic condition probably favored by human activities (*Rivularia* type: 3.1%—sample 11, N-S3). Subsequently, a decrease in percentages (2.2%—sample 10, N-S3) up to the absence of heterocysts (samples 8 and 9) supports the hypothesis of the collapse of this civilization at a time of water crisis and soil depletion due to the overexploitation of natural resources [49]. The poor nutrient supply and widespread arid conditions persisted even after the settlement was abandoned, reflecting the difficulty of local environmental recovery (absence of heterocysts at 103 cm—sample 7, N-S3).
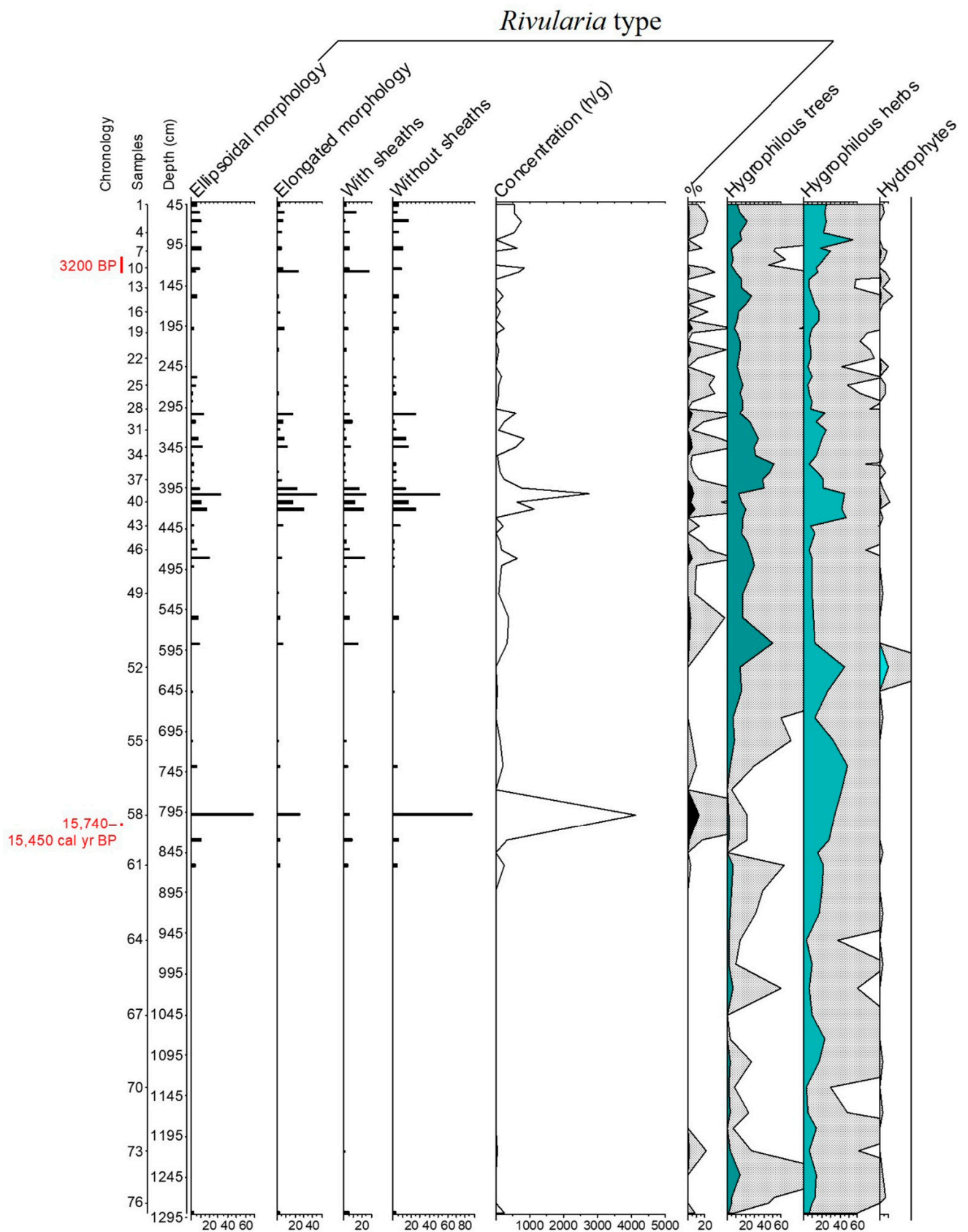
Figure 6. N-S3 core synthetic palynological diagram—*Rivularia* type (heterocysts morphology, presence/absence of sheaths, concentration (h/g), and percentages) and pollen sums percentages of wet environments. Empty curves represent 10% exaggeration.
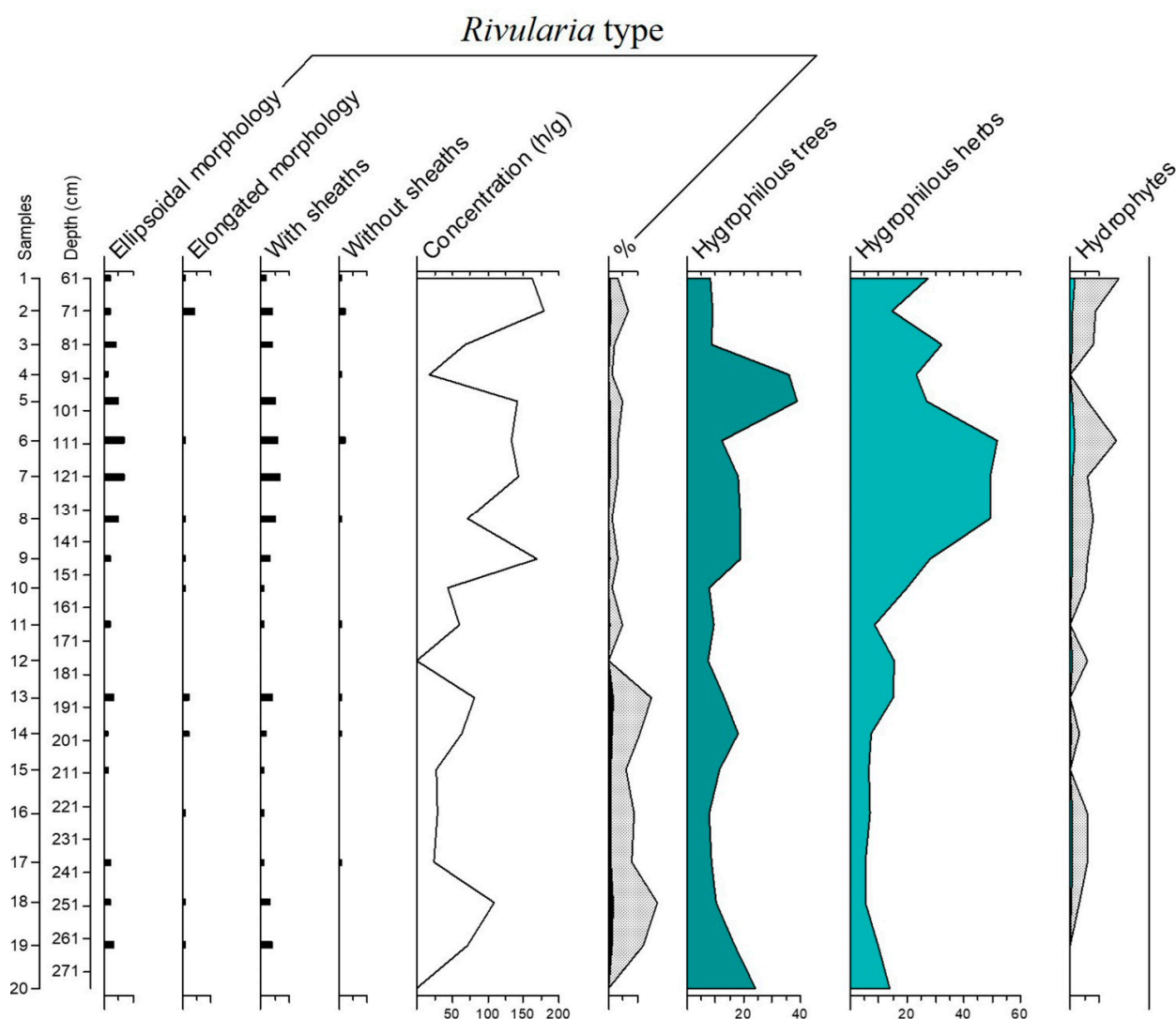
Figure 7. C-S1 core synthetic palynological diagram—*Rivularia* type (heterocysts morphology, presence/absence of sheaths, concentration (h/g), and percentages) and pollen sums percentages of wet environments. Empty curves represent 10% exaggeration.

The amount of the *Rivularia* type in C-S1 is lower than the values observed in the coeval phases of N-S3 (~the first 31 samples). The reason for differentiation may be related to the position of the cores with respect to the archaeological site: core N-S3 is closer to the site than C-S1 and was collected near the moat outside the settlement. The moat, characterized by an almost stable water level, was rich in organic matter (not least because the population presumably threw plant waste into it [50]), which provides nutrients for the cyanobacteria colonies. A comparison of the two cores shows a lower nutrient intake in the C-S1 core, together with less proximity to wet environments necessary for colony development. However, the decline of the *Rivularia*-type percentages documented also in core C-S1 at 177 cm (sample 12) could correspond to the last phases of Terramare settlement in Poviglio.

At the most recent levels, the *Rivularia* type may be a good indicator of the local presence of agriculture and livestock, which lead to trophic and water changes in the soil.

4.2. Comparison with Pollen Curves

In Figures 6 and 7, the trend of the *Rivularia* type is compared with that of the pollen curves of hygrophilous trees, hygrophilous herbs, and hydrophytes [41]. The close relationship

between *Rivularia* and the plants of riparian communities underlines the importance of the direct presence of water or moisture-saturated soil for the development of wet environments.

Hygrophilous trees, here dominated by *Alnus* and *Salix*, closely follow the trend of the *Rivularia* type. *Alnus* and *Salix* need high atmospheric humidity for their development, along with high N concentrations [70,71]. The tendency for these plants and *Rivularia* colonies to grow simultaneously indicates conditions suitable for common development. In particular, the gradual and steady growth of hygrophilous trees begins immediately after the level with the *Rivularia* peak in the N-S3 core (sample 58). These data fit with the climatic change at the beginning of the Holocene, leading to the development of deciduous forests and the spread of cyanobacteria colonies. Conversely, hygrophilous herbs and hydrophytes have many peaks opposite to the *Rivularia* type. This is not surprising, as the abundance of herbaceous plants is usually correlated with phases of constant water flow that allow these populations to occupy the same ecological niche required for cyanobacteria (particularly evident in sample 5 of N-S3, where the absence of the *Rivularia* type corresponds to a peak of hygrophilous herbs). When the flow slows down, sometimes with the lowering of the water level, the woody vegetation prevents the growth of reeds and cattails [72] (p. 199) and favors the proliferation of cyanobacteria in shallow waters.

5. Conclusions

Based on the two new data sequences presented in this paper, considerable local variability in a long-term perspective has emerged in the area surrounding the Bronze Age site of the Terramara di Poviglio. The reconstruction of local environmental dynamics has benefited from the valuable palaeoecological contribution provided by the heterocysts of the *Rivularia* type, which are abundant, of different morphologies, and well preserved in the studied sediment cores.

The *Rivularia* type has provided a complementary source of information on trophic and climatic conditions to integrate the palaeoenvironmental dynamics inferred by pollen spectra. Heterocysts were mostly absent during the Late Pleniglacial and Lateglacial, suggesting that low temperatures were not suitable for the development of cyanobacteria colonies. Rising temperatures and increasing moisture concentrations have allowed colony turnover since the beginning of the Holocene. Subsequently, environmental conditions and human activities act in synergy, influencing nutrient (and water) inputs, resulting in changes in the local trend of the *Rivularia* type.

An attempt to separate heterocysts according to their morphology has been made to get information on the presence of different cyanobacteria species linked to changes in environmental conditions. However, with the current knowledge, it is difficult to answer questions about the relationship between different morphologies of heterocysts and the presence of many species in the palaeoenvironment. A comparison of modern cases and in-depth morphological analysis of these structures could improve the taxonomic identification of heterocysts of the *Rivularia* type.

In modern contexts, *Rivularia* is analyzed together with other N-fixing microorganisms to recognize eutrophication processes and the associated increase in the amounts of organic nutrients, nitrogen, and phosphorous generated by human activities [73]. In addition, some species are invasive in many geographical areas, reflecting polluted conditions and lower water quality [74]. Pioneering research on the characterization of ancient cyanobacteria strains with the perspective of obtaining solutions to the current difficulty of mitigating eutrophication has increased in recent years [75].

Through the study of present-day contexts, it is possible to learn about the relationships between Rivulariaceae species and their habitats. Similarly, the presence of the *Rivularia* type in palaeoenvironmental samples enables us to reconstruct local changes using a long-term approach. As these organisms are sensitive to ecological and environmental conditions, the increasingly accurate interpretation of their signatures in sedimentary archives may lead to a more detailed decoding of their role as a proxy for wetland (and terrestrial) evolution.

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