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Patterns and multi-scale drivers of phytoplankton species richness in temperate peri-urban lakes

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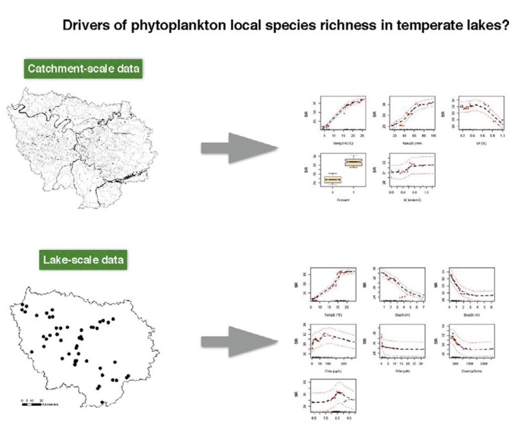
HIGHLIGHTS

- We studied phytoplankton communities in 50 peri-urban lakes.
- We assessed the impact of multi-scale drivers of phytoplankton richness.
- Local- and catchment-scale predictive models performed similarly.
- Seasonal temperature variation and resource availability strongly modulate species richness.
- This approach may be used for the management and conservation of aquatic ecosystems.

GRAPHICAL ABSTRACT



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ABSTRACT

Local species richness (SR) is a key characteristic affecting ecosystem functioning. Yet, the mechanisms regulating phytoplankton diversity in freshwater ecosystems are not fully understood, especially in peri-urban environments where anthropogenic pressures strongly impact the quality of aquatic ecosystems. To address this issue, we sampled the phytoplankton communities of 50 lakes in the Paris area (France) characterized by a large gradient of physico-chemical and catchment-scale characteristics. We used large phytoplankton datasets to describe phytoplankton diversity patterns and applied a machine-learning algorithm to test the degree to which species richness patterns are potentially controlled by environmental factors. Selected environmental factors were studied at two scales: the lake-scale (e.g. nutrients concentrations, water temperature, lake depth) and the catchment-scale (e.g. catchment, landscape and climate variables). Then, we used a variance partitioning approach to evaluate the interaction between lake-scale and catchment-scale variables in explaining local species richness. Finally, we analysed the residuals of predictive models to identify potential vectors of improvement of phytoplankton species richness predictive models.

Lake-scale and catchment-scale drivers provided similar predictive accuracy of local species richness ($R^2 = 0.458$ and 0.424, respectively). Both models suggested that seasonal temperature variations and nutrient supply strongly modulate local species richness. Integrating lake- and catchment-scale predictors in a single predictive

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model did not provide increased predictive accuracy; therefore suggesting that the catchment-scale model probably explains observed species richness variations through the impact of catchment-scale variables on in-lake water quality characteristics.
Models based on catchment characteristics, which include simple and easy to obtain variables, provide a meaningful way of predicting phytoplankton species richness in temperate lakes. This approach may prove useful and cost-effective for the management and conservation of aquatic ecosystems.

1. Introduction

Spatial biogeographic patterns are increasingly studied in order to provide a better understanding of the ecology of living organisms (e.g. Marquet et al., 2004; Azeria et al., 2009) and to identify the processes involved in the maintenance or decline of biodiversity (Bellwood and Hughes, 2001). Evidence on the occurrence of biogeographic patterns in aquatic microorganisms has only recently been provided (Foissner, 2006; Martiny et al., 2006; Green and Bohannan, 2006) and the deterministic or random nature of the underlying processes of microbial biodiversity is still under close scrutiny. However, understanding how the environment acts on biodiversity patterns in microorganisms is critical for mitigating the impact of environmental changes and ensuring the continuity of ecosystems services (Millennium Ecosystem Assessment, 2005). This is particularly true for phytoplankton communities, where shifts in communities' composition (e.g. leading to species poor communities dominated by harmful cyanobacteria) may have profound effects on aquatic ecosystem functioning and on the quality of aquatic resources.

Various processes have been suggested to impact microorganisms' richness patterns across scales, including latitudinal temperature gradients at large spatial scale (Fuhrman et al., 2008), species-area relationships (e.g. Horner-Devine et al., 2004; Smith et al., 2005; Bell et al., 2005), temporal (i.e. stability; Ptacnik et al., 2008b) and spatial (e.g. water column stratification; Streibel et al., 2010) ecosystem heterogeneity and the size of the regional pool of potential colonizers (Ptacnik et al., 2010). Among the various processes linking diversity to ecosystem functioning, the relationship between diversity and productivity (Currie, 1991) has been actively debated in the last decades (Strong, 2010). In essence, productivity corresponds to the ratio of production over biomass and characterizes the efficiency of a biological compartment to use surrounding resources. However, most empirical studies use standing biomass as a surrogate measure of productivity (e.g. Groner and Novoplansky, 2003; Filstrup et al., 2014; Vallina et al., 2014). Current knowledge suggests that the shape of productivity–diversity relationships in both terrestrial and aquatic ecosystems is either positive or hump-shaped (e.g. Dodson et al., 2000; Mittelbach et al., 2001; Chase and Leibold, 2002; Gillman and Wright, 2006; Smith, 2007; Filstrup et al., 2014; Vallina et al., 2014). A number of hypotheses have arisen in the literature to explain how productivity might drive diversity (Palmer, 1994), including the intermediate disturbance hypothesis (Connell, 1978), the species-energy theory (Wright, 1983), the resources-supply ratios hypothesis (Tilman, 1985) or the keystone-predation hypothesis (Leibold, 1996). Alternatively, it was also suggested that diversity might drive productivity (Loreau et al., 2002; Duffy, 2009). These two views on the relationship between diversity and productivity are currently seen as complementary rather than mutually exclusive (Cardinale et al., 2009a, 2009b).

In most aquatic ecosystems, productivity (and standing phytoplankton biomass) is at least partly controlled by resource availability (Vallina et al., 2014). The occurrence of a productivity–diversity relationship in phytoplankton advocates a deterministic control of resource availability on local species richness (SR) and is supported by recent findings (Cardinale et al., 2009a, 2009b). However, to date, most ecological studies on phytoplankton diversity patterns have traditionally focused on understanding among sites variations in SR using explanatory variables quantified at relatively fine scales (e.g. in-lake nutrient concentration). While these studies have provided valuable approaches to test functional hypotheses regarding the drivers of phytoplankton species richness, (i) the hydrogeomorphic (e.g. hydrological connectivity) and anthropogenic features (e.g. land use) occur at multiple scales (Levin, 1992; Turner et al., 2001) and (ii) their interactions with meteorological factors have been seldom studied.

In this study, we examined species richness patterns of phytoplankton communities across 50 freshwater water bodies located in the Paris area (within a 200 km radius), a region characterized by strong gradients in anthropogenic pressure and by different degree of hydrological connectivity of water bodies (Catherine et al., 2008, 2010). We assessed the role of lake-scale and catchment-scale variables in explaining variations of species richness in space and time. Finally, we analysed the residuals of predictive models in order to identify vectors of improvement of predictive models of phytoplankton richness in temperate lakes.

2. Materials and methods

2.1. Study area and sample collection

The Paris area (Fig. 1) is situated in north-central France and constitutes the most densely populated French region and is home to 11.9 million people (19% of the national population; IAURIF, 2014). The region includes many large industrial towns and residential suburbs. However, agricultural and forested areas still cover over 50% and 23% of the region, respectively (IAURIF, 2014), leading to contrasted local environmental contexts. The Paris area includes around 248 lakes and ponds covering over 5 ha (Catherine et al., 2008), most of which are old sand and gravel quarries that were worked between the 1940s and 1980s, or that resulted from peat extraction in the mid-19th century. The remaining water bodies are reservoirs built in the 17th and 18th centuries to provide a reliable water supply for Versailles Castle and the city of Paris. Nowadays, these water bodies support various human activities including water sports and other recreational activities, and fishing.

Data were collected from 50 lakes and reservoirs, which were selected according to a stratified sampling strategy previously described in Catherine et al. (2008). Most selected water bodies are shallow (average depth of water bodies in the area <2.5 m) and represent a wide range of environmental conditions (e.g. size of watershed, land use, hydrology and trophic status) (Catherine et al., 2010).

Sampling was conducted over two summers (50 lakes in August 2006 and 48 lakes in August 2011, hereafter termed Aug06 and Aug11) and one winter (50 lakes in February 2007, hereafter termed Feb07). Each sampling campaign was performed over a short timeframe (approximately two weeks) to obtain a 'snapshot' view of the phytoplankton communities in the selected lakes. Three stations were sampled in each lake to integrate spatial heterogeneity. For each sampling station, a 5 L sample was obtained at three depths (i.e. 0.5–1 m below the surface and at two depths equally spaced according to the lake's depth at the sampling stations) using a Niskin water sampler (KC Denmark, Silkeborg, Denmark). All nine samples per lake were pooled and used for phytoplankton community composition analysis and water chemistry measurements.