Opinion paper

Cryptic diversity, niche displacement and our poor understanding of taxonomy and ecology of aquatic microorganisms

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Abstract The analysis of ecological niche is an important task to correctly identify the role exerted by species within ecosystems, to assess their vulnerability, to plan effective measures addressed at fulfilling the postulates of biological conservation, and ultimately to prevent biodiversity loss. However, for the majority of organisms our knowledge about the actual extent of their ecological niche is quite limited. This is especially true for microscopic organisms. Evidence exists that in different geographical areas allegedly conspecific populations can show different, if not antithetical, ecological requirements and not-overlapping ecological niches. This opinion paper discusses whether this "niche displacement" effectively occurs between conspecific populations or if the pattern is rather due to an inaccurate identification of species and/or to an insufficient knowledge about population and community ecology. Hence, some subjectively selected study cases when alleged phenomena of niche displacements take place are presented, and shortfalls in the correct assessment of the identity and ecological niches of microscopic aquatic eukaryotes, namely phytoplankton, zooplankton, and meiofauna are shown.

Keywords Character displacement · Linnean shortfall · Ecological shortfalls · Phytoplankton · Diaptomid copepods · Rotifers

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Introduction

Human-induced global changes deeply modify the structure and functioning of ecosystems, and in turn affect biodiversity patterns in several ways (Western, 2001). To counteract this tendency, several efforts have been made worldwide to understand and reduce biodiversity loss (Leifeld & Menichetti, 2018; Roberts et al., 2020). Climate change, habitat fragmentation and loss, and biological invasions are often the drivers of species extinction and of alterations of the biological relationships amongst species (Pereira et al., 2012; Malhi et al., 2019). Freshwater biodiversity is globally threatened at increasing rates but the bulk of currently available data deals with vertebrate

and macroinvertebrate taxa (Reid et al., 2019), whereas very little is known about microscopic organisms, from bacteria and archaea to phytoplankton and other protists, fungi, and small metazoans. This is probably due to a limited knowledge about the taxonomy, ecology, and distribution of these taxa: limited, potentially misleading, and biased knowledge can hamper a correct evaluation of ecological niches and our ability to describe biodiversity and to make sound predictions on ecological processes (Gotelli & Stanton-Geddes, 2015; Smith et al., 2019; Lopes-Lima et al., 2021). This is especially true for freshwater microscopic organisms whose biological "identity", ecological requirements and biogeography are still far from being fully resolved.

Although several niche concepts are available in the literature (Chase & Leibold, 2003), the main approaches used to define the ecological niche of a species rely on the analysis (i) of the environmental characteristics of its habitat (Grinnellian niche), and (ii) of the complex network of the biological interactions that each species establishes within its community (Eltonian niche) (see Soberón, 2007; Soberón & Nakamura, 2009). An accurate analysis of the ecological niche of a species is important to correctly identify its role within an ecosystem, to assess its vulnerability, to eventually plan effective measures addressed at fulfilling the postulates of biological conservation (Soulé, 1985), and ultimately to prevent biodiversity loss. However, for the majority of microscopic organisms our knowledge about the actual extent of their ecological niche is quite limited. Evidence exists that in different geographical areas allegedly conspecific populations can show different, if not antithetical, ecological requirements and not-overlapping ecological niches (e.g. Jaturapruek et al., 2021). Are these "displacements" effectively occurring between conspecific populations? Or are they rather due to an inaccurate identification of the species? Moreover, is sound information about the actual niche of even widespread species available?

Species as biological independent entities may not always have clear boundaries and several species concepts are available in the literature (e.g. Agapow et al., 2004; De Queiroz, 2007; Sigwart, 2018). Species can be usually objectively and unambiguously definable in local communities (Mallet, 2013), but boundaries amongst species, being them genetic, morphological, or ecological, may become blurred in

biodiversity surveys over large areas (Prinzing et al., 2002; Bergsten et al., 2012). Moreover, the picture is made even more complex by the existence of the so-called "cryptic species", i.e. those species that are considered different based on some evidence (e.g. genetic) but cannot be at present told apart based on morphology (e.g. Fišer et al., 2018). Misidentification of organisms resulting from an inaccurate taxonomic knowledge can impair our attempt to assess their ecological niches and to retrieve correct information from our assessments. Thus, it is not superfluous to point out that, when studying biodiversity, the first step should be the correct identification of species, eventually analysing the problems that prevent the univocal assignment of an organism to this taxonomic category. Errors in the identification of species make actually null any ecological assessment of the alleged species. Nevertheless, a correct species identification and the evaluation of its ecological niche are not always easy tasks and require efforts and experience.

The aim of this opinion paper is to present some study cases when supposed phenomena of niche displacements take place, and to discuss whether they are real or rather to be ascribed to pitfalls and shortfalls in the correct assessment of the identity and ecological niches of microscopic aquatic eukaryotes, namely phytoplankton, zooplankton, and meiofauna. To fulfil this task, we start with a brief discussion on "niche displacements" and the processes possibly underlying them, followed by a few subjectively selected case studies in aquatic microscopic eukaryotes, concluding with a highlight on the major problems affecting our understanding of biological diversity patterns.
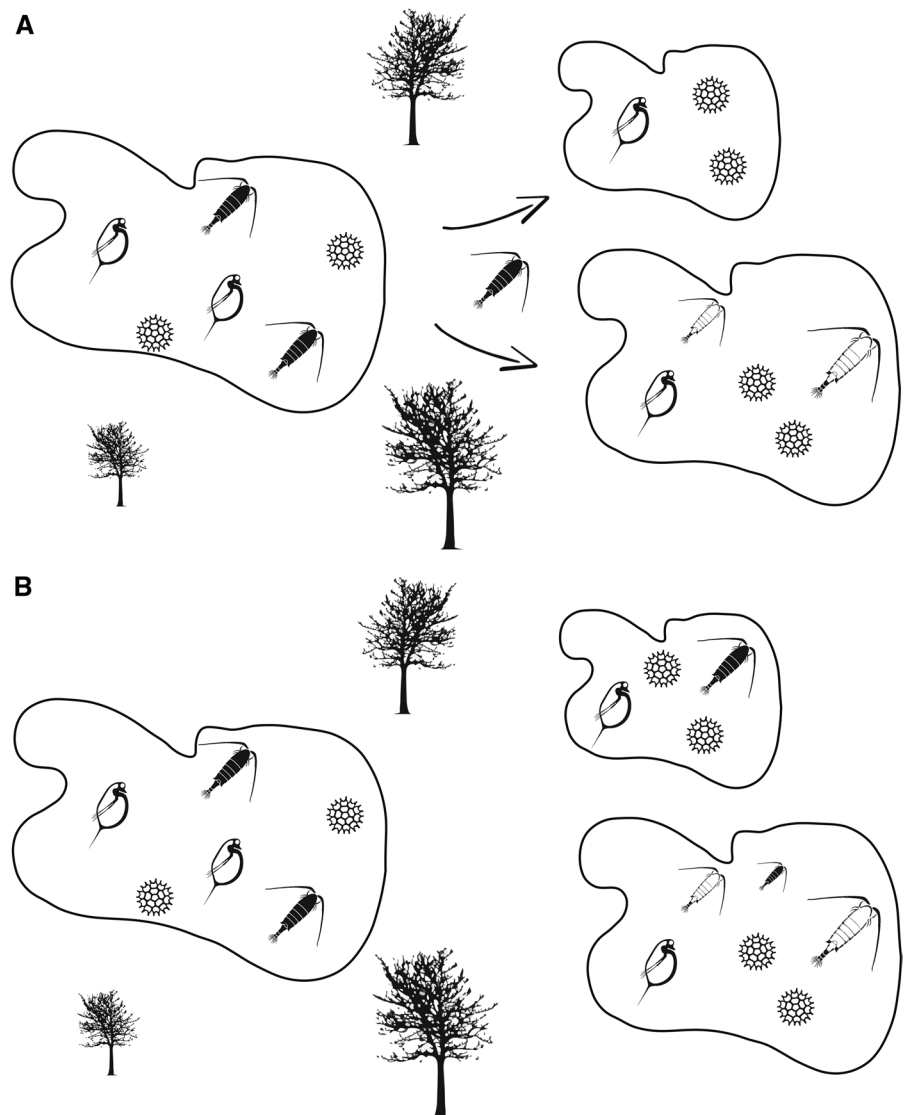
Niche and character displacements

Several examples of phenotypic displacements in space and time are documented in the literature, including morphological, physiological, and ecological differences between conspecific populations. These modifications are mutually connected (e.g. a morphological modification in a species can cause a shift in its ecogeographical range) and all of them synergically cause a "niche displacement". Such a displacement affects the realised niches, i.e. the actual sets of conditions within which populations are observed to occur in different areas, but not the

fundamental niche, i.e. the set of conditions within which a species can live in the absence of competition and other limiting factors (Hutchinson, 1957). By analysing the processes causing these differences we could better understand the real extent of the fundamental niche of the investigated species, i.e. a full understanding of its ecological requirements. However, as suggested by one of the reviewers who revised an earlier draft of this paper, "for most species the fundamental niche remains largely a theoretical conception. Unfortunately, such a niche can rarely be estimated without experimental approaches, contrary to the realised niche which can be directly estimated from the species distribution."

Character displacement occurs when sympatric, similar species differentiate to minimise niche overlap and to avoid competitive exclusion (Brown & Wilson, 1956), e.g. it is a process of phenotypic differentiation of sympatric populations caused by interspecific competition (Fig. 1). However, the process can also be observed within species, e.g. when the different sexes or developmental stages of a species show a marked dimorphism and occupy different niches (De Lisle et al., 2018), when conspecific (sub)populations are spatially and ecologically segregated (Schmit et al., 2013), or when different local adaptations maximise the fitness of the populations to the local biotic or abiotic conditions (Huang et al., 2020).

Fig. 1 A simplified process of character displacement leading to a niche displacement pattern. **A** propagules of a black copepod species (originating from a source habitat where no other copepod species are present) colonise two new ponds through a process of passive dispersal. The first pond is inhabited by *Daphnia* only, the second is also inhabited by two copepod species of different size (white copepods). **B** the population of the species established in absence of other copepods maintains the same body size as its source population; conversely, the population sharing the pond with other copepod species experiences a phenomenon of character displacement mediated by directional selection that leads to a reduction of its size due to the presence of competitors

In microscopic organisms, a large degree of phenotypic plasticity may occur within and between populations and may mediate a "character displacement" that results in a modification of their local realised niches (see Pfennig & Pfennig, 2012), i.e. in a pattern of "niche displacement" which may occur between coexisting (syntopic) or distant (allotopic) populations. The morphology of phytoplankton species can vary in response of fluctuations in resources' availability, temperature, predation, and/or competition (Zohary et al., 2017; Pančić & Kiørboe, 2018; Naselli-Flores et al., 2021); these morphological changes are promoted by more or less subtle changes in the environmental conditions and can increase species fitness. Similarly, environmentally induced phenotypic plasticity, like cyclomorphosis, exhibited by several species amongst cladocerans, rotifers, and dinoflagellates that change their morphology through generations due to epigenetic effects of environmental cues (Black & Slobodkin, 1987; Yurista, 2000; Gilbert, 2017), alters the biological interactions amongst predators and preys and also modifies the life history of the involved species (Dzialowski et al., 2003). Different morphologies not only modify the biological interactions of the species but may differently respond to environmental (e.g. hydrodynamical) constraints, ultimately causing a differentiation of the local ecological niche (i.e. a niche displacement) of those populations undergoing cyclomorphosis compared to those conspecific populations not exposed to cyclomorphosis-inducing stimuli.

Habitat displacement between species occurs when two parapatric species showing similar ecological requirements modify their habitat preferences in those zones, called areas of sympatry, where and when they show a spatial overlap (Iribarne et al., 2003; Peers et al., 2013). Such phenomenon can be observed in the frame of areas of secondary contact between closely related species (Mayfield & Levine, 2010), in the biodiversity patterns following the tropicalisation of the Mediterranean Sea (Bianchi 2007), or when considering biological invasions leading to the establishment of new relationships and to a selection of phenotypic traits amongst native and non-native taxa (Mowery et al., 2021). Moreover, habitat displacement can occur following a process of polyploidisation that allows the polyploid subpopulations to occupy a much wider niche compared to the subpopulation not showing genome duplications (Karunarathne et al., 2018). Although hybridisation and polyploidisation are widely recognised as evolutionarily important phenomena in plants (Fabritzek et al., 2021), they are also not uncommon in animals, where they have important evolutionary implications as drivers of diversification and speciation (Bullini, 1985; Plenet et al., 2000; Wertheim et al., 2013; Ficetola & Stöck, 2016). Unfortunately, studies analysing the ecological implications deriving from genome duplication in animals have been fairly limited to date. However, since "ecology is evolution in progress" (Krebs, 2009), we can easily argue that polyploidisation can offer to animals too a way to avoid niche overlap and to minimise competition.

Character displacements cause the ecological differentiation of populations and represent a first step towards niche displacement. It could be due to local ecological differences (e.g. presence or abundance of predators, preys, and competitors) and/or to local changes in the gene expression granting a different tolerance to abiotic factors, as found in different *Daphnia* clones (Lampert, 2011). In these cases, the realised local niches could differ amongst allotopic populations but the fundamental niche should remain the same (e.g. Soberón & Arroyo-Peña, 2017). However, according to some authors (e.g. Fontaneto & Hortal, 2013) microscopic, passively dispersed freshwater organisms, thanks to the massive production of easily dispersed propagules, can also be found in habitat patches where they cannot "exist indefinitely" (sensu Hutchinson, 1957) due to a negative demographic balance. If such sink habitats are considered as part of the realised niche of the studied species, and the fundamental niche is characterised by a positive or neutral demographic balance (Hutchinson, 1957), one could paradoxically assume that their realised niche is wider than their supposed fundamental niche, thus giving rise to a putative niche displacement. However, following Hutchinson (1957) and Lomolino (2011), such sink habitats (sometimes colourfully referred to as "lands of living dead" or "domains of zombies") should be considered just as parts of their distribution area, but their environmental characteristics should not be used for the assessment of the realised niches of the studied organisms. Accordingly, based on this definition, the realised niches are always comprised within the fundamental one (Fig. 2). The problem remains in how to identify such sink populations.
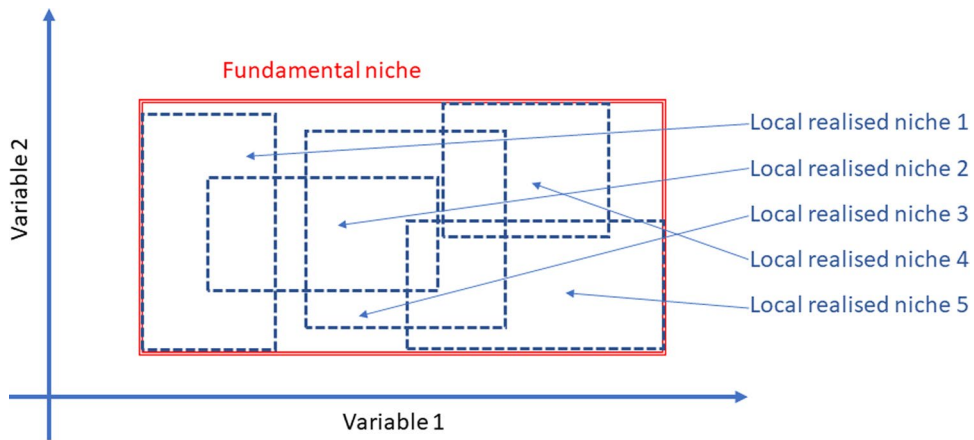
Fig. 2 A bidimensional fundamental niche and some of the different, local realised niches within its boundaries

Conversely, apparent niche displacements could also be due to the presence of cryptic species complexes, not discernible at present using morphological taxonomy, with each cryptic taxon having different niches (Dennis & Hellberg, 2010; Scriven et al., 2016). Molecular tools are questioning the validity of several taxa, and for some groups there is a significant lack of adequate descriptions and type material (e.g. Schlick-Steiner et al., 2007; Fontaneto et al., 2009; Schwentner et al., 2020; Morek et al., 2021). Thus, supposed within-species niche displacement could be either due to different realised local niches exhibited by allopatric or parapatric conspecific populations or to the misidentification of allegedly conspecific populations. Understanding the real extent of niche displacement is thus important since niche displacement between conspecific populations has evolutionary implications and might constitute a first step towards speciation, being a case of interpopulation differentiation due to ecological reasons (Byrom et al., 1993). Such phenomenon can also occur in sympatric conditions, as observed in case of adaptive radiation (Martens & Schön, 1999). In particular, sympatric speciation with gene flow might take place through a process of character displacement mediated by disruptive selection, when extreme values for a trait are favoured over intermediate values thus allowing the exploitation of different niches by co-occurring and initially conspecific individuals (Duffy et al., 2008; Pu et al., 2017; Van Rijssel et al., 2018; but see Schön & Martens, 2004) (Box 1).

Selected examples from literature and case studies

Phytoplankton

Phytoplankton ecologists know well that natural phytoplankton assemblages are generally composed by several, simultaneously coexisting species although all these species are competing for a few resources as light and a variety of nutrients. This paradox of the plankton was first seized by Hutchinson (1961) who suggested that competitive exclusion seldom occurs amongst phytoplankton species because of the high frequency of environmental changes, which prevent competitive equilibrium to get established. The solution proposed by Hutchinson supported a long-standing ecological tenet: true competitors cannot coexist (Hardin, 1960), and truly coexisting species occupy distinct niches (Petersen, 1975). Therefore, if limiting conditions persist uninterrupted for long enough, even for phytoplankton the resource-based competition model postulates that competitive exclusion of all but the fittest (few) species occurs (Reynolds, 2006). Nevertheless, attempts made to verify this assumption by simulating more than two species competing for more than two limiting resources ended up with chaotic and unpredictable outcomes (Huisman & Weissing, 2001). The reasons for this unpredictability probably reside in the phenotypic and genotypic variability of phytoplankton populations, enabling these organisms to quickly adapt to environmental changes or to lessen the biological interactions amongst species (i.e. competition) and/or with predators (i.e.

Box 1 Explanation of terms

Cryptic species	Organisms that appear morphologically identical but are genetically distinct and can be identified as independent evolutionary entities by DNA taxonomy and/or tests on reproductive isolation
Species complex	A group of closely related species that are so similar in appearance that appear as the same morphological species, hiding two or more cryptic species
Syntopic	Organisms occurring in the same site
Sympatric	Organisms occurring in the same region (but not necessarily in the same site)
Allotopic	Organisms occurring in different sites
Allopatric	Organisms occurring in different regions
Grinnellian niche	The determinants of the Grinnellian niche are the habitat abiotic features that allow a species to persist and reproduce
Eltonian niche	The determinants of the Eltonian niche are the biotic interactions (e.g. competition and predation) in the ecological community that allow a species to persist and reproduce
Fundamental niche	The full range of theoretical biotic and abiotic conditions under which a population or a species can persist and reproduce
Realised niche	The set of actual conditions used by a population or a species, where a population or a species can be found
Character displacement	The process of phenotypic differentiation (observable modifications in the physical and/or biochemical characteristics of an organism as determined by both genetic makeup and environmental influences) of sympatric populations caused by interspecific competition to minimise niche overlap and to avoid competitive exclusion
Niche displacement	The pattern deriving from a character displacement that causes a modification in the local realised niche of a species
Phenotypic plasticity	The possibility for one single genotype to produce more than one phenotype that may or may not be permanent throughout an individual's lifespan, and depends on biotic and abiotic stimuli from the environment
Cyclomorphosis	Trans-generational polymorphism induced in some planktic organisms by, e.g. presence of predators or temperature variations

grazing). Moreover, genotypic variability can enhance the invasiveness of phytoplankton species and allow the "expansion" of their alleged fundamental niche (Padisák, 1997; Macêdo et al., 2021).

Phenotypic plasticity has an important adaptive value in phytoplankton (Naselli-Flores, 2014). This group of microalgae collects unicellular and colonial photosynthetic organisms adapted to live in apparent suspension in turbulent water masses. It means that access to resources (light and nutrients) must occur whilst they are entrained in water motion, and this have played an important role in the ecology and evolution of planktic photosynthetic microorganisms (Reynolds, 2006; Stomp et al., 2007); given their short life, hydrodynamic variability represent the most important driver of environmental change for phytoplankton populations, and exert a strong selective pressure on their size and shape (Naselli-Flores & Barone, 2011; Naselli-Flores et al., 2021). Shape and size can be used to identify three life strategies of phytoplankton described by Reynolds (1988, 2006) in his Competitors-Stress tolerants-Ruderals (C-S-R) model. In this model the size and the morphology of

single local species is linked to two environmental factors (light availability and nutrient accessibility) that are considered as the major dimensions of their ecological niche (Brun et al., 2015). By applying the C-S-R model, it can be noticed that the realised niche of phytoplankton species can show displacements since the intraspecific morphology of both unicellular and colonial species can vary (Naselli-Flores & Barone, 2003). In fact, the majority of phytoplankton populations exhibit a high degree of phenotypic plasticity that allow them to persist as the environment changes. Only when the change is strong enough to overcome the limit of its phenotypic plasticity, the population is replaced by another, fitter one (Naselli-Flores & Barone, 2000; Naselli-Flores et al., 2007). Genetic adaptation can also occur via strain selection or selection of new genotypes eventually arising through mutation, recombination, or horizontal gene transfer (Litchman et al., 2012; Foflonker et al., 2018). A recent analysis showed that cell size amongst pico-phytoplankton lineages is partitioned into latitudinal niches following gradients of light and temperature (Flombaum et al., 2020). Temperature not only exerts

a direct influence on metabolism but also modifies water properties (i.e. density and viscosity) linked to phytoplankton sinking and floating. In addition, it influences phytoplankton ability to access resources in several ways, ultimately allowing a local and seasonal variability to their realised niche (Larkin & Martiny, 2017; Ajani et al., 2018). The high phenotypic plasticity of phytoplankton species ensures seasonal and geographical adaptations within a range of environmental variability at both population and community levels (e.g. Zohary et al., 2017; Larkin & Martiny, 2017; Caracciolo et al., 2021; Zohary et al., 2021). Therefore, phenotypic plasticity could be considered as a proxy of niche width but, unfortunately, no data exist on the extent of the environmental range that the phenotypic plasticity of a given phytoplankton species can cover in natural conditions.

Phenotypic plasticity may also be effective as a defence mechanism promoting the change from solitary cells to colonies or other morphological variations as the production of spines or reinforced cell walls (Pančić & Kiørboe, 2018). In some cases, inducible colony formation can mask the taxonomic identity of species (e.g. species can be identified as *Chorella* when found as single cells or as *Micractinium* when found in colonies; see Luo et al., 2006). These defence mechanisms not only modify the biological relationships between phytoplankton and its grazers (Eltonian niche) but also the way in which phytoplankton copes with its physical environment (Grinnellian niche) and should be carefully considered in environmental monitoring and biodiversity assessments. In fact, analysing the phytoplankton realised niches over time represents an effective tool to track environmental changes that happen with a relatively short time lag (Ajani et al., 2018).

Functional classification of phytoplankton sensu Reynolds et al. (2002) describes a method to group species into ecologically coherent clusters (i.e. species showing a high degree of niche overlap) and offers information on the habitat template under which each cluster thrive. It not only reduces the number of functional units in the community making easier ecological evaluations, but also helps to correctly identify species on the basis of the ecological context where they are found (Salmaso et al. 2015). Moreover, it represents a starting point to analyse niche characteristics of functionally grouped species (Nagy-László et al., 2020). However, assigning species to functional groups requires an adequate knowledge on the ecology of phytoplankton species and good taxonomic skills. Species misplacements, often linked to pre-concepts of the users (including species misidentification), frequently occur in literature (Padisák et al., 2009).

Niche displacement of phytoplankton can often arise from errors in the identification of species. This can be due to a lack of experience but also to the molecular revolution that taxonomy and systematics have been experiencing since a few decades ago. Several species were found to be hidden under one single species name due to the morphological stasis that is unmatched by the occurrence of separate evolutionary entities (cryptic species). Moreover, new, less inclusive genera were established, and several new species that are not distinguishable by light microscopy were described (e.g. Krienitz & Bock, 2012; Komárek, 2018). In addition, in several different phytoplankton taxonomic groups, the lack of type material, the insufficient description of many taxa, and the subjectivity of morpho-species approach have caused a frequent classification and re-classification of organisms (e.g. Hoppenrath, 2017). Problems in taxonomy and systematics can arise from objective difficulties in placing biological entities into the appropriate taxon. In addition, splitting genera and renaming species often cause problems to end-users when they have to assign organisms to a given taxon. It is rather common to see taxonomic list of phytoplankton containing epibenthic taxa such as *Oscillatoria* or *Melosira*, or, in the worst cases, species which were originally described as typically growing on tree bark (Komárek, *pers. comm.*).

Diaptomid copepods

Diaptomids, the dominant calanoid copepods in the inland waters of the Palaearctic region, are characterised by quite a stable taxonomy when compared with that of other non-malacostracan crustacean taxa, and the identification of diaptomid morphospecies is often quite straightforward, thus making the information available in regional checklists and studies mostly reliable. This allows to highlight some apparent inconsistencies amongst the niches of allegedly conspecific populations occurring in different regions (see examples below). Conversely, the problematic taxonomy of most copepod genera and species

belonging to the order Cyclopoida and Harpacticoid leads to overestimate the niches of the nominal species, which are mostly considered widespread and euryecious, thus preventing from highlighting possible differences amongst the realised niches of allopatric populations. Accordingly, we here present some case studies dealing with the family Diaptomidae only.

Diaptomus cyaneus Gurney, 1909 is a widespread diaptomid species occurring in western Europe and Maghreb (Dussart & Defaye, 2002; Błędzki & Rybak, 2016). A certain morphological variability was observed within the species, and this brought to the description of some subspecies of uncertain taxonomical value (cf. Kiefer, 1978; Błędzki & Rybak, 2016); to date only *D. c. admotus* Kiefer, 1974 is considered valid and occurring in Dalmatia and Morocco (Kiefer, 1978), whereas the other subspecies are considered junior synonyms of *D. cyaneus* s.s. In Tunisia, Italy and Corsica, only *D. cyaneus* s.s. is unanimously reported to occur (Kiefer, 1978; Alfonso et al., 2021). The species is rather common in low to medium altitude temporary ponds in Tunisia, Sardinia, Sicily and Apulia, co-existing sympatrically and sometimes even syntopically and synchronically with the congener *D. serbicus* Gjorgjweic, 1907 (e.g. in Sicily, see Marrone et al., 2006b). Oddly, the occurrence sites of the species in Corsica and central and northern Italy are limited to high-altitude, sometimes permanent water bodies, being replaced by *D. serbicus* at lower altitudes along the Tyrrhenian coast of the peninsula (Alfonso et al., 2021). In the light of the importance of hydroperiod and climate in determining diaptomid distribution (e.g. Marrone et al., 2017), such a pattern is counter-intuitive in two aspects: first, it is in sharp contrast with the altitude-for-latitude temperature model, according to which a similar climate is expected to occur at the higher altitudes of southern areas and lower altitudes of northern areas (in the northern hemisphere). A species occurring at high altitudes in southern areas is thus expected to occur at lower altitudes in northern areas, as routinely observed for other diaptomid species (e.g. *Hemidiaptomus gurneyi* (Roy, 1927), which is strictly linked to mountainous area in Sicily but a typical lowland species in Peninsular Italy, see Alfonso et al., 2021), whereas the opposite pattern is clearly observed in *D. cyaneus*. Second, the occurrence of *D. cyaneus* in permanent, sometimes even fish-inhabited, water bodies has never been observed in the southernmost regions of the study area (i.e. Tunisia, Sicily, Apulia and Sardinia), whereas the only populations occurring in northern Italy and Corsica are occurring in such a habitat (Alfonso et al., 2021).

Arctodiaptomus alpinus (Imhof, 1885) is a widespread Palearctic species occurring from Mongolia to western Europe, although the actual conspecificity of the Asian and European populations has been questioned by Marrone et al. (2015). In Europe, it is considered a "*cold stenothermal alpine diaptomid species (real high-altitude species with a strong preference for ultraoligotrophic alpine lakes above the timberline)*" (quotation from Błędzki & Rybak, 2016). However, Marrone et al. (2019) found the species in five eutrophic temporary ponds in the Mediterranean island of Crete located at altitudes comprised between 539 and 1330 m a.s.l., co-occurring with typical Mediterranean branchiopods and the paradiaptomin *Neolovenula alluaudi* (Guerne & Richard, 1890), the latter considered a steppic element typical of arid and semi-arid areas (Alfonso & Belmonte, 2013). Analogously to the case of *Diaptomus cyaneus* discussed above, this species shows a counter-intuitive pattern, with a preference for higher altitudes at higher latitudes. Moreover, the habitat type colonised in different region is sharply different, ranging from temporary ponds in the Mediterranean area to high-altitude permanent lakes in the Alps.

Arctodiaptomus wierzejskii (Richard, 1888) is a widespread Palaearctic species occurring from the Azores to Mongolia, and from Maghreb to the Shetland Islands and Novaja Zemlia (Kiefer, 1978; Dussart & Defaye, 2002; Marrone et al., 2017). The actual conspecificity of the Asian and European populations of the species has been questioned by Marrone et al. (2015) based on antennular chaetotaxy. Within its West-Palaearctic distribution range, where the conspecificity of the populations is currently not debated (but see Montevago et al., 2020), the species shows noteworthily different and counterintuitive ecological needs, being typical of permanent, deep, oligotrophic lakes in Great Britain (Fryer & Joyce, 1981), of tundra pools in Russia (Kiefer, 1978) and of temporary ponds and pools in Maghreb (e.g. Gauthier, 1928; F. Marrone, pers. obs.).

Moreover, in addition to the cases mentioned above, the existence of populations with apparent different ecology has been suggested for other diaptomid

species, e.g. *Arctodiaptomus salinus* (Daday, 1885), occurring both in fresh and highly-mineralised water bodies in Spain but linked to saline water bodies throughout its Palearctic-wide distribution range (Alonso, 1998; Błędzki & Rybak, 2016), and *Mixodiaptomus kupelwieseri* (Brehm, 1907), which is strictly linked with poorly mineralised high-altitude ponds in Sicily (Marrone et al., 2006a, b) but proves to be an extremely euryecious and eurytopic species in the rest of its distribution range (Błędzki & Rybak, 2016).

The ecological differences and counter-intuitive patterns sometimes observed amongst allegedly conspecific diaptomid populations should be investigated through a taxonomic approach combining molecular and morphological evidences, aimed at testing their actual conspecificity. In fact, the significant morphological conservatism of Diaptomidae implies the existence of a high number of cryptic or pseudocryptic species, so that under a given binomen several different taxa, possibly with different ecologies could be actually lumped (see Saetang et al., 2022, and references therein). When sound information about the actual conspecificity of the study populations is available, e.g. in the case of the diaptomid *A. alpinus* (see Marrone et al., 2019), the observed inter-populational differences can be ascribed to phenomena of niche displacement, i.e. to the existence of different realised niches of a given species in different regions due in turn to their co-existence with different local biota of competitors, predators, and prey items.

Rotifers

Phenotypic plasticity is one of the main characteristics of rotifers, and is often used as a response mechanism to predators or to environmental changes (Franch-Gras et al., 2017; Gilbert, 2018). Such high phenotypic plasticity is also coupled with predictable or unpredictable trans-generational changes in morphological features in rotifers (Gilbert, 2017), a process termed cyclomorphosis. These features created problems in the delimitation and identification of species in rotifers, given that intraspecific variability could be broader than interspecific differences, with the results that the number of cryptic species is very high (Fontaneto et al., 2009; Garcia-Morales et al., 2013). Almost any known species of rotifers that has been analysed with tools from DNA

taxonomy was revealed as a complex of cryptic species (Gabaldón et al., 2017).

Cryptic species within a species complex often coexist syntopically, and for their co-existence to be allowed, they are expected to differ in at least some axes of their niches. Detailed studies on such expectation are available for the *Brachionus plicatilis s.l.* species complex, a group of at least 15 different species (Mills et al., 2017). Some of the species in the complex frequently coexist (Ortells et al., 2003; Montero Pau et al., 2011; Gabaldon et al., 2015), and when coexisting they often show evidence of niche differences, with temporal turnovers related to differential optima at different salinities. The identification of potential niche displacements in this case is not easy, given that most of the species of the complex have a broad range of salinity tolerance and the actual salinity range for each species is currently unknown. Another species complex within the same genus, *Brachionus calyciflorus s.l.*, with four widely distributed species (Michaloudi et al., 2018), revealed coexistence of taxa that show statistically significant differences in their ecology and morphology (Papakostas et al., 2016; Zhang et al., 2019). Whether this can be considered a case of niche displacement for syntopic species is still premature. Most other rotifer species complexes, such as also those within the genera *Euchlanis*, *Polyarthra,* and *Synchaeta*, revealed cryptic species that differentially respond to the environment (Obertegger et al., 2012, 2014; Kordbacheh et al., 2019). Such ecological differentiation has not been disentangled for all cryptic species, and for several of them the differential niche axes amongst cryptic taxa within each complex have not yet been described, e.g. for *Testudinella clypeata s.l.* and *Philodina flaviceps s.l.* (Fontaneto et al., 2008; Leasi et al., 2013), making it impossible at the moment to provide any inference on their niches.

A case of geographic niche displacement in rotifers could be that of *Rotaria neptunia* (Ehrenberg, 1830), which is considered an indicator of eutrophic water bodies in temperate Europe but avoids eutrophic waters in the tropics in Thailand (Jaturapruek et al., 2021). Whether such geographic displacement of ecological needs could be due to the occurrence of different cryptic species within a species complex in the two geographic areas is still unknown (Jaturapruek et al., 2021).

Taxonomic and ecological shortfalls

From the study cases listed above, it appears that available taxonomy and systematics necessitate deep reappraisal and revisions based on integrating morphological, genetic, and ecological data in order to be able to soundly characterise the fundamental niches of the biological entities under investigation (whether they are species, subspecies, or populations), and to test whether the differences amongst local realised niches of supposedly conspecific populations are rather to be ascribed to our failure to discriminate amongst apparently similar taxa. Lacking such information, which should make the baseline of any biodiversity assessment, it is not possible to distinguish between a biased interpretation of diversity patterns and the actual presence of niche displacement phenomena. Unfortunately, since all the taxa are (more or less) affected by significant taxonomic impediments, the risk that our analyses are biased is real and should not be underestimated.

In those few cases when data soundly attesting the conspecificity of populations with markedly different ecology are available (e.g. in the case of the diaptomid copepod *Arctodiaptomus alpinus*, see above), the existence of different realised local niches is confirmed, implying a fundamental niche often broader than previously hypothesised. Locally different multiple interactions involving both physical and biological factors possibly promote different processes of character displacement in different areas (e.g. Pinceel et al., 2021), ultimately bringing to a within-species niche displacement pattern.

A detailed analysis of niche displacement patterns is mandatory to characterise both the fundamental and realised niches of species, and to better understand their mutual interactions. Accordingly, it is necessary to overcome those shortfalls that prevent any sound assessment of biodiversity (Hortal et al., 2015). First, the Linnean shortfall, according to which our taxonomic knowledge and expertise is largely deficient. It consists in both the incomplete census, description, and characterisation of global biological diversity ("taxonomic gap") and in the insufficient resources devoted to the formation and sustaining of taxonomists and of taxonomic research ("taxonomic impediment"). The existence of a Linnean shortfall is long acknowledged both

by scientists and stakeholders, but to date little has been done to solve it (Engel et al., 2021).

Sometimes the real niche of a species is incorrectly estimated because several different entities with different or partially overlapping niches are lumped under a single binomen bringing to an overestimation of its real niche (e.g. in the rotifer genus *Brachionus*, see Gabaldón et al., 2017; Mills et al., 2017). Although rarer, also the opposite case might happen, with an underestimation of the real niche of a species which is erroneously split under two or more binomia (e.g. the niche of the copepod *Arctodiaptomus alpinus* was underestimated when the Mediterranean populations of the species were ascribed to the taxon *A. piliger* Brehm, 1955, now considered a synonym of the former, see Marrone et al., 2019).

Obviously, the correct assessment of the niche of a species is particularly difficult for the cryptic species complexes, which are widespread amongst different taxa and biogeographical regions (Pfenninger & Schwenk, 2007), so that without accurate morpho-molecular taxonomic revisions the niche of chimeric entities is de facto inferred. This has obvious implications in conservation biology (e.g. Delić et al., 2017). A sound characterisation, delimitation, and identification of species in accordance with an explicit theoretical and methodological approach is thus pivotal for all the subsequent ecological analyses.

A multi-faceted ecological shortfall exists as well. According to Hortal et al. (2015), it can affect our knowledge on evolution ("Darwinian shortfall"), geographical distribution ("Wallacean shortfall"), abiotic tolerances ("Hutchinsonian shortfall"), traits and their trade-off ("Raunkiaeran shortfall"), biotic interactions ("Eltonian shortfall"), and population dynamics ("Prestonian shortfall"). In fact, our understanding of the ecology of microorganisms is often largely inadequate also because we do not know their true distribution ranges, especially in the case of the smaller and "less charismatic" taxa. Unfortunately, rather than being conscious of these limits, we tend to estimate the ecology of species based only on the available evidence, which is often scarce and not fully covering the breadth of their fundamental niche. Moreover, the core distribution area of species and their "typical" ecological needs are in several cases unconsciously linked with their type localities and\or with the areas where they have been most investigated, erroneously considering "exceptions" any

further evidence collected elsewhere or later. The lack of adequate ecological knowledge has important implications when conservation plans are developed. In fact, as pointed out by Lopes-Lima et al. (2021) a further shortfall, the "Ostromian shortfall", resulting from a poor understanding of the ecology of species, can impair the applicability and effectiveness of conservation assessments, as well as its methods, funding, and policies.

Concluding remarks

Nearly two centuries after the revolutionary work of Darwin and the affirmation of evolutionary theories, we are still far from a sound and uncontroversial understanding of the ecology and evolutionary pathways of aquatic microorganisms. The several aforementioned shortfalls "beset large-scale knowledge of biodiversity" (Hortal et al., 2015) and impair our understanding of the complex interactions amongst organisms and those occurring with their habitats. This problem is further exacerbated by the existence and propagation of erroneous or inadequate description, characterisation, and identification of biological entities, which often occur in public scientific repositories and synoptical works (e.g. Meiklejohn et al., 2019), and has obvious consequences in biodiversity assessment, conservation, and management. As stressed by de Faria Peres et al. (2021) in a work dealing with Neotropical deers, it is necessary to improve the process of data check and validation applied to inventories and data collection to avoid producing inconsistent information, as this might affect management and conservation actions. If this holds true for large mammals, the risks of errors when dealing with aquatic microorganisms might even be higher, especially in the light of the long-lasting crisis of taxonomy and taxonomical expertise (e.g. Agnarsson & Kuntner, 2007; Engel et al., 2021).

Character and niche displacements are the resultant of natural selection and have a role in shaping biodiversity (Vellend, 2010); however, habitat modifications and biological invasions are altering these processes jeopardising local and global biodiversity and leading to the global homogenization of biota (Padial et al., 2020). The overcome of the shortfalls affecting our understanding of the actual biological diversity and its functioning is now urgent, starting

from a clear discrimination of real patterns from those due to our ecological and taxonomical prejudices, and from a correct understanding of both fundamental and local realised niches of accurately identified taxa. In this frame, there is much to do with aquatic microorganisms, which support aquatic (and global) ecosystem functioning (Naselli-Flores & Padisák, 2022) but are poorly known by non-specialists and include no "charismatic" species. The nowadays widespread molecular techniques used to investigate biological diversity allow to explore phylogenetic and geographical patterns of diversity, but in the absence of their morphological description, the cryptic species remain taxonomically cryptic (Schlick-Steiner et al., 2007; Morard et al., 2016; Delić et al., 2017): as often advocated, the implementation of an integrative, iterative approach to taxonomy is now fundamental to overcome the Linnean shortfall and all the subsequent limits to a sound understanding of population and community ecology (e.g. Fontaneto et al., 2015 and literature therein).

Declarations

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