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ORIGINAL PAPER

The faunal Ponto-Caspianization of central and western European waterways

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Abstract As alien invasive species are a key driver of biodiversity loss, understanding patterns of rapidly changing global species compositions depends upon knowledge of invasive species population dynamics and trends at large scales. Within this context, the Ponto-Caspian region is among the most notable donor regions for aquatic invasive species in Europe. Using macroinvertebrate time series collected over 52 years (1968–2020) at 265 sites across 11 central and western European countries, we examined the occurrences, invasion rates, and abundances of freshwater Ponto-Caspian fauna. We examined whether: (i) successive Ponto-Caspian invasions follow a consistent pattern of composition pioneered by the same species, and (ii) Ponto-Caspian invasion accelerates subsequent invasion rates. In our dataset, Ponto-Caspian macroinvertebrates increased from two species in 1972 to 29 species in 2012. This trend was parallelled by a non-significant increasing trend in the abundances of Ponto-Caspian taxa.

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Trends in Ponto-Caspian invader richness increased significantly over time. We found a relatively uniform distribution of Ponto-Caspian macroinvertebrates across Europe without any relation to the distance to their native region. The Ponto-Caspian species that arrived first were often bivalves (46.5% of cases), particularly *Dreissena polymorpha*, followed secondarily by amphipods (83.8%; primarily *Chelicorophium curvispinum* and *Dikerogammarus villosus*). The time between consecutive invasions decreased significantly at our coarse regional scale, suggesting that previous alien establishments may facilitate invasions of subsequent taxa. Should alien species continue to translocate from the Ponto-Caspian region,

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our results suggest a high potential for their future invasion success highly connected central and western European waters. However, each species' population may decline after an initial 'boom' phase or after the arrival of new invasive species, resulting in different alien species dominating over time.

Keywords Biological invasion · Biotic homogenization · Invasional meltdown · Invasion corridor · Invasive species · Synergistic interaction

Introduction

Human activities have eroded biogeographical barriers established over geological timescales that separated ecological communities worldwide (Dawson et al. 2017; Duffy et al. 2017; Galil 2011). Rates of invasion by alien species are increasing favored to climate change, global trade and many human activities (Bellard et al. 2013; Seebens et al. 2019). Alien invasive species can impact biotic communities, ecosystem functions, economies and human well-being (Diagne et al. 2021; Gallardo et al. 2019; Russell et al. 2014). Also, they are a major threat to biodiversity across local, regional and global scales (Bellard et al. 2018; IPBES 2019; Pyšek et al. 2020). Thus, it is urgent to understand the processes by which invasions alter biodiversity patterns in an era of rapid environmental change (Ricciardi et al. 2021). The underlying mechanisms that determine the success or failure of invasions vary for each ecosystem but can be related on three factors: introduction to a new range, establishment, and spread (Jeschke and Strayer 2005). Factors influencing invasion success include, among others, dispersal limitation following introduction as species distributions become limited by their own movement abilities (Leuven et al. 2009), propagule (number of released individuals) and colonization pressures (number of released species; Briski et al. 2012a, b; Simberloff 2009), interactions among alien species (Havel et al. 2015), as well as abiotic (e.g. increased water quality and temperature; McLaughlan and Aldridge 2013; Strayer 1999) and biotic factors such as increased frequency of disturbances that reduces native community resilience (Levine et al. 2004; McLaughlan and Aldridge 2013; Strayer 1999), resource availability (e.g. habitat preferences, construction of artificial habitat; Borza et al. 2017; Mooney 2005) or habitat quality (Früh et al. 2012a, b).

Steeply increasing accumulations of introduced species in various large, urbanized aquatic systems worldwide underline the burgeoning risks and potential drivers of homogenization (Ricciardi 2015; Seebens et al. 2021). This is especially the case for Europe's river network, where connectivity was increased through the opening of the Volga-Don Canal in the 1950s, the Volga-Baltic Canal in the 1960s and the Rhine-Main-Danube (RMD) Canal in 1992, facilitating both active and passive spread of Ponto-Caspian macroinvertebrates through, e.g., hull fouling and ballast along these newly expanded shipping corridors (Bij De Vaate et al. 2002; Gallardo and Aldridge 2015). The connection between the Danube and Rhine basins by the RMD Canal represents one of the three main invasion corridors by which Ponto-Caspian macroinvertebrate species have extended across central and western Europe, including the "killer shrimp" *Dikerogammarus villosus* (Bij de Vaate and Klink 1995), the amphipod *Trichogammarus trichiatus* (Podraza et al. 2001) and the polychaete *Hypania invalida* (Klink and Bij de Vaate 1996).

The Ponto-Caspian region (i.e. Black, Azov and Caspian Seas and their adjacent areas) has been a major donor region for invasions of large parts of Europe (Casties et al. 2016; Cuthbert et al. 2020), with the invasion success of Ponto-Caspian macroinvertebrate species enabled by their broad temperature and salinity tolerances (Casties et al. 2019; Cuthbert and Briski 2021; Paiva et al. 2018; Leuven et al. 2009; Pauli and Briski 2018). Several alien macroinvertebrates from the Ponto-Caspian region have been associated with altered food webs and extirpation of native species (Dick et al. 2002; Folino-Rorem et al. 2009; Kestrup and Ricciardi 2009; Ricciardi and MacIsaac 2000) and some alien macroinvertebrates from the Ponto-Caspian region can display synergistic interactions (e.g. Kobak et al. 2014; Ricciardi 2001; Ricciardi and MacIsaac 2000). Noteworthy macroinvertebrate species in this context are the zebra mussel *Dreissena polymorpha* and the killer shrimp *D. villosus*, which can individually and interactively alter communities, change ecosystem functioning and impact economies (Haubrock et al. 2022a; Kouba et al. 2022; Macêdo et al. 2022) and diminish native biodiversity (Aldridge et al. 2014; Rewicz et al. 2014; Waterfield, 2009). For example, mussel patches of *D. polymorpha* provide shelter and suitable habitat structure for amphipods, including *D. villosus* (Devin et al. 2003; Ricciardi et al. 1997), which at the same time offer abundant food sources for Ponto-Caspian gobies (Polačik et al. 2009, Gallardo and Aldridge 2015). These synergistic interactions may facilitate the initial establishment of alien invasive species. However, negative relationships in abundance may occur where invaders coexist and compete for the same resources, as shown between *D. polymorpha* and the Caspian mud shrimp *Chelicorophium curvispinum* (Van der Velde et al. 1998). Within this context, we refer to "Ponto-Caspianization" as the phenomenon by which an increasing number of species from the Ponto-Caspian biogeographic region are becoming established in another biogeographic region, with potential impacts on ecosystems (Copilaş-Ciocianu and Šidagytė-Copilas 2022).

Our study investigates the presence of Ponto-Caspian species in central and western Europe over time. For this, we use a comprehensive dataset of macroinvertebrate time series and investigate trends in the distribution of alien species, their population growth and rates of spread, as well as possible underlying mechanisms modulating their establishment success. To our knowledge, this endeavor represents the largest study to investigate the spatio-temporal accumulation of Ponto-Caspian species and their relative abundance, as well as their potential impact. We hypothesized that: (*i*) the number and dominance (expressed as relative abundances) of Ponto-Caspian macroinvertebrate species across available time series in primarily central and western Europe has increased over time; (*ii*) there is an inverse relationship between the numbers of these Ponto-Caspian species and the distance to their native ranges; and (*iii*) Ponto-Caspian macroinvertebrate invasions result in reduced time intervals between successive invasions.

Methods

Data collection

To investigate the presence of Ponto-Caspian species in central and western European freshwater streams and rivers, we used a recently collated database containing 1816 macroinvertebrate time series from 22 European countries (Haase et al. in review; Haubrock et al. 2022b; Soto et al. 2023a). We define the Ponto-Caspian region as the Black, Azov, and Caspian Seas, as well as the adjacent lagoons and lower river stretches (Fig. 1). Each time series contained samples collected in a minimum of eight, not necessarily consecutive, sampling years. Individual time series were sampled from the same geographic location (hereafter, *site*) in all years. Survey methods (e.g. kick sampling) varied among time series, but were kept constant within each time series (Table S1). Each time series was harmonized to have a comparable sampling effort over time, with sampling occurring once annually within three consecutive months and consistent species-level taxonomic resolution. We selected the time series that contained records of Ponto-Caspian macroinvertebrates (Table S2), comprising 265 time series from 11 central and western European countries (Fig. 1; Table S3). We consider central and western Europe geographically but do not refer to the central corridor defined by Bij de Vaate et al. (2002). Data describing communities of native and alien species from eastern Europe and eastern European canals of adequate (i.e. comparable) time length were—to our knowledge—not available. A lack of records of Ponto-Caspian species in a particular country (e.g. Romania, Italy, and Austria) does not imply that it has not been invaded by these species, but may rather indicate a gap in the geographical coverage of our study. Time series of our data set spanned a mean ± SD of 20.9 ± 9.5 years and contained 13.6 ± 5.4 sampling years between 1968 and 2020 (Figure S1).

The native range of alien species was confirmed by consulting four sources: *Web of Science* (https://webofknowledge.com/), *Google Scholar* (https://scholar.google.com/), the *Global Biodiversity Information Facility* (GBIF; https://www.gbif.org/) and the *European Network on Invasive Alien Species* (NOBANIS; https://www.nobanis.org/). Some of the species in our time series (i.e. *Synurella ambulans* and *Cyptorchestia garbinii*) are native to both the Ponto-Caspian region, and neighbouring areas (Table S2); these species were kept in the analyses due to the complex geological history of the Ponto-Caspian region (Reid and Orlova 2002; Zenkevitch 1963) and the possibility of cryptogenic status

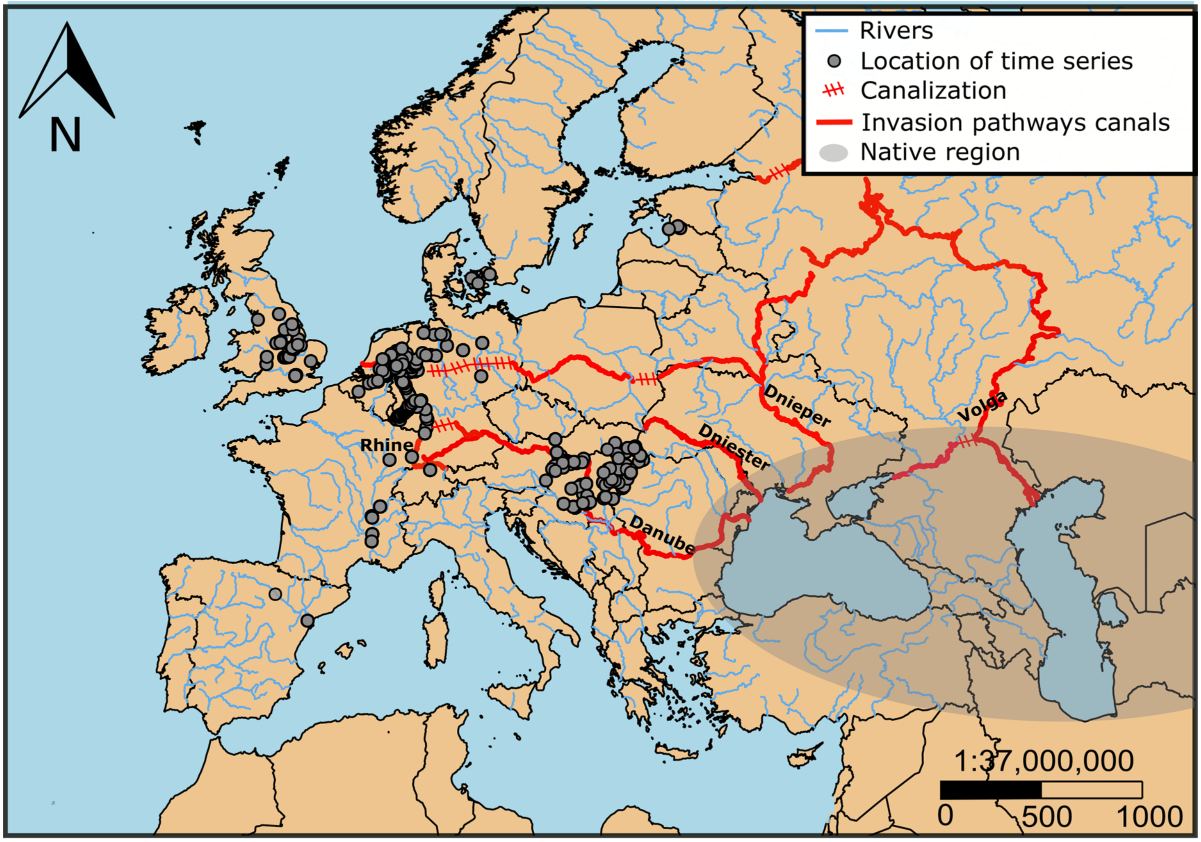


Fig. 1 Locations of time series with Ponto-Caspian species in central and western Europe. The shaded area refers to the overarching native region (Ponto-Caspian) considering the Black, Azov and Caspian Seas and their basins, lagoons and lower river stretches. The thicker red lines represent the main invasion pathways of Ponto-Caspian species (after Bij De Vaate et al. 2002)

(Carlton 2009). We also conducted key analyses without these species and obtained similar results; we thus only present analyses including these species in the main text and present those without them in Supplemental material 2.

Abundance, richness, and accumulation of Ponto-Caspian macroinvertebrates species over time

To test our first hypothesis, i.e. characterize temporal change of Ponto-Caspian macroinvertebrate species across central and western Europe, we conducted a set of meta-regression analyses. Meta-regressions are a powerful tool to synthesize and analyze the results from multiple regressions to evaluate the overall effect (Gurevitch et al. 2018). We constructed a random-effects model assuming sampling variance and different 'true' effects among time series (Nakagawa et al. 2017). For this, we first extracted the effect size (i.e., slope) and variance for every Ponto-Caspian species' raw abundance occurring over a minimum of 5-years using the Mann–Kendall trend test (*S-Statistic*) to identify monotonic trends (Maire et al. 2019). We used a modified version of the Mann–Kendall trend test to account for temporal autocorrelation (Maire et al. 2019; Pilotto et al. 2020). Furthermore, the magnitude of each effect is weighted based on the accuracy of the estimate, meaning that time series with high temporal resolution and large sample size receive more weight than those with lower precision or smaller sample size (Gurevitch et al. 2018). We performed a meta-regression considering all trends (i.e. *S-Statistic*) and their variance to extract an overall trend and assess its significance. This approach enables the comparability among time series by analyzing the individual time series abundance trends (i.e., its slope) rather than the raw abundances (Soto et al. 2023b). In order to correct for spatial autocorrelation between time series, we specified the geographic coordinates as a random effect in the meta-regression model based on a Gaussian correlation structure (Cressie 1993; Maire et al. 2019). This approach was applied to all Ponto-Caspian macroinvertebrates combined, and for the key Ponto-Caspian taxa i.e. amphipods, bivalves, and gastropods, individually. These analyses were performed using the *rma.mv* function of the `metafor` R package (version 3.8–1; Viechtbauer 2010). The same approach was repeated using the richness of all Ponto-Caspian species and within each key taxa in place of raw abundances. Due to an insufficient number of Ponto-Caspian bivalves (n = 2) and gastropods (n = 1), the meta-regressions were not performed on these taxa.

Additionally, for each time series, we extracted the first recorded occurrence of any alien invasive species, and the first occurrence of each Ponto-Caspian species. We then plotted the cumulative richness as an estimate of invasion rates, using the *stat_ecdf* function in the `ggplot2` R package (Wickham et al. 2016). This approach allows us to visualize the cumulative number of invasive species that were newly introduced over time and to provide a comprehensive picture of invasion rates in central and western Europe.

Patterns of Ponto-Caspian invasions

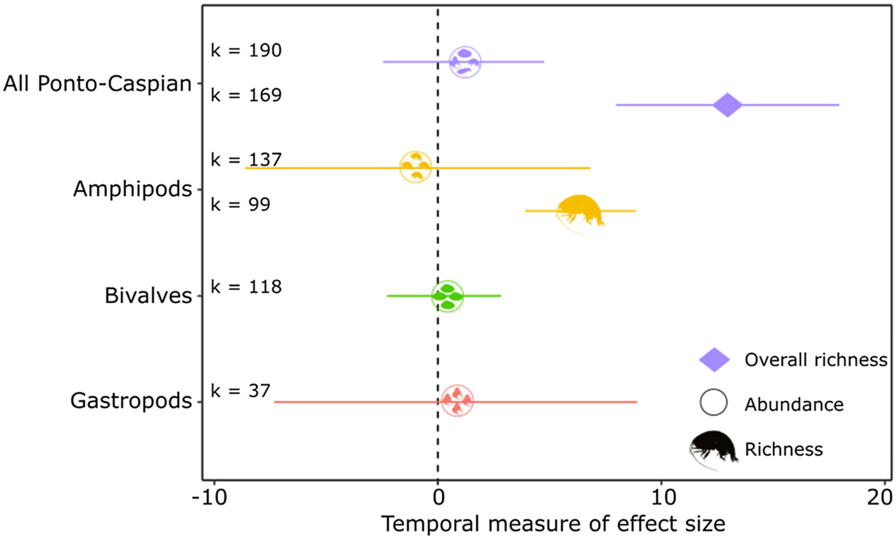
To test our second hypothesis, i.e. the relationship between the numbers of these Ponto-Caspian species and the distance to their native ranges, we assigned Ponto-Caspian macroinvertebrate species to major groups (i.e. Amphipoda, Annelida, Bivalvia, Gastropoda, Hirudinea, Hydrozoa, Isopoda, Mysida, Oligochaeta and Tricladida; Table S2) to identify the presence of potential taxonomic patterns in Ponto-Caspian invasions over time. We first calculated the distance between each site and the Ponto-Caspian region, following the river network (including canals) using the *riverdist* function of `riverdist` R package (Tyers 2022). To standardize distances, we used the Danube delta as the native range for all time series, except for those from Latvia, for which we used the Dnieper delta (Karatayev et al. 2008; Lipinskaya et al. 2020) and for those from the United Kingdom, which were calculated following the marine route that connects Great Britain with the Netherlands and subsequently via the invasion corridors along the river networks (Gallardo and Aldridge 2015). Then, we evaluated the relationship between the number of Ponto-Caspian species recorded in each time series and the distance to their native range using Generalized Linear Mixed Models (GLMMs) with negative binomial family using the *glmer* function of the `lme4` R package (Bates et al. 2015). In order to take into account the dependency between observations (i.e. distances to the native region) within each country, we included ‘country’ as a random effect in the GLMMs. We also included the starting year of each time series to account for the potential effect of the heterogeneous database (i.e. disparity in start of time series)

To test our third hypothesis, i.e. if quantifiable changes in invasion rates lead to a reduction in time intervals between successive invasions, we recorded the first year of occurrence (i.e. the first detection) of each species in each time series, noting that detection may not reflect establishment status over time. We then compared the year of the first occurrence of each Ponto-Caspian macroinvertebrate with the most recent preceding year in which another such species appeared in the same time series. To statistically identify the relationship between sequentially occurring Ponto-Caspian species and the time between the arrival of the subsequent Ponto-Caspian species, we used a GLMM with negative binomial distribution and country as a random effect.

Results

Within the 265 time series spanning the period 1968–2020, we identified 29 Ponto-Caspian macroinvertebrate species. The first records were of the bivalve *Dreissena polymorpha* (n = 12 time series) and the amphipod crustacean *Chaetogammarus ischnus* (n = 1) in 1972 in Germany. The species recorded most frequently across time series were *D. polymorpha* (n = 164) and the amphipods *Chelicorophium curvispinum* (n = 146) and *Dikerogammarus villosus* (n = 132). In contrast, the oligochaete worm *Potamothrix vejdovskyi* (n = 2), the amphipod *Pontogammarus robustoides* (n = 2), and the mysid *Katamysis*

Fig. 2 Trends in raw abundance and richness of all Ponto-Caspian species and for each key taxa (i.e. amphipods, bivalves and gastropods) using meta-regression models. k refers to the number of time series per group



warpachowskyi (n = 3) showed the fewest occurrences (Table S2). Sixty-eight time series contained only one Ponto-Caspian species (25.7%), whereas the highest numbers of Ponto-Caspian species (12, 14, 15, and 16) occurred in four time series from Hungary (Figure S2). In terms of countries, Germany and Hungary had the most Ponto-Caspian macroinvertebrate species (18 and 24, respectively), while the lower number was identified in Spain and Denmark with only one Ponto-Caspian macroinvertebrate.

Trends in the abundances and richness of Ponto-Caspian macroinvertebrates

Across all taxa, the raw abundance of Ponto-Caspian taxa slightly increased over time, but not significantly (Temporal Measure of Effect Size ± SE: = 1.16 ± 1.84; Fig. 2; Table S4). Also not significantly, within taxa, bivalves (TMES ± SE: 0.27 ± 1.29; Fig. 2; Table S4), and gastropods increased over time (TMES ± SE: 0.79 ± 4.14; Fig. 2; Table S4), whereas the raw abundance of amphipods decreased (TMES ± SE: −0.90 ± 3.94; Fig. 2; Table S4). In terms of richness, the number of Ponto-Caspian macroinvertebrates increased significantly over time (TMES ± SE: 12.97 ± 2.54). This trend was supported by an increase of Ponto-Caspian amphipods richness (TMES ± SE: = 6.38 ± 1.26; Fig. 2; Table S4).

The number of all alien invasive species and Ponto-Caspian species recorded per year as well as Ponto-Caspian cumulative richness increased over time (Fig. 3). The increase of Ponto-Caspian macroinvertebrates was especially marked in 2005, when seven Ponto-Caspian macroinvertebrate species were recorded for the first time, while the last new species (*Niphargus hrabei*) was recorded in 2012. There was no clear pattern in the first occurrence of Ponto-Caspian macroinvertebrate species from different taxonomic orders (Fig. 2b). We identified a significant positive, but weak relationship between the length of the time series and the number of Ponto-Caspian

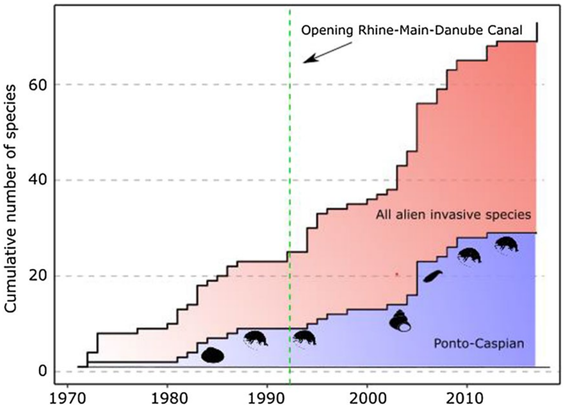


Fig. 3 The cumulative richness of alien species present in our database (red color) and the cumulative richness of Ponto-Caspian species (blue color) across all time series. The green dashed lines represent the opening of the Rhine-Main-Danube Canal in 1992

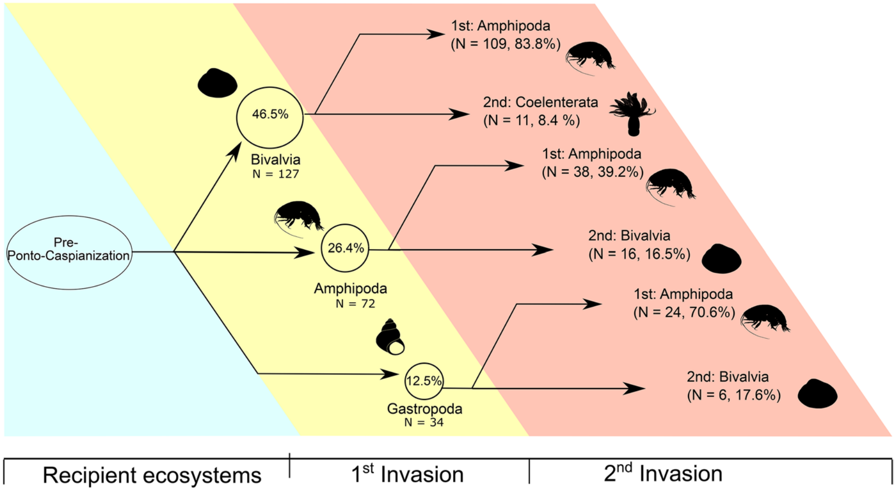


Fig. 4 Sequence of arrival of Ponto-Caspian macroinvertebrate orders in central and western European rivers, expressed as the relative prevalence (%) of first and second invasion records of Ponto-Caspian macroinvertebrate orders across available time series. The first orders to invade are highlighted in yellow, while the second orders to arrive after the first invader are highlighted in red. "Pre-Ponto-Caspianization" refers to the uninvaded state from the Ponto-Caspian donor region. For example, in the first invasion stage, species of Bivalvia constituted 46.5% of the records, which were followed by Amphipoda 83.8% of the time, see Figure S2

macroinvertebrate species ($R^2 = 0.09$; $d.f. = 263$; $p < 0.01$; Figure S4).

Patterns of Ponto-Caspian macroinvertebrate invasions

In 46.5% of time series, the bivalve *D. polymorpha* was most frequently the first Ponto-Caspian macroinvertebrate recorded at a site. At sites where *D. polymorpha* was the first Ponto-Caspian species, amphipods were recorded as the second Ponto-Caspian invader in 83.8% of time series, including *C. curvispinum* in 61.7% of cases, and the freshwater hydroid *Cordylophora caspia* was second in 8.46% of cases (Fig. 4; Figure S5). The second most common Ponto-Caspian macroinvertebrates recorded first in a time series were amphipods (26.4%; mostly *C. curvispinum*). Where amphipods were first to establish a presence, we recorded other amphipods (39.2%; primarily *D. villosus*) and the bivalve *D. polymorpha* (16.5%) most often as second invaders. The third most common initial invader was the gravel snail *Lithoglyphus naticoides* (12.5%), which was most often followed by colonising amphipods (70.6%; mostly *C. curvispinum*) and the bivalve *D. polymorpha* (17.6%) (Fig. 4; Figure S5). Other Ponto-Caspian macroinvertebrate species combined represented < 15% of first arrivals.

We did not find a significant relationship between the number of Ponto-Caspian macroinvertebrate species and the distance to their native region ($p = 0.75$; Fig. 5a; Table S5). We found a significant negative relationship between the time to sequentially occurring Ponto-Caspian macroinvertebrates species averaged across all time series and the average number of invading species in each time series ($p < 0.01$; Fig. 5b; Table S5). Accordingly, the time between successive invasions decreased with the number of Ponto-Caspian macroinvertebrates species already present (Fig. 5b), from 0 to 21 years until the arrival of the next Ponto-Caspian species.

Discussion

Overall, we identified 29 Ponto-Caspian macroinvertebrate species in our European dataset, which is higher than the numbers reported in previous studies (Bij de Vaate et al. 2002; Gallardo and Aldridge 2015; reporting n = 22 and 23 species, respectively). However, differences in sampling effort could have created biases and delays in detecting Ponto-Caspian

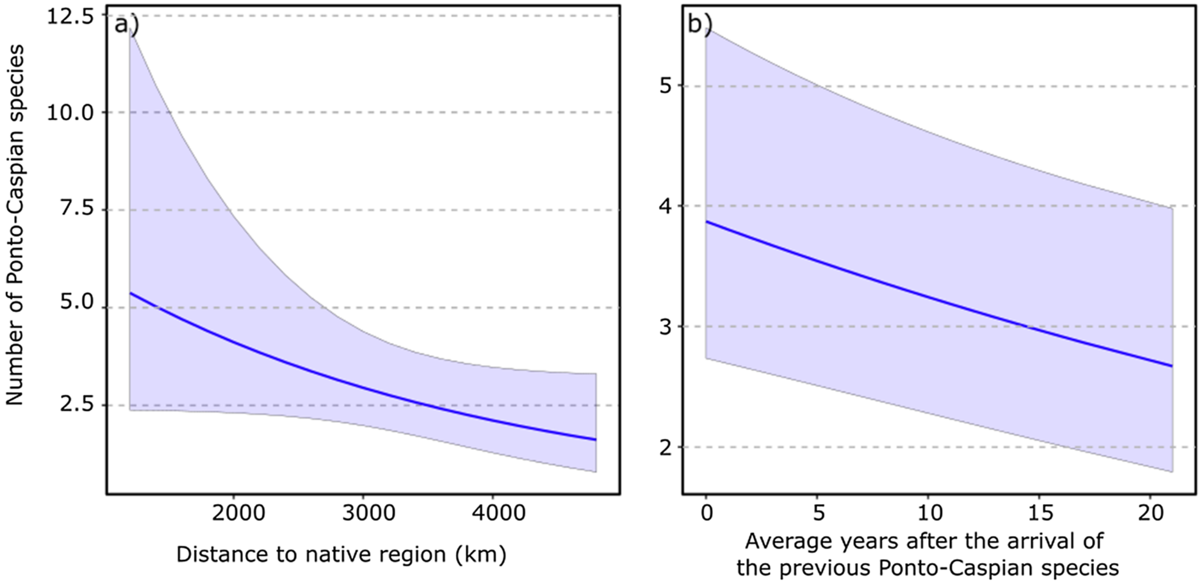


Fig. 5 **a** Relationships between the average distance to the Ponto-Caspian region and the number of Ponto-Caspian macroinvertebrate species per time series. **b** Relationship between the averaged difference in years of sequentially detected Ponto-Caspian macroinvertebrate species per time series and the number of such species per time series

macroinvertebrates at local and regional scales, particularly as the available time series began at variable times relative to actual invasion histories (Aikio et al. 2012; Dawson et al. 2017). The countries represented in our dataset were between 1312 and 4670 km away from the Ponto-Caspian region, whereas several countries were not covered by our data (e.g. Russian Federation, Romania, Bulgaria, Ukraine, Italy, Belarus, Ireland). The vast majority of the Ponto-Caspian macroinvertebrates recorded were found in countries through which the Rhine-Main-Danube (RMD) canal flows (e.g. Hungary and Germany, whose exclusion did not affect the direction of identified trends; Supplementary Material 2). There are two other invasion corridors in Europe, i.e. the southern and the central invasion corridors, connecting the Ponto-Caspian region to other countries (e.g. Latvia; Bij de Vaate et al. 2002; Morton 1997). Although the presence of many Ponto-Caspian macroinvertebrates has been facilitated across these two corridors (see e.g. Jazdzewski et al. 2004; Grabowski et al. 2006; Son 2019), we were unable to identify any suitable (i.e. comparable and sufficiently long) time series data containing entire macroinvertebrate communities from either corridor. However, the included time series contained records of Ponto-Caspian macroinvertebrates in countries unconnected to the main invasion corridors (Spain and the United Kingdom). Invasion of these countries could neither be facilitated by inland water navigation or instream movement of species, but possibly introduced through ballast water of ocean shipping (Binimelis et al. 2007; Gallardo and Aldridge 2015).

Confirming our first hypothesis, we observed a significant increase in the trend of Ponto-Caspian macroinvertebrate species reporting. This increase approximately followed a sigmoid (S-shaped) growth curve (see Fig. 2a; Haubrock et al. 2022b; Kot 2001; Simpson et al. 2022). Although based on correlation and not causation, the steep incline of Ponto-Caspian macroinvertebrates in the years following the opening of the RMD Canal in 1992 (Vučković et al. 2021) suggests that it acted as a primary invasion corridor to countries where it passes through (Leuven et al. 2009). A plateau stage followed this trend later, with only a single new Ponto-Caspian macroinvertebrate species (the amphipod *N. hrabei*) recorded since 2012. The increasing number of Ponto-Caspian species could, however, also be linked to increasing degradation of natural habitats, as several Ponto-Caspian crustaceans have been shown to benefit from an increasing presence of artificial hard substrates

(Borza et al. 2017). The relevance of degradation compared to facilitative biotic interactions, or their potential synergy, remains to be disentangled in future empirical studies. Nevertheless, we found that the number of Ponto-Caspian species was affected by the number of time series in each sampling year, indicating that the saturation observed in recent years likely reflects the reduced number of sampled sites in the most recent years (i.e. 2015–2019). Additionally, a lag time in reporting could have influenced observed trends, despite potential increases in invasive species propagule or colonization pressures.

In combination with the increase in the number of Ponto-Caspian species over time, we observed a slight increase in the abundance trend of Ponto-Caspian species in central and western Europe. This increase was also supported by trends within bivalves and gastropods (albeit represented entirely by *L. naticoides*), which are well-represented in our dataset. Ponto-Caspian amphipod invader trends, however, decreased over time (albeit non-significantly), highlighting that changes over time manifest differently among taxa. This phenomenon can also be observed in the North American Great Lakes, where Ponto-Caspian fishes and invertebrates have become dominant components of food webs (Ricciardi 2001; Vanderploeg et al. 2002); they comprise > 30% of the alien species established in the past few decades—the highest rate of introduction for this group of taxa recorded in the basin's history (Ricciardi 2006). This increase could be explained by a myriad of factors, such as the increase in colonization and propagule pressures driven by the ongoing construction of shipping canals, human modification of rivers, as well as deliberate introductions into human-altered waters (Bij de Vaate et al. 2002; Cassey et al. 2018; MacIsaac et al. 2001) and dynamics and frequency of shipping transits (Capinha et al. 2015; Seebens et al. 2016). In addition, the complex geological history of the Ponto-Caspian region during previous glacial cycles could make these taxa predisposed to invade heterogeneous environments, characterized by broad temperature and salinity gradients (Paiva et al. 2018; Reid and Orlova 2002). The increase of Ponto-Caspian macroinvertebrate trends was mostly driven by bivalves (mostly *D. polymorpha*). We, however, did not span all of its invasion history in Europe (Karatayev and Burlakova 2022), being first recorded in 1847 in France (Kinzelbach 1992) or 1820 in England (CABI 2023). Comparably, gastropod trends—albeit covering only one third of the duration of the other two groups—were found to be increasing, thus possibly being in the boom-phase of a central and western European-wide invasion dynamic (Strayer et al. 2017). This indicates specifically that *L. naticoides* populations might still be expanding across European waterways, posing a higher invasion risk in the near future. In contrast, amphipods exhibited a decreasing albeit non-significant trend, suggesting that may have surpassed the bust-phase of typical invasion dynamics (Strayer et al. 2017).

The present study found that, in many of our time series, the most dominant Ponto-Caspian invader was the bivalve *D. polymorpha*, followed by amphipods. *D. polymorpha* is one of the most successful invaders in Europe due to unique traits, such as a high tolerance to temperature, salinity or pollution, as well as a high fecundity and survival rate during long distance travel (Karatayev and Burlakova 2022; Orlova 2002). Substantial evidence indicates that "ecosystem engineers" such as *D. polymorpha* exhibit a positive relationship with various amphipods (Kobak and Żytkowicz 2007; MacNeil et al. 2010; Gallardo and Aldridge 2015). *Dreissena polymorpha* shells provide refuge from predators to amphipods (e.g. *C. ischnus*; Kobak et al. 2014). In addition, amphipods preferentially settle on habitat structures formed by *D. polymorpha* in the presence of other suitable substrata (Kobak et al. 2013). The absence of experimental data prevents our identification of direct facilitative relationships between Ponto-Caspian macroinvertebrates, although these have been examined in other studies (Kobak and Żytkowicz 2007; Kobak et al. 2014; Ricciardi 2001; Vanderploeg et al. 2002, Gallardo and Aldridge 2015). In addition, the observed pattern could be partly also attributed to the greater ecological importance of bivalves and crustaceans than other taxa such as insects in aquatic ecosystems (Sendek et al. 2022).

The order of recorded arrivals of Ponto-Caspian macroinvertebrates may reflect their ability to actively migrate long distances and to passively hitchhike in ballast tanks, as well as their ability to benefit from already established Ponto-Caspian species (Berezina 2007; Bacela-Spychalska et al. 2013; Gallardo and Aldridge 2015; Kobak et al. 2009). *Chelicorophium curvispinum* was the first amphipod to colonize all newly constructed invasion corridors (Grabowski et al. 2007; Labat et al. 2011) and, as such, was the first amphipod to invade Europe according to our study. *Chelicorophium curvispinum* shows a strong relationship with *D. villosus*: both species were present in 163 of 198 time series with > 1 Ponto-Caspian species (82.32%). The third most common Ponto-Caspian macroinvertebrate in our data was the gastropod snail *L. naticoides*, which is suspected to have spread through the RMD Canal as far as the Netherlands (Bij De Vaate et al. 2002). The differences in order of arrival may be explained by (*i*) trait differences that promote rapid invasion success (e.g. a high intrinsic rate of population growth, asexual reproduction; Casties and Briski 2019; Pauli and Briski 2018), (*ii*) differences in population densities that reflect species habitat preferences (e.g. Ponto-Caspian mysids such as *Hemimysis anomala* are more commonly found in lakes; Kipp and Ricciardi 2007), (*iii*) the variable start and end dates of time series and (*iv*) delays in detection and reporting of new introduced alien species at regional and local scales (e.g. they are commonly longer for cryptic species). Also, it is important to note that some widespread species were established in Europe before our first time series began in 1972. This is the case of *D. polymorpha*, which was introduced into and linked to spread across lentic systems in Germany in the early 1800s, the Netherlands and Belgium in 1826 (Kearney and Morton 1970; Minchin et al. 2002; Seebens et al. 2020), and Denmark in 1840 (Mandahl-Barth 1949).

Contrary to our second hypothesis, we did not observe a difference in the number of detected Ponto-Caspian macroinvertebrate species with increasing distance to the Ponto-Caspian region. This substantiates the enormous invasive potential and the threat to biodiversity presented by Ponto-Caspian macroinvertebrates (e.g. *D. polymorpha*). There are many factors which may explain successful invasion rates, such as high reproductive rates, as well as wide environmental and euryhaline tolerances (Reid and Orlova 2002). These factors in combination with ongoing ecosystem disturbances (e.g. construction of dams) and human activities (e.g. trade intensification) considerably increase the invasion opportunities for these species (Hulme 2021). In addition, it is expected that the number of Ponto-Caspian invasive species will increase in the future with the emergence of new “waves” of invaders from this prominent region (Borza et al. 2017), emphasizing the urgent need for the implementation of control measures to mitigate future impacts (Gallardo and Aldridge 2015; Borza et al. 2017). Indeed, we found a significant increase in richness trends for Ponto-Caspian invaders in the present study, suggesting a further rise in their invasion rates in future.

Changing invasion rates may also be driven by interactions among alien species and the successful establishment of further alien species, which may produce more propagules that enhance downstream propagule pressure. Boom-bust dynamics are also commonly observed in alien invasive species (Haubrock et al. 2022a; Strayer et al. 2017), characterized by exponential population growth, followed by a moderate decline in abundance (Sofaer et al. 2018). Accordingly, as a suite of invasions occurs over time, a newly introduced alien species could ‘boom’ as an established one declines in the ‘bust’ phase, potentially causing a negative, albeit non-causal, correlation. The high risk of invasion from a particular donor region, such as the Ponto-Caspian region, has been described to follow “waves” of invasion where subsequent invaders are replacing each other (Stepien and Tumeo 2006). The observed decrease in the interval between successive introductions could indicate a higher probability for the next alien species to establish, driven potentially through facilitation among co-evolved species that promotes establishment, but not necessarily proliferation (Gallardo and Aldridge 2015; Ricciardi 2001). In accordance with the invasional meltdown (Simberloff 2006; Simberloff and Von Holle 1999) and our third hypothesis presuming reduced time intervals between successive invasions, our results could be explained by synergistic facilitations among Ponto-Caspian macroinvertebrates (possibly through changes in physical habitat structure, community structure or resources) that accelerated the rate of invasion and possibly increased their impact upon recipient communities (Guareschi et al. 2021; Ricciardi 2001; Simberloff and Von Holle 1999). Yet, due to the persistent lack of suitable real-world long-term biodiversity data, documented evidence of interactions between alien species is limited (Gallardo and Aldridge 2015; but see Johnson et al. 2009; Kobak et al. 2013, 2014; Metz et al. 2018) and we cannot confirm the existence of facilitation processes. Nevertheless, it is well known that the replacement of a native species (e.g. of *Gammarus pulex* by the alien *D. villosus* in the Netherlands; MacNeil and Platvoet

2005) could free up niche space and increase the invasibility of an ecosystem (Haubrock et al. 2021), reducing its biotic resistance and potentially triggering an invasional meltdown (De Rivera et al. 2005; Gallardo and Aldridge 2015; Hui et al. 2016), thereby being a driver of biotic homogenization (La Sorte et al. 2007). Thus, although only 5–20% of established species develop harmful impacts (Williamson and Griffiths 1996), the observed gradual increase in the number of Ponto Caspian species across Europe contributes to the major concern of global change and biodiversity loss (Iacarella et al. 2015; Olden and Poff 2004).

Outlook

Potential drivers of an increasing invasion rate are multifaceted and include (*i*) higher colonization pressure, (*ii*) increased disturbance (disrupting biotic resistance; Dar and Reshi 2014; Olden and Rooney 2006) and *(iii)* facilitation (Byers and Noonburg 2003; Green et al. 2011; Lockwood et al. 2009). Due to the presence of existing and emerging Ponto-Caspian macroinvertebrates in Europe (Baars et al. 2022; Lucy et al. 2020) and considering the lag time in the detection and reporting alien invasive species, our identified number of Ponto-Caspian macroinvertebrate species is likely a conservative estimate (Bij de Vaate et al. 2002). Additionally, including other well-known Ponto-Caspian groups, such as fish species (e.g. the round goby *Neogobius melanostomus*) already widespread in Europe, makes this Ponto-Caspianization even more prominent (Le Hen et al. 2023). Accordingly, there are a variety of potential explanations for the increase of Ponto-Caspian fauna in Europe, including Europe's history of canal-building and asymmetric interactions among introduced species with the initial invader facilitating the subsequent invader at the potential cost of its own population growth rate. While it remains difficult to predict future invasion rates, even for prominent groups with a notorious origin such as the Ponto-Caspian region, increasing invasion rates due to 'stepping-stones' from previously invaded areas (Bertelsmeier and Ollier 2021) are also expected (Seebens et al. 2018). The steep increase in Ponto-Caspian invaders in recent decades highlights the need for coordinated efforts to slow further spread and to manage already established invader populations. Without such management intervention, biological invasions from the Ponto Caspian region could ultimately reshape the entire continental aquatic community over time. Strict control of the vectors of introduction and spread of alien species, such as aquaria and garden ornamentation stores (Dickey et al. 2023), ship ballast and ship and recreation boat hulls (Sylvester and MacIsaac 2010; Briski et al. 2012b; Kelly et al. 2013), and increased sampling efforts that promote earlier detection of alien species (e.g. via eDNA methods; Thomas et al. 2020), together with sharing information between governments and stakeholders are needed for effective management. There should be a focus on prevention and control of biological invasions in the current contexts of globalization, global change and accelerating rates of species introductions.

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Data avalability The data underlying this study will be made available upon reasonable request. Requests for data should be directed to Ismael Soto (Isma-sa@hotmail.com).

Declarations

Competing interests The authors have no relevant fnancial or non-fnancial interests to disclose.

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