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Using functional approaches to study phytoplankton communities in a temperate region exposed to tropical species dispersal

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Abstract Functional characteristics play an important role in shaping phytoplankton distributions. This approach can help to explain the success of tropical taxa in temperate ecosystems. We used functional groups (FG) and functional traits (FT) to assess the phytoplankton distribution in five temperate lakes exposed to tropical taxa dispersal. We ran redundancy analyses to assess the relationship between each functional classification and the environment. Both approaches showed similar variance of the phytoplankton biomass and responded to similar environmental variables. The FG approach separated lakes by trophic status (total phosphorus: TP), while the FT approach reflected the lakes' hydromorphology (conductivity, depth, mixing regime). The traits of motility and mixotrophy coincided with low mixing and high light. Tropical taxa were dominant in two lakes, rare in one and absent in two lakes. When dominant, tropical taxa exerted an overwhelming effect on phytoplankton biomass and community composition, and contributed to foam occurrences. The success of tropical taxa in only two lakes seems related to the interplay of their traits (accessory pigments, morphology) and the prevailing environmental filters (low light, deep mixing, and intermediate TP). Their rarity or absence in the other lakes evidences how traits can increase fitness in one environment but not in other.

Keywords Phytoplankton · Functional groups · Functional traits · Tropical taxa · Temperate lakes

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Introduction

Ecosystem properties depend greatly on the functional characteristics of the organisms present and their distribution and abundance over space and time (Hooper et al., 2005). The opposite is also true, as

strong environmental filters can limit functional composition to a relatively restricted range of characteristics (Hooper et al., 2005). Phytoplankton ecology seeks to unravel the mechanisms responsible for patterns in species distribution and explain why certain species or functional traits are more favored than others in the assembly of communities. The occurrence of a dominant phytoplankton species depends upon a complex combination of factors, including the physical structure of the water column, nutrient availability, and grazing pressure (Reynolds, 1980). Likewise, functional traits to a large extent define the ecological niche of a species, determining their distribution along environmental gradients (Litchman & Klausmeier, 2008). Hence, the identity of a dominant species is tightly linked to its traits and the interplay of the traits with the prevailing biotic and abiotic factors.

Phytoplankton species adopt diverse strategies in response to environmental forces. These are related to morphological (size, shape) and physiological (nutritional status, buoyancy) changes which influence essential processes such as growth, sedimentation, and nutrient acquisition (Reynolds, 2006). Compared to individual species responses, functional characteristics provide a better understanding of how communities respond to the environment (Souza et al., 2008) and vice versa. Functional approaches reduce system complexity by aggregating species by some shared role they play in a particular ecosystem (Simberloff & Dayan, 1991). There is current interest and debate in the assessment of phytoplankton ecology using functional approaches. A commonly utilized functional scheme is the phytoplankton functional groups (FG) proposed by Reynolds et al. (2002), with more than 130 citations reviewed in Padisák et al. (2009). This FG scheme assembles planktonic and meroplanktonic taxa into 40 groups (coda) (updated by Padisák et al., 2009). Each coda pools species which respond in similar way to a suite of ecological conditions, which may or not share phylogenies or morphologies. The FG approach has been widely used as a tool for studying phytoplankton ecology in lakes, reservoirs, and rivers in multiple geographical regions (Huszar et al., 2003; Devercelli, 2006; Caputo et al., 2008; Abonyi et al., 2012). Further advances in assessing phytoplankton function were proposed in terms of functional traits (FT) (Weithoff, 2003; Litchman & Klausmeier, 2008; Kruk et al., 2010). An important

step in the trait-based approaches is translating traits into fitness (McGill et al., 2006). Litchman & Klausmeier (2008) classified phytoplankton FT in terms of ecological function (reproduction, resource acquisition and grazing resistance) and type (morphological, physiological, behavioral and life history). Phytoplankton FT are easily identified and quantifiable, which makes this community an ideal model for exploring trait–trait and trait–environment relations (Litchman et al., 2010). The FT approach is acknowledged as a useful tool in ecology to explain and predict species distribution along environmental gradients (Litchman et al., 2010), and have been used by many researchers (Naselli-Flores & Barone, 2007; O'Farrell et al., 2007; Salmaso & Padisák, 2007). However, studies jointly assessing phytoplankton ecology in terms of FG and FT and their interplay with the environment are scarce (Izaguirre et al., 2012a). Moreover, Kruk et al. (2011) showed that FT better explain the phytoplankton variance from environmental conditions than the FG approach. It is still unclear if the FG and FT approaches provide similar, different or complementary information in explaining phytoplankton distributions.

The Aquitaine region, located along the southwest coast of France, encompasses lakes with different hydromorphological characteristics (connectivity, depth, surface, trophic status). Studies on phytoplankton in the area are scarce and focused on floristic lists (Capdevielle & Couté, 1980; Capdevielle, 1982; Capdevielle, 1985; Cellamare et al., 2010). This underscores the need for assessing the ecology of phytoplankton in the region. Interestingly, some phytoplankton taxa previously reported only in African lakes and other tropical areas are dominant in some of these systems. These tropical species are probably introduced by migratory birds as the region is an important corridor and staging post for bird migration in Europe (Cellamare et al., 2010). Moreover, foam formations are recurrently observed on the shores of several of these coastal Aquitaine lakes, decreasing their recreational value. It is unclear if the tropical phytoplankton is implicated in the production of the foams. It is also unknown which traits govern the fitness of these species in the region, the environmental conditions favoring their success and the consequences of their dominance in the ecosystem.

In this study, we used the FG sensu Reynolds et al. (2002) (updated by Padisák et al., 2009) and FT sensu

Fig. 1 Location of the five lakes studied in the Aquitaine region. The subset shows an example of the three sampling sites per lake (*1* pelagic deepest area free of vegetation, *2* vegetated western littoral, *3* vegetated eastern littoral)
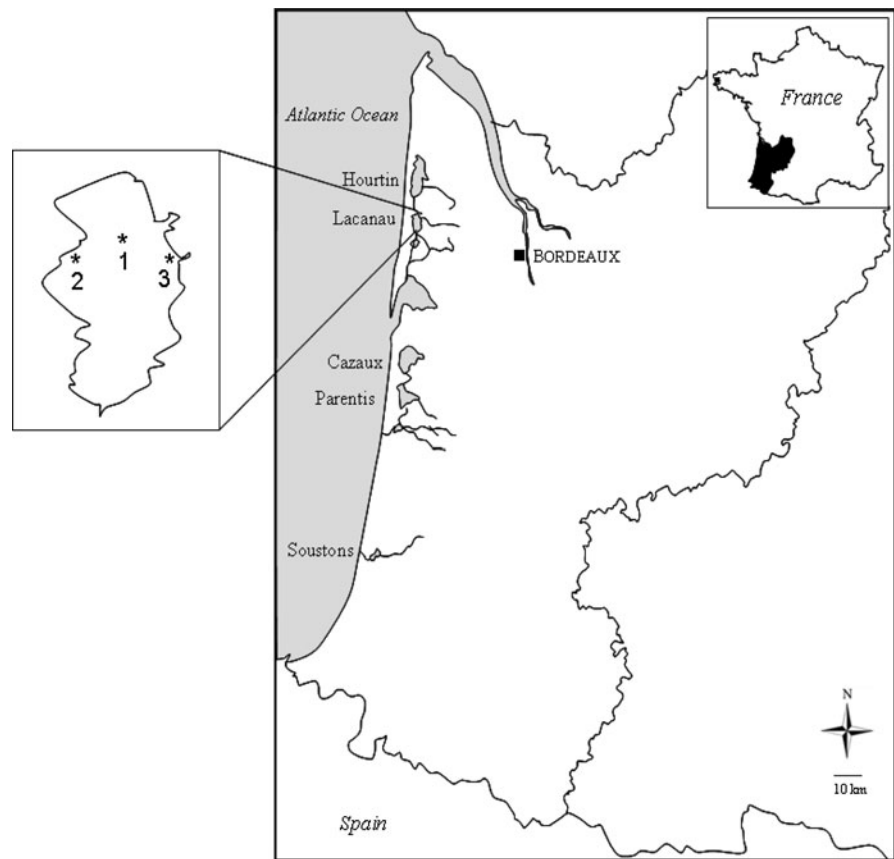
Weithoff ([2003](#)) and Litchman & Klausmeier ([2008](#)) for assessing the phytoplankton distribution in lakes located in the French Aquitaine region, and the success and impact of tropical taxa in this temperate area. We aimed to answer the following questions:

(1) Do the FG and FT explain the distribution of phytoplankton in the region? Is the variance explained by both approaches similar, different or complementary? Can we identify functional–environmental responses for the phytoplankton community?

(2) Are tropical taxa successful in all lakes in the region? What is the impact of these species in the temperate phytoplankton community? What are the environmental variables (connectivity, trophic status, abiotic forcing) and traits (resource acquisition, predation avoidance or reproduction) that favor the dominance of the tropical species?

(3) Are tropical taxa responsible for the foam occurrences?

Materials and methods

Study sites

We studied five freshwater lakes distributed along a 160 km coastline in southwest France: Hourtin, Lacanau, Cazaux, Parentis, and Soustons (Fig. [1](#)). These lakes are situated <6 km away from the Atlantic Ocean. Two pairs of lakes are connected by a channel: Hourtin with Lacanau, and Cazaux with Parentis (Fig. [1](#)). Lakes Hourtin and Lacanau are brown colored due to the drainage of waters from pine forests. All lakes are located at low altitude (≤ 20 m above sea level), have low alkalinity (<1 meq l^{-1}) and sandy substrate. They differ in size, shape, depth, and residence time (Capdevielle, [1978](#); Dutartre et al., [1989](#); S.A.G.E., [2004](#)) (Table [1](#)). The climate is temperate oceanic: air temperature ranges between 5 and 25°C. The cold season extends from November to April and the warm season from May to October. The rainy season occurs between October and December

Table 1 Main characteristics of the studied lakes

Characteristics	Lake Hourtin	Lake Lacanau	Lake Cazaux	Lake Parentis	Lake Soustons
Latitude	N45°11′14″	N44°58′33″	N44°29′30″	N44°20′41″	N43°46′36″
Longitude	W 01°03′23″	W01°07′31′′	W01°09′00′′	W01°10′49′′	W01°18′55′′
Surface (km^2)	62	20	58	36	3.8
Max depth (m)	11	8	23	20.5	1.9
Mean depth (m)	3.4	2.6	8.6	6.7	0.6
Residence time (years)	1.8	0.4	4	1	0.02
Volume (millions of m^3)	210	53	500	240	2.5

Lakes are sorted by latitude

and the dry season from June to September; mean annual precipitation is 950 mm (S.A.G.E., 2004).

Field sampling

The five lakes were sampled seasonally (Spring, Summer, Autumn, Winter) between May 2006 and February 2007, at three sites per lake ($n = 60$ samples). Sampling sites included a pelagic area in the deepest part of the lake free of aquatic vegetation (site 1) and two littoral vegetated areas (sites 2 and 3). Littoral site 2 corresponded to the western shore, which is protected from wind action by a dune cord. Littoral site 3 was located in the eastern shore, which is impacted by the west wind in spring and summer (≥ 8 m s^{-1}) and by the east wind in autumn and winter (2–8 m s^{-1}) (S.A.G.E., 2004) (Fig. 1). The littoral areas in Lake Soustons had scarce vegetation. In all lakes, the western shore (site 2) was deeper than the eastern shore (site 3). At each sampling site, we took integrated samples from the euphotic zone for biological and physico-chemical analyses: in the deepest area (site 1) we used a water pump, and in each littoral zone (sites 2 and 3), we took six sub-superficial samples (0.5 m) from the area surrounding the macrophyte beds and pooled them together. When foams were conspicuous, we collected samples directly from the lake surface.

Sample analysis

The following variables were measured in situ: water temperature, pH, oxygen, and conductivity using WTW probes (pH340, Oxi340, and LF340, respectively) and transparency with a Secchi disk. The mixing depth (Z_{mix}) was estimated from temperature

profiles measured every 1 m. When a lake showed stratification, mixing depth was considered as the depth where water temperature changed by 1°C or more (onset of thermocline). In the absence of stratification, the mixing depth was considered as the average lake depth (Scheffer et al., 1997; Naselli-Flores & Barone, 2003). The euphotic depth (Z_{eu}) was calculated as 2.5 times the Secchi depth (Golterman et al., 1978). The Z_{mix}:Z_{eu} ratio was used as a proxy for mixing and light availability. When the Z_{mix}:Z_{eu} ratio is high (Z_{mix}:$Z_{eu} > 1$), the relative amount of time that phytoplankton spends in darkness increases (Reynolds, 1984), hence impairing photosynthesis and growth. Conversely, when the ratio is low (Z_{mix}:$Z_{eu} < 1$) phytoplankton is mixed within the euphotic zone (well-illuminated layer).

In the laboratory, the following variables were measured: dissolved and total nitrogen and phosphorus (N-NO$_3^-$, N-NO$_2^-$, N-NH$_4^+$, TN, SRP, and TP, respectively), soluble reactive silicate (SRSi), dissolved organic carbon (DOC) and chlorophyll a, following standard methods (NF EN ISO 13395, 11732, 25663; NF T 90-023, 90-007, 90-117; and NF EN 1484, 13475). Dissolved nutrients were considered to limit phytoplankton growth when DIN (dissolved inorganic N, including N-NO$_3^-$, N-NH$_4^+$, N-NO$_2^-$) ≤ 7 μM, SRP ≤ 0.16 μM, and SRSi ≤ 0.24–2.49 μM (Reynolds, 2006). Trophic status was determined based on the mean concentrations of total phosphorus (TP), chlorophyll a, and Secchi depth (OECD, 1982).

Phytoplankton samples were fixed in situ with Lugol's solution. Counting was performed with an inverted microscope (OLYMPUS IX70) following the Utermöhl method (Lund et al., 1958). For each sample, at least 400 individuals (filament, colony, and single-celled organisms) were enumerated and the

results were expressed as biomass. Phytoplankton biomass (mg l^{-1}) was estimated using specific biovolume, obtained by geometrical approximations from the measure of 30–40 individuals per species (whenever possible) following Hillebrand et al. (1999) and Olenina et al. (2006). Species identification was carried out using updated phytoplankton taxonomic literature.

Each species contributing to at least 2% of the total biomass in one sample was classified into:

(i) Functional groups (FG) sensu Reynolds et al. (2002) (updated by Padisák et al., 2009). A FG (codon) was considered dominant if it contributed to at least 20% of the total biomass in one sample.

(ii) Functional traits (FT) used in this study combine the approaches of Weithoff (2003) and Litchman & Klausmeier (2008) spanning the axes of the ecological function (R: reproduction, RA: resource acquisition and PA: predator avoidance) and trait types (M: morphological, P: physiological and B: behavioral) proposed by Litchman & Klausmeier (2008):

  (a) Biovolume (R, RA and PA, M): This trait was used as a proxy of size, which is a major trait in phytoplankton, as it spans the three axes of ecological function (R, RA, and PA) (Litchman & Klausmeier, 2008). Phytoplankton was classified into four biovolume categories based on the organism size: <100 μm^3, 100–1,000 μm^3, 1,001–10,000 μm^3, >10,000 μm^3, as done by Fonseca & Bicudo (2010).

  (b) Greatest axial linear dimension (GALD) (PA, M): Taxa with GALD <35 μm encompass small and edible specimens whereas taxa with GALD >35 μm encompass large and inedible organisms (Hulot et al., 2000).

  (c) Life form (PA, M): Taxa were sorted into unicellular or multicellular forms. Multicellular taxa included: colonies (no physiological nor mechanical contact between cells, without a fixed cell number), coenobia (colony with a fixed number of interconnected cells embedded in a common matrix before release from the parental colony), filaments (row of consecutive aligned cells sharing a common cell wall), and pseudofilaments (chain of individual cells held together by mucilage or attached by cell walls). The splitting of the diversity of life forms allow testing if taxa with similar morphologies (filaments–pseudofilaments, colonies–coenobia), but different physiology, share similar or contrasting functions. Each species was classified into the corresponding life form based on the literature. Certain species can be found either single-celled or in colonies. Classification of these species was performed based on the most frequently observed life form in our samples.

  (d) Motility (RA, B): We considered motile taxa specimens with flagella, which allow tridimensional movements (Jones, 1993).

  (e) Silicate requirements (RA, P) allow discriminating diatoms and Chrysophytes (which require silicate) from other phytoplankton groups (Reynolds, 2006).

  (f) Phycobiliproteins (RA, P): Phycobiliproteins absorption peaks (phycoerythrin = 560 nm and phycocyanin = 620 nm) occur between the chlorophyll *a* absorption peaks (420 and 663 nm) (Graham & Wilcox, 1999), hence markedly increase the range of light absorption for photosynthesis of taxa possessing this trait (Cyanobacteria and Cryptophytes).

  (g) Nitrogen fixation (RA, P) allows supplementing N-requirements. We classified a species as capable of N-fixation if it fixes N in specialized cells (heterocytes) (Nostocales, Cyanobacteria).

  (h) Mixotrophy (RA, P and B): Mixotrophic phytoplankton is capable of combining both autotrophic and heterotrophic modes of nutrition (Jones, 1994). We classified a species as mixotroph if there is evidence in the literature for its capability of phagotrophic heterotrophy (we excluded taxa capable of osmotrophic nutrition).

All traits were binary categorized (1 = trait presence and 0 = trait absence; and for GALD: 1 = >35 μm and 0 = <35 μm). We multiplied the biomass of each sampling site and date for each positive

Table 2 Main environmental and biological characteristics in the pelagic area of the studied lakes

Parameters	Lake Cazaux	Lake Lacanau	Lake Parentis	Lake Hourtin	Lake Soustons
Water temperature (°C)	6–25 ± 4	5.6–27.9 ± 5	7–26 ± 4	5.8–27.8 ± 5	3.1–27.5 ± 5
Mixing regime	Monomictic	Polymictic	Monomictic	Polymictic	Polymictic
pH	7.6 ± 0.2	7.7 ± 0.2	7.7 ± 0.6	8.2 ± 0.4	8.4 ± 0.8
Secchi transparency (m)	4.2 ± 0.7	1.2 ± 0.2	2.6 ± 0.3	0.7 ± 0.1	0.8 ± 0.3
Conductivity ($\mu S\ cm^{-1}$)	168 ± 16	245 ± 19.4	160.5 ± 7.2	328 ± 11.4	162.4 ± 3.9
O_2 ($mg\ l^{-1}$)	10 ± 1.3	9.8 ± 0.6	10.1 ± 0.7	11 ± 1.2	11.5 ± 1.7
$N\text{-}NH_4^+$ (μM)	1.6 ± 1.3	3.0 ± 1.6	5.3 ± 2.4	3.8 ± 1.3	4.8 ± 1.6
$N\text{-}NO_3^-$ (μM)	<d.l.	<d.l.	<d.l.	<d.l.	19.2 ± 18.3
$N\text{-}NO_2^-$ (μM)	0.1 ± 0.06	0.3 ± 0.1	0.3 ± 0.1	1.0 ± 0.2	1.0 ± 0.2
TN (μM)	37.5 ± 1.8	52.5 ± 5.3	52.5 ± 1.8	115 ± 3.6	75 ± 24.8
SRP (μM)	0.14 ± 0.05	0.3 ± 0.1	0.2 ± 0.08	0.74 ± 0.1	0.59 ± 0.24
TP (μM)	0.49 ± 0.05	0.88 ± 0.11	1.03 ± 0.14	1.14 ± 0.09	4.22 ± 1.09
SRSi (μM)	0.04 ± 0.003	0.11 ± 0.01	0.02 ± 0.007	0.046 ± 0.01	0.19 ± 0.02
DOC ($mg\ l^{-1}$)	6.8 ± 0.9	17 ± 1	6.1 ± 0.4	24.6 ± 0.9	4.9 ± 0.7
Z_{max} (m)	23	8	20.5	11	1.9
Z_{mix} (m)	8.7 ± 0.1	2.6	8.6 ± 1.3	3.4	0.6
Z_{eu} (m)	10.4 ± 1.6	3 ± 0.4	6.6 ± 0.8	1.8 ± 0.18	1.3 ± 0.2
$Z_{mix}{:}Z_{eu}$	0.9 ± 0.1	1 ± 0.1	1.3 ± 0.1	2 ± 0.2	0.5 ± 0.06
Chlorophyll a ($\mu g\ l^{-1}$)	3.2 ± 0.7	8.9 ± 2.7	10.2 ± 2.2	20.5 ± 1.3	73.4 ± 22.7
Algal biomass ($mg\ l^{-1}$)	0.6 ± 0.1	3.4 ± 1.4	1.8 ± 0.2	6 ± 1.3	19.6 ± 6.4
Dominant FG	**B, C, E, Lo, MP, Y**	**K, N, S1**	**B, D, E, H1, N, P, Y**	**K, Lo, N, S1**	**C, D, E, J, H1, K, Lo, MP, P, S1, Y**
Trophic status (OECD, 1982)	Oligo-mesotrophic	Meso-eutrophic	Meso-eutrophic	Eutrophic	Hypereutrophic

Lakes are sorted based on their trophic status. Values represent the annual mean and standard error, except for temperature which reports minimum and maximum values and standard error. *d.l.* detection limit = 70 μM $N\text{-}NO_3$. Z_{max} from Table 1 is also included for comparing Z_{mix} and Z_{eu} versus Z_{max}. Standard error is reported for Z_{mix} only for stratified lakes. In lakes were the stratification was not observed, mixing depth was considered equal to the average depth of the lake (Scheffer et al., 1997; Naselli-Flores and Barone 2003). FG functional group. For FG description, see Table 3

trait. This allowed weighting the occurrence of each trait with spatial and temporal resolution.

Foams were analyzed qualitatively under a light microscope (OLYMPUS BX51).

Data analysis

A multivariate ordination method was used to estimate how much the variance of the phytoplankton biomass in terms of functional groups (FG) and traits (FT) was explained by the environmental variables, pooling all five lakes. The environmental variables used in the analysis were standardized and the biological data

transformed (Hellinger transformation). The detrended correspondence analysis (DCA) (Hill & Gauch, 1980) suggested that a linear method was appropriate, since the gradient length of species did not exceed 3 standard deviations. Accordingly, a redundancy analysis (RDA) was used (ter Braak & Šmilauer, 2002). A co-linearity test was performed to determine the correlation between variables. For determining the significant variables ($p < 0.01$), we performed a pre-selection using a Monte Carlo test (999 permutations without restriction). The RDAs were carried out with R software version 2.10.0 (2011-10-10) using the package ade4, vegan (R Development Core Team, 2008).

Results

Environmental variables

The studied lakes showed contrasting features (Table 2) and ranged from oligo-mesotrophic (Cazaux), meso-eutrophic (Lacanau and Parentis), eutrophic (Hourtin) to hypereutrophic (Soustons) status. The deepest lakes Cazaux and Parentis (Z_{max} 23 and 20 m, respectively) were stratified in summer (warm monomictic regime); for the other lakes we did not find stratification at any sampling occasion. Dissolved organic carbon (DOC) was very high in the humic lakes Hourtin and Lacanau (mean of 25 and 17 mg l^{-1}, respectively); concentrations in all other lakes were at least two times lower. Lake conductivities ranged from 160 to 328 μS cm^{-1}, being highest in Hourtin, intermediate in Lacanau and lower in all other lakes. The Z_{mix}:Z_{eu} ratio was ≥1 in Hourtin, Lacanau, and Parentis, implying low light availability for phytoplankton; the opposite happened for the other lakes. Average TP was lowest in Cazaux, intermediate in Lacanau, Parentis, and Hourtin, and highest in Soustons. SRP concentrations in Lacanau, Cazaux, and Parentis were close to values potentially limiting phytoplankton growth. In all lakes, total nitrogen was sufficient for phytoplankton growth but dissolved inorganic nitrogen (N-NO$_3^-$, N-NH$_4^+$, N-NO$_2^-$) was recurrently below values potentially limiting phytoplankton growth. SRSi concentrations in all lakes were within the range of phytoplankton limitation. In each sampling period, temperature (3–7°C in winter and 25–28°C in summer) and pH (ca. 8) were similar in all lakes (Table 2).

Phytoplankton functional characterization

A total of 687 phytoplankton taxa were identified with 85 species contributing ≥2% to the total biomass (5 being tropical species, see "Tropical taxa" section). The sorting of the 85 species using the functional approach rendered 18 FG (Table 3) and 15 FT (Appendix 1—Supplementary Table). Table 2 shows the dominant FG in each lake. Remarkably, while Lacanau and Parentis had similar trophic status, they differed in the dominant FG (Table 2). Species belonging to a same FG usually shared similar traits, except for FG which pool polyphyletic taxa (e.g. **Lo**, **P**, **N**) (Appendix 1—Supplementary material).

Species within a genus shared most traits, albeit for GALD and biovolume (Appendix 1—Supplementary material).

Phytoplankton functional–environmental responses

Figure 2 shows the RDA biplots of the phytoplankton FG (a) and FT (b) with respect to the environmental variables in the five Aquitaine lakes studied. The results based on the FG approach indicated that the total variance explained by the first two axes accounted for 71% (axis 1: 48%; axis 2: 23%) (Fig. 2a). The first axis was mainly defined by conductivity ($r = 0.85$), Z_{mix}:Z_{eu} ratio ($r = 0.50$) and TP ($r = -0.45$), and the second axis by Secchi depth ($r = -0.76$). Phytoplankton FG in the humic and connected lakes Hourtin and Lacanau shared similar composition, including desmids in **N** and Cyanobacteria in **K** and **S1**. Remarkably, these coda were dominated by tropical taxa (see "Tropical taxa" section). In the cold season, phytoplankton composition in Hourtin was different from Lacanau, mostly due to the dominance of the codon **Lo** (colonial Cyanobacteria *Chroococcus minutus*) (Figs. 2a, 3). FG in these lakes were related to high conductivity (DOC co-linearity $r > 0.94$), deep mixing and low light availability (low Secchi depth). Both these lakes generally showed high spatial homogeneity within sampling periods (Figs. 2a, 3).

Phytoplankton in Parentis and Soustons shared several FG from spring to autumn (**H1**, **D**, **P**) but differed in species composition (Fig. 3). The dominant phytoplankton assemblage in Parentis included three species of N-fixing cyanobacteria in **H1** (*Dolichospermum circinalis*, *D. flos-aquae*, and *Aphanizomenon flos-aquae*), a big centric diatom in **D** (*Actinocyclus normanii*), desmids and diatoms in **P** (the single-celled *Staurastrum pingue* and *Xanthidium antilopaeum*, and the chained *Fragilaria crotonensis* with up to 60 cells long) (Figs. 2a, 3). Dominant FG in Soustons were **H1** (*Aphanizomenon gracile*), **J** (several species of *Scenedesmus* and *Tetraedron caudatum*), **D** (*Nitzschia intermedia*, *N. palea*, *Staurosira berolinensis*), and **P** (*Staurastrum chaetoceras*) (Figs. 2a, 3). All these FG were shaped by high TP (Fig. 2a). Phytoplankton in Soustons in winter shared some similar FG to those in Cazaux (Figs. 2a, 3). The winter FG assemblage in Soustons had about ten times lower biomass than all other

Table 3 Phytoplankton functional groups (FG) recorded in the five Aquitaine lakes

FG	FG description	Taxa
A	Diatoms in clear-waters	*Cyclotella comensis* Grun. In Van Heurck (C), *C. cyclopuncta* Håkansson & Carter (C), *Urosolenia longiseta* (Zach.) M. B. Edlund & Stoermer (L)
B	Centric diatoms in mesotrophic systems	*Aulacoseira italica* (Ehr.) Sim. (L, C, P, S), *A. muzzanensis* (Meister) Kramm. (S), *Puncticulata radiosa* (Lemm.) Håk. (H, L, C)
C	Diatoms in eutrophic systems	*Aulacoseira ambigua* (Grun.) Sim. (L, C, P, S), *Cyclotella meneghiniana* Kütz. (S)
D	Diatoms in turbid systems	*Actinocyclus normanii* (Greg. ex Grev.) Hust. (P), *Nitzschia gessneri* Hust. (S), *N. intermedia* Hantz. ex Cl. & Grun. (S), *N. palea* (Kütz.) W. Smith (S), *Staurosira berolinensis* (Lemm.) Lange-Bert. (S)
E	Chrysophytes	cf. *Erkenia* (C, P), unidentified Chrysophyte (C), *Dinobryon bavaricum* Imh. (L, C, S), *Mallomonas lefevriana* Bour. (S), *Mallomonas* sp. (H)
H1	Filamentous nitrogen-fixing Cyanobacteria	*Dolichospermum circinalis* (Rabenh. ex Born. & Flah.) Wack., Hoff. & Kom. (P), *D. flos-aquae* (Bréb. Ex Born. & Flah.) Wack., Hoff. & Kom. (P), *Aphanizomenon flos-aquae* Ralfs ex Born. & Flah. (P), *A. gracile* Lemm. (S)
J	Coenobial Chlorophytes	*Pediastrum boryanum* (Turp.) Menegh. (P), *P. tetras* (Ehr.) Ralfs (L), *Scenedesmus acuminatus* (Lagerh.) Chod. (S), *S. magnus* Meyen (S), *S. opoliensis* Richt. (S), *S. quadricauda* (Turp.) Bréb. (S), *S. spinosus* Chod. (S), *Tetraedron caudatum* (Cord.) Hansg. (H, L, C, S)
K	Small-celled colonial Cyanobacteria	*Aphanothece nidulans* Richt. (H, L), *A. stagnina* (Spreng.) A. Braun (H), *Aphanothece* sp.1 (H), *Aphanothece* sp.2 (H), *Synechocystis* sp.1 (H), *Synechocystis* sp.2 (H), **Cyanodictyon tropicale Senna, Delazari & Sant'Anna** (H, L), *Cyanonephron styloides* Hickel (S)
Lo	Colonial Cyanobacteria and dinoflagellates	*Chroococcus minutus* (Kütz.) Näg. (H, L), *Coelosphaerium kuetzingianum* Näg. (P), Peridiniales (C, P, S), *Peridiniopsis elpatiewskyi* (Ostenf.) Bour. (C), *Peridinium umbonatum* Stein (C), *Peridinium* sp. (C), *Radiocystis aphanothecoidea* Hind. (H, L, C)
M	*Microcystis*	*Microcystis aeruginosa* (Kütz.) Kütz. (P), *M. wesenbergii* (Kom.) Kom. (S)
MP	Meroplanktonic diatoms	*Amphora oligotraphenta* Lange-Bert. (C), *Aneumastus tusculus* (Ehr.) Mann & Stickle (C, P), *Brachysira neoexilis* Lange-Bert. (H), *Cymbella helvetica* Kütz. (C), *Encyonopsis cesatii* (Rabenh.) Kram. (C), *E. subminuta* Kram. & Reich. (C), *Fragilaria virescens* Ralfs (C), *Gomphonema acuminatum* Ehr. (H), *G. lateripunctatum* Reich. & Lange-Bert. (C), *Navicula radiosa* Kütz. (H, C), *Staurosira construens* Ehr. (S), *Ulnaria biceps* (Kütz.) Comp. (S), *U. ulna* (Nitzsch.) Comp. (S)
N	Diatoms and desmids in mesotrophic lakes	*Tabellaria flocculosa* (Roth) Kütz. (H, L, C, P, S), *Spondylosium clepsydra* Beck (P), *S. papillosum* West & West (H, L), *Staurastrum* cf. *longipes* (L), **S. excavatum var. planctonicum Krieg.** (H, L), *S. messikomeri* Lundb. (P), *S. tetracerum* Ralfs (L), *Staurodesmus cuspidatus* (Bréb. ex Ralfs) Teiling (L), *Teilingia excavata* (Ralfs) Bour. (H, P)
P	Diatoms and desmids in eutrophic lakes	*Fragilaria crotonensis* Kitton (P), *F. nanana* Lange-Bert. (S), *Staurastrum pingue* Teil. (P), *S. chaetoceras* (Schr.) Smith (S), *Xanthidium antilopaeum* (Bréb.) Kütz. (P)
S1	Filamentous non-fixing Cyanobacteria	**Planktolyngbya circumcreta (West) Anag. & Kom**. (L, S), *P. limnetica* (Lemm.) Kom.-Legn. & Cron. (H, L, C, S), **P. microspira Kom. & Cron.** (H, L), **P. minor (Geitler) Kom. & Cron.** (S), *Pseudanabaena* sp.1 (L), *Pseudanabaena* sp.2 (S)
X1	Small Chlorophytes in eu-hypereutrophic systems	*Didymocystis planctonica* Korš. (L), *Monoraphidium contortum* (Thur. in Bréb.) Kom.-Legn. (P, S)
X2	Small flagellates in meso-eutrophic systems	*Plagioselmis nannoplanctica* (Skuja) Novar., Lucas & Morr. (P)
X3	Small Chlorophytes and Chrysophytes in oligotrophic systems	*Chromulina* cf. *magnifica* (P)
Y	Large Cryptomonads	*Cryptomonas* spp. (C, P, S)

Each row shows the FG (bold), its description and the species belonging to the FG. In the taxa column, letters in parenthesis (H: Hourtin; L: Lacanau; C: Cazaux; P: Parentis; S: Soustons) show the lakes where each species was found. Tropical species are in bold
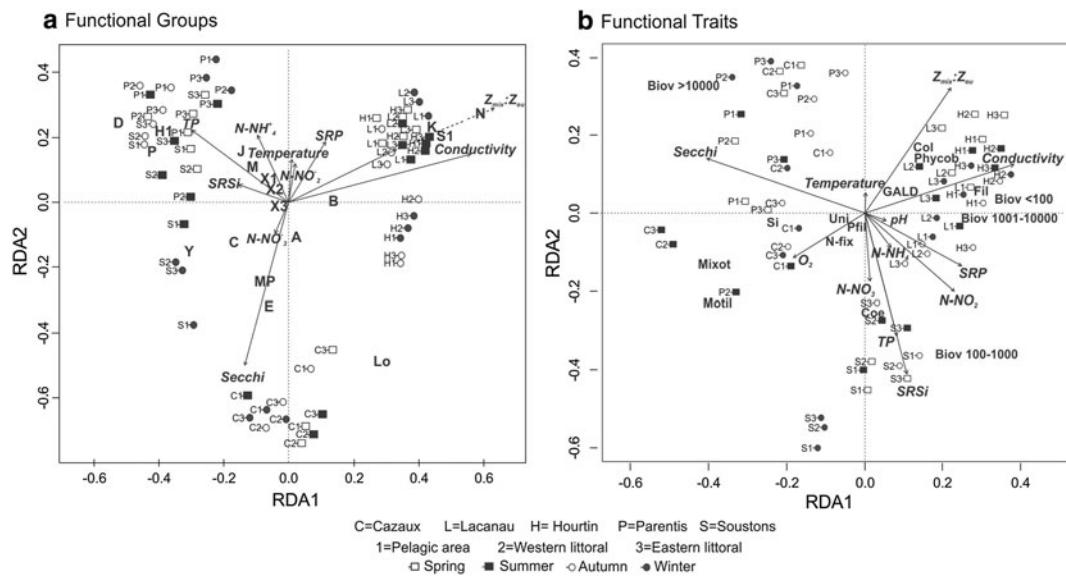
Fig. 2 RDA applied to the phytoplankton data: **a** functional groups and **b** functional traits in the five Aquitaine lakes during the studied period. Functional groups: **S1**, **Lo**, **B**, **N**, **MP**, **D**, **K**, **E**, **C**, **Y**, **P**, **J**, **H1**, **M**, **A**, **X1**, **X2**, **X3**. Functional traits: **GALD**, greatest axial linear dimension; **Biov**, biovolume (μm^3); **Motil**, motility; **Si**, silica requirements; **Phycob**, phycobiliproteins; **Mixot**, mixotrophy; **Fil**, filament; **Pfil**, pseudofilament; **Uni**, unicellular; **Col**, colony; **Coe**, coenobium; **N-fix**, N-fixation. Functional groups and traits are represented with *bold character*. Environmental variables are in *italic character*

seasons, with dominance (up to 49% biomass) of Chrysophytes in **E** (*Mallomonas lefevriana*) (Fig. 3) linked to high light availability (high Secchi depth) (Fig. 2a). FG in Cazaux were characterized by the coda **Lo** (colonial Cyanobacteria *Radiocystis aphanothecoidea* and the dinoflagellate *Peridiniopsis elpatiewskyi*), **MP** (meroplanktonic diatom *Cymbella helvetica*), and **E** (several species of Chrysophytes); these FG were linked to high transparency (Secchi depth) (Fig. 2a). In particular, the polyphyletic species within the codon **Lo** were distributed in different sites of the lake: *R. aphanothecoidea* dominated in the stratified pelagic area whereas *P. elpatiewskyi* dominated in both littoral areas (Fig. 3). Interestingly, Parentis and Cazaux which are both deep and connected showed contrasting FG–environment relations mostly due to trophic status (Fig. 2a).

The distribution of the FG reflected the key environmental conditions in the five lakes: eutrophic FG (**D**, **H1**, **P**, **J**, **M**) occurred at high TP, while oligotrophic/clear-water FG (**A**, **E**, **Lo**) happened at low TP or at high Secchi depth (Fig. 2a; Tables 2, 3). Likewise, low light adapted FG (**S1**) occurred at high conductivity (high DOC) and high $Z_{mix}:Z_{eu}$ ratio (Fig. 2a; Table 2). FGs containing flagellated taxa (the

monophyletic coda **Y** and **E**, and the polyphyletic codon **Lo**) were found at high light availability (high Secchi depth) (Fig. 2a).

In the FT approach, the total variance explained by the first two axes accounted for 72% (axis 1: 52%; axis 2: 20%) (Fig. 2b). The first axis was mainly defined by the Secchi depth ($r = -0.82$), conductivity ($r = 0.78$), and SRP ($r = 0.50$), and the second axis was mainly correlated with SRSi ($r = -0.85$), $Z_{mix}:Z_{eu}$ ratio ($r = 0.66$) and TP ($r = -0.66$). The FT–environmental response was similar in the connected lakes Lacanau and Hourtin: filaments and colonies with phycobiliproteins, organism biovolume between <100 and 10,000 μm^3 and GALD >35 μm were linked to high conductivity (high DOC), high SRP, deep mixing and low light (Fig. 2b). The deep and connected lakes Parentis and Cazaux also shared similar FT-environmental responses: large organisms (>10,000 μm^3) and taxa with silicate requirements were linked to high transparency (Fig. 2b). Soustons behaved differently from the other four lakes (Fig. 2b); the FT coenobium and organism biovolume of 100–1,000 μm^3 were linked to the nutrient concentrations ($N-NO_3^-$, $N-NO_2^-$, $N-NH_4^+$, SRP, TP, SRSi) (Fig. 2b). The traits of mixotrophy and motility were
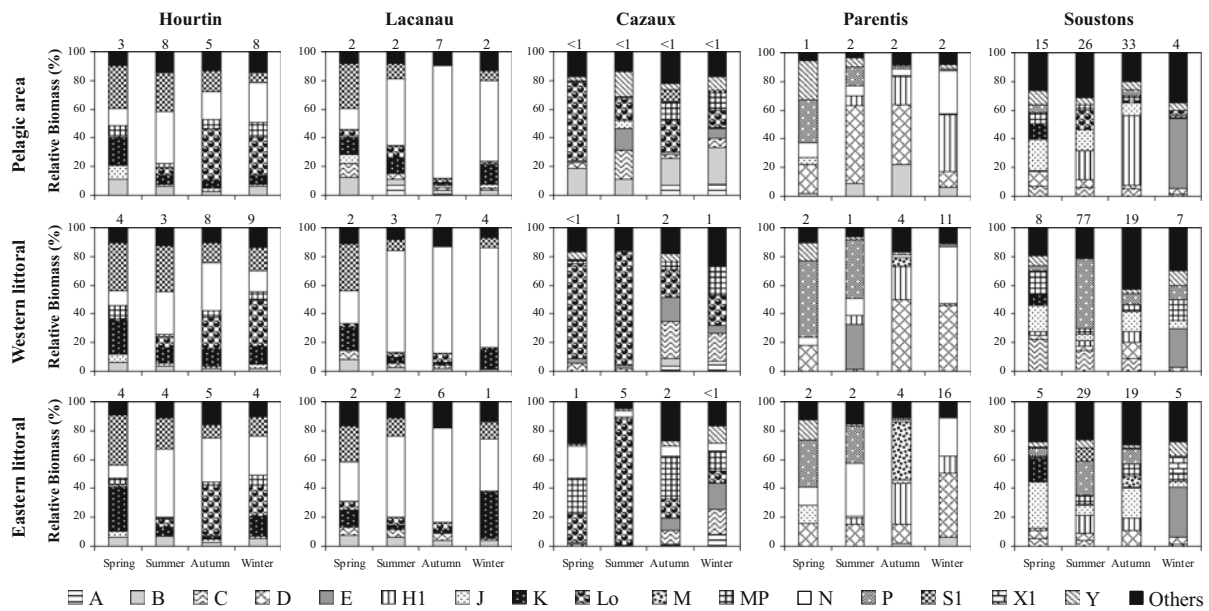
Fig. 3 Phytoplankton functional group structure and species within coda for the five Aquitaine lakes during the studied period. **Hourtin**: **B** (*Puncticulata radiosa*), **K** (*Aphanothece nidulans, A. stagnina*), **Lo** (*Chroococcus minutus*), **N** (*Spondylosium papillosum, Staurastrum excavatum* var. *planctonicum*), **S1** (*Planktolyngbya limnetica, P. microspira*); **Lacanau**: **B** (*P. radiosa*), **K** (*A. nidulans, Cyanodictyon tropicale*), **N** (*S. excavatum* var. *planctonicum, S. tetracerum, Tabellaria flocculosa, Staurodesmus cuspidatus*), **S1** (*P. limnetica, P. microspira, P. circumcreta*), **J** (*Tetraedron caudatum, Pediastrum tetras*); **Cazaux**: **B** (*Aulacoseira italica*), **C** (*A. ambigua*), **E** (*Dinobryon bavaricum,* unidentified Chrysophyte), **Lo** (*Radiocystis aphanothecoidea, Peridiniopsis elpatiewskyi*), **MP** (*Cymbella helvetica*), **N** (*T. flocculosa*), **Y** (*Cryptomonas* spp.); **Parentis**: **B** (*A. italica*), **D** (*Actinocyclus normanii*), **E** (cf.

Erkenia), **H1** (*Dolichospermum circinalis, D. flos-aquae, Aphanizomenon flos-aquae*), **M** (*Microcystis aeruginosa*), **N** (*T. flocculosa, Staurastrum messikomeri*), **P** (*Fragilaria crotonensis, Xanthidium antilopaeum, Staurastrum pingue*), **Y** (*Cryptomonas* spp.); **Soustons**: **C** (*A. ambigua*), **D** (*Nitzschia intermedia, N. palea, Staurosira berolinensis*), **E** (*Mallomonas lefevriana*), **H1** (*Aphanizomenon gracile*), **J** (*Scenedesmus opoliensis, S. quadricauda*), **K** (*Cyanonephron styloides*), **Lo** (Peridiniales), **MP** (*Staurosira construens, Ulnaria biceps, U. ulna*), **P** (*Staurastrum chaetoceras*), **X1** (*Monoraphidium contortum*). Values above each graphic represent the total biomass (mg l^{-1}). Only taxa whose relative biomass represent ≥5% in at least one sample were considered in this figure. Lakes are sorted by latitude

related to high light availability and shallow mixing (Fig. 2b). Organisms sharing similar morphologies but different physiologies (filaments and pseudofilaments, as well as colonies and coenobia) displayed contrasting environmental responses. Filaments occurred at high conductivity (high DOC) and deep mixing, while pseudofilaments seem unrelated to these variables. Colonies occurred at deep mixing while coenobia were linked to shallow mixing (Fig. 2b). The FT–environment relation seems to be driven by the lakes' hydromorphology, as lakes with similar features (depth, size, mixing regime) and connected (Hourtin and Lacanau, Cazaux and Parentis) were grouped together (Fig. 2b; Table 1).

In both functional approaches, the percentage of the explained variance was similar (>70%) and shared

most of the significant environmental variables (Figs. 2a, b). Both classifications coincided in separating the humic lakes Hourtin and Lacanau from the other systems. However, in the FG approach, phytoplankton in Parentis and Soustons were similar and separated from Cazaux, while in the FT approach Parentis and Cazaux were similar and separated from Soustons. When confronting both approaches, we observed that trait distributions within a polyphyletic FG showed different links with the environment. For example, the codon **Lo** (colonial Cyanobacteria and dinoflagellates) which was dominant in Cazaux was linked to high light (Fig. 2a). However, when using the trait-based approach, the traits associated with dinoflagellates (mixotrophy, motility) were related to high light availability and shallow mixing (Fig. 2b),

while those of colonial Cyanobacteria (colonies, phycobiliproteins) were related to deep mixing (low light availability).

Tropical taxa

The five tropical species found in the studied lakes comprised four Cyanobacteria (*Planktolyngbya microspira*, *P. circumcreta*, and *P. minor* in the codon **S1**, and *Cyanodictyon tropicale* in the codon **K**) and one desmid (*Staurastrum excavatum* var. *planctonicum* in the codon **N**) (Table 3). These species were dominant in the humic lakes Hourtin and Lacanau (up to 46 and 45% of the total biomass, respectively), and occurred at low biomass in Soustons (up to 5% of the total biomass), but were absent in Parentis and Cazaux. The higher number of tropical taxa occurred in Lacanau (4 species, 3 FG), followed by Hourtin (3 species, 3 FG) and Soustons (2 species, 1 FG) (Table 3). In Hourtin and Lacanau, the tropical taxa contributed with high biomass to the phytoplankton community: *P. microspira* and *P. circumcreta* constituted 40–50% of the biomass of the codon **S1**, *C. tropicale* contributed to the 60–88% of the biomass in the codon **K**, and *S. excavatum* var. *planctonicum* to the 70–90% of the biomass in the codon **N** (Fig. 3). Interestingly, the coda **K** and **S1** displayed very similar ecologies (Fig. 2a). Species turnover occurred among tropical taxa: groups **S1** and to a lesser extent **K** prevailed in spring, whereas **N** dominated or co-dominated from summer till winter in Hourtin and Lacanau (Fig. 3). The relative biomass of **N** was higher in Lacanau than in Hourtin. In Soustons, the tropical taxa were represented by the codon **S1** (*Planktolyngbya circumcreta*, *P. minor*). The traits characterizing these tropical taxa were: phycobiliproteins in **S1** and **K**, pseudofilaments in **K**, filaments in **S1**, unicellularity in **N**, small biovolume in **S1** and **K** (<100 and 100–1,000 μm^3), large biovolume in **N** (1,001–10,000 μm^3) and GALD >35 μm in **S1**, **K**, and **N** (Supplementary Table 1).

Foams

Foams were mainly observed in Hourtin and to a lesser extent in Lacanau, mostly concentrated on the eastern shore, which is impacted by the dominant west winds during spring and summer (Supplementary Figure 1). Also, sparse foams happened in the oligo-mesotrophic

lake Cazaux (Supplementary Figure 1). The microscopic analysis of the foams showed prevalence of Cyanobacteria and diatom species (Supplementary Figure 2). Cyanobacteria found in these foams included three FG: **S1** (*P. microspira*, *P. circumcreta*, and *P. limnetica*), **Lo** (*C. minutus*), and **K** (*Aphanothece* spp.). Diatoms found in the foams belonged to two FG: **MP** (*Navicula radiosa*) and **N** (*Tabellaria flocculosa*) (Supplementary Figure 2). Two of the five tropical taxa happened in the foams: *P. microspira* and *P. circumcreta* (**S1**).

Discussion

The functional approaches explained well the variability of phytoplankton under different environmental conditions. In both approaches, phytoplankton functional distributions responded to similar environmental variables: light availability, deep mixing, and phosphorus concentration. Moreover, both approaches allowed reducing the system complexity from a wide range of species to a few FG and FT. The FG approach allowed splitting lakes by trophic status: eutrophic (**D**, **H1**, **P**, **J**, **M**) and oligotrophic/clear-water (**A**, **E**, **Lo**) FG, coinciding with Reynolds et al. (2002) (updated by Padisák et al., 2009) classification. The FT approach reflected well the lakes' hydromorphology: connectivity, depth, size, mixing regime. Lakes with similar nutrient concentrations and biomasses (e.g., the meso-eutrophic lakes Parentis and Lacanau) had markedly different FG composition.

The joint analysis of the phytoplankton community in terms of FG and FT rendered comparable results for the humic lakes, but differed for the other lakes. Izaguirre et al. (2012a), in a study using three morpho-functional approaches in lakes from the Salado basin (Argentina) found that all approaches were able to split turbid from clear lakes. Also, coinciding with our findings, they found for all approaches, that the phytoplankton variance explained by the environmental variables was high. Nevertheless, Kruk et al. (2011) found that FT explain better the phytoplankton variance from environmental conditions than the FG approach.

Functional and environmental responses

In humic ecosystems, light is strongly attenuated and red wavelengths prevail (Kirk, 1994). Hence, deep

mixing should select for low light adapted taxa with pigments capable of absorbing red light (phycocyanin) such as Cyanobacteria and some Cryptophytes. To an extent, this occurred in the humic and polymictic lakes Hourtin and Lacanau, as revealed by the high biomass of Cyanobacteria FG (**S1**, **K**, and **Lo**). Nevertheless, motile taxa containing phycocyanin (such as Cyano-bacteria with gas vesicles in **H1**, S_N, **M**, and flagel-lated Cryptophytes in **Y**) were not found in these ecosystems. It seems that in environments with deep mixing, buoyant taxa are not favored (Bormans & Condie, 1998; Huisman et al., 2004), even if these possess traits that favor light capture. Likewise, the trait of motility (i.e., flagellates in **Y**, **E**, **Lo**) was negatively related to high mixing. Taxa capable of mixotrophy (phagotrophic) were linked to high light availability and low mixing. Several authors found mixotrophs at high light (Caron et al., 1993; Hansen & Hjorth, 2002; Izaguirre et al., 2012b) as these may depend on energy and carbon derived from photosyn-thesis (Bergström et al., 2003). The trait of nitrogen fixation (codon **H1**) only happened in two lakes, even if all the lakes studied were at some point limited by inorganic nitrogen availability. Likewise, de Tezanos Pinto & Litchman (2010) suggested that dissolved inorganic nitrogen *per se* is not an adequate proxy for forecasting N-fixers distribution. Nevertheless, in our study, nitrogen concentrations (dissolved and total) played minor roles in shaping the phytoplankton distributions in the landscape (as evidenced in both RDAs).

Regarding the trait of life form, several authors treat filaments or colonies as a whole without explicitly differentiating pseudofilaments (within filaments) and coenobia (within colonies) (O'Farrell et al., 2007; Fonseca & Bicudo, 2010), or alternatively classify life forms in terms of coloniality (Litchman & Klausmeier, 2008). Nevertheless, our results show that taxa with similar morphologies but from polyphyletic origin (i.e., colonies in Cyanobacteria and coenobia in green algae, and filaments in Cyanobacteria versus pseudo-filaments in Cyanobacteria/diatoms/desmids) showed different FT–environmental responses. This suggests that, in addition to morphology, organism physiology plays an important role in determining the phyto-plankton functional response. This underscores the need to split filaments from pseudofilaments, and colonies from coenobium when studying phytoplank-ton life forms.

Tropical species success in temperate lakes

The five tropical phytoplankton taxa identified are commonly found in tropical and subtropical lakes worldwide (reviewed in Cellamare et al., 2010). Their dispersal along the Aquitaine region is likely due to birds migrating from Africa (Capdevielle, 1985; Cellamare et al., 2010). Tropical taxa were found along the 160 km range, in the two further north lakes (Hourtin and Lacanau) and in the further south lake (Soustons), underscoring a similar dispersion capabil-ity. Nevertheless, tropical species managed to thrive only in three of the five lakes studied: they were dominant in the humic lakes Hourtin and Lacanau, rare in Soustons and absent in Parentis and Cazaux. Hence, suggesting that environmental variables shape their success (see below).

When dominant, the tropical taxa exerted an overwhelming effect on the ecosystem in terms of biomass, community composition and succession, and also contributed to foam occurrences. The lakes where tropical taxa succeeded (humic Hourtin and Lacanau) had high DOC content, low transparency, high mixing, and intermediate TP concentrations. Deep mixing should select for low light adapted taxa with pigments capable of absorbing red light (phycocyanin) as described above for humic lakes. Cyanobacteria are acknowledged as the best low light adapted phyto-plankton group (Schwaderer et al., 2011). Indeed, the tropical Cyanobacteria (coda **S1** and **K**) have phyco-biliproteins (physiological trait common to all Cya-nobacteria) as well as morphological traits (elongated shape, small biovolume, and high S:V ratio) which improve light harvesting capabilities (Kirk, 1994). The success of the tropical desmid (codon **N**) seems a paradox, as desmids as a group are high light adapted organisms (Schwaderer et al., 2011) and the humic lakes are colored (decreased light availability). Coin-ciding with the desmid light trait, the relative biomass of *Staurastrum excavatum* var. *planctonicum* was higher in the lake with more light availability (Laca-nau, shallower mixing than in Hourtin). Morpholog-ical traits of this species may help explain their occurrence in the humic lakes, as it has very long and skinny arms. This latter feature could be a strategy to maximize the surface exposed to light in turbid systems (Padisák et al., 2003). All the tropical taxa found had a GALD >35 µm that hinders predation (Hulot et al., 2000). In brief, the traits that seem to

provide fitness to the tropical taxa span the axes of ecological function related to predator avoidance and resource acquisition: size (GALD >35), shape (elongated forms) and photosynthesis (in Cyanobacteria because of phycobiliproteins).

Coincident with our results, in other tropical lakes worldwide (e.g. South America, Africa) (reviewed in Cellamare et al., 2010) the tropical species found in this study are consistently found in waters with low transparency, regardless of conductivity, altitude, or depth (Begg, 1970; Hare & Carter, 1984; Senna et al., 1999; Magadza, 2006). The desmid seems to have a broad trophic spectrum (oligo- to eutrophic) (Compère & Iltis, 1983; Biswas & Nweze, 1990), while Cyanobacteria seem less favored in nutrient-poor conditions (Senna et al., 1999; Komárek & Cronberg, 2001; Cózar et al., 2007).

It is a challenge to explain why the tropical species manage to thrive in only some lakes in the Aquitaine region. This is probably related to the species fitness in the environment. Traits impact fitness indirectly via effects on growth, reproduction, and survival (Violle et al., 2007). Moreover, a trait can provide fitness in one environment but not in other, depending on the environmental filters. Based on the evidence gathered on our study, the success of the tropical taxa seems strongly linked to the interplay between the traits (predator avoidance and resource acquisition) and a particular environment (low light availability, deep mixing, and intermediate TP concentrations). This could be the cause for the absence of tropical taxa in Cazaux and Parentis and their rareness in Soustons. In particular, TP availability may set a constraint to the tropical taxa distribution: at extreme low TP (Cazaux, oligo-mesotrophic) tropical taxa could be unable to grow, whereas at very high TP (e.g. Soustons) they may be out-competed by the native community. The absence of tropical taxa in Parentis, which shares similar TP concentrations with the humic lakes, may be explained in terms of light availability: Parentis is clear (high Secchi depth) whereas in the humic lakes light availability is low (colored waters and deep mixing).

Finally, while bird migrations should provide a continuous input of tropical taxa into the studied lakes, it is possible that increased mean temperatures in the Aquitaine region favor their success. In particular, increases in the minimal temperatures (+0.6°C since 1975) probably play a key role in the overwintering of these taxa in these temperate systems (Cellamare et al., 2010). Our study is the first on phytoplankton ecology in the region. Hence, we are unable to answer if the tropical taxa are becoming invasive or if it is an enlargement of their home range due to a change in environmental conditions. Paleolimnological studies should determine if the trend in tropical taxa success is increasing. This is important to assess as global warming is allowing the broadening of the geographical ranges of many potentially invasive species (Hughes, 2000; Parmesan, 2006) that can be toxic (Padisák, 1997), representing a potential public health problem with important ecological and economical consequences.

Foam occurrences

Conspicuous foams occurred in lakes dominated by tropical taxa. Nevertheless, sparse foams were also observed in lakes without these species. Foams were mainly composed by Cyanobacteria (including the tropical ones) and diatoms. Several taxa in these groups are known to produce exopolysaccharides (De Philippis et al., 2005). Indeed, chemical analyses on the foams confirmed that these were composed by plant polysaccharides (Cellamare, 2009). Hence, while tropical taxa were abundant in the foams, we cannot ascertain that they are the sole player responsible for the foam occurrences. The dominance of species capable of producing polysaccharides in combination with strong wind action seem to better explain the foam events.

Sorting species into FG: new proposals

In the phytoplankton FG approach, not all the coda are defined with the same level of accuracy, hence the sorting of non-previously listed species may be sometimes challenging. For example, the location for the tropical Cyanobacteria *Cyanodictyon tropicale* is uncertain. We chose to classify it into codon **K** that includes other species of the genus *Cyanodictyon* but this group consists of "small-celled Cyanobacteria colonies" (Padisák et al., 2009). Nevertheless, based on our results we suggest that *C. tropicale* should be placed into group **S1**, because: (a) its colony morphology (flat cell arrayed in row) resembles more a thin filament of *Planktolyngbya* (**S1**) than a **K** type colony and (b) when *C. tropicale* was dominant in codon **K**, this group displayed very similar ecologies to codon **S1**.

FG or FT for studying community attributes?

The FG and FT approaches encompass polyphyletic groups within their categories; these groups should display similar functional–environmental relations. However, we observed that species within polyphyletic FG (e.g., **Lo**, **N**, and **P**, which differed in their traits) responded differently to the environment. For example, the polyphyletic codon **Lo**, composed by dinoflagellates and colonial Cyanobacteria, was linked to high transparency. However, when the species were analyzed in terms of FT, the traits characterizing dinoflagellates (mixotrophy, motility) were linked to high light while those of the colonial Cyanobacteria (phycobiliproteins, colonies) showed the opposite behavior. Further studies considering traits will allow identifying if FG containing polyphyletic groups need to be redefined to better reflect the behavior of the taxa within coda.

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