



Species complexes within epiphytic diatoms and their relevance for the bioindication of trophic status



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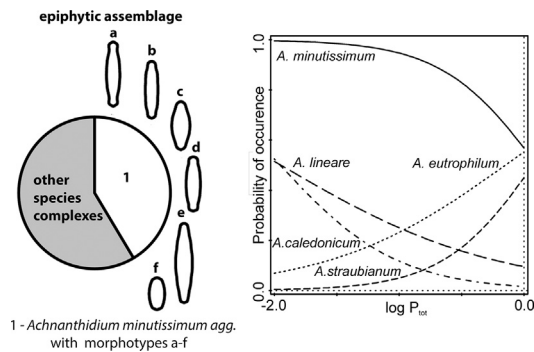
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HIGHLIGHTS

- Freshwater diatoms were examined at localities along a trophic gradient.
- Number of indicator species increased with fine taxonomic resolution.
- Species complexes showed low sensitivity to changes in phosphorus concentration.
- Cryptic species had contrasting relationships to trophic gradient.
- Some cryptic species have potential to improve bioassessment models.

GRAPHICAL ABSTRACT



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ABSTRACT

The popularity of aquatic bioassessments has increased in Europe and worldwide, with a considerable number of methods being based on benthic diatoms. Recent evidence from molecular data and mating experiments has shown that some traditional diatom morphospecies represent species complexes, containing several to many cryptic species. This case study is based on epiphytic diatom and environmental data from shallow fishponds, investigating whether the recognition and use of fine taxonomic resolution (cryptic species) can improve assessment of community response to environmental drivers and increase sharpness of classification, compared to coarse taxonomic resolution (genus level and species level with unresolved species complexes). Secondly, trophic bioindication based on a species matrix divided into two compartments (species complexes and remaining species) was evaluated against the expectation that species complexes would be poor trophic indicators, due to their expected wide ecological amplitude. Finally, the response of species complexes and their members (cryptic species) to a trophic gradient (phosphorus) were compared. Multivariate analyses showed similar efficiency of all three taxonomic resolutions in depicting community patterns and their environmental correlates, suggesting that even genus level resolution is sufficient for routine bioassessment of shallow fishponds with a wide trophic range. However, after controlling for coarse taxonomic matrices, fine taxonomic resolution (with resolved cryptic species) still showed sufficient variance related to the environmental variable (habitat groups), and increased the sharpness of classification, number of indicator species for habitat categories, and gave better separation of habitat categories in the ordination space. Regression

Abbreviations: P_{tot} , total phosphorus concentrations; SPC, species complexes; RSP, remaining species; GL, genus level resolution; SLC, species level resolution with unresolved species complexes; SL, species level resolution with cryptic species recognized; DCA, detrended correspondence analysis; CCA, canonical correspondence analysis; CoCA, co-correspondence analysis; pCCA, partial canonical correspondence analysis; ANOVA, analysis of variance.

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analysis of trophic bioindication and phosphorus concentration showed a weak relationship for species complexes but a close relationship for the remaining taxa. GLM models also showed that no species complex responded to phosphorus concentration. It follows that the studied species complexes have wide tolerances to, and no apparent optima for, phosphorus concentrations. In contrast, various responses (linear, unimodal, or no response) of cryptic species within species complexes were found to total phosphorus concentration. In some cases, fine taxonomic resolution to species level including cryptic species has the potential to improve data interpretation and extrapolation, supporting recent views of species surrogacy.

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1. Introduction

Cryptic species can be defined as two or more distinct species that are classified as a single taxon (Bickford et al., 2007), a “species complex” or “aggregate”. Cryptic species are morphologically similar, superficially indistinguishable, but separable with molecular data or other techniques (Poulíčková et al., 2016). Cryptic species have been recognized for nearly 300 years but research into them has increased exponentially over the past three decades due to the increasing availability of DNA sequences (Bickford et al., 2007). Cryptic diversity is recorded from various groups of organisms (Bickford et al., 2007; Fernandez et al., 2006; Funk et al., 2016; Trontelj and Fišer, 2009), including microalgae and diatoms (Degerlund et al., 2012; Kaczmarska et al., 2014; Kulichová and Fialová, 2016).

Bickford et al. (2007) surveyed the literature for references containing the phrases “cryptic species” or “sibling species” in the title, abstract or keywords, and found surprisingly few papers reporting cryptic species in higher plants or microbes. Botanists do not use these phrases, but species complexes due to polyploidy in angiosperms are common (e.g., Dančák et al., 2012; Duchoslav et al., 2013; Husband et al., 2013; Koblíková et al., 2016; Soltis et al., 2007). Barker et al. (2015) recently estimated that there are ca 50–60,000 cryptic polyploid species in angiosperms that await discovery and naming. Microorganismal molecular data are still limited because of problems associated with DNA isolation. To obtain sufficient material microorganisms must be grown up in clonal culture. Single cell/filament PCR potentially solves this problem but is time consuming. In addition, some microorganismal groups have cell wall structures that complicate DNA isolation, e.g. different types of frustules, loricas, and particularly different types of mucilage envelope (Mareš et al., 2015; Mazalová et al., 2011).

Many reasons have been given for the value of recognizing cryptic species, e.g. biodiversity, conservation, disease treatment and bioprospecting (Barker et al., 2015; Geller, 1999). Bioindication and biomonitoring are based on organisms having known, distinctive ecological requirements, or specific responses to environmental stressors, such as pollution and nutrient enrichment (Adams, 2002; Diekmann, 2003; Zonneveld, 1983). Aquatic bioassessments have increased in popularity in Europe, methods being based mostly on macrophytes and benthic invertebrates (54%), phytoplankton (21%), fish (15%) and phytobenthos (10%; Birk et al., 2012). Bioindication requires standardized sampling, sample processing and identification of collected organisms, mostly (74%) to species level (Birk et al., 2012). However, species complexes are often common, widespread and euryvalent (Poulíčková et al., 2008b; Schlick-Steiner et al., 2007) and thus suitable (Diekmann, 2003). The importance of recognizing cryptic species is relevant when entities within species complexes are ecologically differentiated (Poulíčková et al., 2008b). Knowledge of the bioindication value of cryptic species could improve the sensitivity of bioassessment methods, particularly for the European Water Framework Directive (European Commission, 2000), which requires an assessment of ecological quality at an ecoregional level (Rimet and Bouchez, 2012a).

Diatoms are widespread organisms playing a key role in all freshwater ecosystems (Round, 1981). Therefore, they are considered powerful indicators for recent and past water quality and climates (Birks et al.,

1990; Smol and Stoermer, 2010). Recent evidence from molecular data and mating experiments has shown that some traditional diatom morphospecies represent species complexes containing several to many cryptic species (Kulichová and Fialová, 2016). *Sellaphora pupula* agg., a characteristic epipelagic taxon (Supplementary Fig. S1), is an excellent example of diatom cryptic diversity, with >50 morphotypes (probably cryptic species) in Great Britain alone (Mann et al., 2008), some of which have been found to be ecologically differentiated with respect to trophic gradients (Poulíčková et al., 2008b). *Achnanthis minutissimum* agg. (Supplementary Fig. S1) is another example of cryptic diversity. Although many ecological studies have reported its dominance (lentic vs lotic freshwaters, epiphyton, epilithon; Rimet and Bouchez, 2012a; Cantonati et al., 2014), few have tried to document cryptic diversity within this complex (Potapova and Hamilton, 2007; Wojtal et al., 2011). Together with a few other complexes, *A. minutissimum* can dominate stream and pond epiphyton, contributing up to 97% of the assemblage (Kollár et al., 2015; Supplementary Table S1), not a trivial percentage.

Ignoring taxonomic heterogeneity and potential ecological differentiation within such species complexes may bias ecological assessments of water quality, despite evidence that evaluations adopting lower taxonomic resolution (genus, family, life-forms or guilds; ‘taxonomic sufficiency’ or ‘taxonomic surrogates’; Terlizzi et al., 2003) show similar, or even better pollution assessment than species-level resolution (e.g., Grouns, 1999; Hill et al., 2001; Rimet and Bouchez, 2012b). Indeed, a requirement for cost-effective methods for elucidating the response of ecosystems (across terrestrial, freshwater and marine environments) to anthropogenic impacts has focused on the use of higher taxa as surrogates for species (reviewed by Terlizzi et al., 2003), stemming from the idea of phylogenetic niche conservatism (Losos, 2008; Webb et al., 2002; Keck et al., 2016). However, our knowledge of the extent to which ecological similarity is related to phylogenetic relatedness among species is generally limited (Bevilacqua et al., 2012), partly because the taxonomic classification of many organisms does not mirror phylogenetic relatedness (Wheeler, 2004). More recently, Bevilacqua et al. (2012, 2013) found that the statistical power to detect environmental changes with coarse taxonomic resolution depends on the degree of species aggregation (i.e., the higher taxa/species ratio) rather than the taxonomic resolution (see also Siqueira et al., 2012). Due to the discovery of closely related taxa (cryptic species) (Bickford et al., 2007) that can exhibit ecological niche differentiation (Vanellander et al., 2009), the continual increase in the number of diatom species may decrease the usefulness of coarse taxonomic resolution for the assessment of community responses to environmental variables. In this respect, Bevilacqua et al. (2012, 2013) suggested combining species surrogacy (difficult taxa, tolerant species) with the retention of high taxonomic detail when necessary (indicator taxa, sensitive species, easy recognizable species). Following these ideas we focused on the potential utility of diatom cryptic species for improving the identification of community response to environmental variation. The philosophy of this study is based on expectation that species complexes are generally euryvalent and blur community response to environmental variation, while cryptic species should be ecologically differentiated and thus might be useful for the detection of (subtle) community responses to

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