

Floristic diversity, richness and distribution of Trentepohliales (Chlorophyta) in Neotropical ecosystems

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Received: 7 December 2016 / Accepted: 7 April 2017 / Published online: 28 April 2017
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Abstract Trentepohliales is one of the most diverse and abundant algal group of the terrestrial microflora in tropical regions; however, information about composition, richness and distribution of these algae in Neotropical regions are scarce. We described the flora and evaluated species richness and composition of Trentepohliales in four Brazilian different phytophysiognomies and analyzed the influence of environmental and spatial factors on species richness and distribution. Specimens of Trentepohliales were gathered from six natural areas in Brazil, and they were studied according to their vegetative and reproductive morphological traits. We applied tests to evaluate the richness and similarity in species composition in the different environments: rarefaction curves to compare richness; dendrogram with Jaccard's index to evaluate the similarity of species composition; Mantel's test to detect the influence of the spatial geographic distance on the assemblages; and partial linear regression to analyze the influence of the spatial and environmental factors on species richness. Thirty-three morphospecies were recorded; most of them in one location and none was observed occurring in all sampled areas. Rainforest areas showed the highest species richness and

the species composition was variable among the areas. Partial linear regression revealed that the spatial features plus environmental features drove the Trentepohliales' species richness gradient. The composition of species of communities presented distance decay of similarity pattern, since differences in composition of such assemblages were positively related to the distance among the areas. In this way, the dispersion jointly with the variation of the environmental conditions may determine the Trentepohliales species composition in each ecosystem.

Keywords Community structure · Distance decay pattern · Green algae · Terrestrial algae

Introduction

Photosynthetic microorganisms living in terrestrial environments consist of a set of heterogeneous organisms, belonging to several evolutionary lineages (Rindi et al. 2009). Green algae and cyanobacteria are known as the best succeeded algal groups inhabiting the terrestrial environments, although other groups, as Heterokontophyta, are also diverse (López-Bautista et al. 2007). Trentepohliales are very common among the terrestrial green algae and constitute one of the most diverse and abundant algal group of the terrestrial microflora in tropical regions (López-Bautista et al. 2007).

Trentepohliales belongs to Ulvophyceae and comprises one family, Trentepohliaceae, five (*Cephaleuros*, *Phycopeltis*, *Stomatochroon*, *Trentepohlia* and *Printzina*) or six genera (including *Physolinum*) according to morphological criteria and depending on the classification system chosen, and about 100 species have been recognized (Guiry and Guiry 2017). This algal group exhibits diverse forms,

Electronic supplementary material The online version of this article (doi:10.1007/s40415-017-0390-3) contains supplementary material, which is available to authorized users.

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including branched filaments, pseudoparenchymatous and reduced thallus (Chapman 1984; López-Bautista et al. 2002).

Despite trentepohlialeans can be found in a range of environments, comprising tropical and temperate regions, they have been usually referred to humid tropical forest around the world, indicating that these regions may be a more suitable environment to the development of the terrestrial algae (López-Bautista et al. 2007). Records of Trentepohliales can be found for almost all continents, including Australia (Cribb 1958, 1963, 1970, 1989), Europe (Rindi and Guiry 2003; Rindi et al. 2003), Africa (Rindi et al. 2006; Allali et al. 2013), Asia (Islam 1960; Jose and Chowdary 1980; Panikkar and Sindhu 1993; Neustupa and Sejnohová 2003; Neustupa 2005) and America (Tracanna 1989; Rindi et al. 2005; Rindi and López-Bautista 2008; Rindi et al. 2008). In Brazil, information on Trentepohliales diversity is compiled in only three specific surveys, all of them carried out in Atlantic forest areas from São Paulo State (Akiyama 1971; Bicudo and Santos 2001; Lemes-da-Silva et al. 2010). These surveys presented a very diversified Trentepohliales flora, and the expansion of the sampling is essential to enhance the knowledge of this algal group diversity.

The patterns of geographic distribution and of the communities' richness of the Trentepohliales and the greatest part of terrestrial algae are poorly understood in world scale, mostly due to the lack of knowledge on their biodiversity (Rindi et al. 2009). Tropical regions comprise ecosystems, such as savannah and mixed forest, which are underserved on the knowledge of Trentepohliales diversity. Thus, while the richness of Trentepohliales in tropical forests is remarkably high (Rindi and López-Bautista 2008; Rindi et al. 2008), information about this flora in different ecosystems remains to be produced, as well as evaluations on different aspects of species distribution.

Considering the poor knowledge of Trentepohliales in Neotropical regions, the aims of this study were: (1) to access the floristic biodiversity, species composition and richness of Trentepohliales, covering different Brazilian ecosystems; (2) to evaluate the influence of selected environmental conditions on species occurrence and richness distribution; and (3) to investigate the role of the space (distance) on the similarity of floristic composition of Trentepohliales among the localities.

Materials and methods

Study area – Samples of Trentepohliales were gathered between 2009 and 2010, in six natural areas, including two biomes, savanna and Atlantic forest, distributed in south-eastern and Midwestern Brazil (Fig. 1, appendix 1 of

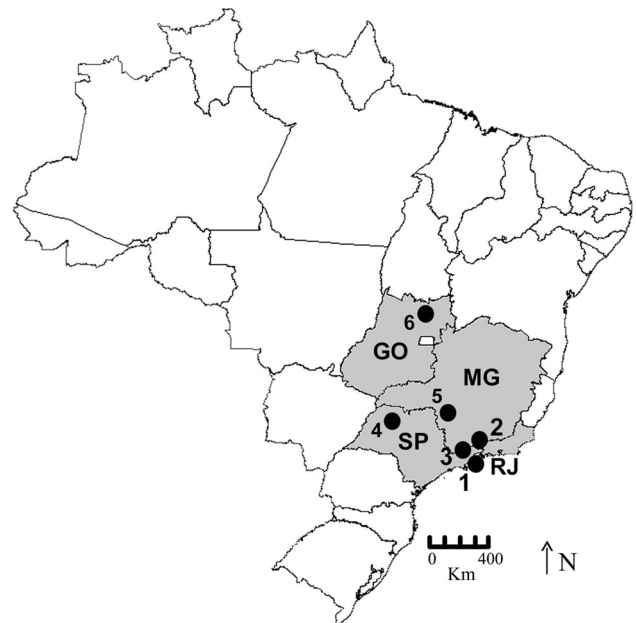


Fig. 1 Map showing sampling locations for Trentepohliales. Brazilian states (gray) where the sampling areas are located (black dots). (1) SMSP—Serra do Mar State Park; 2 INP—Itatiaia National Park; 3 CJR—Campos do Jordão Region; 4 SPFF—São Paulo forest fragments; 5 SCNP—Serra da Canastra National Park; 6 CVNP—Chapada dos Veadeiros National Park)

Electronic supplementary material): savannah, in the states of Minas Gerais (Serra da Canastra National Park—SCNP) and Goiás (Chapada dos Veadeiros National Park—CVNP); and Atlantic rainforest, comprising three ecosystem types—(1) rainforest, in the states of São Paulo (Serra do Mar State Park—SMSP) and Rio de Janeiro (Itatiaia National Park—INP); (2) mixed forest, in the state of São Paulo (Campos do Jordão municipality and surrounding region—CJR); and (3) seasonal semideciduous forest, in the state of São Paulo (forest fragments spread throughout northwestern region of the state—SPFF).

Savannah biome is the second largest biome in Brazil, covering the central territory of the country, and is recognized as the richest savannah of the world (Klink and Machado 2005). It is characterized by predominantly dried climate, outstanding seasonality and herbaceous, shrub and tree formations (Ribeiro and Walter 1998). Atlantic forest covers the littoral region along Brazilian coast (Barbosa and Thomas 2002) and is composed by a set of forest formations (ombrophilous rainforest, mixed forest, semideciduous seasonal forest and deciduous seasonal forest). Due to latitudinal, longitudinal, topography and climate gradients, the Atlantic forest shows changes in vegetation whereas it maintains a degree of homogeneity (Barbosa and Thomas 2002). This study covered three vegetation types in Atlantic forest: rainforest, mixed forest and seasonal semideciduous forest. While rainforest areas

exhibit a warm and wet climate without a dry season, seasonal semideciduous forest presents high temperatures but seasonal climate with a relatively severe dry season (generally from April to September) (Morellato et al. 2000; Oliveira Filho and Fontes 2000). The mixed forest or Araucaria forest is characterized by the presence of the Brazilian pine (*Araucaria angustifolia* Kunze), a gymnosperm, and it is distributed along the subtropical, displaying a wet climate and low temperatures in the coldest months (Lammel et al. 2007).

Sampling protocol – The sampling sites were determined for the presence of Trentepohliales. The distinguishable masses were randomly sought from all available substrates (soil, rocks, barks and leaves) and the specimens were taken with knives and stored in paper bags labeled with the area name, substrate and data.

In the sampling sites, irradiance, substrate pH, temperature and atmospheric humidity were measured in addition to the altitudinal and geographic coordinate (GPS Garmin E-trex Vista) data. Irradiance was measured (quantameter Li-Cor with spherical sensor) close to the algal masses and also in an opened area as near as possible to the sampled mass. In this way, complementarily to the absolute values, the irradiance was also evaluated by the proportion (%) of that value measured close to the algal mass in relation to the value of the opened area. Substrate pH was evaluated by the dissolution of portions of the substrate in distilled/deionized water and reading with pH indicator paper (Merck®) (Strauss et al. 2012). Temperature and atmospheric humidity values were taken using thermo-hygrometer (PeakTech 5090®) close to the algal mass.

The collected specimens were initially examined under stereoscopic microscope (Olympus SZX7) and latter under light microscope (Olympus BX50) coupled with an image capture system (Olympus DP71). The morphological identification was based on Printz (1939), Sarma (1986) and Thompson and Wujek (1997).

Data analyses – Rarefaction curves were made to compare Trentepohliales richness in each area using the species richness per number of populations (Gotelli and Colwell 2001). The order of the samples in the curves was randomized 1000 times, so that each point in the curve corresponded to the average of the accumulated richness in the 1000 curves with confidence interval of 95%. The rarefaction was obtained with EstimateS 8.2.0 software (Colwell 2006).

The similarity of species composition among the areas was evaluated by Jaccard's index, which considers qualitative data (presence/absence). The cluster analysis was performed by applying the algorithms unweight average method (UPGMA), Ward's method and *single linkage*

(Legendre and Legendre 1998). The value of the cophenetic correlation index (r) was calculated to each algorithm, and a cophenetic correlation coefficient was calculated to analyze the extent to which the resulting dendrogram represents the original similarity matrix; this aimed to select the better algorithm for this dataset, i.e., the one that graphically keeps the greatest amount of the information in the triangular matrix. Besides, the consistency of each branch in the dendrogram was assessed by bootstrap randomization, in which the matrix was randomized 1000 times, using the software PAST, v. 3.0 (Hammer et al. 2001).

The influence of the spatial geographic distance among the communities was evaluated through the Mantel matrix correlation test, using similarity matrix based on community composition data (Jaccard index) and the geographic distance matrix. Pairwise distances (in km) among localities were calculated using the geographic coordinates of the areas, adjusted by the earth curvature, as implemented in the "rdist.earth" function in the fields package (Furrer et al. 2012) of software R v. 2.15.1 (R Development Core Team 2012).

Partial linear regression was used to partition the variation in species richness into spatial and environmental components. This method allows to evaluate the influence of pure environmental component, pure spatial and the spatial structuring shared by the environmental data on Trentepohliales species richness (Borcard et al. 1992). The partial regression analysis was carried out with the software SAM (Rangel et al. 2010). The environmental predictors of the richness distribution were altitude, temperature, irradiance and air humidity, and the spatial component was the positive eigenvector produced by principal coordinates of neighbor matrices (PCNM). Due to different measurement units among environmental variables, they were standardized using the Z statistics. Variance inflation factor (VIF) was implemented with variance less than three to reduce the multicollinearity (Zuur et al. 2010).

Results

Floristic survey – Trentepohliales morphospecies were distributed through the four genera: *Cephaleuros* (three species), *Phycopeltis* (nine species), *Printzina* (one species) and *Trentepohlia* (20 species) (Table 1).

* DL^{-1} = diameter/length ratio⁻¹

Cephaleuros Kunze ex Fries

Cephaleuros cf. *karstenii* Schmidle (Fig. 2)

Table 1 Presence (1) and absence (0) of the Trentepohliales morphospecies in the sampled areas

	Atlantic forest				Savanna	
	SMSP	INP	CJR	SPFF	SCNP	CVNP
Pseudoparenchymatous						
<i>Cephaleuros</i> cf. <i>karstenii</i> Schmide	0	0	0	1	0	0
<i>C.</i> cf. <i>parasiticus</i> Karsten	0	0	0	0	1	1
<i>Cephaleuros</i> sp.	1	0	1	1	0	0
<i>Phycopeltis</i> <i>amboinensis</i> Printz ^a	1	1	0	0	0	0
<i>P.</i> <i>arundinacea</i> De Toni	1	1	1	1	1	0
<i>P.</i> <i>epiphyton</i> Millardet ^a	1	0	0	0	0	0
<i>P.</i> <i>flabellata</i> Thompson & Wujek ^a	1	0	0	0	0	0
<i>P.</i> <i>pilosa</i> Thompson & Wujek ^a	1	1	0	0	0	0
<i>P.</i> <i>treubii</i> Karsten ^a	0	1	0	0	0	0
<i>P.</i> <i>vaga</i> Thompson & Wujek ^a	1	1	0	0	0	0
<i>Phycopeltis</i> sp.1	1	1	0	0	0	0
<i>Phycopeltis</i> sp.2	1	0	0	0	0	0
Filamentous						
<i>Printzina</i> <i>lagenifera</i> Thompson & Wujek ^a	0	1	0	0	0	0
<i>Trentepohlia</i> <i>abietina</i> Hansgirg	1	1	1	1	0	0
<i>T.</i> <i>abietina</i> var. <i>tenue</i> Cribb ^a	1	0	1	0	1	0
<i>T.</i> <i>arborum</i> Hariot	1	1	0	0	1	0
<i>T.</i> <i>aurea</i> Martius	0	1	1	1	1	0
<i>T.</i> cf. <i>chapmanii</i> Rindi & López-Bautista ^b	1	0	0	0	0	0
<i>T.</i> <i>depressa</i> Hariot ^a	1	0	0	0	0	0
<i>T.</i> <i>diffracta</i> Hariot	1	0	0	0	0	0
<i>T.</i> <i>dusenii</i> Hariot	0	0	1	0	0	0
<i>T.</i> cf. <i>iolithus</i> Wallroth ^b	0	0	1	0	0	0
<i>T.</i> <i>monilia</i> De Wildemann	0	0	0	1	0	0
<i>T.</i> <i>odorata</i> Wittrock ^a	0	1	0	0	0	0
<i>T.</i> <i>peruana</i> Printz	1	0	0	0	0	0
<i>T.</i> cf. <i>rigidula</i> Hariot	0	0	0	0	1	0
<i>T.</i> <i>umbrina</i> Bornet ^a	0	0	0	0	1	0
<i>Trentepohlia</i> sp.1	1	1	1	1	1	0
<i>Trentepohlia</i> sp.2	1	0	0	0	0	0
<i>Trentepohlia</i> sp.3	0	1	0	0	0	0
<i>Trentepohlia</i> sp.4	0	1	0	0	0	0
<i>Trentepohlia</i> sp.5	1	0	0	1	0	0
<i>Trentepohlia</i> sp.6	0	1	0	0	0	0

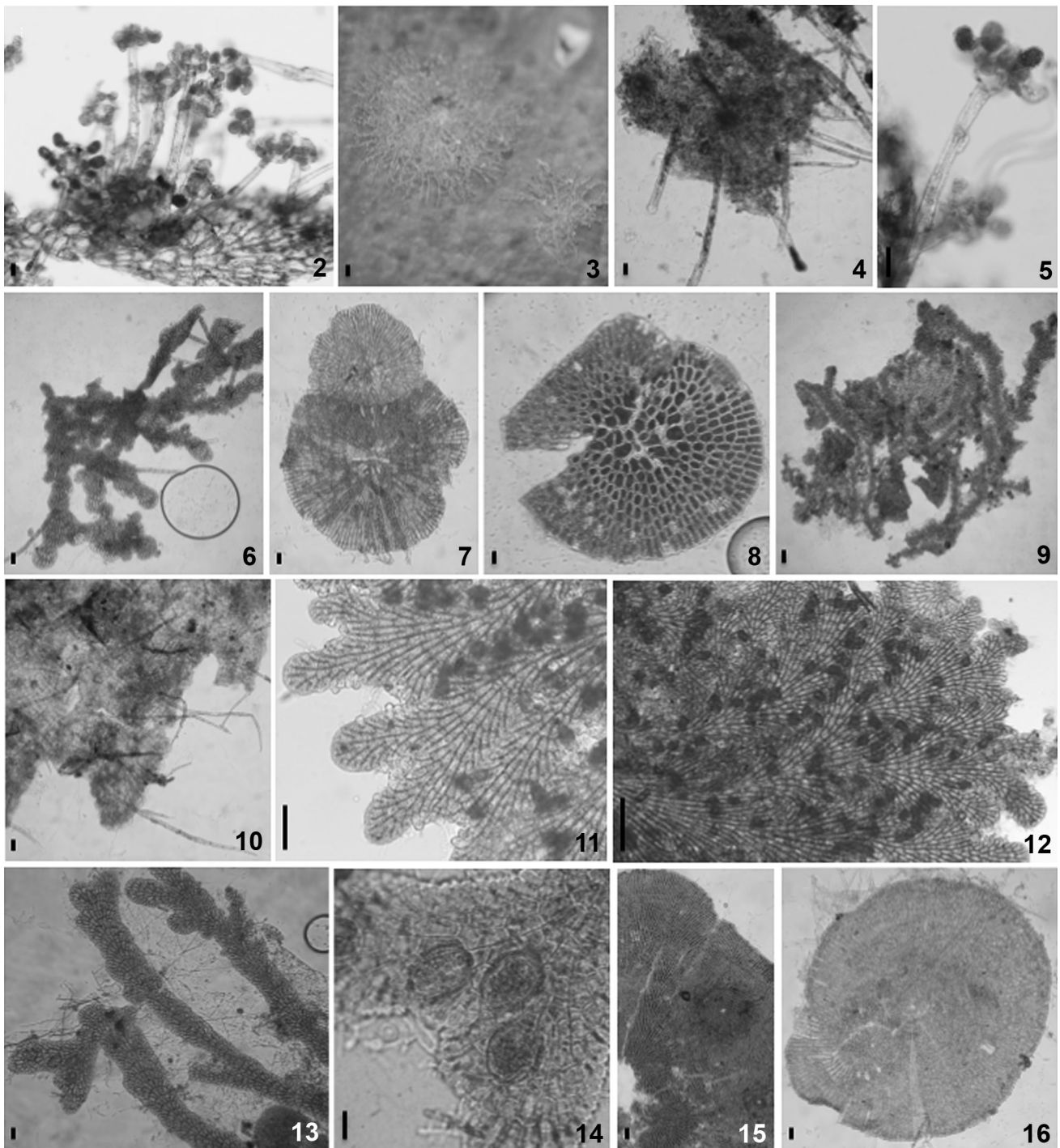
SMSP Serra do Mar State Park, INP Itatiaia National Park, CJR Campos do Jordão Region, SPFF São Paulo forest fragments, SCNP Serra da Canastra National Park and CVNP Chapada dos Veadeiros National Park

^a New records to Brazil, ^b New records to Brazil if identifications are confirmed

Thallus irregular, orange or green, subcuticular on tree leaves; prostrate system formed by dichotomizing branches, cells elliptical or irregular; erect sterile filaments not tapered in the apex, not branched, chloroplast parietal, apical cell rounded, cell cylindrical, 14.4–23.2 μm diam., 57.6–92.0 μm long, $D L^{-1}$ 3.3–5.8; sporangiate lateral developed on top of erect filaments, in clusters of 5–10;

sporangia elliptical, 17.6–19.2 μm diam., 24.0–25.4 μm long, $D L^{-1}$ 1.2–1.4.

The specimens presented morphological features similar to *C. karstenii*, mainly the thallus and the erect sterile filaments; however, details of the cells of the prostrate system could not be observed, due to the penetration of the cells into the host leaf tissue.

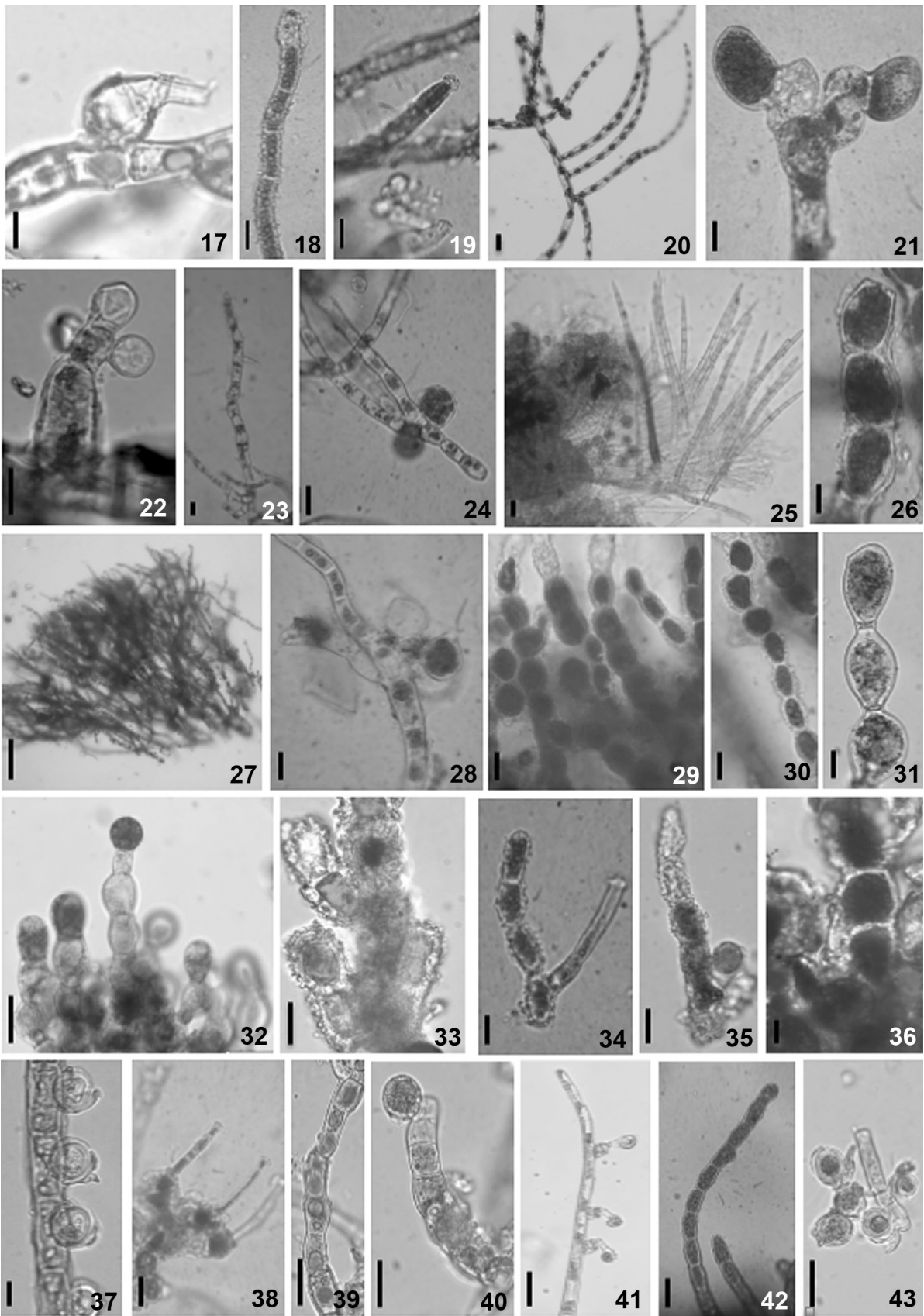


Figs. 2–16 2 *Cephaleuros* cf. *karstenii*; 3 *C.* cf. *parasiticus*; 4, 5 *Cephaleuros* sp.; 6 *Phycopeltis* *amboinensis*; 7 *P.* *arundinacea*; 8 *P.* *epiphyton*; 9 *P.* *flabellata*; 10 *P.* *pilosa*; 11, 12 *P.* *treubii*; 13, 14 *P.* *vaga*; 15 *Phycopeltis* sp.1; 16 *Phycopeltis* sp.2. Scale bars indicate 10 μm

Cephaleuros parasiticus Karsten (Fig. 3)

Thallus rounded, orange, subcuticular on tree leaves; prostrate system irregular formed by dichotomizing branches, cells irregular; erect sterile filaments not tapered in the apex, not branched, chloroplast parietal, apical cell

rounded, cell cylindrical, 12.0–15.2 μm diam., 36.0–64.0 μm long, $D L^{-1}$ 2.4–4.7; sporangiate lateral developed on top of erect filaments, in clusters of 2–5; sporangia elliptical, 20.0–24.0 μm long, 25.6–29.6 μm long, $D L^{-1}$ 1.1–1.4.



◀ **Figs. 17–43** 17 *Printzina lagenifera*; 18 *Trentepohlia abietina*; 19 *T. abietina* var. *tenuis*; 20, 21 *T. arborum*; 22 *T. aurea*; 23, 24 *T. cf. chapmanii*; 25 *T. depressa*; 26 *T. diffracta*; 27, 28 *T. duseinii*; 29, 30 *T. cf. iolithus*; 31, 32 *T. monilia*; 33 *T. odorata*; 34 *T. peruana*; 35 *T. cf. rigidula*; 36 *T. umbrina*; 37 *Trentepohlia* sp.1; 38 *Trentepohlia* sp.2; 39, 40 *Trentepohlia* sp.3; 41 *Trentepohlia* sp.4; 42 *Trentepohlia* sp.5; 43 *Trentepohlia* sp.6. Scale bars indicate 10 µm

Cephaleuros sp. (Figs. 4, 5)

Thallus irregular, orange, subcuticular on tree leaves; prostrate system irregular formed by irregular cells; erect sterile filaments not tapered in the apex, not branched, chloroplast parietal, apical cell rounded, cell cylindrical, 12.0–16.8 µm diam., 61.6–88.0 µm long, RC L⁻¹ 3.7–7.0; sporangiate lateral develop on top of erect filaments, in clusters of 3–8; sporangia elliptical, 16.8–22.4 µm diam., 24.0–32.0 µm long, D L⁻¹ 1.2–1.5.

Phycopeltis Millardet

Phycopeltis amboinensis (Karsten) Printz (Fig. 6)

Thallus ramulated, formed by dichotomizing branches; marginal cells not lobed; cells cylindrical, 4.8–8.0 µm diam., 17.6–21.6 µm long, D L⁻¹ 2.1–3.3; sterile filaments and sporangiophores short, 5–12 cells, not branched, cells cylindrical, 8.0–10.4 µm diam., 16.0–20.0 µm long, D L⁻¹ 1.7–2.0; sporangia elliptical, 12.0–15.2 µm diam., 16.0–20.0 µm long, D L⁻¹ 1.3; gametangia not observed.

Phycopeltis arundinacea (Montagne) De Toni (Fig. 7)

Thallus discoid or irregular, formed by dichotomizing branches; marginal cells lobed; central cells irregular, 4.0–4.8 µm diam., 8.0–12.0 µm long, D L⁻¹ 1.8–2.8; distal cells cylindrical, 6.0–7.2 µm diam., 12.0–19.2 µm long, D L⁻¹ 1.8–3.4; sporangia subspherical, 8.8–9.6 µm diam., 11.2–12.0 µm long, D L⁻¹ 1.2–1.3; gametangia not observed.

Phycopeltis epiphyton Millardet (Fig. 8)

Thallus discoid, formed by dichotomizing branches; marginal cells lobed; central cells irregular; distal cells cylindrical, 4.8–8.8 µm diam., 10.4–12.8 µm long, D L⁻¹ 1.7–2.5; sporangia subspherical, 14.4–16.0 µm diam., 16.8–20.0 µm long; gametangia not observed.

Phycopeltis flabellata Thompson and Wujek (Fig. 9)

Thallus ramulate, formed by dichotomizing branches; marginal cells lobed, 5.6–9.6 µm diam., 16.0–25.6 µm long, D L⁻¹ 1.7–4.4; central cells cylindrical, 4.8–8.8 µm long, 8.0–16.0 µm long, D L⁻¹ 1.2–2.0; sterile erect filaments short, 4–5 cells, not branched, cells cylindrical, 3.2–6.4 µm diam., 4.8–10.4 µm long, D L⁻¹ 1.1–2.0; gametangia globular, 9.6 diam; sporangia not observed.

Phycopeltis pilosa Thompson and Wujek (Fig. 10)

Thallus discoid, formed by dichotomizing branches; marginal cells lobed, 4.8–8.0 µm diam., 11.2–22.4 µm long, D L⁻¹ 2.0–3.5; central cells cylindrical, 4.8–6.4 µm diam., 8.0–14.4 µm long, D L⁻¹ 1.4–2.5; sterile erect filaments long, tapered in the apex, not branched; sporangia elliptical, 14.4 µm diam., 19.4 µm long, D L⁻¹ 1.3; gametangia not observed.

Phycopeltis treubii Karsten (Figs. 11, 12)

Thallus discoid, formed by dichotomizing branches; marginal cells lobed; marginal and central cells cylindrical, 8.0–11.2 µm diam., 20.0–32.0 µm long, D L⁻¹ 2.1–3.0; marginal cells with glandular papillae dorsally; sporangia elliptical, 13.6–15.2 µm diam., 14.4–16.0 µm long, D L⁻¹ 1.3; gametangia not observed.

Phycopeltis vaga Thompson and Wujek (Figs. 13, 14)

Thallus ramulate, formed by dichotomizing branches; ramuli with 2–3 filaments rows; marginal cells lobed; marginal and central cells cylindrical, 3.2–6.4 µm diam., 6.4–13.6 µm long, D L⁻¹ 1.5–3.3; gametangia elliptical, 12.0–16.8 µm diam., 1.6–25.6 µm long, D L⁻¹ 1.2–1.5; sporangia not observed.

Phycopeltis sp.1 (Fig. 15)

Thallus discoid or irregular, formed by dichotomizing branches; yellowish patches in the center of disk; marginal cells lobed; marginal and central cells cylindrical, 3.2–8.0 µm diam., 8.8–13.6 µm long, D L⁻¹ 1.3–3.4; gametangia and sporangia not observed.

Phycopeltis sp.2 (Fig. 16)

Thallus discoid or irregular, formed by dichotomizing branches; marginal cells not lobed; marginal and central cells cylindrical, 5.0–8.0 µm diam., 12.0–20.0 long, D L⁻¹ 1.5–3.4; gametangia and sporangia not observed.

Printzina Thompson and Wujek

Printzina lagenifera (Hildebrand) Thompson and Wujek (Fig. 17)

Filaments forming orange mass; filaments short, 3–10 cells, not tapering in the apex, not branched; chloroplast parietal; apical cell undifferentiated; cells moniliform or cylindrical, 7.0–10.0 µm diam., 8.5–13.3 µm long, D L⁻¹ 0.8–1.7; gametangia lateral or intercalary, globular with a long neck bearing an ostiole, 13.0–17.6 µm diam., 16.0–21.3 µm long, D L⁻¹ 1.1–1.3; sporangia not observed.

Trentepohlia Martius

Trentepohlia abietina (Flotow) Hansgirg (Fig. 18)

Filaments forming a cottony mass, orange; filaments long, not tapered in the apex, branches abundant, usually in 90°, chloroplast parietal, apical cells rounded, cells

cylindrical, 6.8–12.0 μm diam., 12.0–29.6 μm long, $D L^{-1}$ 1.5–3.2; gametangia single, lateral or apical, globular, 17.6–36.0 μm diam., 13.6–36.0 μm long, $D L^{-1}$ 0.8–1.1; sporangia single, globular, 21.6 μm diam., 19.2 μm long, $D L^{-1}$ 1.1.

Trentepohlia abietina (Flotow) Hansgirg var. *tenuis* (Zeller) Cribb (Fig. 19)

Filaments forming rounded patches, orange; thallus differentiated in prostrate and erect systems; prostrate system pseudoparenchymatous, cells elliptic, 7.2–9.6 μm diam., 7.2–11.2 μm long, $D L^{-1}$ 0.9–1.3; erect filaments not tapering in the apex, rarely branched; apical cells conic rounded with an apical cap, cells cylindrical to elliptic, 4.0–10.0 μm diam., 11.2–26.4 μm long, $D L^{-1}$ 1.5–4.3; gametangia single, globular, lateral, 8.8–11.2 μm diam., 8.8–11.2 μm long, $D L^{-1}$ 1.0; sporangia not observed.

Trentepohlia arborum (Agardh) Hariot (Figs. 20, 21)

Filaments forming a cottony mass, orange or green; filaments long, not tapering in the apex, branches in 90° ; chloroplast discoid; apical cell rounded to pointed; cells cylindrical, 12.8–21.6 μm diam., 32.0–67.2 μm , $D L^{-1}$ 2.3–3.5; gametangia single, lateral, rounded, 25.6–47.2 μm diam., 25.6–47.2 μm long, $D L^{-1}$ 0.9–1.3; sporangia in clusters of 2–5, elliptic, 17.6–28.0 μm diam., 20.8–35.6 μm long.

Trentepohlia aurea (Linnaeus) Martius (Fig. 22)

Filaments forming a cottony mass, orange or green; filaments long, not tapered in the apex, branches in 90° or less; lateral branches with cylindrical or barrel-shaped cells; chloroplast parietal; apical cells rounded; cells cylindrical, 14.4–27.2 μm diam., 28.0–52.0 μm long, $D L^{-1}$ 1.7–2.8; gametangia single or in cluster of 2, lateral, globular, 28.0–37.4 μm diam., 24.0–32.0 μm long, $D L^{-1}$ 0.8–1.0; sporangia single or in clusters of 2–5, elliptic, 17.6–28.0 μm diam., 20.8–35.6 μm long, $D L^{-1}$ 0.9–1.5.

Trentepohlia cf. *chapmanii* Rindi and López-Bautista (Figs. 23, 24)

Filaments forming a mat, yellow; thallus differentiated in prostrate and erect systems; prostrate system pseudoparenchymatous, cells irregular, 8.0–11.0 μm diam., 8.0–16.8 μm long; erect filaments long, not tapered in the apex, rarely branched; apical cells pointed; cells cylindrical or elliptic, 4.0–7.2 μm diam., 8.8–15.2 μm long, $D L^{-1}$ 1.8–3.0; gametangia lateral or apical, oval, 12.0–17.0 μm diam., 14.4–21.6 μm long, $D L^{-1}$ 1.0–1.7; sporangia not observed.

The population presented morphology correspondent to *T. chapmanii*; however, it possess erect filaments longer than that described by Rindi and López-Bautista (2007).

Trentepohlia depressa (Müller Arg.) Hariot (Fig. 25)

Filaments forming rounded patches, orange; thallus differentiated in prostrate and erect systems; prostrate system pseudoparenchymatous, cells cylindrical, 5.0–6.0 μm diam., 12.0–17.0 μm long, $D L^{-1}$ 2.5–3.0; erect filaments long, not tapered in the apex, not branched, apical cell pointed, cells cylindrical, 2.4–4.0 μm diam., 8.0–14.4 μm long, $D L^{-1}$ 2.6–4.0; gametangia born in the base of the erect filament, single, elliptic, 11.2–13.6 μm diam., 16.0–21.6 μm long, $D L^{-1}$ 1.2–1.9; sporangia not observed.

Trentepohlia diffracta (Krempelhüner) Hariot (Fig. 26)

Filaments forming crustose mass, orange; filaments long, not tapered in the apex, branches short, 1–3 cells, chloroplast parietal, apical cells rounded, cells cylindrical or elliptic, 20.8–26.7 μm diam., 26.1–38.9 μm long, $D L^{-1}$ 1.4–3.0; gametangia single, apical, globular, 30.2–45.3 μm diam., 33.1–53.30 μm long, $D L^{-1}$ 0.9–1.1; sporangia not observed.

Trentepohlia dusenii Hariot (Figs. 27, 28)

Filaments forming cottony mass, green; filaments long, not tapered in the apex, chloroplast parietal, apical cell rounded, cells cylindrical, 7.2–12.8 μm diam., 13.6–28.0 μm long, $D L^{-1}$ 1.4–3.0; gametangia single, lateral, globular, 13.6 μm diam., 16.0 μm long, $D L^{-1}$ 1.2; sporangia single, globular, 16.0–20.0 μm diam.

Trentepohlia cf. *iolithus* (Linnaeus) Wallroth (Figs. 29, 30)

Filaments forming a crustose mass, yellowish; filaments long, not tapered in the apex, not branched, chloroplast parietal, apical cell elliptical, cells elliptical, 6.0–20.0 μm diam., 32.0–40.0 μm long, $D L^{-1}$ 1.7–3.6; gametangia and sporangia not observed.

The population presented vegetative features similar to *T. iolithus* (Printz 1939); however, for correct identification of this species, it is necessary the presence of reproductive structures.

Trentepohlia monilia De Wildemann (Figs. 31, 32)

Filaments forming a cottony mass, green; filaments short, 7–10 cells, not tapered in the apex, chloroplast discoid, apical cells moniliform, cells moniliform, 17.6–26.4 μm diam., 21.6–36.0 μm long, $D L^{-1}$ 1.1–1.7; sporangia and gametangia not observed.

Trentepohlia odorata (Wiggers) Wittrock (Fig. 33)

Filaments forming a crustose mass, orange; filaments long, not tapered in the apex, chloroplast parietal, apical cells cylindrical or elliptic, cells cylindrical or elliptic,

10.4–16.0 µm diam., 12.0–20.8 µm long, $D L^{-1}$ 1.0–1.8; gametangia single, lateral, globular, 30.2–45.3 µm diam., 33.1–53.3 µm long, $D L^{-1}$ 0.9–1.1; sporangia not observed.

Trentepohlia peruana (Kützing) Printz (Fig. 34)

Filaments forming patches, orange; filaments short, not tapered in the apex, rarely or not branched, apical cells elliptic, cells elliptic, 6.4–12.0 µm diam., 8.8–26.4 µm long, $D L^{-1}$ 1.3–2.0; unicell hairs, hyaline born in the middle of the cell; gametangia single, apical or intercalary, elliptical, 13.6–16.0 µm diam., 12.8–16.0 µm long, $D L^{-1}$ 0.85–1.1; sporangia not observed.

Trentepohlia cf. *rigidula* (J. Müller) Hariot (Fig. 35)

Filaments forming crustose mass, orange; filaments long, not tapered in the apex, rarely branched, chloroplast parietal, apical cell rounded, cell wall ornamented, cells elliptic, 6.4–10.4 µm diam., 13.6–16.0 µm long, $D L^{-1}$ 1.5–2.6; gametangia single, lateral, globular, 12.0–15.2 µm diam., 13.6–18.4 µm long, RCL^{-1} 1.0–1.3; sporangia not observed.

Although these specimens had presented the greatest part of morphological features correspondent to *T. rigidula*, they showed smaller cells than the descriptions found in the literature.

Trentepohlia umbrina (Kützing) Bornet (Fig. 36)

Filaments forming a crustose mass, orange or reddish; filaments short, until five cells, not tapered in the apex, rarely branched, chloroplast parietal, apical cells rounded or elliptical, cells rounded or elliptical, 9.6–20.0 µm diam., 14.4–21.6 µm long, $D L^{-1}$ 0.8–1.8; sporangia single, globular, 20.0 µm diam.; gametangia not observed.

Trentepohlia sp.1 (Fig. 37)

Filaments forming a cottony mass, brownish; filaments long, not tapered in the apex, branches in 90°, chloroplast discoid, apical cell rounded, cell wall colored, thick, cells

cylindrical, 12.8–15.2 µm diam., 20.8–31.2 µm long, $D L^{-1}$ 1.7–2.0; gametangia single, globular, 16.0–20.8 µm diam., 13.6–21.6 µm long, $D L^{-1}$ 0.8–1.1; sporangia not observed.

Trentepohlia sp.2 (Fig. 38)

Filaments forming patches, orange; thallus differentiated in prostrate and erect systems; prostrate system pseudo-parenchymatous, cells rounded, 8.8–15.2 µm diam., 8.8–14.4 µm long, $D L^{-1}$ 0.9–1.1; erect filaments short, 3–5 cells, not tapered in the apex, not branched, chloroplast parietal, apical cell rounded, cells cylindrical, 2.4–4.0 µm diam., 10.4–25.6 µm long, $D L^{-1}$ 3.2–7.2; gametangia and sporangia not observed.

Trentepohlia sp.3 (Figs. 39, 40)

Filaments forming a mat, yellow; thallus differentiated in prostrate and erect systems; prostrate system pseudo-parenchymatous, cells irregular; erect system formed by filaments tapered in the apex, with few branches, chloroplast parietal, apical cell pointed, cells cylindrical, 4.0–12.0 µm diam., 17.6–52.0 µm long, $D L^{-1}$ 1.9–8.1; sporangia globular or oval, 12.0–20.0 µm diam., 12.0–24.0 µm long, $D L^{-1}$ 1.0–1.3; gametangia not observed.

Trentepohlia sp.4 (Fig. 41)

Filaments forming a cottony mass, green; thallus differentiated in prostrate and erect systems; prostrate system pseudoparenchymatous, cells rounded or irregular; erect system formed by filaments tapering in the apex, very branched, chloroplast parietal, apical cell rounded or pointed; cells cylindrical, 12.0–19.2 µm diam., 28.8–57.6 µm long, $D L^{-1}$ 1.8–3.3; sporangia single or in cluster of 2–5, globular, 13.6–22.4 µm diam.; gametangia not observed.

Trentepohlia sp.5 (Fig. 42)

Filaments forming a cottony mass, orange; thallus differentiated in prostrate and erect systems; prostrate system

Table 2 Species richness and environmental conditions of the studied areas

	S	Alt (m)	Temp	AH	Irrad
SMSP	20 (60.6%)	396.1	24.0 (1.3)	91.2 (26.6)	71.4 (1273.5)
INP	16 (48.5%)	1418.8	18.6 (11.5)	63.5 (99.5)	37.3 (900.7)
CJR	9 (27.3%)	1620.7	19.8 (24.5)	56.4 (67.1)	43.1 (1457.8)
SPFF	8 (24.2%)	501.2	25.1 (29.7)	66.6 (109.5)	51.1 (706.7)
SCNP	7 (21.2%)	1127.9	26.1 (22.5)	59.2 (126.2)	80.9 (901.3)
CVNP	1 (3.0%)	913.4	28.6 (43.4)	57.9 (214.9)	100.0 (0)

S number of morphospecies (=richness; percentage in relation to the total number of morphospecies recorded in all areas—33—in parenthesis), Alt altitude average (meters above sea level) of the localities sampled in each area, Temp temperature average (variance in parenthesis), AH air humidity average (variance in parenthesis), Irrad irradiance average (variance in parenthesis). SMSP Serra do Mar State Park, INP Itatiaia National Park, CJR Campos do Jordão Region, SPFF São Paulo forest fragments, SCNP Serra da Canastra National Park and CVNP Chapada dos Veadeiros National Park

Fig. 44 Rarefaction curves of the sampled areas in *black* and standard deviation in *gray* (SMSP—Serra do Mar State Park, INP—Itatiaia National Park, CJR—Campos do Jordão Region, SPFF—São Paulo forest fragments, SCNP—Serra da Canastra National Park and CVNP—Chapada dos Veadeiros National Park)

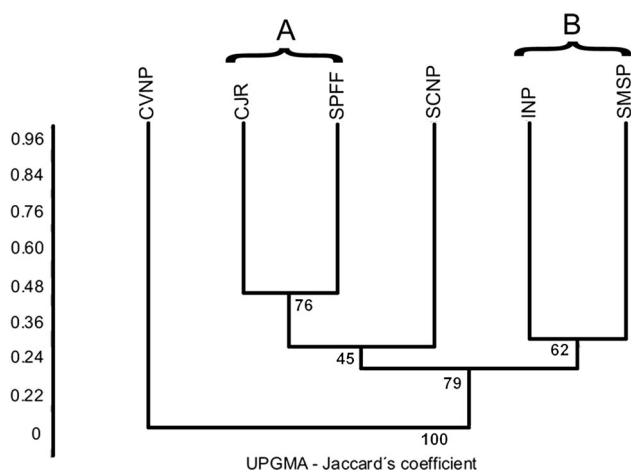
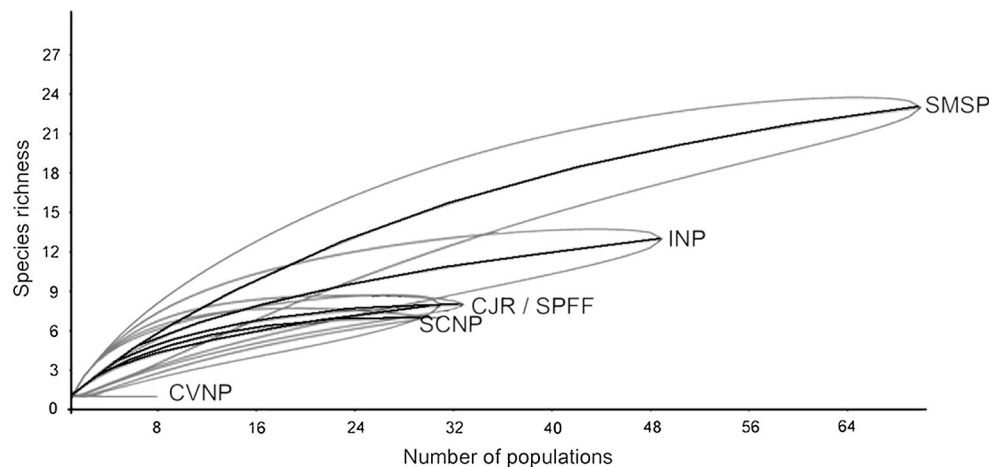


Fig. 45 Cluster analysis of the floristic composition of Trentepohliales using Jaccard's index and UPGMA algorithm (SMSP—Serra do Mar State Park, INP—Itatiaia National Park, CJR—Campos do Jordão Region, SPFF—São Paulo forest fragments, SCNP—Serra da Canastra National Park and CVNP—Chapada dos Veadeiros National Park). **A**, **B** Clusters formed by the most similar areas in species composition. The value of the cophenetic correlation coefficient (r) was 0.96

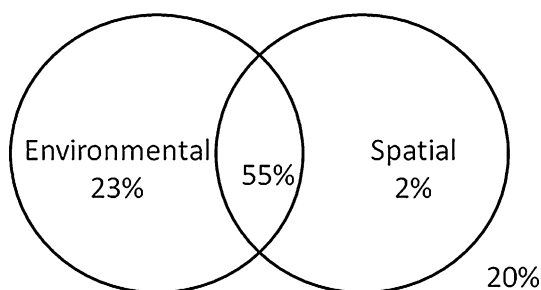


Fig. 46 Partial linear regression of the variation in trentepohlialean species richness into spatial and environmental components

pseudoparenchymatous, cells irregular; erect system formed by long filaments, not tapering in the apex, very branched, chloroplast parietal, apical cell rounded, cells

moniliform, cylindrical or irregular, 6.4–8.8 μm diam., 8.0–16.0 μm long, $D L^{-1}$ 1.2–2.5; gametangia lateral, globular, 15.2–17.6 μm diam., 16.0 μm long; sporangia not observed.

Trentepohlia sp.6 (Fig. 43)

Filaments forming mat, yellow or green; thallus differentiated in prostrate and erect systems; prostrate system pseudoparenchymatous, cells rounded or irregular, 2.0–12.0 μm diam., 8.0–15.2 μm long, $D L^{-1}$ 1.0–2.1; erect system formed by short filaments, 3–5 cells, not tapering in the apex, not branched; apical cell irregular, cells cylindrical, 6.4–7.2 μm diam., 11.2–23.2 μm long, $D L^{-1}$ 2.0–5.0; gametangia and sporangia not observed.

Species composition – Thirty-three morphospecies of Trentepohliales were found considering all localities studied (Table 1), being eleven considered new records to Brazil. Seventeen taxa (51.5%) were found in just one location and the most frequent morphospecies was *Trentepohlia* sp.1, being recorded in five of the six sampled areas and none morphospecies occurred in all areas. Regarding the morphology, 21 morphospecies were filamentous (Figs. 2–16): one species of *Printzina* and twenty species of *Trentepohlia*; and twelve taxa were pseudoparenchymatous (Figs. 17–43): three *Cephaleuros* and nine *Phycopeltis* species with eight new taxonomic records to Brazil (Table 1). Some taxa presented morphologically distinct from the already described species (*Cephaleuros* sp.1, *Phycopeltis* sp.1, *Phycopeltis* sp.2, *Trentepohlia* sp.1, *Trentepohlia* sp.2, *Trentepohlia* sp.3, *Trentepohlia* sp.4, *Trentepohlia* sp.5 and *Trentepohlia* sp.6), and probably constitute new species of Trentepohliales.

Rainforest regions showed the highest species richness (26 species), while savanna (eight species in both areas) and seasonal semideciduous forest (eight species) had low species richness. SMSP was the richest species area, with

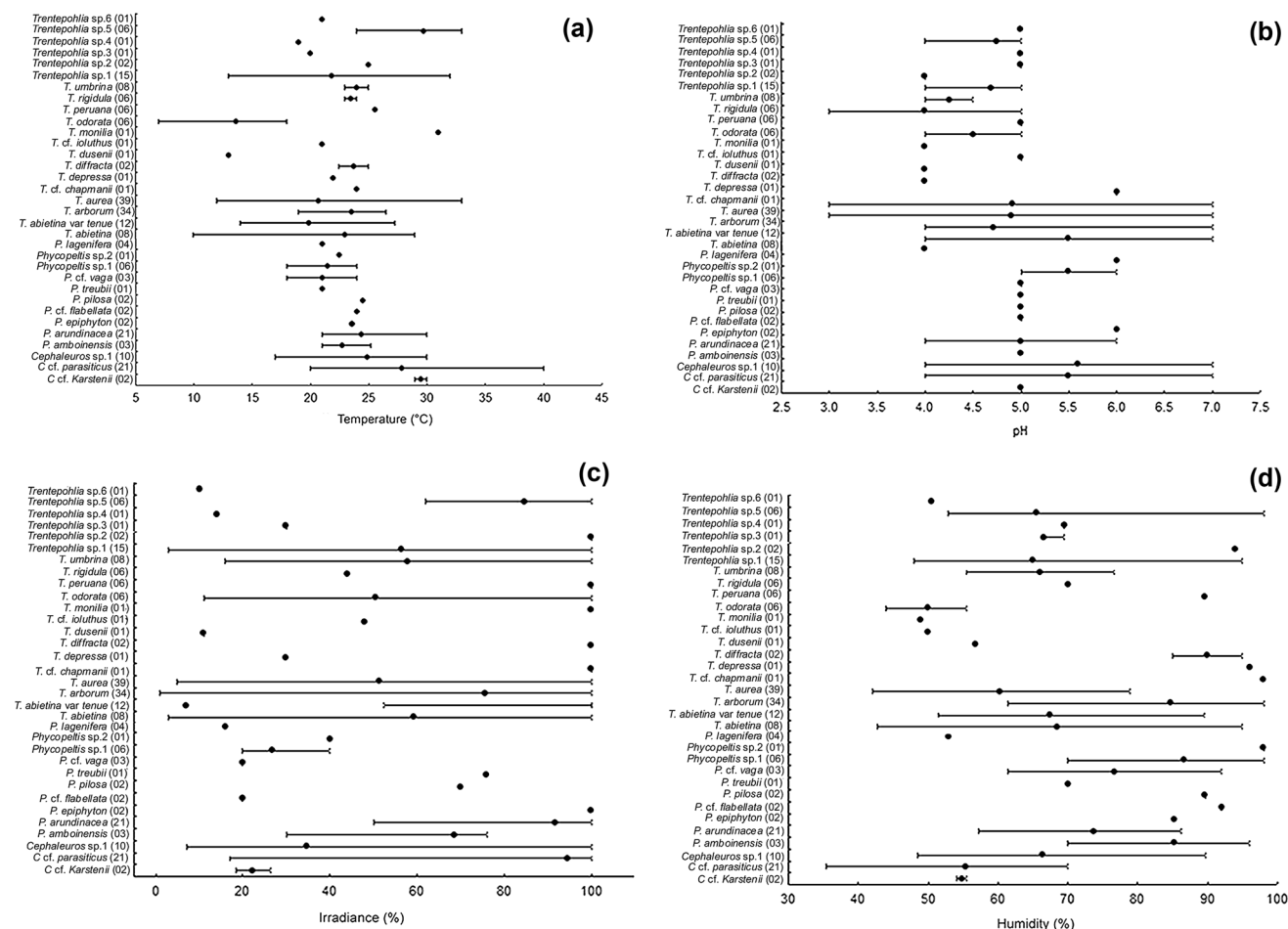


Fig. 47 Range of occurrence values of the trentepohlialean species found according to the environmental variables evaluated. **a** Temperature; **b** substrate pH; **c** irradiance; **d** humidity (*In parenthesis* = the number of populations of each species, *black dots* = average, *bars* = minimum and maximum values)

20 morphospecies (60.6% of the total recorded in all the areas), followed by INP, CJR, SPFF and SCNP, with seven morphospecies, and CVNP, with only one morphospecies (Table 2). The rarefaction curve showed that the highest Trentepohliales species richness was found in the rainforest areas, with highest species richness housed in the SMSP followed by INP (Fig. 44). Similar values of species richness were found in the other localities (SCNP, SPFF and CJR). Also from the rarefaction curve it is high probability that more Trentepohliales species are recorded in rainforest areas, since the curve did not reach the asymptote.

The dendrogram based on floristic composition reveals the clear separation of CVNP from the other areas, whereas the remaining localities composed two clusters (Fig. 45). CJR and SPFF grouped as the most similar areas among all sampled areas (around 45% of similarity; Fig. 45, cluster A), with the savanna SCNP positioned close to these areas, but with lower similarity. Rainforest areas (SMSP and INP) grouped (Fig. 45, cluster B) with about 30% of the floristic similarity.

The result of Mantel test indicated that the differences in communities' composition were positively related to the distance among the areas, ($r = 0.74$; $P = 0.05$). The greater the geographical distance between the areas, the greater the difference in the composition of the communities, thereby presenting distance decay similarity pattern.

Influence of the environmental variables on the species distribution – Trentepohliales were found growing under diversified environmental conditions (Table 2), however, neither environmental nor spatial factors explained the richness variation ($r_{adj}^2 = 0.66$; $F = 2.657$; $P = 0.07$; Fig. 46). Nevertheless, it is noteworthy that the spatially structured environmental variation accounts for the greatest fraction (55%) of variation in species richness.

Rainforest regions presented milder temperatures compared to savanna regions and seasonal semideciduous forest (Table 2). In general, the temperature of the localities sampled ranged between 15 and 30 °C, while some species were recorded in more extreme conditions (populations of

the *C. cf. parasiticus* were observed growing in 40 °C and *T. odorata* in areas with temperatures reaching 6 °C (Fig. 47a).

The distribution of the species varied in relation to the substrate pH, being that the morphospecies occurred in substrates with pH ranging from 3.0 to 7.0, and the majority of the species was found growing in acidic substrate (5.0; Fig. 47b).

The species displayed different distribution between shaded and exposed areas (Fig. 47c). While most *Trentepohlia* species (filamentous) occurred in exposed areas (above 50% irradiance), most of the *Phycopeltis* species (pseudoparenchymatous) occurred only inside the forest, under the canopy, with low values of irradiance. Among the *Phycopeltis* species, only *P. arundinacea* had occurred also in exposed environments.

Most of the species (87.9%) was observed in environments with humidity above 50%, whereas some species, as *T. abietina*, *T. aurea* and *T. odorata*, were also found above 40% humidity. *Cephaleuros cf. parasiticus* was the unique species recorded in environments with air humidity below 40% (Fig. 47d).

Discussion

This study revealed a rich flora of Trentepohliales (33 morphospecies) in the studied areas, which can be considered similar to other tropical regions (e.g., 28 taxa were recorded in rainforest from French Guiana by Rindi and López-Bautista 2008, and 24, in rainforest from Panama by Rindi et al. 2008). Although the present study had been carried out in different vegetation formations from different geographic Brazilian regions, most of the Trentepohliales diversity was recorded in rainforest areas, reaffirming the great potential of these regions to harbor terrestrial algal communities, of which Trentepohliales representatives compose a large portion of that diversity (López-Bautista et al. 2007).

Considering the vegetation formations sampled, rainforest regions showed the highest species richness, while savanna and seasonal semideciduous forest regions presented low species richness. The results of partial linear regression revealed that the spatial features (geographical distances among the areas) jointly with environmental features (climatic conditions) drove the Trentepohliales' species richness gradient. Indeed, the rainforest areas sampled are geographically close to each other, presenting similar climatic conditions, which enable these localities to host a similar species richness, although their species composition presented differences.

Light intensity and atmospheric humidity have been assigned as the most important factors influencing growth

and development of the terrestrial algae (Fritsch 1907; Islam 1960). In the present study, the greatest richness of Trentepohliales was observed inside of rainforest areas, which are characterized by low light and high humidity. However, exposed areas apparently offer more suitable conditions to the growth in abundance of some *Trentepohlia* species. Neustupa and Škaloud (2008) found that light was the most important factor to the richness and composition of the corticolous algae and cyanobacteria in mountainous regions of Indonesia and Trentepohliales was found growing on trunks, specially, in exposed microhabitats. Given the ecosystems sampled, filamentous Trentepohliales (*Trentepohlia* and *Printzina*) were poorly recorded inside the forest areas with dense canopy cover, whereas *Phycopeltis* was greatly observed in such shaded areas, growing on leaves. The occurrence of the *Phycopeltis* in shaded and wet environments was observed by Rindi and López-Bautista (2008) in rainforest areas of French Guiana. Most filamentous morphotypes were found mostly in exposed areas, which probably represents irradiance-tolerant organisms. *Cephaleuros cf. parasiticus* was frequent in savanna regions (areas characterized by low humidity and high temperatures), which may be related to the microhabitat that this species occurs, since it usually inhabits endophytic microhabitats (Thompson and Wujek 1997), which promote more protected spaces and reduce the water loss to the environment.

Trentepohliales occurrence exhibited differences according to the temperature and pH variance. Most populations were recorded between 16 and 32 °C, with few species occurring in the extremes 6 or 40 °C. Neustupa and Škaloud (2013) observed that the abundance of Trentepohliales was positively related to warmer and/or more humid climatic conditions. In relation to pH, it was firstly noticed by the cited authors that Trentepohliales distribution in temperate regions of Europe was most strongly affected by the pH of the bark and their abundance increased in high pH values of the barks. In the present study, however, the pH of the diverse substrates occupied by the Trentepohliales presented always acid or neutral values (3–7), showing that Trentepohliales may respond differently to the environmental factors in temperate and tropical regions.

The species composition of Trentepohliales of the areas studied revealed a distance decay of similarity pattern (Nekola and White 1999). In the present study, the rise of the dissimilarity in species composition followed the increase in the distance among the areas. The pattern of distance decay of similarity has already been recorded for several taxa (Soininen et al. 2007), including diatoms (Wetzel et al. 2012) and plants (Nekola and White 1999), but this result represents the first record of this pattern for terrestrial algae. The dispersal limitation is considered one

of the main mechanisms that can generate this pattern (Nekola and White 1999; Wetzel et al. 2012). Trentepohliales may easily be disseminated by wind, rain and insects, and their zooporangia require wet environments to release the water-dependent zoospores (Thompson and Wujek 1997). Although dispersion should not represent a barrier for some trentepohlialeans considering that there is a reasonable number of cosmopolitan species, the increasing of distance appears to be important to the changes in species composition, probably due to the specific requirements of each species, the dispersal limitation for some species, or both occurring jointly. In general, the composition of Trentepohliales was greatly divergent among different sampled areas, wherein the majority of the species (51.5% of the species) revealed a restrict distribution, occurring in only one vegetation formation.

In synthesis, Atlantic rainforest areas tend to present higher Trentepohliales species richness than savanna, probably due to irradiance levels and humidity conditions. Beside the richness, the species composition of the trentepohlialean assemblages also displayed differences among the areas due to the restrict occurrence of most species, resulting in distance decay pattern and suggesting that there are species-specific requirements determining their composition. Trentepohliales diversity in warm and wet regions was already target of previous studies (e.g., Rindi and López-Bautista 2008), but the present one was the broadest carried out in Neotropical region, since it encompasses different geographical regions with a wide environmental variation and ecosystem types, contributing to the understanding of the diversity and distribution pattern of this algal group across ecosystems of a Neotropical region.

Acknowledgements Authors are grateful to Fapesp (2008/10740-3, 2009/03587-7, 2012/19468-0) for the Ph.D. fellowship to NMLS and financial support.

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