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ORIGINAL PAPER

Microbial biogeography through the lens of exotic species: the recent introduction and spread of the freshwater diatom *Discostella asterocostata* in the United States

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Abstract The large population sizes and high dispersal potential of microbes suggests that a given microbial species should be found in all suitable habitats worldwide. Consequently, microbes should not exhibit the kinds of biogeographic patterns seen in macroorganisms. This paradigm is challenged by a growing list of exotic microbes with biogeographic disjunctions that instead promotes microbial dispersal as inherently limited. We sampled water bodies in the United States and compiled records from the literature and public databases to characterize the distribution of the freshwater planktonic diatom, *Discostella asterocostata* (Xie, Lin, and Cai) Houk and Klee. *Discostella asterocostata* was thought to be restricted to the Far East, but we report its presence in ecologically similar water bodies across the eastern United States. Populations from the U.S. and China are indistinguishable morphometrically, suggesting they may be recently separated—a hypothesis supported by paleolimnological data, which support an introduction of *D. asterocostata* into the U.S. as recently as the mid-1980s. The overlapping distributions of *D. asterocostata* and invasive carp species, in both their native and nonnative ranges, highlighted Asian carp as a possible vector for introduction of the diatom in the U.S. The existence of exotic diatoms underscores natural constraints on microbial dispersal, resulting in biogeographic distributions that can be upended through human activity.

Keywords Asian carp · Baas–Becking hypothesis · Bighead carp · Freshwater · Reservoirs · Silver carp

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Introduction

According to the Baas–Becking hypothesis (BBH), the small size and rapid growth rates of microbes lead to large population sizes, facilitating passive dispersal and allowing them to colonize suitable habitats worldwide (Baas Becking 1934). The ability of many species to form resilient resting cells should further enable dispersal across long distances. As a result, with few if any barriers to dispersal, microbes should not exhibit the kinds of biogeographic patterns that characterize vertebrates, land plants, and other macroorganisms (Fenchel and Finlay 2004). This paradigm has shaped much of the debate and research focused on understanding the patterns of species richness and biogeography of prokaryotic and eukaryotic microbes. The BBH is challenged, however, by a large and growing number of studies which show, for example, that not all microbes are present in the vast numbers assumed by the BBH. Like other species (Preston 1948), many microbes exist in low abundance (Curtis et al. 2002; Ashby et al. 2007; Jia et al. 2018), and these species are often more narrowly distributed than those with higher abundance (Finlay 2002; Nemergut et al. 2011). In addition, several studies have also shown compelling evidence for dispersal limitations across a range of spatial scales and in a diverse set of both prokaryotic and eukaryotic microbes (Martiny et al. 2006; Telford et al. 2006; Vyverman et al. 2007). Other challenges to the BBH include species–area relationships (Bell et al. 2005; Peay et al. 2007) and credible reports of endemism (Foissner 2006). Finally, if dispersal is truly unconstrained, then we should not find evidence for recent human-mediated dispersal of microbes into areas outside of their known (native) ranges (Vanormelingen et al. 2008; Spaulding et al. 2010).

Unless they are pathogenic or ecologically disruptive, invasive microbes can easily evade detection (Litchman 2010). Detection can be hampered by lack of long-term baseline data on the microbial community composition of an area, which makes it difficult to identify and characterize microbes as nonnative. Detection is further challenged by the inability to discern foreign and native microbes in groups that are notoriously difficult to classify because of their paucity of distinguishing phenotypic characters. These challenges are exacerbated in cases where the nonnative species is present but in low abundance. Alternatives to traditional cell counting, such as high-throughput metabarcoding and metagenomic sequencing, can help offset, but not necessarily fully overcome, some of these problems (Darling and Mahon 2011).

Due to the ecological importance and worldwide distributions of many species, diatoms have factored prominently into debates about microbial biogeography, cosmopolitanism, and endemism (Finlay et al. 2002; Telford et al. 2006; Vanormelingen et al. 2008). These studies are also driven by the goal of identifying the underlying drivers of diatom diversification: diatoms are a hyperdiverse lineage of tens of thousands or more species that have diversified throughout marine, freshwater, and terrestrial ecosystems worldwide (Malviya et al. 2016; Nakov et al. 2019; Pinseel et al. 2020). They play cornerstone roles in the global cycling of carbon, oxygen, and silica (Tréguer et al. 1995; Field et al. 1998), and their persistent silicon cell walls are preserved in marine and freshwater sediments dating back tens of millions of years. Diatom cell walls are rich in ultrastructural features that are the basis for species delimitation and taxonomic classification (Round et al. 1990). Although many diatom species are defined by subtle quantitative or morphometric differences evident mainly to specialists, other so-called “flagship” taxa (Tyler 1996; Foissner 2006) are so unmistakable morphologically that they are virtually impossible to overlook or misidentify.

Discostella asterocostata (Xie, Lin, and Cai) Houk and Klee is one such species. Originally described as *Cyclotella asterocostata* from reservoirs in central China (Xin et al. 1985), this species is distributed across the Far East, including sites in China (Houk 1992), Japan (Tanaka 2007), South Korea (Lee et al. 1995; Houk et al. 2010), and eastern Russia (Medvedeva et al. 2009). *Discostella* species are commonly found in the phytoplankton communities of large rivers, ponds, lakes, and reservoirs worldwide. Although many small *Discostella* species are distinguishable only by subtle morphological differences, *D. asterocostata* stands out as one of the most distinct and easily recognizable members of the genus based on its large size, strong concentric undulation of the valve face, further undulation in the valve center, and prominent external extensions of the strutted processes (Xin et al. 1985; Houk et al. 2010). *Discostella asterocostata* has not been reported from Europe or the Western Hemisphere, where freshwater diatom floras have been intensively documented for decades (e.g., Patrick and Reimer 1966; Simonsen 1987; Krammer and Lange-Bertalot 1991). In other words, absence of this conspicuous taxon from Western Hemisphere floras cannot be attributed to mere oversight (Fig. 1).

We compiled records from the literature, water monitoring projects in the U.S., and our own collections to characterize the global distribution of *D. asterocostata*, including the first reports in the U.S. Paleolimnological, ecological, and morphometric datasets together support the hypothesis that *D. asterocostata* was recently introduced and has quickly spread across the central and eastern U.S. Although the mode of introduction is unknown, overlap in the native and introduced ranges of *D. asterocostata* and invasive planktivorous Asian carp species suggests that they may have been vectors for the introduction. This study adds to a growing number of records of exotic diatom species, which taken together, indicate that many diatoms do, in fact, have restricted biogeographic ranges.

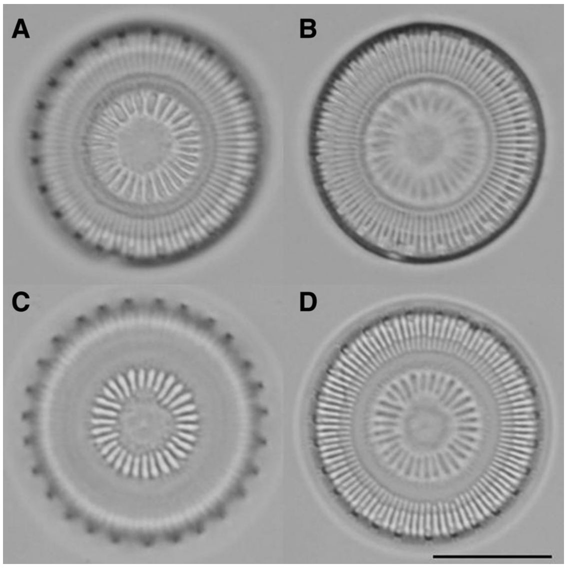

Fig. 1 Light micrographs of the freshwater planktonic diatom, *Discostella asterocostata*. The different focal planes show the concentrically undulated valve surface, which tapers downward from the central apex to an outer ring of regularly spaced strutted processes, which resemble spines. In **a**, **c** the focus is on the center of the cell and the distal ends of the marginal extensions of the strutted processes. In **b**, **d** the focus is on the outer margin of the cell. Panels A and B show a specimen from the type locality in China. **c**, **d** show a specimen collected from Beaver Lake, Arkansas, USA. The diatoms were photographed at 1000× magnification. Scale bar=10 µM

Materials and methods

Diatom sampling and community composition

We sampled a total of 11 sites in Arkansas, Oklahoma, and Indiana (USA) that contained *D. asterocostata* (see Appendix S1 in Supporting Information). Most sites were sampled on one occasion. We collected near-surface phytoplankton with a 10 µM mesh net, and we sampled surface cores from two lakes in Arkansas (Beaver Lake and Lake Fayetteville) and five lakes in Indiana (Izaak Walton Lake, Sisters of Providence Lake, Beall Woods Lake, and ponds from Dobbs and Maple Avenue Parks in Terre Haute, Indiana) over the course of five years (Appendix S1). A portion of each sample was weighed into scintillation vials, and organic components were digested in 30% hydrogen peroxide at room temperature for up to three weeks. After digestion, samples were rinsed with reverse-osmosis purified water four times then dried onto no. 1 type coverslips. Coverslips were mounted onto microscope slides with Naphrax®, a heat-cured epoxy with a high refractive index.

We discovered additional U.S. records of *D. asterocostata* in The Academy of Natural Sciences of Drexel University database (https://diatom.ansp.org/taxa/taxon2506007.html) and the Neotoma Pale oecology Database (https://www.neotomadb.org/) (see Appendix S1). In addition to reported records of *D. asterocostata* in these databases, we examined diatom slides from samples collected in years 2015–2018 in which the original analyst reported unidentified *Discostella*. *Discostella asterocostata* was described from reservoirs in China, and we were also able to obtain and analyze isotype material from the original species description (Xin et al. 1985).

The diatom community composition of a water body is broadly indicative of its ecology (Smol and Stoermer 2010; Stevenson 2014). We characterized the diatom community from each site in our collection and from the type locality in China, to determine whether *D. asterocostata* lives in water bodies with similar conditions in the U.S. and China. We identified diatoms to species level and counted at least 600 diatom valves per sample. All counts were made by a single investigator (KMM) using a Leica DM2500 microscope with differential interference contrast optics and attached Leica DFC295 camera. The raw count data are available in the Supporting Information (see Appendix S2). For sedimentary records, a minimum of 300 fossil diatom valves were counted for each slide. The relative abundance is reported in samples where *D. asterocostata* was present in the 300-valve count. If *D. asterocostata* was not present in the count transect, the entire slide was scanned for its presence in the assemblage. If one or more valves were discovered in whole-slide scans, we considered it as present in 'trace' abundance.

We converted absolute diatom counts to relative abundances and used the vegan package (Dixon 2003) in R to ordinate the water bodies with non-metric multidimensional scaling (NMDS) and Bray–Curtis distances.

Morphometrics

We chose samples from the type locality in China and eight sites in the U.S. for morphometric analysis. Measurements included five diameter measurements that mark discrete morphological breakpoints on the valve face (Fig. 2, circles) as well as three meristic variables, including total count of marginal strutted processes (Fig. 2, squares), total outer striae count (Fig. 2, black ovals), and total central striae count (Fig. 2, radiating lines in valve center). Approximately 20 specimens per site were photographed at 1000× magnification with the goal of capturing the full range of cell sizes in the population. For phytoplankton samples, diatoms were imaged using a Zeiss Axio Imager.A2 light microscope with a Canon EOS Rebel T2i camera, and measurements were made on digitized images using the Image J software package (Schindelin et al. 2015). Cells from sediments were imaged with a Leica DM2500 upright light microscope and measured with the integrated Leica Application Suite software. As necessary, we made measurements from images captured at different focal planes of the valve (see Fig. 1). The morphometric data are available in the Supporting Information (see Appendix S3).

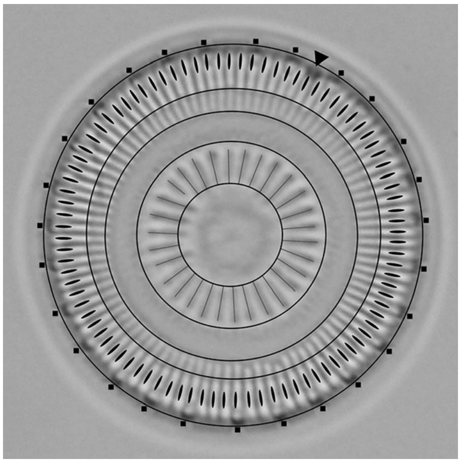

Fig. 2 Morphometric data collected for *Discostella asterocostata*. The dataset included counts of marginal strutted processes (small squares) and one outer and one inner set of striae (radiating filled ovals and gray lines, respectively). Concentric black circles show continuous measurements of cell diameter and diameters that mark discrete transition zones on the cell surface. The triangle shows the position of the labiate process

We used principal component analysis (PCA) as implemented in the R package FactoMineR (Lê et al. 2008) to determine whether populations from the U.S. and China could be separated in morphometric space. The measurements included both meristic and continuous variables, so we performed the PCA on the correlation matrix, rather than the covariance matrix, to standardize these two different data types. We validated results of the PCA using canonical discriminant analysis as implemented in Systat ver. 13.2 and with default settings.

Sediment cores and dating

Surface cores were collected using an inflatable boat and rope-deployed HTH Gravity Corer (Hansson and Renberg 2008). Following sampling, the sediment–water interface of each core was stabilized using the polymer gel Zorbitrol (sodium polyacrylate) before transport to the Indiana State University Paleolimnology Laboratory where the cores were stored at 4 °C prior to subsampling. The two coring sites in Arkansas were sampled because *D. asterocostata* had been previously found in phytoplankton samples by AJA, whereas *D. asterocostata* was discovered by chance in the Indiana coring sites as part of other coring surveys conducted between 2013 and 2018 that targeted natural and human-constructed lakes across Indiana.

Each core was extruded in 0.5-cm increments into WhirlPak bags, and subsamples were dried in a convection oven at 40 °C. A fraction of each subsample was weighed into scintillation vials, and organic components were digested before mounting cleaned diatoms onto microscope slides as described above. Samples in which *D. asterocostata* was not rare were analyzed by identifying and counting 250–300 diatom valves per sample. When *D. asterocostata* abundance was less than 0.3% (trace abundance) in the count, entire slides were scanned and marked if the species was present to help determine the depth of first occurrence in the core.

The age–depth models were generated from the sediments of Lake Fayetteville (18-FAY) and Izaak Walton Lake (18-IW2) using ^{210}Pb (see Appendix S4 in Supporting Information), which was determined using alpha spectrometry (via ^{210}Po proxy) as described by Yeager et al. (2004). In the case of 18-FAY, age models were combined with the date of lake origin since it is a human-made impoundment. Age models for all cores assumed constant sedimentation rates from collection date to their human-made origin or dredging dates for the lake basins. Core sediments were dated using the constant flux-constant supply (CF-CS) model (Appleby and Oldfieldz 1983):

$$\left[{}^{210}\mathrm{Pb}_{\mathrm{xs}}(z)\right] = \left[{}^{210}\mathrm{Pb}_{\mathrm{xs}}(0)\ \exp\left(-\alpha z\right)\right]$$

$$\alpha = (\lambda/S)$$

where $[{}^{210}\mathrm{Pb}_{\mathrm{xs}}(z)]$ and $[{}^{210}\mathrm{Pb}_{\mathrm{xs}}(0)]$ = activity concentrations of $^{210}\mathrm{Pb}_{\mathrm{xs}}$ at depth z and at the sediment surface, respectively; S = sediment accumulation rate (cm y^{-1}); and λ = ^{210}Pb decay constant (0.03114 year^{-1}).

Results

Distribution and ecology of *Discostella asterocostata*

We first discovered *D. asterocostata* in 2012 in plankton samples from Beaver Lake, Arkansas (USA) and the Wabash River, Indiana (USA). Expanded searches revealed additional populations in northwest Arkansas, eastern Oklahoma, and Indiana (see Appendix S1). We discovered additional U.S. records of *D. asterocostata* in The Academy of Natural Sciences of Drexel University database and the Neotoma Paleoecology Database (see Appendix S1). We report *D. asterocostata* from a total of 37 sites in the U.S. (Fig. 3 see Appendix S1). Published records of *D. asterocostata* outside of the U.S. include eight sites in China, nine sites in Japan, one site in Russia, and three sites in S. Korea (Fig. 3 and see Appendix S1). Our literature search revealed no reports of *D. asterocostata* outside of these areas.

We characterized the diatom communities of the type locality of *D. asterocostata* in China and 11 sites in the U.S. (Fig. 4). *D. asterocostata* comprised <3% of the diatom community in the type locality in China, whereas it comprised between <1% to >37% of the total diatom community at U.S. sites (Figs. 4 and 5; see Appendix S2 for raw data). Some of the highest numbers of *D. asterocostata* were recorded from a small human-made lake in Dobbs State Park (Terre Haute, Indiana, USA). We characterized the change in abundance of *D. asterocostata* at this site and found that *D. asterocostata* has increased from trace abundances in the 1980s to comprise roughly one-quarter of the present-day diatom community (see Appendix S5 in Supporting Information). The high abundance of *D. asterocostata* in these samples was responsible, in part, for the separation of sites on NMDS1 (Fig. 4).

In addition to *D. asterocostata*, sites in China and the U.S. shared several common and widespread diatoms (e.g., *Achnanthidium minutissimum*, *Aulacoseira ambigua*, *Cyclotella meneghiniana*, *Discostella stelligera*, *Fragilaria crotonensis*, *Nitzschia palea*, and *Synedra acus*) that exemplify the types of cosmopolitan distributions that have been interpreted as supportive of the BBH (Fig. 4; Finlay et al. 2002). A total of 23 of the 25 diatoms identified to the species level in the single sample from China were also present in one or more of the U.S. sites, underscoring the broad ecological similarities among sites containing *D. asterocostata* on the two continents. Additional sampling of sites throughout the U. S. and Far East will help us better understand the ecological preferences of *D. asterocostata* and whether Dobbs Park Lake, which lies in a unique portion of ordination space (Fig. 4), falls within or outside of the natural range of habitats for *D. asterocostata*.

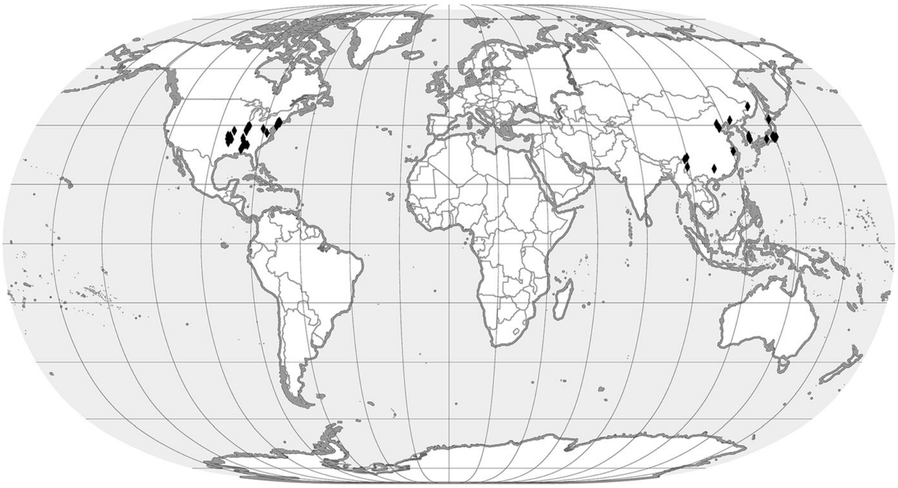

Fig. 3 Global distribution of the freshwater planktonic diatom, *Discostella asterocostata*. Black diamonds show reported occurrences of *D. asterocostata*. See Appendix S1 for a table of records

Paleolimnological record of *Discostella asterocostata*

Discostella asterocostata was observed in the top sediment intervals of all seven cores analyzed and typically was encountered dating back to at least the mid-1980s in all sediment cores with records that extended through this time interval (Fig. 5). *Discostella asterocostata* was absent from the sediment records below ca. 1985 in cores with the longest records in time and with age models based on ^{210}Pb dating (including 18-FAY and 18-IW2) (Fig. 5). In the record from Beall Woods Lake (18-BWL), the age estimate suggests that the first occurrence of *D. asterocostata* may extend beyond this point, i.e., around the time of the formation of this lake (1972), but uncertainty regarding whether this core represents the entire record from this site leaves open the possibility that *D. asterocostata* was present in Beall Woods Lake prior to 1985 and as early as 1972.

In most sediment cores, *D. asterocostata* comprised $<5\%$ of the overall fossil assemblage. In Lake Fayetteville (18-FAY) and Izaak Walton Lake (16-IW1), *D. asterocostata* was present in trace numbers initially but gradually increased in abundance, reaching maximum relative abundances of nearly 20% and 40%, respectively, in the past two decades (Fig. 5). One of the sediment cores from Izaak Walton Lake (16-IW1) was from a part of the lake with a high sedimentation rate, whereas the other, deeper core (18-IW2) was from a part of the lake with a lower sedimentation rate and, consequently, lower abundance of *D. asterocostata* (Fig. 5).

Morphometric analyses

We collected morphometric data for 16–20 individuals per site for a total of nine sites, including the type locality in China and eight sites in the U.S. Principal component analysis showed that PC1 accounts for $>80\%$ of the variance in the dataset, and the strong positive correlation between cell diameter and PC1 indicates that PC1 captured variation in cell size (Fig. 6a), which is common for this type of dataset (Theriot 1987). Principal component axes 2 and 3 accounted for 8.4% of the variance, and the broad overlap between U.S. and China specimens on these two axes indicates that the two populations are indistinguishable both qualitatively (Fig. 1) and quantitatively (Fig. 6b). Results of a canonical discriminant analysis, which separated the dataset into the U.S. and China populations a priori, also failed to separate the U.S. and China populations (see Appendix S6 in Supporting Information).

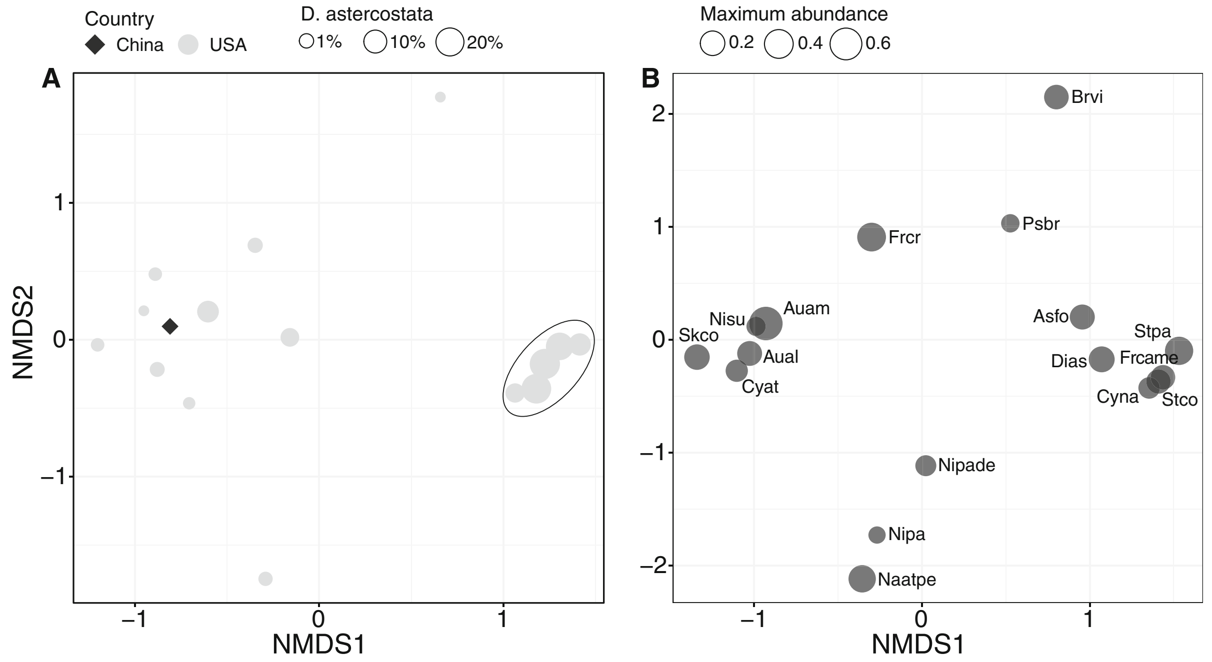

Fig. 4 **a** Nonmetric multidimensional scaling (NMDS) ordination of sites in the United States (n = 11) and China (n = 1) with *D. asterocostata*. The distance between sites in ordination space reflects similarity in their diatom communities, which is a proxy for the ecology of a water body. Point sizes in panel a are scaled to show the relative abundance of *D. asterocostata* at each site. The encircled cluster of points shows a series of samples taken across a sediment core from Dobbs Park Lake (Indiana, USA), a site with a high abundance of *D. asterocostata*. **a** NMDS ordination of diatom species. For simplicity, only species with a relative abundance ≥ 0.1 in at least one site and with an NMDS score ≥ 0.75 or ≤ − 0.75 on NMDS1 or NMDS2 are shown. Point sizes in panel **b** are scaled to show the maximum relative abundance of each species. Species abbreviations in panel b are as follows: *Asterionella formosa* **(Asfo)**, *Aulacoseira alpigena* **(Aual)**, *Aulacoseira ambigua* **(Auam)**, *Brachysira vitrea* **(Brvi)**, *Cyclotella atomus* **(Cyat)**, *Cyclotella nana* **(Cyna)**, *Discostella asterocostata* **(Dias)**, *Fragilaria capucina* v. *mesolepta* **(Frcame)**, *Fragilaria crotonensis* **(Frcr)**, *Navicula atomus* v. *permitis* **(Naatpe)**, *Nitzschia palea* **(Nipa)**, *Nitzschia palea* v. *debilis* **(Nipade)**, *Nitzschia subacircularis* **(Nisu)**, *Pseudostaurosira brevistriata* **(Psbr)**, *Skeletonema potamos* **(Skpo)**, *Staurosira construens* **(Stco)**, *Stephanodiscus parvus* **(Stpa)**

Discussion

Evidence for dispersal limitations from native and nonnative species

Broad similarities in the diatom communities of the water bodies in the U.S. and China studied here exemplify the types of patterns supportive of Baas Becking's hypothesis, which emphasizes ubiquitous dispersal as the predominant factor shaping the global distributions of prokaryotic and eukaryotic microbes (Baas Becking 1934; Fenchel and Finlay 2004). The large number of familiar diatom species in these sites was punctuated, however, by the equally unmistakable presence of one species, *D. asterocostata*, whose presence does not appear to be the result of the same natural dispersal processes of well-known cosmopolitan species (Finlay et al. 2002; Vanormelingen et al. 2008).

Evidence for human activity as the mode of introduction of *D. asterocostata* in the U.S. from its native East Asia comes from several sources. Despite decades of work documenting the diatom flora of the U.S.—one that includes *Discostella* species (Lowe 1975)—*D. asterocostata* has not been reported in North America until now. *Discostella asterocostata* is a “flagship” taxon that is easily recognizable with a light microscope (Fig. 1) and has reached high abundance in several of the sites in our study (Fig. 4). Taken together, it is unlikely that *D. asterocostata* is naturally present but has been historically overlooked in the U.S. By contrast, *D. asterocostata* has been

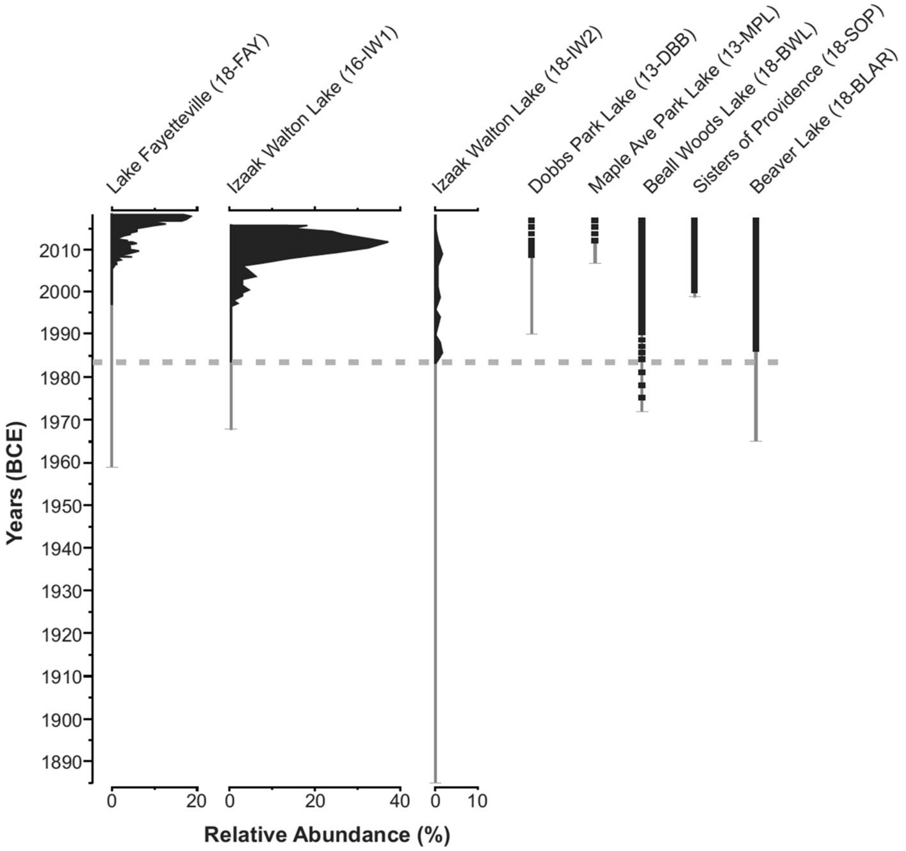

Fig. 5 Relative abundance of *Discostella asterocostata* in the paleolimnological records of eight sites in the central United States. For each site, the grey vertical bar indicates the full extent of the sediment core, whereas black lines show presence, and silhouettes show relative abundances. The grey dashed horizontal line (ca. 1985) marks the earliest reliable estimates of the first occurrence of *D. asterocostata* across all sediment cores based upon trace occurrences in fossil assemblages and sediment core ages

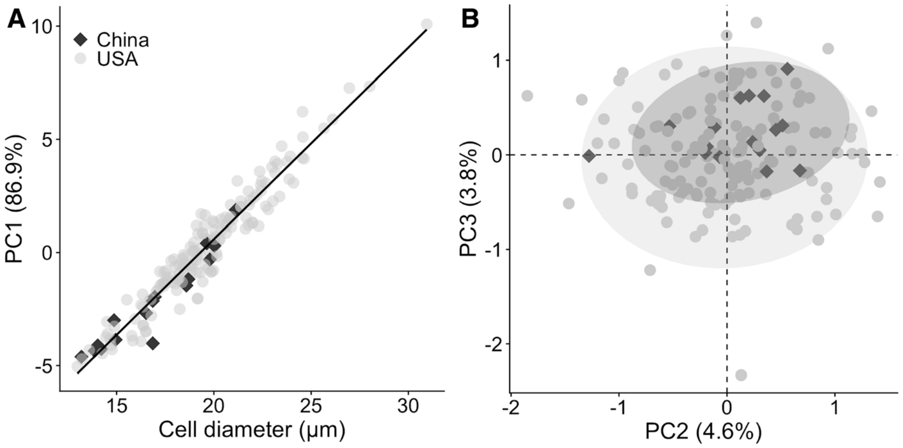

Fig. 6 Principal component analysis (PCA) of eight morphometric characters (Fig. 2) for eight populations of *Discostella asterocostata* in the U.S. and one in China. **a** The first PC axis was strongly correlated with cell size. **b** U.S. and China populations were fully overlapping on PC axes 2 and 3

documented across the Far East dating back to the 1980s (Xin et al. 1985). This includes one report of *D. asterocostata* in sediment cores dating to at least 1920 (Zou et al. 2015), but our sediment cores—one of which dates back to as early as the 1880s—did not contain *D. asterocostata* until 100 years later in the mid-1980s. The hypothesis of a recent arrival in the U.S. was also supported by morphometric data, which failed to distinguish populations from the U.S. and China. Although this pattern could also be the result of ongoing gene flow across continents, in the context of our other findings, it seems more likely that the morphological homogeneity of U.S. and China populations is due to recent separation, a hypothesis that could be tested with population genetic data.

The ubiquity of many freshwater diatoms is indisputable and underscores their vast dispersal potential (Finlay et al. 2002), but this does not appear to be true of all diatoms, many of which appear to experience dispersal limitations across regional and continental scales (Telford et al. 2006; Vyverman et al. 2007; Bennett et al. 2010). These patterns include longstanding reports of endemism—at scales ranging from single lakes (Theriot et al. 2006) to geographic regions (Telford et al. 2006; Vyverman et al. 2007) and hemispheres (Vyverman et al. 1998)—that have yet to be falsified. The validity of these natural historical patterns is reinforced by observations of abrupt, contemporary disjunctions related to human activity (Foissner 2006; Vanormelingen et al. 2008; Spaulding et al. 2010). Detection of nonnative diatoms is facilitated by long-term preservation of their siliceous cell walls in stratified lake sediments, where both relative and absolute time can be measured with great accuracy (Edlund et al. 2000). Such studies have revealed, for example, some 20 exotic diatom species in the Laurentian Great Lakes (Sturtevant et al. 2019). These were likely introduced through transport in ballast water, where diatoms can survive for as long as a month (Klein et al. 2010). Introductions elsewhere appear to be the byproducts of intentional introductions of nonnative fish (Harper 1994).

Asian carp as a possible vector

Invasive macroorganisms often serve as vectors for the cointroduction of associated microbes (Litchman 2010). We explored whether nonnative Asian carp, which are abundant in large rivers and reservoirs across the U.S., may have been vectors for the introduction of *D. asterocostata* in the U.S. Two of the four invasive carp species—*Hypophthalmichthys nobilis* (Bighead Carp) and *Hypophthalmichthys molitrix* (Silver Carp)—are planktivores that feed on diatoms, including ones that are similar in size, morphology, and habitat to *D. asterocostata* (Ping and Jiankang 1994). Direct and indirect evidence has shown that diatoms can survive the digestive process in planktivorous carp (Vörös et al. 1997; Görgényi et al. 2016; Borsodi et al. 2017), making cotransport inside the fish a plausible hypothesis for establishment of *D. asterocostata* in the U.S.

We used the global freshwater fish occurrence database (Tedesco et al. 2017) to extract the worldwide distributions of the four Asian carp species in the U.S. and decomposed the ranges into presence/absence values at the major drainage scale (Fig. 7). Superimposing sites containing *D. asterocostata* revealed overlap with the native ranges of all four Asian carp (Fig. 7), including both planktivorous species. Juxtaposition of the historical timeline of the invasions of Asian carp in North America with paleolimnological records (Fig. 5) lends further support for a vector-borne introduction. Both planktivorous species (Bighead and Silver Carp) were prolifically introduced beginning in the mid- to late-1970s in Arkansas as a biological control agent for nuisance phytoplankton, including intentional stocking into Beaver Lake, Arkansas, by 1988 (Kolar 2007). By that time, Grass Carp had also been intentionally stocked in multiple states (Greenfield 1973; Robison and Buchanan 2020). Although stocking records do not exist for the other Arkansas site we surveyed, Lake Fayetteville, the earliest wild records in nearby tributaries in the Nonindigenous Aquatic Species database maintained by the U.S. Geological Survey were 1988–1995 (https://nas.er.usgs.gov/). Taken together, plausible introduction dates of Asian carp into the Arkansas sites juxtapose well with the earliest paleolimnological records of *D. asterocostata* reported here (Fig. 5).

Silver Carp escapees were likewise recorded in Arkansas by 1980 (Freeze and Henderson 1982) and soon after in 1982 were reported in multiple states throughout the Mississippi River drainage basin (Carter and Beadles 1983). Wild occurrences of Bighead Carp were also reported in multiple

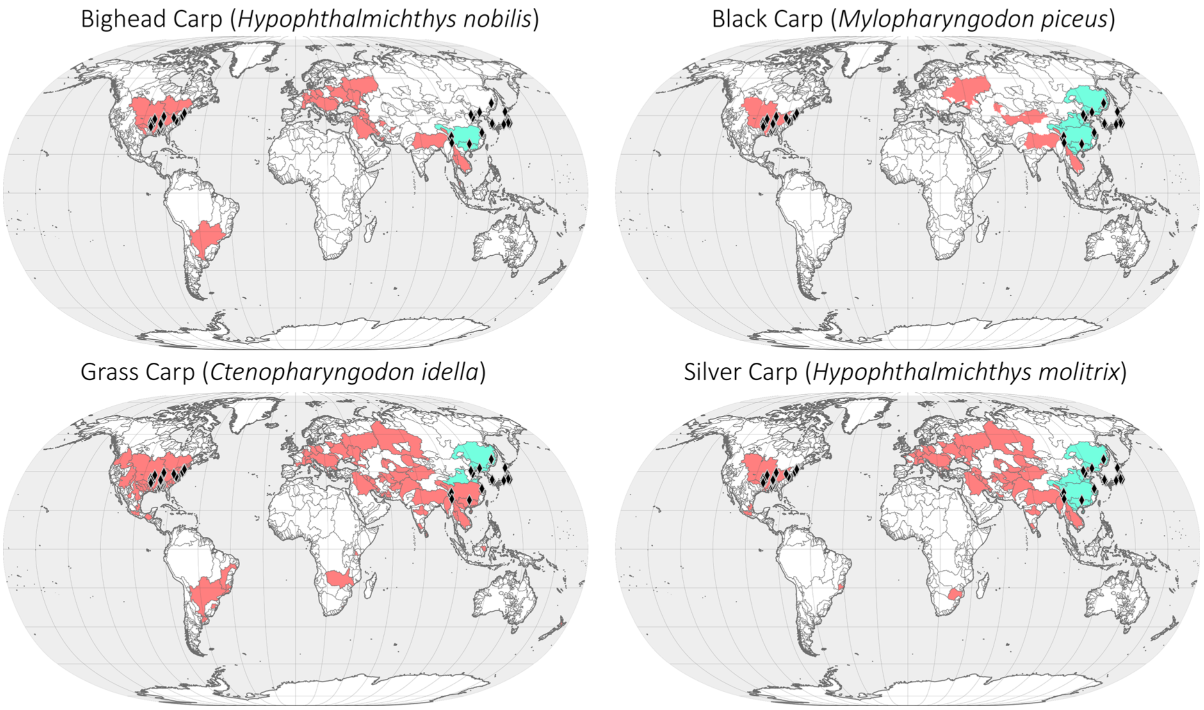

Fig. 7 Overlapping distributions of *Discostella asterocostata* and four species of invasive Asian carp in their native (blue) and non-native (red) ranges. Black diamonds show reported occurrences of *D. asterocostata*

disparate localities throughout the Mississippi River drainage basin by the mid- to late-1980s (Jennings 1988; Tucker et al. 1996). Occurrence records in the main stem of the Illinois River (near Izaak Walton Lake) for Grass and Bighead Carp suggest establishment sometime between 1990 and 1995. The earliest wild occurrence records for Bighead and Silver Carp in the drainage encompassing the Beall Woods Lake, Maple Avenue pond, Dobbs Park Lake, and Sisters of Providence Lake sites were from 1999 to 2004, which is in general agreement with sediment records presented here (Fig. 5). The putative timing of establishment for multiple invasive carp species thus overlaps well with the appearance of *D. asterocostata*. Beall Woods Lake (Fig. 5, site 18-SOP) is an apparent exception in that the paleolimnological record extends back to the mid- to late-1970s, though there is some uncertainty regarding the bottom age of this core. We note, however, that some of the earliest 'wild' records of planktivorous Asian carp were from Illinois (Jennings 1988), and importation of the species was occurring in Illinois by ca. 1977 (Kelly et al. 2011). This lends plausibility to an earlier establishment of exotic diatoms in the Wabash River drainage basin, including Beall Woods Lake, particularly given the lower detectability of exotic species with the methods available at the time. Microsatellite studies have found Silver Carp in the Wabash River drainage basin to be strongly differentiated from those found elsewhere in Illinois (Stepien et al. 2019), further supporting the possibility of a separate and potentially earlier establishment of Asian carp (and *D. asterocostata*) in Beall Woods Lake.

Although overlap in the distributions of the diatom and carp is confounded by their ability to disperse independently of one another following establishment in the U.S., the much broader introduced ranges of Asian carp compared to *D. asterocostata* can either be interpreted as undermining our hypothesis of carp-based introduction of *D. asterocostata* in the U.S. or, alternatively, reflecting a rarity of successful co-transport and/or establishment of the diatom commensurate with the small founding sizes of invasive carp populations. A number of confounding factors likely contribute to variable success of hitchhiking planktonic invaders via aquaculture (Duggan and Pullan 2017), such as the sources of stocked individuals (Pearson and Duggan 2018), seasonality of plankton communities in source or aquaculture ponds (Duarte et al. 2019), biotic resistance or environmental/demographic stochasticity in recipient ponds (Branford and Duggan 2017), and the aquaculture conditions within captive or rearing environments prior to release (Çelekli et al. 2014; Eichmiller et al. 2016). Finally, although diatoms have a demonstrated capacity to retain viability following digestion (Görgényi et al. 2016), the proportion of cells being either fragmentary or exhibiting some form of damage increases longitudinally through the digestive tract (Ping and Jiankang 1994), thereby further reducing potential propagule pressure (i.e., number of invading individuals), and thus contributing to stochasticity in invasion success (Lockwood et al. 2005; Acosta et al. 2015). We note, however, that colonization success of diatoms from ballast water has instead been linked to selective pressures during transport, irrespective of propagule pressure (Briski et al. 2012). With a disproportionate survivorship of diatoms relative to other potential hitchhiking species (Ping and Jiankang 1994) and a demonstrable ability for planktivorous carp species to shape planktonic community composition in an aquaculture setting (Mitchell et al. 1984; Domaizon and Devaux 1999), a reasonable outcome may actually be enrichment of non-digestible species (including *D. asterocostata*) in captivity prior to release. Given observed co-establishment of non-native zooplankton species into recipient Grass Carp ponds (Branford and Duggan 2017), we would posit that the potential for co-establishment diatoms—which are known to survive the digestive process (Vörös et al. 1997; Görgényi et al. 2016; Borsodi et al. 2017)—is also plausible.

Conclusions

Given all of the available information—including the presence of *D. asterocostata* in East Asia dating back >100 years and its much more recent discovery in the U.S.—the simplest explanation for the geographic disjunction described here is human-mediated introduction of *D. asterocostata* into U.S. waters. Our hypothesis rests on the assumption that the absence of *D. asterocostata* species from U.S. diatom floras, which date back to the mid-1900s, along with our failure to detect it in sediments predating the 1970s, represents true absence rather than failures to detect it. Rejecting the null hypothesis of cosmopolitanism is a persistent challenge in microbial biogeography (Foissner 2006; Williams and Reid 2006). One can argue that we have simply missed a flagship taxon that has been in the U.S. all along. Likewise, one might also argue that the native range of *D. asterocostata* also extends westward from the Far East across Europe, but that it simply has not been detected in these areas. The >100 years of floristic research on European diatoms makes this argument, which is unfalsifiable, nevertheless exceedingly unlikely. Our hypothesis—that the U.S. is outside the native range of *D. asterocostata*—is a stronger one because it can be easily falsified by the discovery of *D. asterocostata* in lake sediments that predate European settlement. Likewise, our hypothesis that the introduction was mediated by carp will be falsified if *D. asterocostata* is discovered in sediments that predate the introduction of Asian carp in the U.S. There are several examples of diatoms that were once thought to be exotic but were later found to be more likely native based on new paleolimnological discoveries (Hawryshyn et al. 2012; Shaw Chraïbi et al. 2014).

Although all available evidence points to East Asia as the native range for *D. asterocostata*, we were not able to decisively test this hypothesis. Additional paleolimnological data from sites in Asia and the U.S. will show how long *D. asterocostata* has been present in these areas. Sampling should include natural lakes, which have sediments that go back tens or hundreds of thousands of years or more, as opposed to reservoirs that go back only decades. Still, our data clearly showed an appearance of *D. asterocostata* well after the construction of these systems, but a sampling of natural systems will reveal more decisively the natural age, history, and ecological preferences of this species. Further studies will show precisely which niche this species fills in North American freshwaters, whether it will lead to local extirpations of native species, and what if any harmful impacts it may have. Population genomic data will provide important insights into the invasion history and biology of this species (Cristescu 2015): Where precisely did it come from and when did it arrive? Were there one or many introductions? Are the genomic data consistent with East Asia as the native range, followed by a genetic bottleneck consistent with a recent introduction into the U.S.?

The temporal controls afforded by a fine-scale paleolimnological record, coupled with population genomic data, highlight unique strengths of diatom systems for understanding invasive species biology.

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Availability of data and materials Distribution records, diatom community counts, and morphometric measurements are available as Supplementary Information.

Code availability Not applicable.

Compliance with ethical standards

Conflict of interest Not applicable.

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