

## Global distribution and diversity of alien Ponto-Caspian amphipods

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### Abstract

The Ponto-Caspian region is an important donor of aquatic alien species throughout the Northern Hemisphere, many of which are amphipod crustaceans. Despite decades of ongoing spread and negative effects on native biota, a complete picture of the global diversity and distribution of these amphipods has yet to emerge, hampering efficient monitoring and predictions of future invasions. Herein, we provide a comprehensive summary of alien species taxonomic and ecomorphological diversity, as well as high-resolution distribution maps and biogeographical patterns based on >8000 global records. We find that up to 39 species in 19 genera and five families, belonging to all four currently recognized ecomorphs, are potentially alien, their diversity gradually decreasing with distance from the native region. Most species (62%) have limited distributions, 15% are widespread, and 23% exhibit intermediate ranges. We also find that regions adjacent to the native areal are comparatively less well-sampled than more distant regions. Biogeographical clustering revealed three faunal provinces that largely correspond with the Southern, Central and Northern invasion corridors. We conclude that 1) alien amphipods are a representative subsample of the native Ponto-Caspian phylogenetic and ecomorphological diversity, and 2) that their biogeographical patterns are driven by anthropogenic factors acting on distinct native regional species pools.

**Keywords:** biogeography, Corophiidae, distribution, Gammaridae, non-native, Pontogammaridae

### Declarations

**Funding** Lithuanian Research Council (contract no. S-MIP-20-26)

**Conflicts of interest** None

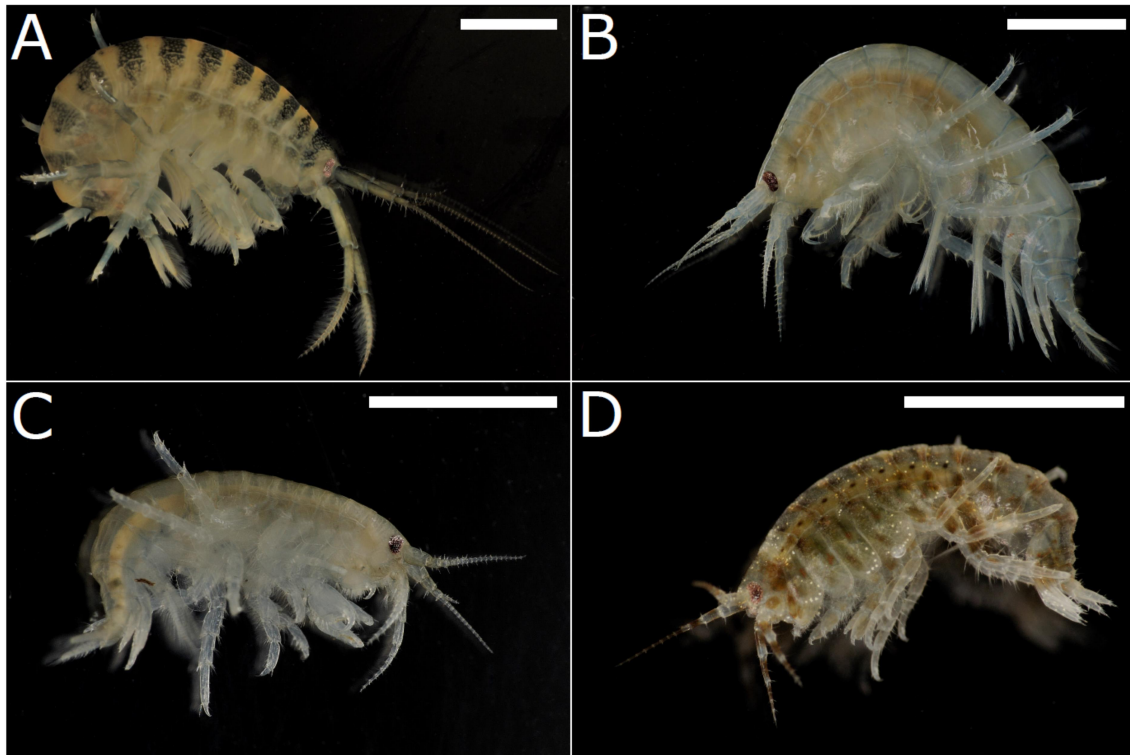
**Availability of data and material (data transparency)** Data is available at Figshare.

**Authors' contributions** DCC, ESC and DS—conceptualization, DCC, ESC and DS—literature screening, DCC—data collection and formal analysis, DCC—led the writing; all authors approved the final version of the manuscript.

45 **Introduction**

46 The Ponto-Caspian region harbors a unique fauna adapted to withstand a broad regime of salinity  
47 conditions (Reid and Orlova 2002). Human mediated dispersal via shipping, artificial canals,  
48 intentional introductions, and increased ionic content in inland water has enabled some of these  
49 species to disperse throughout the Northern Hemisphere as far west as the North American Great  
50 Lakes, and east into Central Asia, sometimes with enormous economic and ecological consequences  
51 (Vanderploeg et al. 2002; Strayer 2009). Among these invasive Ponto-Caspian species, amphipod  
52 crustaceans are the most numerous and diverse (Fig. 1) (Bij de Vaate et al. 2002; Cuthbert et al.  
53 2020).

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56 **Fig. 1** Ecomorphological diversity of Ponto-Caspian gammarid amphipods. A) *Dikerogammarus villosus* (crawler  
57 ecomorph), B) *Pontogammarus robustoides* (digger ecomorph), C) *Obesogammarus crassus* (digger ecomorph),  
58 D) *Chaetogammarus warpachowskyi* (clinger ecomorph). Scale bar = 0.5 cm. Photographs Denis Copilaș-  
59 Ciocianu.

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61

62 Invasions of alien Ponto-Caspian amphipods (hereafter APCAs) are often followed by extinction of  
63 native species, and restructuring of ecological communities (Dermott et al. 1998; Van Riel et al. 2006;  
64 Arbačiauskas 2008; Grabowski et al. 2009; Arbačiauskas et al. 2017). It is generally thought that  
65 native species replacement is due to the higher aggressiveness, reproductive output and adaptability  
66 of the Ponto-Caspian invaders (Dick and Platvoet 2000; Grabowski et al. 2007; Arbačiauskas et al.  
67 2013; Bacela-Spychalska and Van Der Velde 2013; Šidagytė and Arbačiauskas 2016). However,  
68 relatively few alien Ponto-Caspian amphipods have been studied thus far, most attention being  
69 focused on a handful of the most widespread species.

70

71 The dispersal of APCAs has a long history dating back more than a century. Their range expansions  
72 have been primarily facilitated by the opening of artificial canals in the 18<sup>th</sup> century, which connected  
73 the river basins of Central/Western Europe to those of the Black Sea (Bij de Vaate et al. 2002). Some  
74 of the earliest species known to have expanded their ranges are *Chaetogammarus ischnus* and  
75 *Chelicorophium curvispinum*, possibly as early as the late 19<sup>th</sup> century (Jarocki and Demianowicz  
76 1931; Crawford 1935). A second important wave of invasions took place in the 1960s where a  
77 number of species were deliberately introduced and successfully acclimatized in reservoirs and lakes  
78 in the Baltic region, from where they subsequently expanded (Bij de Vaate et al. 2002; Arbačiauskas  
79 et al. 2017). At the same time, similar patterns of deliberate introductions took place also in other  
80 areas of the former Soviet Union, especially in newly built reservoirs on the Dnieper, Volga and Kura  
81 rivers (Ioffe 1973; Jazdzewski 1980; Grigorovich et al. 2002). The opening of the Rhine-Main-Danube  
82 canal in 1992 has promoted the dispersal of many amphipods into Western Europe (Bij de Vaate et  
83 al. 2002). From here, *C. ischnus* has even been transferred into the Great Lakes region in North  
84 America through shipping activity, where it successfully established along with other Ponto-Caspian  
85 species (Witt et al. 1997; Cristescu et al. 2004). Several species are already established in the British  
86 Isles as well (MacNeil et al. 2010). Nowadays, the distribution of APCAs in Eurasia stretches from  
87 Ireland to eastern Kazakhstan, where they are common in most of the large rivers and their  
88 estuaries.

89

90 Despite their wide distribution and documented negative effects, few studies have previously  
91 documented the distribution of APCAs at the continental scale (Jazdzewski 1980; Barnard and  
92 Barnard 1983). However, these studies are decades old, and, since then, the ranges of these species  
93 have increased dramatically. Thus, to the extent of our knowledge, there are no high resolution, up  
94 to date, distribution maps comprising the global ranges of APCAs, despite that numerous studies  
95 have provided such data at a regional scale (Jazdzewski and Konopacka 1988; Bollache et al. 2004;  
96 Grudule et al. 2007; Žganec et al. 2009; Arbačiauskas et al. 2011; Borza 2011; Borza et al. 2015;  
97 Meßner and Zettler 2018), and range expansions are routinely reported (Copilaş-Ciocianu and  
98 Arbačiauskas 2018; Moedt and Van Haaren 2018; Minchin et al. 2019; Lipinskaya et al. 2021). Even  
99 though the spatio-temporal dispersal patterns are relatively well known for many species (Bij de  
100 Vaate et al. 2002; Grigorovich et al. 2002; Cristescu et al. 2004; Rewicz et al. 2015; Jazdzewska et al.  
101 2020), a lack of high resolution distribution data precludes efficient global monitoring and hampers  
102 predictions of future invasions. Such predictions are crucial for an effective management aimed at  
103 preventing further dispersal (Gallardo and Aldridge 2015).

104

105 Apart from sparse knowledge on distribution ranges, it is also unclear how many APCAs occur outside  
106 their native area. To the extent of our knowledge, a comprehensive list of these species along with  
107 their taxonomic and ecomorphological diversity, as well as modes of introduction has never been  
108 compiled. Such information is, again, of high relevance in forecasting future invasions (Borza et al.  
109 2017).

110

111 Considering the above shortcomings, with this paper we aim to compile for the first time information  
112 regarding the diversity and global distribution of all Ponto-Caspian amphipods that are known to  
113 occur outside their native range. Specifically, we aim to bring insight into patterns of taxonomic and  
114 ecomorphological diversity, as well as a better understanding of biogeographical patterns based on  
115 up-to-date, high resolution distribution data.

116

## 117 **Material and Methods**

### 118 *Defining the native range*

119 The boundary between the native and non-native areas of a species' distribution is often not  
120 straightforward to define (Courchamp et al. 2020; Pereyra 2020). We acknowledge that a single  
121 definition applicable to all APCA species is difficult given the high taxonomic and ecological diversity  
122 of the group (Copilaş-Ciocianu and Sidorov 2021). Many species have well-documented introductions  
123 (Grigorovich et al. 2002, 2003; Arbačiauskas et al. 2011) and spatio-temporal dispersal patterns (Bij  
124 de Vaate et al. 2002) outside the native area, while in some cases it is assumed that they dispersed  
125 since the Late Pleistocene (Cristescu et al. 2004). As such, we aim for an operational definition that is  
126 generally applicable.

127

128 We consider that the native range of APCAs encompasses the seas themselves (Black, Azov, Caspian  
129 and Aral) as well as the adjacent lagoons, river mouths and deltaic/estuarine regions. This is mainly  
130 because Ponto-Caspian amphipods have inhabited and diversified in this area (i.e. Paratethys Sea)  
131 since the late Miocene, as evidenced by fossils as well as time-calibrated phylogenies (Derzhavin  
132 1927; Hou et al. 2014; Hou and Sket 2016; Copilaş-Ciocianu et al. 2020; Copilaş-Ciocianu and Sidorov  
133 2021). Only four non-alien species that belong to the Ponto-Caspian amphipod group (ca. 4%) are  
134 found exclusively outside the Ponto-Caspian realm, all of these being found in the nearby Balkan  
135 Peninsula or the Caucasus (Copilaş-Ciocianu and Sidorov 2021). Therefore, our definition is  
136 conservative as it does not include lower sections of rivers that stretch further than the deltaic  
137 regions (Gogaladze et al. 2020). Drawing a line between the native and invasive areal is not  
138 straightforward in such linear habitats (Pereyra 2020). Likewise, setting a fixed threshold distance is  
139 not feasible as each river has its idiosyncrasies.

140

### 141 *Taxonomic framework*

142 As a taxonomic framework we used a recent review of Ponto-Caspian amphipod diversity (Copilaş-  
143 Ciocianu and Sidorov 2021). Two species were found to be taxonomically ambiguous and should be  
144 treated with caution. First, we do not consider that the north-western Black Sea (including Central  
145 and Western Europe) populations of *Trichogammarus trichiatus* are conspecific with the eastern  
146 Black Sea ones (Caucasus region) based on which this species was originally described (Martynov  
147 1932). The north-western populations were initially described as *Chaetogammarus tennelus major* by  
148 Cărăușu (1943) from lagoons in Romania and Bulgaria, and were later synonymized with *T. trichiatus*  
149 (Dedju 1967; Straškraba 1969), a situation that is currently accepted (Rachalewski et al. 2013).  
150 However, unpublished molecular and morphological data confirms the distinctiveness of both taxa,  
151 which are not even closely related (Copilaş-Ciocianu in prep.). As such, all the non-Caucasian  
152 populations are provisionally referred to as *Trichogammarus* cf. *trichiatus*, pending further study.  
153 Second, we do not distinguish between the records of *Yogmelina pusilla* and *Y. limana*, since the  
154 latter has never been reported outside its type locality, probably due to misidentification with the  
155 former (Karaman and Barnard 1979).

156

### 157 *Data collection*

158 We collected data from any available source (publication, conference proceedings, report or online  
159 database) which provided precise locality information (either coordinates or locality name). Our own  
160 unpublished data was included as well. Whenever possible, data was also extracted from maps (~10

161 km accuracy) if locality information was not provided in the text. We generally focused on collecting  
162 data from non-native areas. However, for the most widespread species we also collected all available  
163 data from their native ranges as well.

164 Data from online databases was obtained from GBIF (<https://www.gbif.org/>;  
165 <https://doi.org/10.15468/dl.iddp60>; <https://doi.org/10.15468/dl.uvqzia>;  
166 <https://doi.org/10.15468/dl.ythkoe>; <https://doi.org/10.15468/dl.qrkyj>;  
167 <https://doi.org/10.15468/dl.i8uafv>; <https://doi.org/10.15468/dl.h40xk1>;  
168 <https://doi.org/10.15468/dl.agjzc4>; <https://doi.org/10.15468/dl.kkgszv>;  
169 <https://doi.org/10.15468/dl.xmntxw>) and the Czech Hydrometeorological Institute  
170 (<http://hydro.chmi.cz/>). Data collection ended in March 2021.

171

172 On each species we collected further data regarding its mode(s) of introduction, ecomorphology and  
173 taxonomy. Following Grigorovich et al. (2002) we distinguished five types of species introduction  
174 modes: deliberate, accidental, facilitated by hydrotechnical constructions (canals and reservoirs),  
175 shipping, and natural dispersal. Ecomorph and taxonomic assignment followed Copilaş-Ciocianu and  
176 Sidorov (2021). The corophiid genus *Chelicorophium* was not included in the ecomorphological  
177 classification as ecomorphs have been established only for gammaroidean Ponto-Caspian amphipods  
178 (Copilaş-Ciocianu and Sidorov 2021).

179

#### 180 *Data analysis*

181 We examined the relationship between the total number of species and total number of alien  
182 species within a genus using Pearson correlation. We also tested whether the number of species  
183 within ecomorphs statistically differs between the native and non-native regions. For this we used  
184 Fisher's exact test with 9999 permutations. Statistical analyses were performed with PAST 3  
185 (Hammer et al. 2001).

186

187 We explored to what extent the phylogenetic diversity of the alien species represents the total  
188 endemic diversity of gammaroidean and corophioidean Ponto-Caspian amphipods. For this we used  
189 the PhyRe python script (Plazzi et al. 2010), running the analysis at the species level with 1000  
190 random replicates and default settings. For each species we also added the superfamily, family and  
191 genus level. The master list with the reference taxonomy followed Copilaş-Ciocianu and Sidorov  
192 (2021).

193

194 Distribution maps were created with QGIS 3.10 (QGIS Development Team 2016). We estimated the  
195 number of alien species per country and per freshwater ecoregion (Abell et al. 2008) with the help of  
196 layers downloaded from <https://geospatial.tnc.org/>. Species richness and sampling redundancy grids  
197 were created with Biodiverse 2.0 software (Laffan et al. 2010) using 1° cells. Biogeographical  
198 regionalization was performed using the Infomap Bioregions server  
199 (<https://www.mapequation.org/bioregions/>) (Edler et al. 2017). The analysis was run with default  
200 settings, except the number of trials which was set to 10 (maximum) and the value of the cluster cost  
201 parameter was set to 1.2. This was the most conservative value as increasing it resulted in only one  
202 biogeographical region. For the last two analyses only records from the non-native regions were  
203 used.

204

## 205 **Results**

206 Overall, we reviewed 527 sources, of which 322 had precise locality information (supplementary  
 207 references will be provided during the review process). Overall, we obtained 8145 distribution  
 208 records. Data collection ended in March 2021. The full dataset is available at Figshare (doi will be  
 209 provided after acceptance).

210

211 *Biodiversity and modes of introduction*

212 In total, we consider that up to 39 species (in 19 genera and five families) are potentially alien, as  
 213 they were reported occurring outside their native region (Table 1). This number represents  
 214 approximately 40% of all currently known Ponto-Caspian endemic amphipod diversity (96 species,  
 215 Copilaş-Ciocianu and Sidorov 2021).

216

217 Table 1. Checklist of alien Ponto-Caspian amphipods, their non-native distribution, biogeographical pattern,  
 218 mode of introduction and ecomorphological classification.

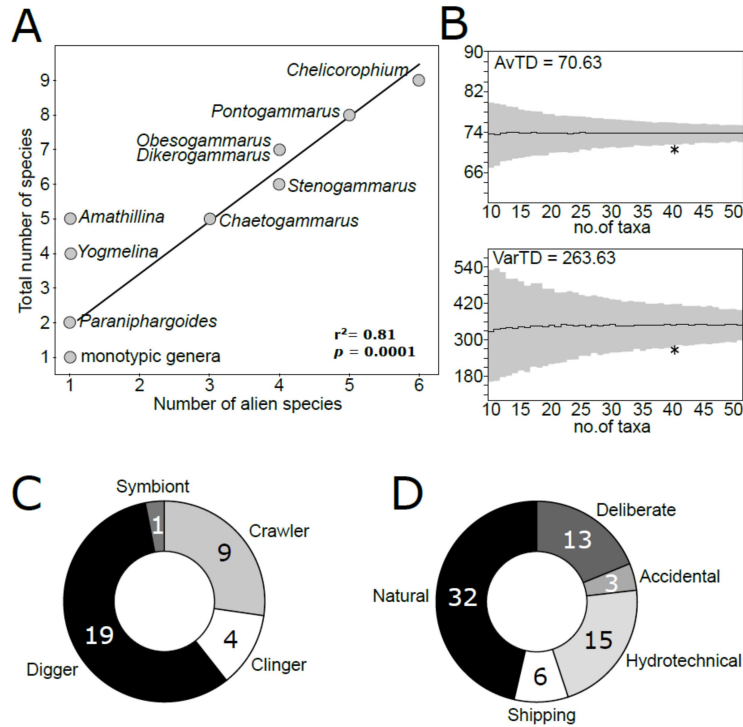
Species	Family	Sea drainage				Distribution type				Introduction mode				Ecomorph			
		BL	ME	NO	BA	A	CA	I	II	III	IV	D	A		H	S	N
<i>Amathillina cristata</i>	Gam.	*									*	*					clinger
<i>Chaetogammarus ischnus</i>	Gam.	*		*	*	*	*	*				*		*	*	*	crawler
<i>Chaetogammarus placidus</i>	Gam.	*									*					*	crawler
<i>Chaetogammarus warpachowskyi</i>	Gam.	*			*		*				*	*			?	*	clinger
<i>Chelicorophium chelicorne</i>	Cor.	*									*	*				*	N/A
<i>Chelicorophium curvispinum</i>	Cor.	*	*	*	*	*	*	*				*		*	*	*	N/A
<i>Chelicorophium maeoticum</i>	Cor.	*					*				*		*			*	N/A
<i>Chelicorophium nobile</i>	Cor.	*					*				*	*				*	N/A
<i>Chelicorophium robustum</i>	Cor.	*		*					*			*		*	?	*	N/A
<i>Chelicorophium sowinskyi</i>	Cor.	*	*	*			*	*						*	?	*	N/A
<i>Dikerogammarus bispinosus</i>	Gam.	*		*			*		*					*	?	*	crawler
<i>Dikerogammarus caspius</i>	Gam.	*					*			*		?		*		*	crawler
<i>Dikerogammarus haemobaphes</i>	Gam.	*		*	*	*	*	*				*		*	*	*	crawler
<i>Dikerogammarus villosus</i>	Gam.	*	*	*	*	*	*		*			*		*	*	*	crawler
<i>Iphigenella acanthopoda</i>	Iph.	*					*				*		?				symbiont
<i>Lanceogammarus andrussovi</i>	Gam.	*									*	*					crawler
<i>Kuzmelina kusnezowi</i>	Gam.	*									*		*				clinger
<i>Niphargogammarus intermedius</i>	Pon.	*									*					*	digger
<i>Obesogammarus crassus</i>	Pon.	*		*	*	*	*	*		*	*	*	?	?	*	*	digger
<i>Obesogammarus obesus</i>	Pon.	*		*		*	*						*	?	*	*	digger
<i>Obesogammarus platycheir</i>	Pon.					*					*	?	?			*	digger
<i>Obesogammarus subnudus</i>	Pon.	*									*		*				digger

<i>Paraniphargoides motasi</i>	Pon.	*								*					*	digger
<i>Pontogammarus abbreviatus</i>	Pon.	*				*			*		?	?			*	digger
<i>Pontogammarus aestuarius</i>	Pon.	*							*	*	?	?			?	digger
<i>Pontogammarus maeoticus</i>	Pon.	*				*			*	*		*			*	digger
<i>Pontogammarus robustoides</i>	Pon.	*	*	*	*	*	*	*		*	*	*	*	*	*	digger
<i>Pontogammarus sarsi</i>	Pon.	*				*			*		?	?			*	digger
<i>Shablogammarus shablensis</i>						*			*		?	?	*		*	crawler
<i>Stenogammarus compressus</i>	Pon.					*			*	*	?	?			*	digger
<i>Stenogammarus deminutus</i>	Pon.					*			*	*	?	?			*	digger
<i>Stenogammarus macrurus</i>	Pon.					*			*	*	?	?			*	digger
<i>Stenogammarus similis</i>	Pon.					*			*	*	?	?			*	digger
<i>Trichogammarus cf. trichiatus</i>	Gam.	*		*	*			*					*		*	crawler
<i>Turcogammarus aralensis</i>	Pon.	*				*			*	*	?	?			*	digger
<i>Uroniphargoides spinicaudatus</i>	Pon.	*							*						*	digger
<i>Wolgagammarus dzjubani</i>	Pon.					*			*	*	?	?			*	digger
<i>Yogmelina pusilla/limana</i>	Gam.	*							*				*		*	clinger
<i>Zernovia volgensis</i>	Beh.					*			*	*	?	?			?	digger

219 Gam. – Gammaridae, Cor. – Corophiidae, Iph. – Iphigenellidae, Pon. – Pontogammaridae, Beh. – Behningiellidae, BL – Black  
 220 Sea, ME – Mediterranean Sea, NO – North Sea, BA – Baltic Sea, A – Atlantic, CA – Caspian Sea;  
 221 D – deliberate, A – accidental, H – hydro technical construction, S – shipping, N – natural spread  
 222  
 223

224 We identified a strongly positive correlation between the total number of species and alien species  
 225 within a genus (Pearson correlation,  $r^2 = 0.81$ ,  $p = 0.0001$ ) (Fig. 2A). With respect to ecomorphology,  
 226 we find that 19 species are diggers, 9 are crawlers, 4 are clingers and one is a symbiont (Fig. 2B, Table  
 227 1). We did not find significant differences between the number of non-native and native species  
 228 within ecomorphs ( $X^2 = 1.148$ ,  $p = 0.76$ ), meaning that the ecomorphological diversity in the non-  
 229 native area is similar to that in the native area.

230  
 231 The phylogenetic representativeness analysis revealed that the alien species represent a relatively  
 232 good proportion of the total phylogenetic diversity of the endemic gammaroidean and  
 233 corophioidean amphipod fauna. The average taxonomic distinctness (AvTD = 70.63) and variation in  
 234 taxonomic distinctness (VarTD = 263.63) were slightly below the lower bound of the 95% interval, the  
 235 former indicating modest representativeness while the latter indicating good representativeness (Fig.  
 236 2B). Moreover, von Euler's index of imbalance (= 0.19) was well below the recommended threshold  
 237 of 0.25, which also indicates good representativeness (Plazzi et al. 2010).



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**Fig. 2** A) Relationship between the total number of species and number of invasive species within a genus. B) Funnel plots indicating the average taxonomic distinctness (AvTD) and variation in taxonomic distinctness (VarTD) of alien Ponto-Caspian amphipods. Asterisks indicate the empirical parameter values, thick black lines indicate mean, and gray area reflects the 95% confidence interval of the 1000 replicates. C) Pie-chart indicating the number of species that belong to each of the four currently recognized ecomorphs. D) Pie-chart indicating the number of species that have expanded their ranges via different introduction modes. Note that one species may have dispersed via several modes.

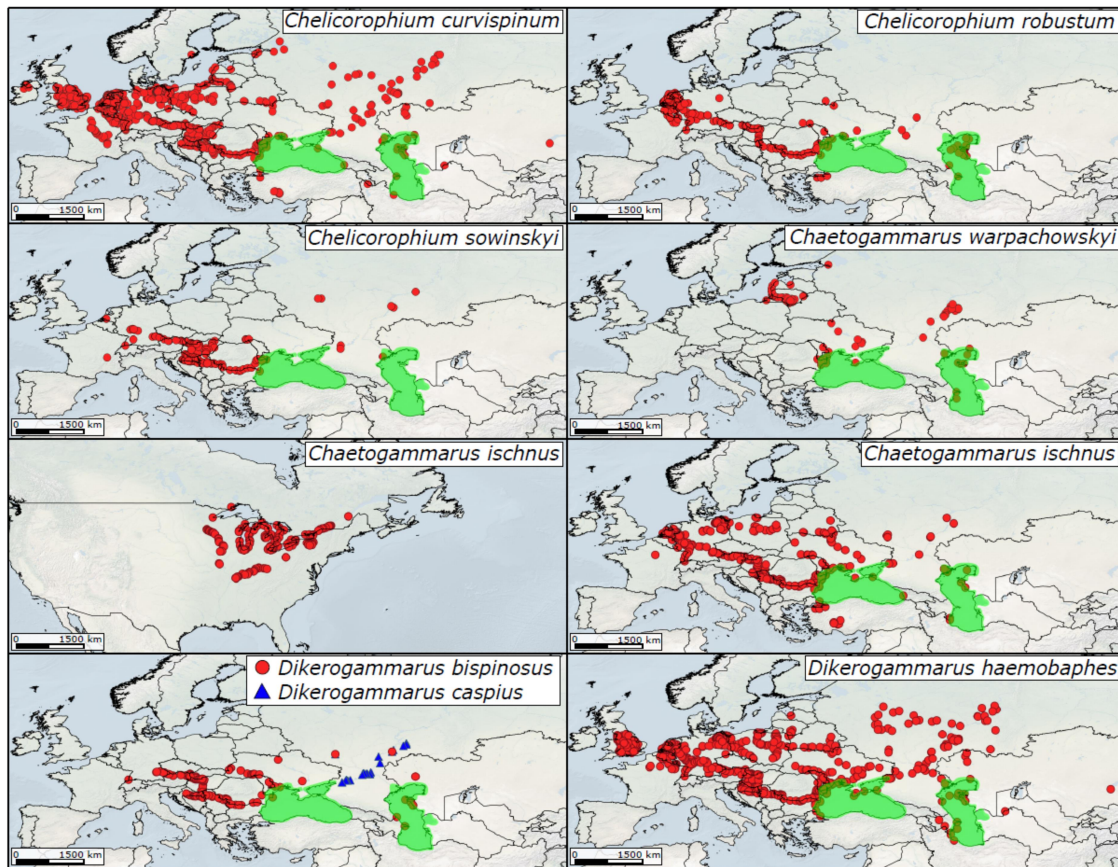
Regarding introduction mode, we find that up to 32 species seem to have dispersed naturally (Fig. 2C). However, this dispersal type is almost always associated with human activity (Table 1). A total of 16 species have been documented as introduced (13 deliberately and 3 accidentally), 15 have spread via hydrotechnical constructions (reservoirs and canals), and 6 have spread through shipping activity (Fig. 2C). For a number of species, the exact dispersal mode is still uncertain (Table 1).

### Biogeography

Distribution maps of all 39 species are presented in Figures 3-5. For the 14 most widespread species we present records spanning their entire distribution area, including the native region (Figs. 3-4). For the remainder of species we present only non-native distribution records (Fig. 5).

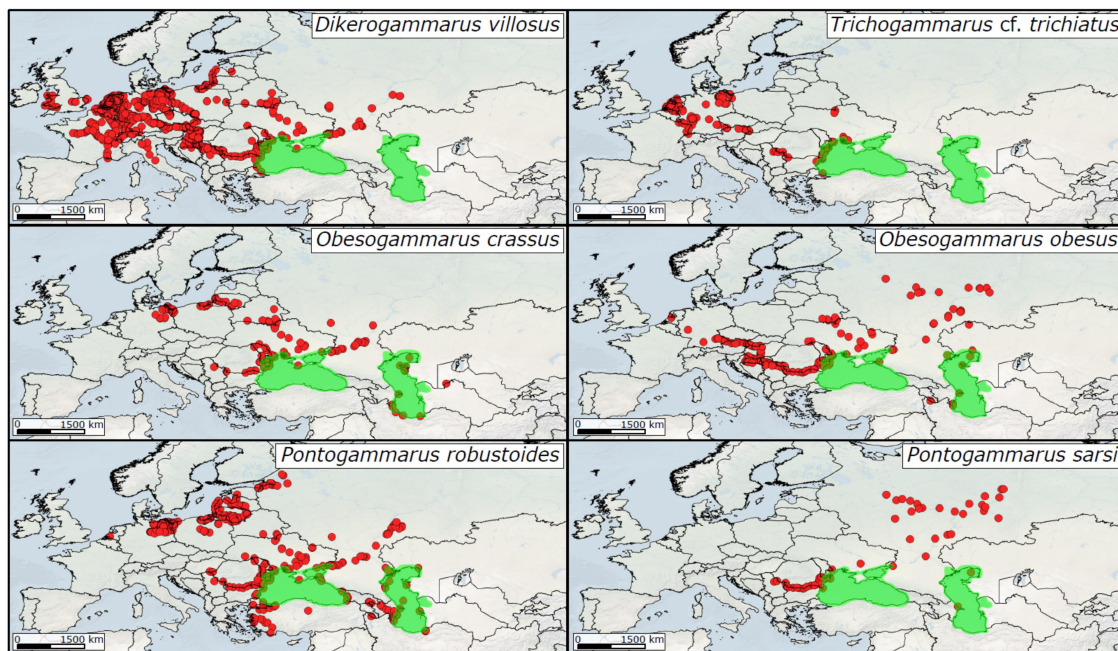
Altogether, 34 countries spanning the Northern Hemisphere were found to harbor alien amphipods (Fig. 6A). The highest number of species was observed in countries adjacent to Ponto-Caspian water bodies such as Russia (30), Ukraine (24), Bulgaria (17), and Romania (16). A total of 25 freshwater ecoregions contained non-native species, the highest number being found in the ones closest to the Ponto-Caspian realm. These were the Volga-Ural (27 species), Dniester-Lower Danube (23), Dnieper-South Bug (22), and Don (20) (Fig. 6B).





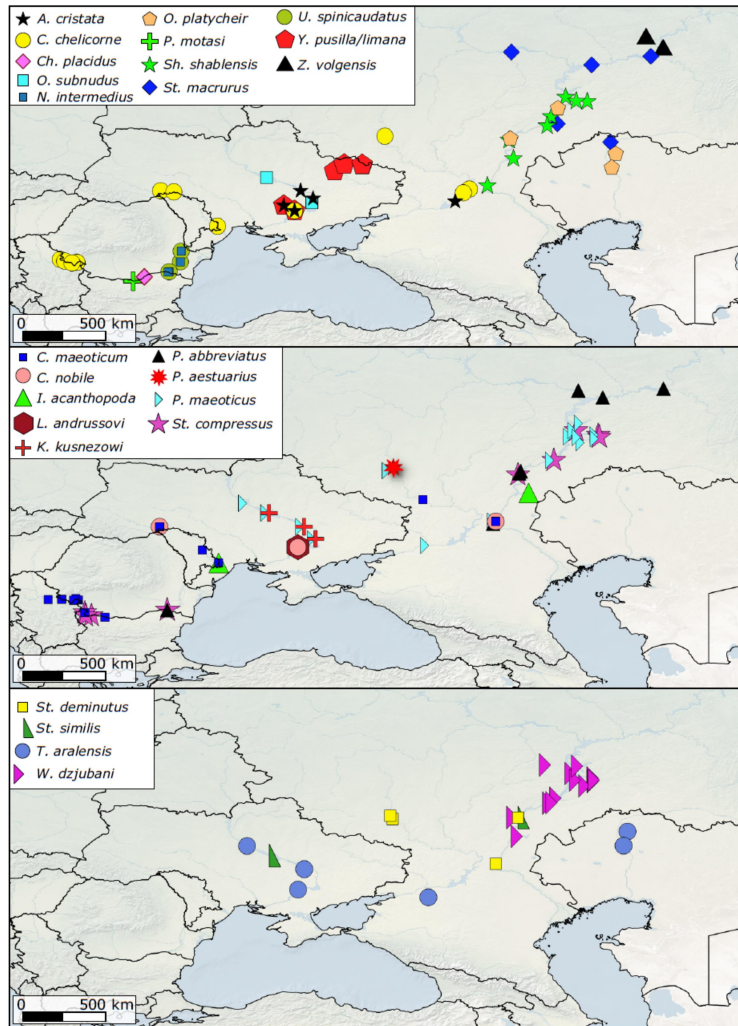
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**Fig. 3** Distribution of widespread Ponto-Caspian amphipods in native and non-native areas (except *Dikerogammarus caspius* for which only non-native records are shown). Green shading denotes the native areal.



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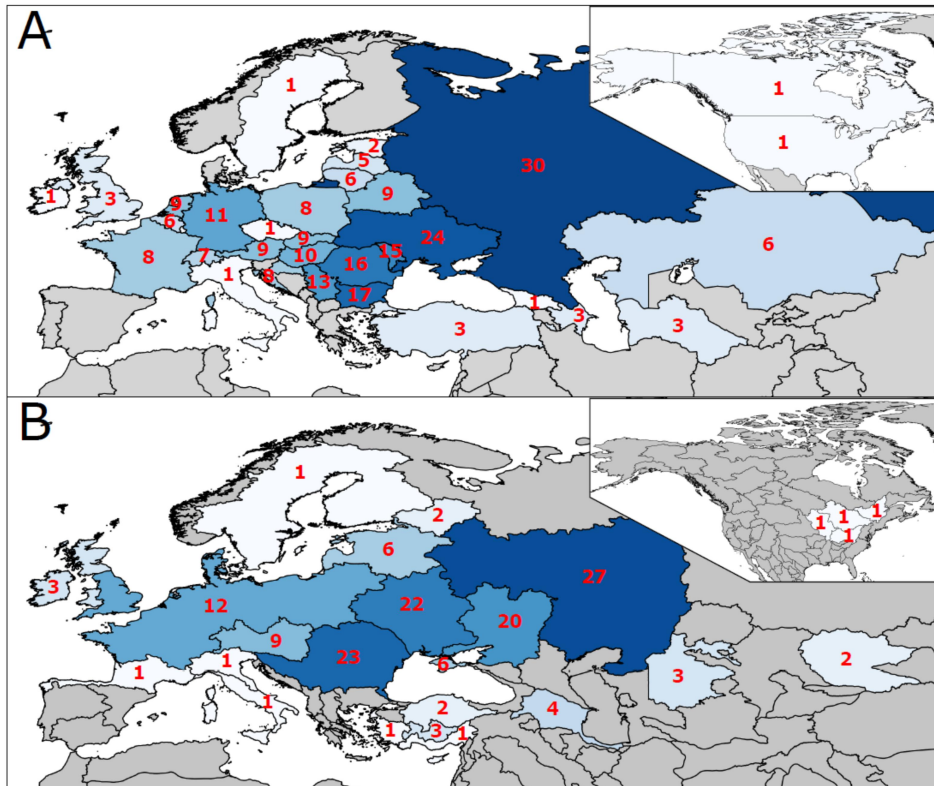
**Fig. 4** Distribution of widespread Ponto-Caspian amphipods in native and non-native areas. Green shading denotes the native areal.



273  
 274 **Fig. 5** Distribution of Ponto-Caspian amphipods that have a less extended area. All distribution points are non-  
 275 native records.

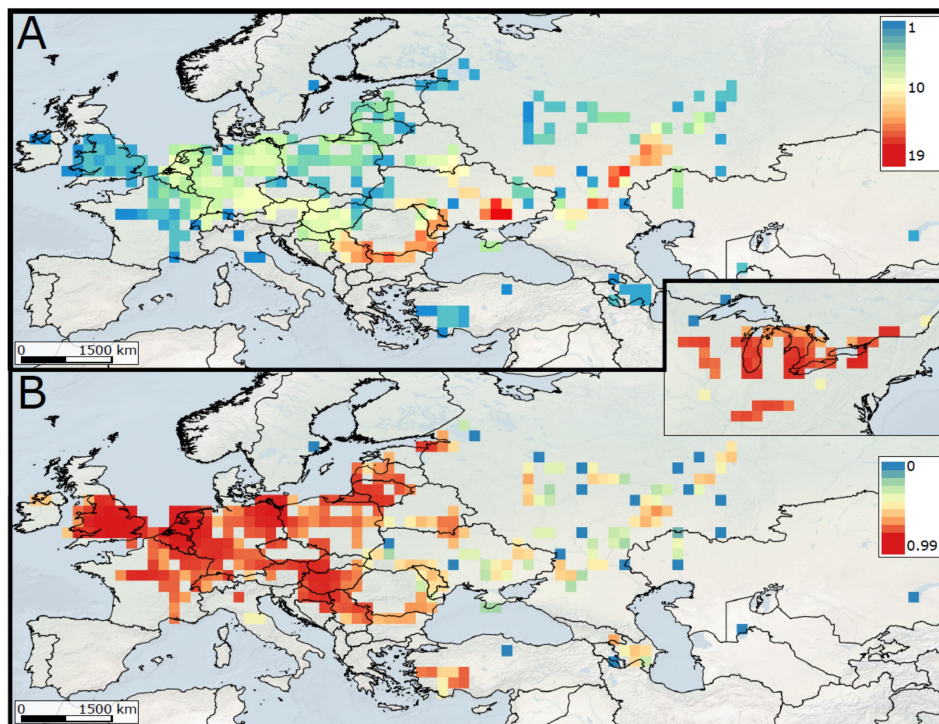
276  
 277 Species richness analysis at a finer spatial scale revealed that the highest concentration of alien  
 278 species is found throughout the lower courses of the largest rivers: Volga, Don, Dnieper and Danube.  
 279 Generally, the number of alien species decreases gradually with distance from the native area (Fig.  
 280 7A). We also find that, in general, the sampling intensity is comparatively greater in the species-poor  
 281 regions located further away from the Ponto-Caspian realm (Fig. 7B).

282  
 283 Biogeographical clustering based on spatial species composition revealed three distinct faunistic  
 284 regions (Fig. 8). Region 1 mainly encompasses the river drainages connected to the north-western  
 285 part of the Black Sea (Rhine, Danube and Dniester) as well as a few areas of the upper-most reaches  
 286 of the Volga basin. The most common species here is *C. curvispinum*. This region mainly corresponds  
 287 to the Southern invasion corridor (Bij de Vaate et al. 2002). Region 2 encompasses the south and  
 288 south-eastern edges of the Baltic Sea. The most common species is *P. robustoides*. It partially  
 289 corresponds with the Central invasion corridor. Finally, region 3 comprises drainages that flow to the  
 290 northern Black Sea, the Azov Sea and the Caspian Sea (Dnieper, Don and Volga). The most common  
 291 species is *D. haemobaphes*. This region partially corresponds with the Northern invasion corridor.



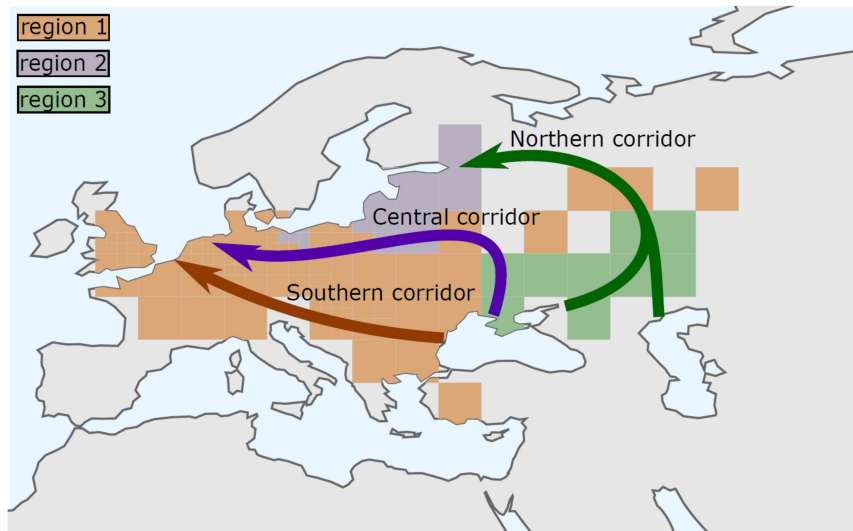
292  
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Fig. 6 Number of alien Ponto-Caspian amphipod species per A) country and B) freshwater ecoregion.



295  
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299

Fig. 7 Species richness and sampling intensity of Ponto-Caspian amphipods in non-native areas. A) Distribution of species richness. Warmer colors indicate higher species number. B) Sampling redundancy. Warmer colors indicate higher sampling effort. Inset map represents the Great Lakes Region in North America.



300  
301 **Fig. 8** Biogeographical regions based on species composition. The colored arrows indicate the main invasion  
302 corridors through which Ponto-Caspian species have dispersed.  
303

304

305 Additionally, we classified the geographical patterns of distribution into four categories (Table 1):

- 306 a) Type I - Species which are widespread in both Black Sea and Caspian basins, and their  
307 connected rivers (6 species).  
308 b) Type II - Species mainly distributed in the Black Sea basin and connected rivers, with  
309 limited/no distribution in the Caspian basin (5 species).  
310 c) Type III - Species mainly distributed in the Caspian basin with limited/no distribution in the  
311 Black Sea basin and connected rivers (4 species).  
312 d) Type IV - Species with limited distribution in either or both basins (24 species).

313 Therefore, we can summarize that 24 species (62%) have restricted distributions, six species (15%)  
314 are widespread, and nine species (23%) have intermediary range sizes.

315

## 316 **Discussion**

317 Our study provides the first comprehensive overview of the diversity and distribution of APCAs at the  
318 global scale. We find that the non-native species are a representative subsample of the total Ponto-  
319 Caspian amphipod diversity in terms of taxonomy and ecomorphology. Our detailed, high-resolution  
320 distribution maps provide a first global perspective on the spatial extent of these species,  
321 emphasizing the role of anthropogenic corridors in shaping their non-native biogeography.

322

### 323 *Biodiversity*

324 The total number of Ponto-Caspian amphipods that were found to occur outside the native region is  
325 quite high. Up to 39 species can be considered alien, representing about 40% of the entire endemic  
326 diversity. At higher taxonomic levels we find that 19 genera (out of 39, i.e. ~49%) and five families  
327 (out of 10, i.e. 50%) contain alien species. It therefore appears that the non-native species represent  
328 approximately half of the entire endemic Ponto-Caspian amphipod taxonomic diversity.

329 Furthermore, we also find that the alien species represent a good part of the total endemic  
330 phylogenetic diversity.

331

332 It appears that species rich genera have the highest number of alien species since we found a strong  
333 and positive relationship between the total number of species and alien species within genera.  
334 However, it is yet unclear whether this relationship reflects particular intrinsic generic traits that  
335 favor invasiveness, or is an artifact due to human activity. Perhaps these two factors are not mutually  
336 exclusive either.

337  
338 From an ecomorphological perspective, our study reveals that the alien species belong to all of the  
339 four currently recognized Ponto-Caspian gammarid ecomorphs (Copilaş-Ciocianu and Sidorov 2021).  
340 Half of the species (49%) are diggers, and up to a quarter are crawlers (23%), while clingers and  
341 symbionts represent a small fraction (10% and 2%, respectively). These proportions reflect very well  
342 the situation in the native region, with the most common ecomorph being the digger (49%), followed  
343 by crawlers (26%), clingers (19%) and symbionts (6%) (Copilaş-Ciocianu and Sidorov 2021).  
344 Furthermore, we also did not find significant differences regarding the number of native and non-  
345 native species within ecomorphs. As such, we can deduce that alien species represent a significant  
346 subsample of the total ecomorphological diversity of endemic Ponto-Caspian amphipods. Further  
347 detailed morphometric analyses are necessary to paint a clearer picture regarding the morpho-  
348 functional differentiation (if any) among the native and alien species. Such insight can be useful in  
349 identifying the functional traits that favor invasiveness (Ordóñez et al. 2010; Petruzzellis et al. 2021).

350  
351 It remains to be seen whether the more numerous diggers and crawlers have certain advantages that  
352 promote invasiveness over clingers and symbionts. The first two are more associated with coarse  
353 substrates (fine sand to rocks) than the last two (Copilaş-Ciocianu and Sidorov 2021). An affinity for  
354 hard substrata has been proposed as an important factor favoring the dispersal of Ponto-Caspian  
355 peracarid crustaceans into heavily anthropized habitats (Borza et al. 2017). Indeed, numerous studies  
356 reported a preference of alien Ponto-Caspian amphipods for hard substrates, although relatively few  
357 species were studied thus far (Dermott et al. 1998; Hesselschwerdt et al. 2008; Jermacz et al. 2015;  
358 Borza et al. 2018; Poznańska-Kakareko et al. 2021). Clingers and symbionts seem to be associated  
359 with more specific substrates, which may limit dispersal potential. Therefore, our study also leans  
360 towards the hypothesis that preference for hard substrates is an important trait that characterizes  
361 non-native Ponto-Caspian crustaceans.

362  
363 We consider that the introduction modes of many species are not yet certainly known. Most species  
364 have probably spread naturally, but this is only in conjunction with human activities, such as after  
365 being deliberately introduced, or after the construction of dams and canals (Grigorovich et al. 2002).

### 366 367 *Biogeography*

368 Our high resolution maps capture for the first time the global spread of APCAs, providing a greater  
369 resolution and extent than any previous studies (Jazdzewski 1980; Bij de Vaate et al. 2002). We find  
370 that range sizes vary greatly among species, from highly localized to intercontinental. Nevertheless,  
371 despite the relatively large number of alien species, it appears that most of them (62%) have limited  
372 distributions. Only six species are widespread in both the Black Sea and Caspian basin, and nine are  
373 widely distributed only in one basin.

374  
375 As expected, the highest alien species diversity is in the regions adjacent to the native areal,  
376 especially in the lower course of large rivers such as the Volga, Don, Dnieper and Danube. In Central

377 Europe the highest diversity is observed in the Danube and Rhine rivers. Towards the outermost  
378 edges of the invaded areal the number of species is always low, these usually being the oldest  
379 invaders such as *C. curvispinum*, *C. ischnus* and *D. haemobaphes*.

380

381 Lower sampling intensity in areas close to the native areal suggests that more intensive monitoring is  
382 required here, as well as in the native region. This is especially important since many introductions  
383 took place among these regions, and most of the species diversity is found here (Grigorovich et al.  
384 2002). Despite a few more recent studies (Uzunova 1999; Petrescu 2009; Zinchenko and Kurina 2011;  
385 Konopacka et al. 2014; Copilaş-Ciocianu et al. 2020; Kurina 2020; Son et al. 2020), there is a  
386 significant lack of new data in many of these areas. It is very likely that some of the introduced  
387 species are extinct, or their distributions could have changed significantly.

388

389 Biogeographical clustering of species composition revealed three faunistic provinces that correspond  
390 remarkably with the Northern, Central and Southern invasion corridors used by the Ponto-Caspian  
391 fauna (Bij de Vaate et al. 2002). These corridors consist of artificially connected large rivers and have  
392 limited to no connectivity among each other. This overlap between corridors and faunistic provinces  
393 highlights, on one hand, that human mediated dispersal plays a crucial role in the spreading of Ponto-  
394 Caspian fauna outside its native area. On the other hand, this overlap also emphasizes that the  
395 distinct faunal composition between region 1 (corresponding to the Southern corridor with species  
396 originating from the Black Sea) and region 3 (corresponding to the Northern corridor with species  
397 originating from the Azov and Caspian Seas) is connected to the biogeography of the area, since the  
398 Black and Caspian Seas have distinct biotas (Mordukhai-Boltovskoi 1964, 1979; Copilaş-Ciocianu and  
399 Sidorov 2021). Moreover, our results show that the Azov drainages have a greater similarity in alien  
400 species composition to the Caspian Sea rather than to the nearby Black Sea. This similarity is  
401 sometimes reflected in phylogeographic studies which identified a closer genetic connection of the  
402 Azov with the Caspian rather than the Black Sea (Audzijonyte et al. 2006; Nahavandi et al. 2013),  
403 most likely reflecting the region's geological past (Krijgsman et al. 2019; Palcu et al. 2021). As such, it  
404 appears that the regional species pools in the native areal coupled with a strong anthropogenic  
405 influence play a critical role in shaping the non-native distributions of Ponto-Caspian amphipods.

406

#### 407 *Prospects for further dispersal*

408 Europe and temperate Asia are the most affected regions by alien crustacean species, and their  
409 number is predicted to significantly rise by 2050 (Seebens et al. 2021). Borza et al. (2017) concluded  
410 that the possibility for additional Ponto-Caspian peracarid crustaceans of becoming invasive in the  
411 future is low. Nevertheless, given that the current number of non-native species is already quite high,  
412 further dispersal into new regions is unavoidable. This is exemplified by the regular reporting of new  
413 APCAs records (e.g. Csabai et al. 2020; Son et al. 2020; Lipinskaya et al. 2021). As such, additional  
414 monitoring is needed, coupled with the implementation of management measures aimed at  
415 minimizing further dispersal (Vander Zanden and Olden 2008).

416

417 It remains to be seen how much further APCAs will spread in the future. Although local range  
418 expansions are constantly being reported, most of them occur in Europe. Eastward dispersal into  
419 large Siberian rivers such as Ob and Yenisei is likely, as this pattern has been recently observed in  
420 pond mussels and was connected to fish stocking (Kondakov et al. 2020). The species with the most  
421 eastward occurrence are *C. curvispinum* and *D. haemobaphes*, being present in the delta of the Ille

422 River and some parts of Lake Balkhash (Petr 1992; Khassengazyeva and Mamilov 2020). Considering  
423 that these two species are also the most widespread of all Ponto-Caspian amphipods, they are the  
424 prime candidates for being detected in the large Siberian rivers in the future. However, the possibility  
425 of jump dispersal due to shipping activity make future predictions less straightforward given the  
426 apparent haphazard nature of these events (Copilaş-Ciocianu et al. 2020). Nevertheless, climatically  
427 suitable areas that may support such populations can be identified on the basis of modeling.

428

429 Our high resolution distribution data will be invaluable for modeling future distributions and  
430 predicting future invasion pathways of APCAs (Mainali et al. 2015; but see Liu et al. 2020). This is  
431 especially critical under future climate warming scenarios (Zhang et al. 2020). Predicting which  
432 invasive species will spread further and which native species will go extinct or decline is of major  
433 importance for implementing adequate conservation measures (Porfirio et al. 2014). Another  
434 important aspect of our data is that it will also allow testing whether APCAs experience climatic niche  
435 shifts and/or expansions in the non-native areal relative to their native areal (Broennimann et al.  
436 2007; Guisan et al. 2014). This will be critical for assessing long-term dynamics, persistence, and  
437 adaptation of APCAs in non-native habitats.

438

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442

#### 443 **References**

- 444 Abell R, Thieme ML, Revenga C, et al (2008) Freshwater ecoregions of the world: A new map of biogeographic units for  
445 freshwater biodiversity conservation. *Bioscience* 58:403–414. <https://doi.org/10.1641/B580507>
- 446 Arbačiauskas K (2008) Amphipods of the Nemunas River and the Curonian Lagoon, the Baltic Sea basin: Where and which  
447 native freshwater amphipods persist. *Acta Zool Litu* 18:10–16. <https://doi.org/10.2478/v10043-008-0002-3>
- 448 Arbačiauskas K, Lesutiene J, Gasiunaite ZR (2013) Feeding strategies and elemental composition in Ponto-Caspian  
449 peracaridans from contrasting environments: Can stoichiometric plasticity promote invasion success? *Freshw Biol*  
450 58:1052–1068. <https://doi.org/10.1111/fwb.12108>
- 451 Arbačiauskas K, Šidagytė E, Šniaukštaitė V, Lesutienė J (2017) Range expansion of Ponto-Caspian peracaridan Crustaceans in  
452 the Baltic Sea basin and its aftermath: Lessons from Lithuania. *Aquat Ecosyst Heal Manag* 20:393–401.  
453 <https://doi.org/10.1080/14634988.2017.1328229>
- 454 Arbačiauskas K, Višinskienė G, Smilgevičienė S, Rakauskas V (2011) Non-indigenous macroinvertebrate species in Lithuanian  
455 fresh waters, Part 1: Distributions, dispersal and future. *Knowl Manag Aquat Ecosyst* 402:12.  
456 <https://doi.org/10.1051/kmae/2011076>
- 457 Audzijonyte A, Daneliya ME, Väinölä R (2006) Comparative phylogeography of Ponto-Caspian mysid crustaceans: Isolation  
458 and exchange among dynamic inland sea basins. *Mol Ecol* 15:2969–2984. <https://doi.org/10.1111/j.1365-294X.2006.03018.x>
- 460 Bacela-Spychalska K, Van Der Velde G (2013) There is more than one “killer shrimp”: Trophic positions and predatory  
461 abilities of invasive amphipods of Ponto-Caspian origin. *Freshw Biol* 58:730–741. <https://doi.org/10.1111/fwb.12078>
- 462 Barnard JL, Barnard CM (1983) *Freshwater Amphipoda of the World*. Hayfield Associates, Mt. Vernon, Virginia
- 463 Bij de Vaate A, Jazdzewski K, Ketelaars HAM, et al (2002) Geographical patterns in range extension of Ponto-Caspian  
464 macroinvertebrate species in Europe. *Can J Fish Aquat Sci* 59:1159–1174. <https://doi.org/10.1139/f02-098>
- 465 Bollache L, Devin S, Wattier R, et al (2004) Rapid range extension of the Ponto-Caspian amphipod *Dikerogammarus villosus*  
466 in France: Potential consequences. *Arch fur Hydrobiol* 160:57–66. <https://doi.org/10.1127/0003-9136/2004/0160-0057>
- 467
- 468 Borza P (2011) Revision of invasion history, distributional patterns, and new records of Corophiidae (Crustacea: Amphipoda)  
469 in Hungary. *Acta Zool Acad Sci Hungaricae* 57:75–84
- 470 Borza P, Csányi B, Huber T, et al (2015) Longitudinal distributional patterns of Peracarida (Crustacea, Malacostraca) in the  
471 River Danube. *Fundam Appl Limnol / Arch für Hydrobiol* 187:113–126. <https://doi.org/10.1127/fal/2015/0769>
- 472 Borza P, Huber T, Leitner P, et al (2017) Success factors and future prospects of Ponto-Caspian peracarid (Crustacea:  
473 Malacostraca) invasions: Is ‘the worst over’? *Biol Invasions* 19:1517–1532. <https://doi.org/10.1007/s10530-017-1375-7>
- 474
- 475 Borza P, Huber T, Leitner P, et al (2018) How to coexist with the ‘killer shrimp’ *Dikerogammarus villosus*? Lessons from

- 476 other invasive Ponto-Caspian peracarids. *Aquat Conserv Mar Freshw Ecosyst* 28:1441–1450.  
477 <https://doi.org/10.1002/aqc.2985>
- 478 Broennimann O, Treier UA, Müller-Schärer H, et al (2007) Evidence of climatic niche shift during biological invasion. *Ecol*  
479 *Lett* 10:701–709. <https://doi.org/10.1111/j.1461-0248.2007.01060.x>
- 480 Cărăușu S (1943) Amphipodes de Roumanie I. Gammarides de type Caspian. Institutul de Cercetari Piscicole al Romaniei,  
481 Bucharest
- 482 Copilaș-Ciocianu D, Arbačiauskas K (2018) First record of *Dikerogammarus bispinosus* Martynov, 1925 in Kazakhstan:  
483 invasive or overlooked native in the Caspian Sea basin? *Biol Invasions Rec* 7:285–291.  
484 <https://doi.org/10.3391/bir.2018.7.3.09>
- 485 Copilaș-Ciocianu D, Berchi GM, Mumladze L (2020) First survey of shallow-water Amphipoda along the Georgian Black Sea  
486 coast reveals new faunistic records and the unexpected Atlantic invader *Melita nitida*. *Mediterr Mar Sci* 21:460–463.  
487 <https://doi.org/10.12681/mms.22844>
- 488 Copilaș-Ciocianu D, Borko Š, Fišer C (2020) The late blooming amphipods: Global change promoted post-Jurassic ecological  
489 radiation despite Palaeozoic origin. *Mol Phylogenet Evol* 143:106664. <https://doi.org/10.1016/j.ympev.2019.106664>
- 490 Copilaș-Ciocianu D, Sidorov D (2021) Taxonomic, ecological and morphological diversity of Ponto-Caspian gammaridean  
491 amphipods: a review. *bioRxiv* 1–36. <https://doi.org/10.1101/2021.01.21.427559>
- 492 Courchamp F, Hulme P, Pyšek P (2020) Invasion biology and uncertainty in native range definitions: response to Pereyra  
493 2019. *Conserv Biol* 34:1041–1043. <https://doi.org/10.1111/cobi.13528>
- 494 Crawford GI (1935) *Corophium curvispinum* G.O. Sars var. *devium* Wundsch, in England. *Nat* 136:685
- 495 Cristescu MEA, Witt JDS, Grigorovich IA, et al (2004) Dispersal of the Ponto-Caspian amphipod *Echinogammarus ischnus*:  
496 invasion waves from the Pleistocene to the present. *Heredity (Edinb)* 92:197–203.  
497 <https://doi.org/10.1038/sj.hdy.6800395>
- 498 Csabai Z, Borza P, Rewicz T, et al (2020) Mass appearance of the Ponto-Caspian invader *Pontogammarus robustoides* in the  
499 River Tisza catchment: Bypass in the southern invasion corridor? *Knowl Manag Aquat Ecosyst* 2020-Janua:  
500 <https://doi.org/10.1051/kmae/2020003>
- 501 Cuthbert RN, Kotronaki SG, Dick JTA, Briski E (2020) Salinity tolerance and geographical origin predict global alien amphipod  
502 invasions. *Biol Lett* 16:2–7. <https://doi.org/10.1098/rsbl.2020.0354>
- 503 Dedju II (1967) Amphipody i mizidy basseinov rek Dniestra i Pruta. Izdatelstvo “Nauka,” Moskva
- 504 Dermott R, Witt J, Um YM, González M (1998) Distribution of the ponto-caspian amphipod *Echinogammarus ischnus* in the  
505 great Lakes and replacement of native *Gammarus fasciatus*. *J Great Lakes Res* 24:442–452.  
506 [https://doi.org/10.1016/S0380-1330\(98\)70834-2](https://doi.org/10.1016/S0380-1330(98)70834-2)
- 507 Derzhavin AN (1927) Notes on the Upper Sarmatian Amphipods of the Ponto-Caspian region. *Bull Ia Soc des Nat Moscou*  
508 2:183–196
- 509 Dick JTA, Platvoet D (2000) Invading predatory crustacean *Dikerogammarus villosus* eliminates both native and exotic  
510 species. *Proc R Soc B Biol Sci* 267:977–983. <https://doi.org/10.1098/rspb.2000.1099>
- 511 Edler D, Guedes T, Zizka A, et al (2017) Infomap bioregions: Interactive mapping of biogeographical regions from species  
512 distributions. *Syst Biol* 66:197–204. <https://doi.org/10.1093/sysbio/syw087>
- 513 Gallardo B, Aldridge DC (2015) Is Great Britain heading for a Ponto-Caspian invasional meltdown? *J Appl Ecol* 52:41–49.  
514 <https://doi.org/10.1111/1365-2664.12348>
- 515 Gogaladze A, Raes N, Biesmeijer JC, et al (2020) Social network analysis and the implications for Pontocaspian biodiversity  
516 conservation in Romania and Ukraine: A comparative study. *PLoS One* 15:1–20.  
517 <https://doi.org/10.1371/journal.pone.0221833>
- 518 Grabowski M, Bacela K, Konopacka A (2007) How to be an invasive gammarid (Amphipoda: Gammaroidea) - Comparison of  
519 life history traits. *Hydrobiologia* 590:75–84. <https://doi.org/10.1007/s10750-007-0759-6>
- 520 Grabowski M, Bacela K, Konopacka A, Jazdzewski K (2009) Salinity-related distribution of alien amphipods in rivers provides  
521 refugia for native species. *Biol Invasions* 11:2107–2117. <https://doi.org/10.1007/s10530-009-9502-8>
- 522 Grigorovich IA, Maclsaac HJ, Shadrin N V, Mills EL (2002) Patterns and mechanisms of aquatic invertebrate introductions in  
523 the Ponto-Caspian region. *Can J Fish Aquat Sci* 59:1189–1208. <https://doi.org/10.1139/f02-088>
- 524 Grigorovich IA, Therriault TW, Maclsaac HJ (2003) History of aquatic invertebrate invasions in the Caspian Sea. *Biol*  
525 *Invasions* 5:103–115. <https://doi.org/10.1023/A:1024050824073>
- 526 Grudule N, Parele E, Arbačiauskas K (2007) Distribution of Ponto-Caspian amphipod *Pontogammarus robustoides* in Latvian  
527 waters. *Acta Zool Litu* 17:28–32. <https://doi.org/10.1080/13921657.2007.10512812>
- 528 Guisan A, Petitpierre B, Broennimann O, et al (2014) Unifying niche shift studies: Insights from biological invasions. *Trends*  
529 *Ecol Evol* 29:260–269. <https://doi.org/10.1016/j.tree.2014.02.009>
- 530 Hammer Ø, Harper DAT, Ryan PD (2001) PAST: paleontological statistic software package for education and data analysis.  
531 *Palaeontol Electron* 4:1–9
- 532 Hesselschwerdt J, Meeker J, Wantzen KM (2008) Gammarids in Lake Constance: Habitat segregation between the invasive  
533 *Dikerogammarus villosus* and the indigenous *Gammarus roeselii*. *Fundam Appl Limnol* 173:177–186.  
534 <https://doi.org/10.1127/1863-9135/2008/0173-0177>
- 535 Hou Z, Sket B (2016) A review of Gammaridae (Crustacea: Amphipoda): The family extent, its evolutionary history, and  
536 taxonomic redefinition of genera. *Zool J Linn Soc* 176:323–348. <https://doi.org/10.1111/zoj.12318>
- 537 Hou Z, Sket B, Li S (2014) Phylogenetic analyses of Gammaridae crustacean reveal different diversification patterns among  
538 sister lineages in the Tethyan region. *Cladistics* 30:352–365. <https://doi.org/10.1111/cla.12055>



- 539 Ioffe TI (1973) Pool for acclimatization of invertebrates in the USSR. *Izv Gos Nauchno-Issled Inst Ozern Rechn Rybn Khoz*  
540 84:8–67
- 541 Jarocki J, Demianowicz A (1931) Über das Vorkommen des ponto-kaspischen Amphipoden *Chaetogammarus tenellus*  
542 (G.O.Sars) in der Wisla (Weichsel). *Bull Int Acad Pol Sci Lett, Cl Math Nat Ser B(II)* 513–530
- 543 Jażdżewska AM, Rewicz T, Mamos T, et al (2020) Cryptic diversity and mtDNA phylogeography of the invasive demon  
544 shrimp, *Dikerogammarus haemobaphes* (Eichwald, 1841), in Europe. *NeoBiota* 57:53–86.  
545 <https://doi.org/10.3897/neobiota.57.46699>
- 546 Jazdzewski K (1980) Range extensions of some gammaridean species in European inland waters caused by human activity.  
547 *Crustaceana* 6:84–107
- 548 Jażdżewski K, Konopacka A (1988) Notes on the Gammaridean Amphipoda of the Dniester River Basin and Eastern  
549 Carpathians. In: *Proceedings of the VIth International Colloquium on Amphipod Crustaceans, Ambleteuse, France, 28*  
550 *June-3 July 1985.* pp 72–89
- 551 Jermacz Ł, Dzierżyńska A, Poznańska M, Kobak J (2015) Experimental evaluation of preferences of an invasive Ponto-Caspian  
552 gammarid *Pontogammarus robustoides* (Amphipoda, Gammaroidea) for mineral and plant substrata. *Hydrobiologia*  
553 746:209–221. <https://doi.org/10.1007/s10750-014-1963-9>
- 554 Karaman GS, Barnard JL (1979) Classificatory Revisions In Gammaridean Amphipoda Crustacea 1. *Proc Biol Soc Washingt*  
555 92:106–165
- 556 Khassengaziyeva GK, Mamilov NS (2020) Diversity of hydrobionts in delta of the Ile river in changing human impact. *Vestn*  
557 *Kazn Ser Ekol* 1:78–86
- 558 Kondakov A V., Bespalaya Y V., Vikhrev I V., et al (2020) The Asian pond mussels rapidly colonize russia: Successful invasions  
559 of two cryptic species to the Volga and Ob rivers. *BiolInvasions Rec* 9:504–518.  
560 <https://doi.org/10.3391/bir.2020.9.3.07>
- 561 Konopacka A, Hupało K, Rewicz T, Grabowski M (2014) Species inventory and distribution patterns of freshwater amphipods  
562 in Moldova. *North West J Zool* 10:382–392
- 563 Krijgsman W, Tesakov A, Yanina T, et al (2019) Quaternary time scales for the Pontocaspian domain: Interbasinal  
564 connectivity and faunal evolution. *Earth-Science Rev* 188:1–40. <https://doi.org/10.1016/j.earscirev.2018.10.013>
- 565 Kurina EM (2020) Specific Features of Distribution of Alien Species of Macrozoobenthos in the Bays of Reservoirs (by  
566 Example of Water Bodies of the Middle and Lower Volga Basins). *Russ J Biol Invasions* 11:118–125.  
567 <https://doi.org/10.1134/S2075111720020058>
- 568 Laffan SW, Lubarsky E, Rosauer DF (2010) Biodiverse, a tool for the spatial analysis of biological and related diversity.  
569 *Ecography (Cop)* 33:643–647. <https://doi.org/10.1111/j.1600-0587.2010.06237.x>
- 570 Lipinskaya T, Makaranka A, Razlutskiy V, Semenchenko V (2021) First records of the alien amphipod *Dikerogammarus*  
571 *haemobaphes* (Eichwald, 1841) in the Neman River basin (Belarus). *BiolInvasions Rec* 10:319–325
- 572 Liu C, Wolter C, Xian W, Jeschke JM (2020) Species distribution models have limited spatial transferability for invasive  
573 species. *Ecol Lett* 23:1682–1692. <https://doi.org/10.1111/ele.13577>
- 574 MacNeil C, Platvoet D, Dick JTA, et al (2010) The Ponto-Caspian “killer shrimp”, *Dikerogammarus villosus* (Sowinsky, 1894),  
575 invades the British Isles. *Aquat Invasions* 5:441–445. <https://doi.org/10.3391/ai.2010.5.4.15>
- 576 Mainali KP, Warren DL, Dhileepan K, et al (2015) Projecting future expansion of invasive species: Comparing and improving  
577 methodologies for species distribution modeling. *Glob Chang Biol* 21:4464–4480. <https://doi.org/10.1111/gcb.13038>
- 578 Martynov A (1932) Contribution to the knowledge of the fresh-waterfauna of the Black Sea coast of Caucasus. I.  
579 Amphipoda. *Trav l’Institut Zool l’Academie des Seiences l’URSS* 1:73–98
- 580 Meßner U, Zettler ML (2018) The conquest (and avoidance?) of the brackish environment by Ponto-Caspian amphipods: A  
581 case study of the German Baltic Sea. *BiolInvasions Rec* 7:269–278. <https://doi.org/10.3391/bir.2018.7.3.07>
- 582 Minchin D, Arbačiauskas K, Daunys D, et al (2019) Rapid expansion and facilitating factors of the Ponto-Caspian invader  
583 *dikerogammarus villosus* within the Eastern Baltic sea. *Aquat Invasions* 14:165–181.  
584 <https://doi.org/10.3391/ai.2019.14.2.02>
- 585 Moedt S, Van Haaren T (2018) *Pontogammarus robustoides* (Sars, 1894), a new non-indigenous amphipod in the  
586 Netherlands (Crustacea: Amphipoda). *Lauterbornia* 85:123–126
- 587 Mordukhai-Boltovskoi (1964) Caspian Fauna Beyond the Caspian Sea. *Int Rev der gesamten Hydrobiol und Hydrogr* 49:139–  
588 176. <https://doi.org/10.1002/iroh.19640490105>
- 589 Mordukhai-Boltovskoi PD (1979) Composition and Distribution of Caspian Fauna in the Light of Modern Data. *Int Rev der*  
590 *gesamten Hydrobiol und Hydrogr* 64:1–38. <https://doi.org/10.1002/iroh.19790640102>
- 591 Nahavandi N, Ketmaier V, Plath M, Tiedemann R (2013) Diversification of Ponto-Caspian aquatic fauna: Morphology and  
592 molecules retrieve congruent evolutionary relationships in *Pontogammarus maeoticus* (Amphipoda:  
593 *Pontogammaridae*). *Mol Phylogenet Evol* 69:1063–1076. <https://doi.org/10.1016/j.ympev.2013.05.021>
- 594 Ordóñez A, Wright IJ, Olff H (2010) Functional differences between native and alien species: A global-scale comparison.  
595 *Funct Ecol* 24:1353–1361. <https://doi.org/10.1111/j.1365-2435.2010.01739.x>
- 596 Palcu DV, Patina IS, Şandric I, et al (2021) Late Miocene megalake regressions in Eurasia. *Sci Rep* 11:1–12.  
597 <https://doi.org/10.1038/s41598-021-91001-z>
- 598 Pereyra PJ (2020) Rethinking the native range concept. *Conserv Biol* 34:373–377. <https://doi.org/10.1111/cobi.13406>
- 599 Petr T (1992) Lake Balkhash, Kazakhstan. *Int J Salt Lake Res* 1:21–46. <https://doi.org/10.1007/BF02904950>
- 600 Petrescu I (2009) New mentions of amphipods (Crustacea:Amphipoda) from romanian waters of the Danube. *Trav du*  
601 *Muséum Natl d-Histotire Nat “Grigore Antipa”* 52:73–86

- 602 Petruzzellis F, Tordoni E, Tomasella M, et al (2021) Functional differentiation of invasive and native plants along a leaf  
603 efficiency/safety trade-off. *Environ Exp Bot* 188:104518. <https://doi.org/10.1016/j.envexpbot.2021.104518>
- 604 Plazzi F, Ferrucci RR, Passamonti M (2010) Phylogenetic representativeness: a new method for evaluating taxon sampling in  
605 evolutionary studies. *BMC Bioinformatics* 11:209. <https://doi.org/10.1186/1471-2105-11-209>
- 606 Porfirio LL, Harris RMB, Lefroy EC, et al (2014) Improving the use of species distribution models in conservation planning  
607 and management under climate change. *PLoS One* 9:1–21. <https://doi.org/10.1371/journal.pone.0113749>
- 608 Poznańska-Kakareko M, Lis M, Kakareko T, et al (2021) Near-shore distribution of alien ponto-caspian amphipods in a  
609 european dam reservoir in relation to substratum type and occurrence of macroinvertebrate taxa. *Knowl Manag*  
610 *Aquat Ecosyst* 2020-Janua: <https://doi.org/10.1051/kmae/2021005>
- 611 QGIS Development Team (2016) QGIS Geographic Information System. Open Source Geospatial Found. Proj.  
612 <http://www.qgis.org>
- 613 Rachalewski M, Grabowski M, Konopacka A, Bączela-Spychalska K (2013) *Echinogammarus trichiatus* (Martynov, 1932) — A  
614 new Ponto-Caspian amphipod invader in Poland with remarks on other alien amphipods from the Oder river.  
615 *Crustaceana* 86:1224–1233. <https://doi.org/10.1163/15685403-00003228>
- 616 Reid DF, Orlova MI (2002) Geological and evolutionary underpinnings for the success of Ponto-Caspian species invasions in  
617 the Baltic Sea and North American Great Lakes. *Can J Fish Aquat Sci* 59:1144–1158. <https://doi.org/10.1139/f02-099>
- 618 Rewicz T, Wattier R, Grabowski M, et al (2015) Out of the Black sea: Phylogeography of the invasive killer shrimp  
619 *Dikerogammarus villosus* across Europe. *PLoS One* 10:1–20. <https://doi.org/10.1371/journal.pone.0118121>
- 620 Seebens H, Bacher S, Blackburn TM, et al (2021) Projecting the continental accumulation of alien species through to 2050.  
621 *Glob Chang Biol* 27:970–982. <https://doi.org/10.1111/gcb.15333>
- 622 Šidagytė E, Arbačiauskas K (2016) Resistance to low oxygen in the Ponto–Caspian amphipod *Pontogammarus robustoides*  
623 varies among lentic habitats of its northern invaded range. *Limnologia* 61:7–13.  
624 <https://doi.org/10.1016/j.limno.2016.09.001>
- 625 Son MO, Prokin AA, Dubov PG, et al (2020) Caspian invaders vs. Ponto-caspian locals – range expansion of invasive  
626 macroinvertebrates from the Volga Basin results in high biological pollution of the lower Don river. *Manag Biol*  
627 *Invasions* 11:178–200. <https://doi.org/10.3391/mbi.2020.11.2.02>
- 628 Straškraba M (1969) Review of: J. J. Dedju, Amphipods and Mysids of the basins of the rivers Dniestr and Prut (systematics,  
629 ecology, zoogeographical analysis and economic importance). *Crustaceana* 17:110–112
- 630 Strayer DL (2009) Twenty years of zebra mussels: Lessons from the mollusk that made headlines. *Front Ecol Environ* 7:135–  
631 141. <https://doi.org/10.1890/080020>
- 632 Uzunova S (1999) On the biodiversity of the Ponto-Caspian Amphipoda (Crustacea) from the Bulgarian Black Sea coast. *Proc*  
633 *Inst Fish - Varna* 25:175–186
- 634 Van Riel MC, Velde G Van Der, Rajagopal S, et al (2006) Trophic relationships in the Rhine food web during invasion and  
635 after establishment of the Ponto-Caspian invader *Dikerogammarus villosus*. *Hydrobiologia* 565:39–58.  
636 <https://doi.org/10.1007/s10750-005-1904-8>
- 637 Vander Zanden MJ, Olden JD (2008) A management framework for preventing the secondary spread of aquatic invasive  
638 species. *Can J Fish Aquat Sci* 65:1512–1522. <https://doi.org/10.1139/F08-099>
- 639 Vanderploeg HA, Nalepa TF, Jude DJ, et al (2002) Dispersal and emerging ecological impacts of Ponto-Caspian species in the  
640 Laurentian Great Lakes. *Can J Fish Aquat Sci* 59:1209–1228. <https://doi.org/10.1139/f02-087>
- 641 Witt JDS, Hebert PDN, Morton WB (1997) *Echinogammarus ischnus*: Another crustacean invader in the Laurentian Great  
642 Lakes basin. *Can J Fish Aquat Sci* 54:264–268. <https://doi.org/10.1139/f96-292>
- 643 Žganec K, Gottstein S, Hudina S (2009) Ponto-Caspian amphipods in Croatian large rivers. *Aquat Invasions* 4:327–335.  
644 <https://doi.org/10.3391/ai.2009.4.2.4>
- 645 Zhang Z, Capinha C, Usio N, et al (2020) Impacts of climate change on the global potential distribution of two notorious  
646 invasive crayfishes. *Freshw Biol* 65:353–365. <https://doi.org/10.1111/fwb.13429>
- 647 Zinchenko TD, Kurina EM (2011) Distributional patterns of alien species in the open shallow areas of the Saratov Reservoir.  
648 *Russ J Biol Invasions* 2:183–190. <https://doi.org/10.1134/S2075111711030209>
- 649  
650  
651