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1 Geographic patterns in freshwater gammarid invasions: an analysis at
2 the pan-European scale

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15 **Abbreviated title** : Biogeography and invasive gammarids

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16 ABSTRACT

17 Biogeographic characteristics of freshwater gammarids at a pan-European scale were
18 investigated to describe spatial gradients of richness and their relationships with the pattern of
19 invasive species distribution. Species richness appeared to be linked to latitude and among the 25
20 European biogeographical areas, the Ponto-Caspian basin exhibited a particular position, being
21 by far the most diverse area. A link between the species richness of an area and the number of
22 invasive species coming from this area was observed, showing that rich areas are more prone to
23 shelter potential invaders than others. The patterns of gammarid dispersals among European
24 waterways suggest that, rather than a random distribution of invaders, a clump occurred in basins
25 which served as refuge areas during the last glaciations. Several reasons explaining the pattern
26 are discussed, including the possibility that among species evolving in a stimulating environment
27 some of them have had the opportunity to develop special competitive attributes.

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30 Key-words : biological invasions, amphipods, biogeography, species transfers

31 INTRODUCTION

32 Identifying potential invaders generally requires paying attention to the role of the biological and
33 ecological features of invaders in order to draw a general profile of species at risk (Williamson
34 and Fitter, 1996; Kolar and Lodge, 2001). This kind of analysis, already performed for
35 gammarids, revealed the predominant role of ecological traits (Devin and Beisel, 2007). An
36 innovative and complementary method is the investigation of geographic patterns in the
37 distribution of invasive and non-invasive species within a taxonomic group. Such a
38 biogeographical approach has already been adopted for plant invasions, with most of the focus
39 on the differences in species traits according to the donor region, or on differences between
40 native and invasive traits within a region (Pyšek et al., 2004 and references therein). To date, no
41 study has reported how the biotic context of donor areas can enhance their capacity to supply
42 invasive species. Biotic context includes characteristics such as the number of endemic species,
43 the species richness within a clade, and the latitudinal distribution.

44 In Europe, the Ponto-Caspian basin (Black, Azov, and Caspian Seas) has been identified
45 as a donor region for numerous freshwater species now found in Western Europe (bij de Vaate et
46 al., 2002; Devin et al., 2005b) and the North American Great Lakes (Ricciardi and MacIsaac,
47 2000; MacIsaac et al., 2001). The two main causes evoked are the broad salinity tolerance and
48 the potential displacement of Ponto Casopian species via important shipping traffic on several
49 particular routes (MacIsaac et al., 2001). While these two conditions contribute to explain how
50 the first two steps of the invasion process (dispersal and establishment) are completed, they are
51 not sufficient to fully explain the geographical clump of the invader origin area.

52 Among introduced freshwater species, gammarids constitute a homogenous phylogenetic
53 clade with numerous invaders. In Western Europe, non-indigenous crustaceans have met with

54 more success than other taxa (Devin et al., 2005b). The ecology of most European gammarid
55 species is well documented with recent studies devoted to the dispersal of invasive species
56 among different European basins (Jazdzewski, 1980; bij de Vaate et al., 2002; van der Velde et
57 al., 2002; Jazdzewski et al., 2004). Thus, amphipod crustaceans constitute an interesting model
58 to analyse mechanisms underlying an invasion process.

59 We investigated several biogeographic characteristics of gammarids to explore the
60 existence of spatial gradients in gammarid richness and to analyse the link between a
61 biogeographic gradient and the pattern of invasive species distribution. These points allowed us
62 to discuss whether common biogeographic features are shared by invasive gammarids and
63 potential evolutionary explanations related to these patterns.

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MATERIAL AND METHODS

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Analysis of gammarid distribution at a pan-European scale

69 The analysis of geographical gradients in Gammaridae distribution at a pan-European scale was
70 based on the 25 biogeographical areas defined by Illies (1978) in *Limnofauna Europaea* and on
71 information provided in Barnard and Barnard synthesis (1983). The number of fresh and
72 brackish water Gammaridae species within each zone was determined, excluding groundwater
73 species. Species occurring in a unique area (e.g. endemic species) were counted and reported on
74 a map showing the biogeographic areas (Fig. 1). The mean geographic coordinates of each zone
75 were determined by checking those of a point located at the graphically estimated gravity centre

76 of each area. To simplify the statistical analysis, areas positioned westward of the Greenwich
77 Meridian were noted negatively.

78 To assess whether latitudinal and longitudinal clines influence species richness in Europe,
79 linear regression analyses of species richness against latitude and longitude were performed.
80 Student t-tests allowed us to assess whether these relationships were significant.

81

82 **Origin of exotic gammarids**

83 The analysis of geographical origin of invasive gammarids within European freshwaters was also
84 based on the biogeographical zones defined by Illies (1978). Only species of European origin
85 that have moved from at least one area to another were taken into account (i.e. species
86 movements within an area were not considered). Species with a European origin that only moved
87 outside of Europe or those with an extra-European origin that invaded Europe, such as
88 *Gammarus tigrinus* Sexton, 1939 or *Gmelinoides fasciatus* Stebbing, 1899, were not considered.
89 Based on the bibliography, a list of 15 gammarid species that have moved in Europe during the
90 last 150 years was established. Once this species list was established, their geographic origin was
91 defined based on the work of Illies (1978). A linear regression between the number of species
92 within a given area and the number of exotic species that came from this area was performed. A
93 student t-test allowed us to assess whether this relationship was significant.
94 Exponential and log-linear models were tested on each scatterplot but the linear regression
95 provided the best fit to the observed data with normally distributed residuals.

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98 **Results**

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100 When plotting the number of species in each area according to their average latitude, a
101 significant latitudinal gradient appeared (Fig. 2a), showing that species richness decreased
102 significantly ($r_{\text{Pearson}} = -0.50$, $n = 25$, $p = 0.005$) from south (38° latitude) to north (69° latitude) in
103 Europe. Two areas, the Pontian province and the Caspian lowlands, defining the Ponto-Caspian
104 basin, were distinguished by a high number of species (43 and 51, respectively), 30% higher than
105 the next richest area (Iberian Peninsula with 29 species). Two corrections could be performed on
106 the dataset to validate the legacy of lineage hypothesis between species richness and latitude.
107 First, we excluded the two particular areas evoked to assess how they contribute to the latitudinal
108 gradient. The new Pearson coefficient ($r_{\text{Pearson}} = -0.63$, $n = 23$, $p < 0.001$) exceeded the value
109 previously obtained with the whole dataset. Second, we weighted the richness by the surface area
110 expressed in natural logarithm (Fig. 2b) and a significant correlation was still observed ($r_{\text{Pearson}} =$
111 -0.52 , $n = 23$, $p = 0.005$).

112 The same analyses were performed between species richness and the longitudinal data. A
113 slight but significant gradient was observed ($r_{\text{Pearson}} = 0.363$, $n = 25$, $p = 0.037$), with a small
114 decrease in species number from east (52° longitude east) to west (18° longitude west).
115 However, when we excluded the Ponto-Caspian area, the pattern was no longer significant,
116 whatever the weight applied to the richness.

117 A correlation between the number of gammarid species in an area and the number of
118 invasive species originating from this area was observed (Fig. 3; $r_{\text{Pearson}} = 0.78$, $n = 25$, $p <$
119 0.001), showing that rich areas provide more exotic species than poorly diversified areas. The
120 Ponto-Caspian basin is by far the most important European pool of invasive species.

121 Finally, the mean richness of the donor areas can be analysed versus that of the receptor
122 areas (Fig. 4), showing that invasive species come from areas where the mean richness is higher

123 than that of the invaded areas (Wilcoxon paired test, $p < 0.01$). The second panel of this figure
124 shows the same data, but takes into consideration the overlap in species composition by
125 removing, in pairwise region comparisons, species present in both regions. It shows that species
126 composition of donor and receptor areas is independent, with only a few species present in both.
127 Moreover, it confirms that donor areas are richer than receptor areas (Wilcoxon paired test, $p <$
128 0.01). To complete this approach a synthesis of the flux of gammarids in Europe (Fig. 5) was
129 performed based on several articles dealing with amphipod invasions (Jazdzewski, 1980;
130 Arbaciauskas, 2002; bij de Vaate et al., 2002; Nehring, 2002; Slynko et al., 2002; Van der Velde
131 et al., 2002; Jazdzewski et al., 2004; Devin et al., 2005a,b). It allowed us to illustrate that the
132 main invasion corridors are from east to west (Ponto-Caspian basin and Balkans to Western
133 Europe) and from south to north (Pyrenees to Northern France, Western continental Europe to
134 Ireland, Ponto-Caspian basin to Northern Europe).

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DISCUSSION

137 We found a negative correlation between species number and latitude, a robust pattern in
138 biogeography seen in the great majority of taxonomic groups (Blondel, 2000; Sax, 2001). As a
139 result, species richness decreases from south to north. Many explanations have been proposed to
140 elucidate the origins of this gradient (Blondel, 2000); a preponderant role in recent theories gives
141 to biotic interactions as the factor that regulates diversity (France, 1992). In Europe, this decrease
142 in species richness of freshwater gammarids could be linked to recent geological history of the
143 continent. During the Würm glaciation (80,000-10,000 BP), a major part of Western Europe was
144 covered by ice or in a permafrost state. Thus, at the end of this period, defaunated freshwater
145 ecosystems appeared that were recolonised by fish species that survived in refuge areas that were

146 outside of the range of ice extension (according to Oberdorff et al., 1997). The same mechanism
147 of recolonisation of defaunated ecosystems from refuge areas also occurred for
148 macroinvertebrates in Europe and in North America (France, 1992; Vainio and Väinölä, 2003).
149 The two main refuge areas in Europe were Mediterranean Europe and the Danube basin (Persat
150 and Keith, 1997). Each played a key role of a ‘living museum’ during the glacial periods and
151 thus explains the species gradient observed by the number of endemic species in each area (Fig.
152 1).

153 The Ponto-Caspian basin fits with the geographical gradient found, but is remarkable for
154 being by far the richest area in Europe for gammarid species. Remnants of the intracontinental
155 Paratethys basin, an area home to a spectacular radiation of crustaceans (Cristescu et al., 2003),
156 led Zenkevich (1963) to propose that the Caspian Sea should be called the ‘Crustacean Sea’. In
157 the Caspian Sea, adaptive radiation has occurred in many groups and endemisms at the species
158 level often reach 80% (Dumont, 2000). Endemism is so important that it rivals that of Lake
159 Baikal, where about 300 gammarid species occurred (France, 1992; Dumont, 2000) as a result of
160 a long evolutionary history without a glaciation period. The Ponto-Caspian basin is the most
161 frequent donor basin implied in freshwater invasions by gammarids as well as several other taxa
162 (Ricciardi and Macisaac, 2000; bij de Vaate et al., 2002; Reid and Orlova, 2002; Devin et al.,
163 2005b). We can therefore wonder whether the species diversity of a basin favours the emergence
164 of invasive species. The correlation between the gammarid species richness of an area and
165 invasive gammarids coming from this area confirms that invasive European gammarid species
166 underwent the majority of their evolution in areas rich in closely-related species. Nevertheless,
167 five areas exhibited particular results, and have provided few invasive gammarids to other
168 European areas compared to their richness: the Western lowlands, Iberian Peninsula, Italy,

169 Dinarian, and Hellenic Western Balkans. The low number of invaders coming from the last four
170 areas could easily be explained by their strong geographic isolation, having a low connectivity
171 with the main European waterways.

172 From a probabilistic approach, if invasive species are distributed randomly among
173 ecological areas, a larger pool of species is more likely to become invasive in highly diversified
174 area than in areas with a low number of species. Nevertheless, if a species has a broad
175 distribution range in its natural habitat area, co-occurring with many other closely-related species
176 and exploiting a broad spectrum of resources, this species possesses the attributes needed to
177 establish itself more surely in a recipient ecosystem than a specialized species narrowly
178 distributed and poorly adapted to competition. Thus, evolving in a species-rich area can lead to
179 selection, within a pool of species, for some species to acquire the attributes needed to compete
180 efficiently. This particular profile could be useful to spread among non-naïve ecosystems already
181 sheltering closely related species, while the profile of invaders will be less important for success
182 in a naïve ecosystem.

183 Our results alone did not allow us to fully determine whether the invader origins are
184 randomly distributed or related to particular competitive abilities developed in species-rich areas.
185 Our results support that invasive species come from areas where the mean richness is higher than
186 that of invaded areas. The synthesis of gammarid dispersals in Europe (Fig. 5) highlighted that
187 the main invasion corridors are unidirectional from east to west and from south to north. This
188 suggests that species invaded areas with a lower diversity, thus with a lower competition, than
189 the donor basin or, to keep the same terminology, that the recipient ecosystem is more naïve than
190 the donor. However, this pattern could be linked to asymmetrical species transfers due to current
191 trade patterns (Ricciardi and MacIsaac, 2000).

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Biotic context and invasiveness

We postulate that an environment with rich, complex assemblages of closely-related species evolving in their natural range is more likely to favour the emergence of potential invasive species. This hypothesis does not link invasiveness to species biological/ecological characteristics directly, but contributes to an understanding of reasons allowing some species to be more successful than others. We focused on the innovative assumption that species evolving in areas with a high number of closely-related species (from a taxonomic point of view) leads to selection for a set of species developing their competitive potential. This implies that such ecological areas would be more frequently identified as the native region of successfully introduced species. These areas are, more extensively, the cradles of potential exotic species even if the mechanism shaping these species is unknown. In particular, the lack of phylogeny at a large scale for European species did not allow us to test either the hypothesis of a common ancestor with singular competitive features or the phylogenetic relatedness to the native community (Darwin's naturalisation hypothesis).

From an evolutionist point of view, it can seem paradoxical that a species introduced into a new ecosystem is a better competitor than an autochthonous species having evolved in that same ecosystem. Sax and Brown (2000) proposed two patterns to demonstrate the logic of this situation. The first pattern is explained by an exotic species' pre-adaptation for altered environments and opportunities created by an absence of enemies (Keane and Crawley, 2002). The most invaded ecosystems, such as the Rhine River (Den Hartog et al., 1992) or San Francisco Bay (Cohen and Carlton, 1998), are generally disturbed environments suffering high levels of anthropogenic stress. In most estuaries and large rivers, autochthonous relic species are

215 poorly adapted, lagging behind in their evolution while their environment has continued to
216 change quickly over the last century. Due to this evolutionary anachronism, introduced species in
217 a disturbed ecosystem can easily become the best competitors. A second pattern proposed by Sax
218 and Brown (2000) is that introduced species can benefit from environmental stochasticity and a
219 global release of introduced species from pressure due to competitors, predators, parasites and
220 diseases. This view can be completed with two supplementary elements related to biogeography:
221 the positive interaction between introduced species from the same area of origin (suggested in
222 the invasional meltdown hypothesis proposed by Simberloff and Von Holle, 1999; Simberloff,
223 2006) and the advantages due to the biogeographical origin of invaders (already evoked by Sax
224 and Brown, 2000). According to our results, a species' biogeographical origin can confer a
225 particularly high potential upon it for being a competitor. A few species in a rich area could be
226 pre-adapted to compete successfully with closely-related species with different profiles (a
227 'biogeographic bonus'). As an example, a recent article (Kelly et al., 2006) described the
228 alteration of native communities by the invasive amphipod *Gammarus pulex* in Ireland. Among
229 the different mechanisms evoked, a better acquisition and assimilation of resources by the
230 invasive species than by the native *G. duebeni celticus* suggest that competition could have
231 driven the regression of the latter. Moreover, a complementary explanation might be found in the
232 fact that facilitation relationships can increase the invasion success of a group of species having
233 co-evolved in the same donor ecosystem. These positive interactions among invading species
234 have been found to be more common than previously assumed for the North American Great
235 Lakes (Ricciardi, 2001). Hence, biogeographical features such as species traits should be used in
236 the general framework of invader predictions to identify species at risk within regions at risk.
237

238 Finally, our results are in accordance with the hypothesis that the evolutionary context is an
239 element to consider as determinant to select special features of invaders, while alternative
240 explanations could be advanced (asymmetrical species transfer and random distribution of
241 invaders). The way a species evolves in a rich biota, in terms of closely-related species, needs to
242 be further investigated, to test the validity of the ‘biogeographic bonus’ hypothesis.

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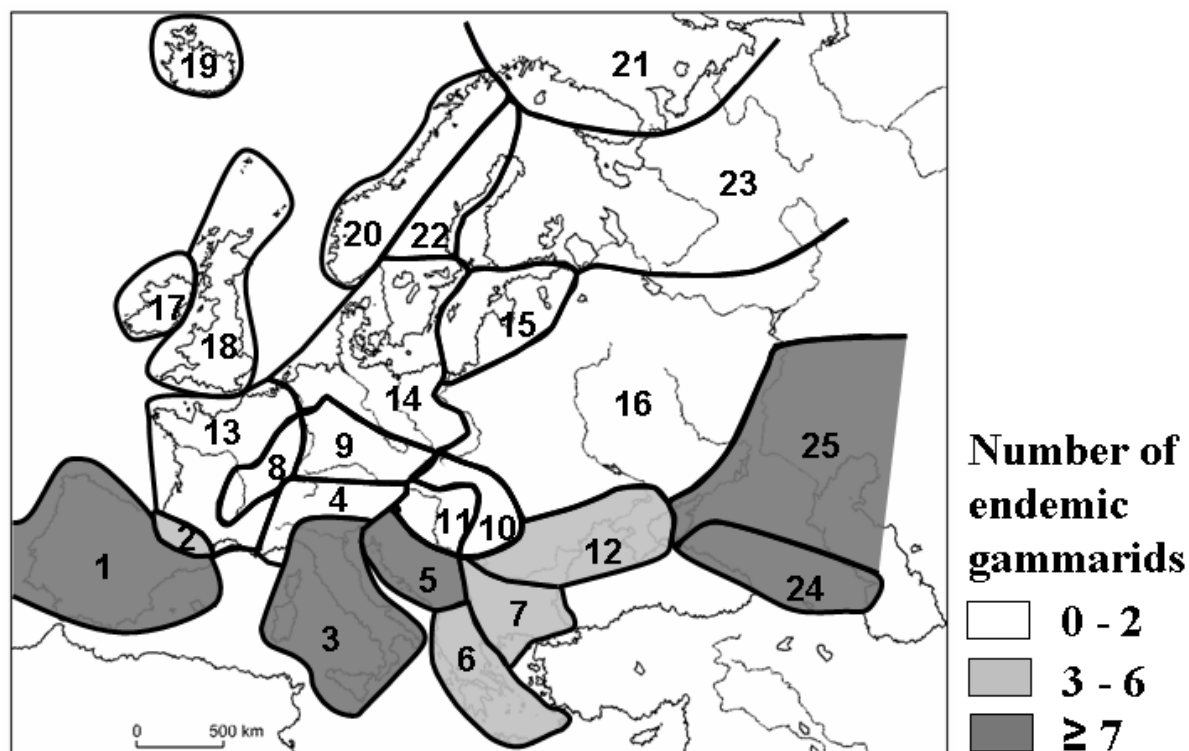
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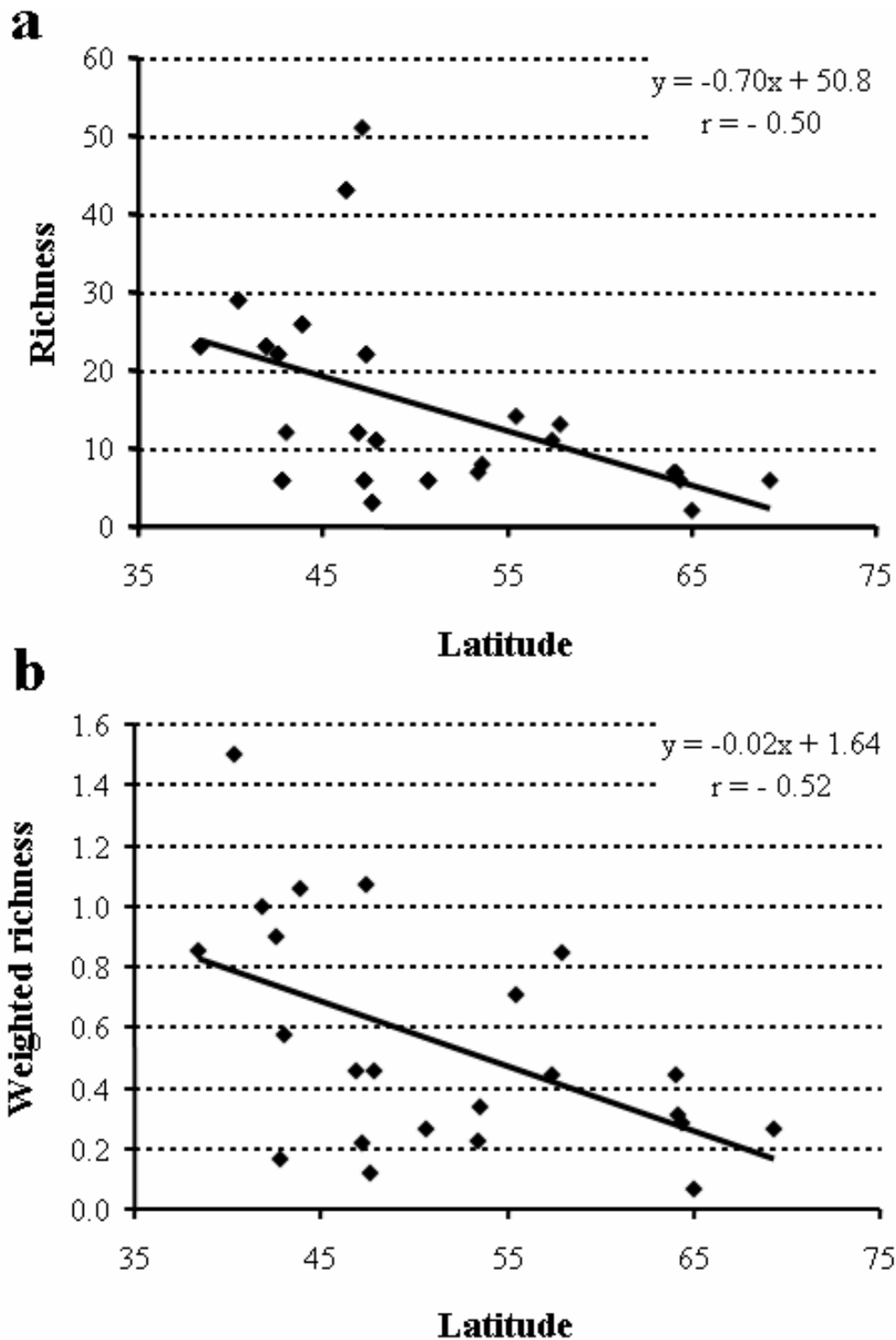
345 Figure 1: Map of the 25 European biogeographical areas, redrawn after Illies (1978). Shaded
 346 areas represent the number of endemics.

347 1: Iberian Peninsula - 2: Pyrenees - 3: Italy - 4: Alps - 5: Dianarian Westen Balkans - 6:
 348 Hellenic Western Balkans - 7: Eastern Balkans - 8: Western Sub-alpine mountains - 9: Central
 349 Sub-alpine mountains - 10: Carpathian - 11: Hungarian Plain - 12: Pontian Province - 13:
 350 Western Lowlands - 14: Central Lowlands - 15: Baltic Province - 16: Eastern Lowlands - 17:
 351 Ireland - 18: England - 19: Iceland - 20: Boreal Highlands - 21: Tundra - 22: Northern Sweden -
 352 23: Taiga - 24: Caucasus - 25: Caspian Lowlands.

353 Figure 2: Gradients of gammarid species number among the 25 biogeographical areas of Illies
 354 (1978) according to their mean latitude. (a) Raw data and (b) richness weighted by the natural
 355 logarithm of the surface area, with the exclusion of the Pontian province and Caspian lowlands.

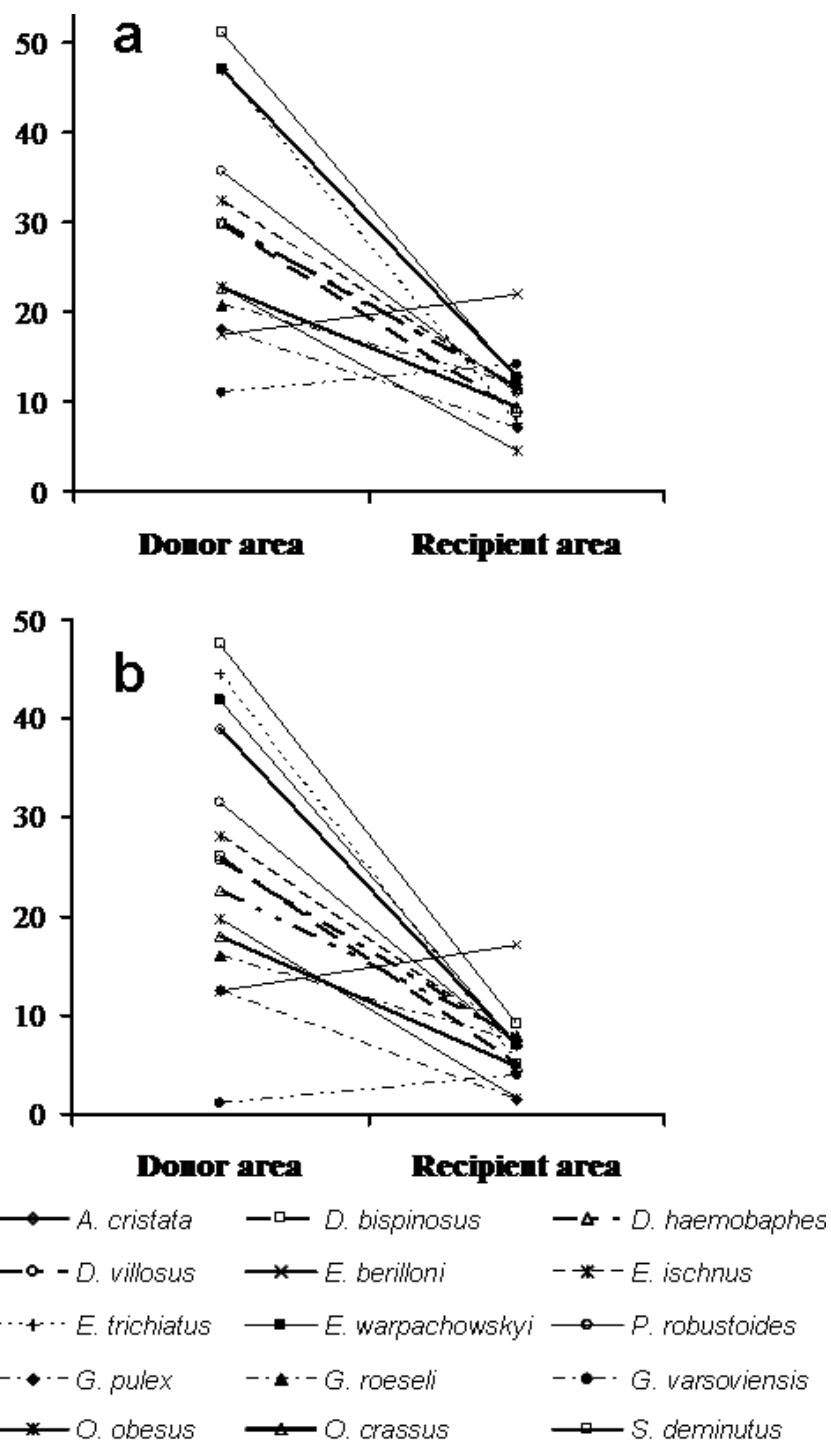
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 362 (1978) according to their mean latitude. (a) Raw data and (b) richness weighted by the natural
 363 logarithm of the surface area, with the exclusion of the Pontian province and Caspian lowlands.

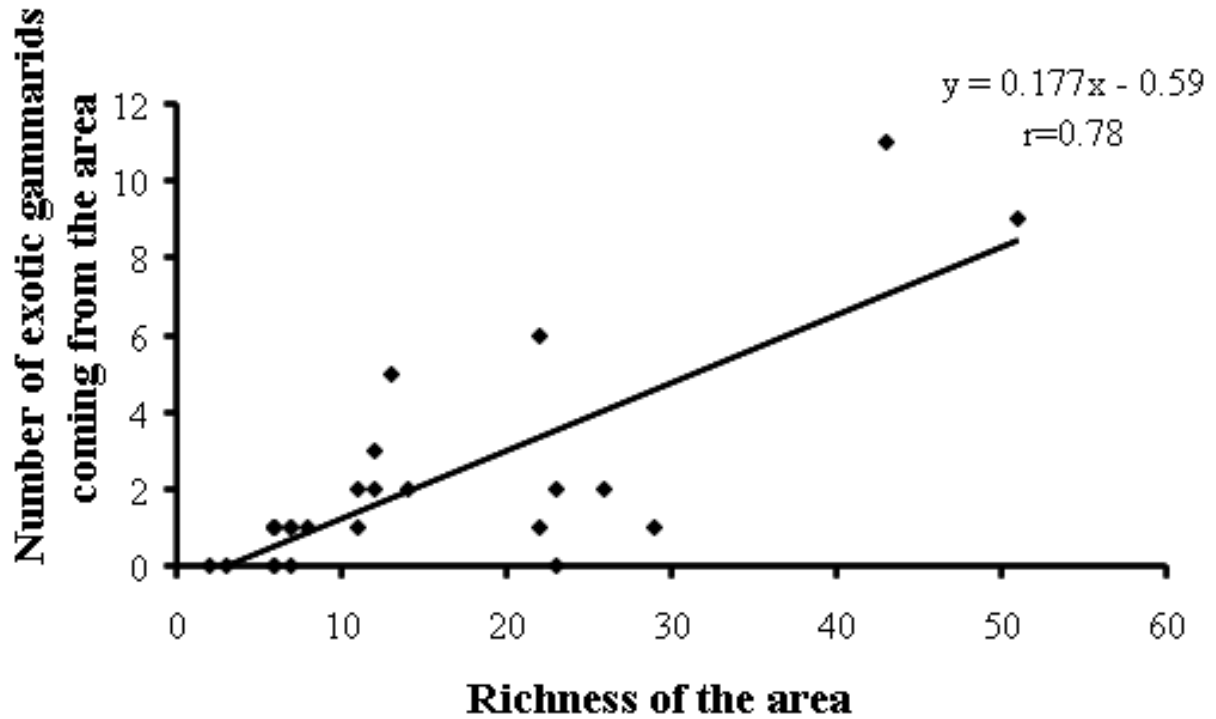


364

365

366 Figure 3: Relationship linking the total number of gammarid species in an area to the number of
 367 exotic gammarid species coming from this area.

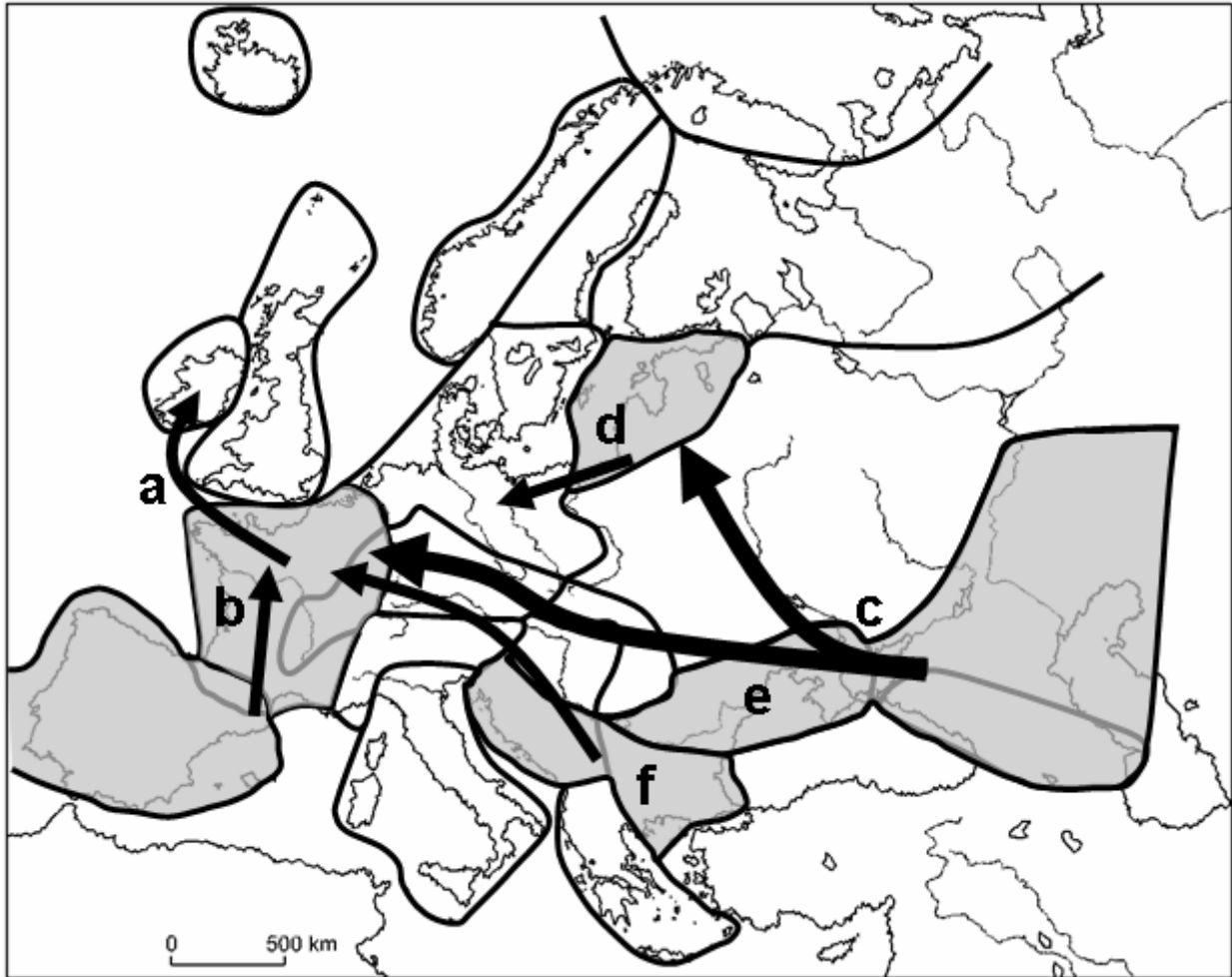
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370 Figure 4: Mean richness of the donor and receptor areas for the 15 gammarid species that moved
 371 inside Europe. (a) Raw data. *D. haemobaphes* and *D. villosus* curves are merged, as well as those
 372 for *E. warpachowski* and *A. cristata* (b) species richness once species present in both donor and
 373 recipient areas were removed.

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376

377 Figure 5: Main flux of gammarid species in Europe according to a bibliographic review (see text
 378 for references and Barnard and Barnard 1983 for species authorities).

379 South – North transfers. a: *Gammarus pulex*; b: *Echinogammarus berilloni*; c: *Amathillina*
 380 *cristata*, *Dikerogammarus haemobaphes*, *D. villosus*, *E. ischnus*, *E. warpachowskyi*,
 381 *Obesogammarus crassus*, *Pontogammarus robustoides*, *Stenogammarus deminutus*.

382 East – West transfers. d: *Gammarus varsoviensis*; e: *Dikerogammarus haemobaphes*, *D. villosus*,
 383 *D. bispinosus*, *Echinogammarus ischnus*, *E. trichiatus*, *E. warpachowskyi*, *Obesogammarus*
 384 *crassus*, *O. obesus*, *Pontogammarus robustoides*; f: *Gammarus roeseli*.