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

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ABSTRACT

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

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

INTRODUCTION

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

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

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

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

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

MATERIAL AND METHODS

Analysis of gammarid distribution at a pan-European scale

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

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

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

Origin of exotic gammarids

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

Results

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

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

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

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

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

DISCUSSION

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

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

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

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

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

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

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

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

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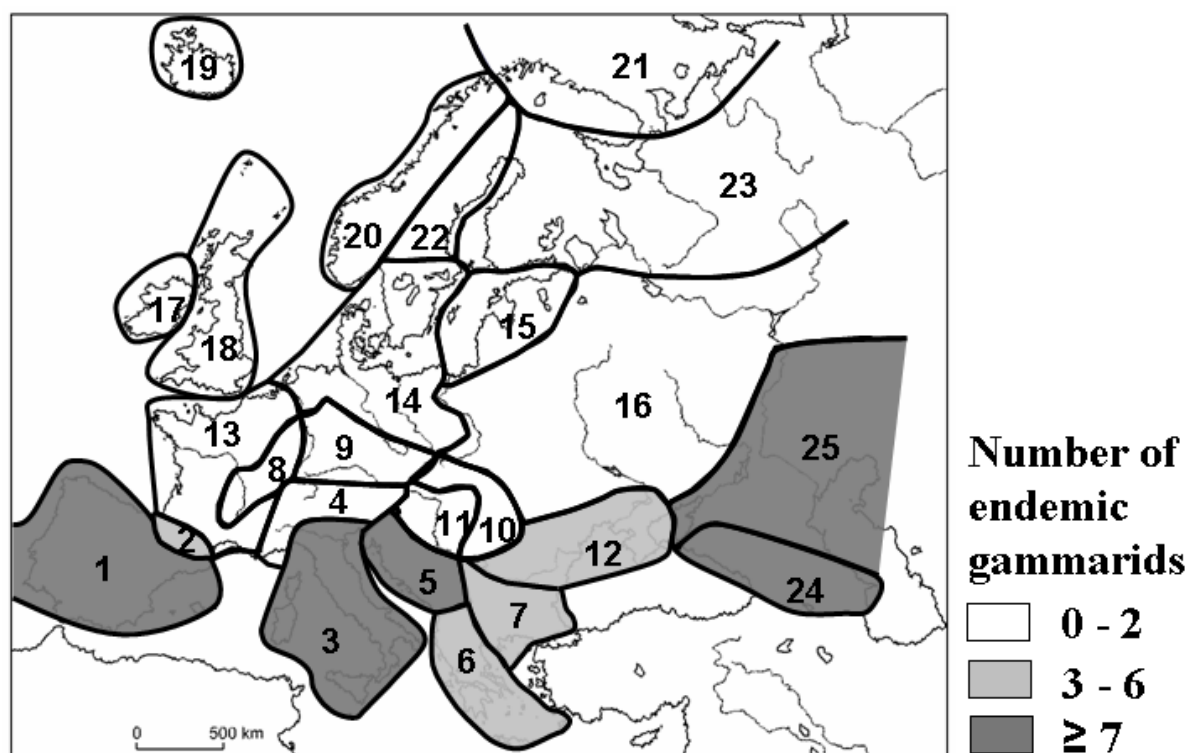
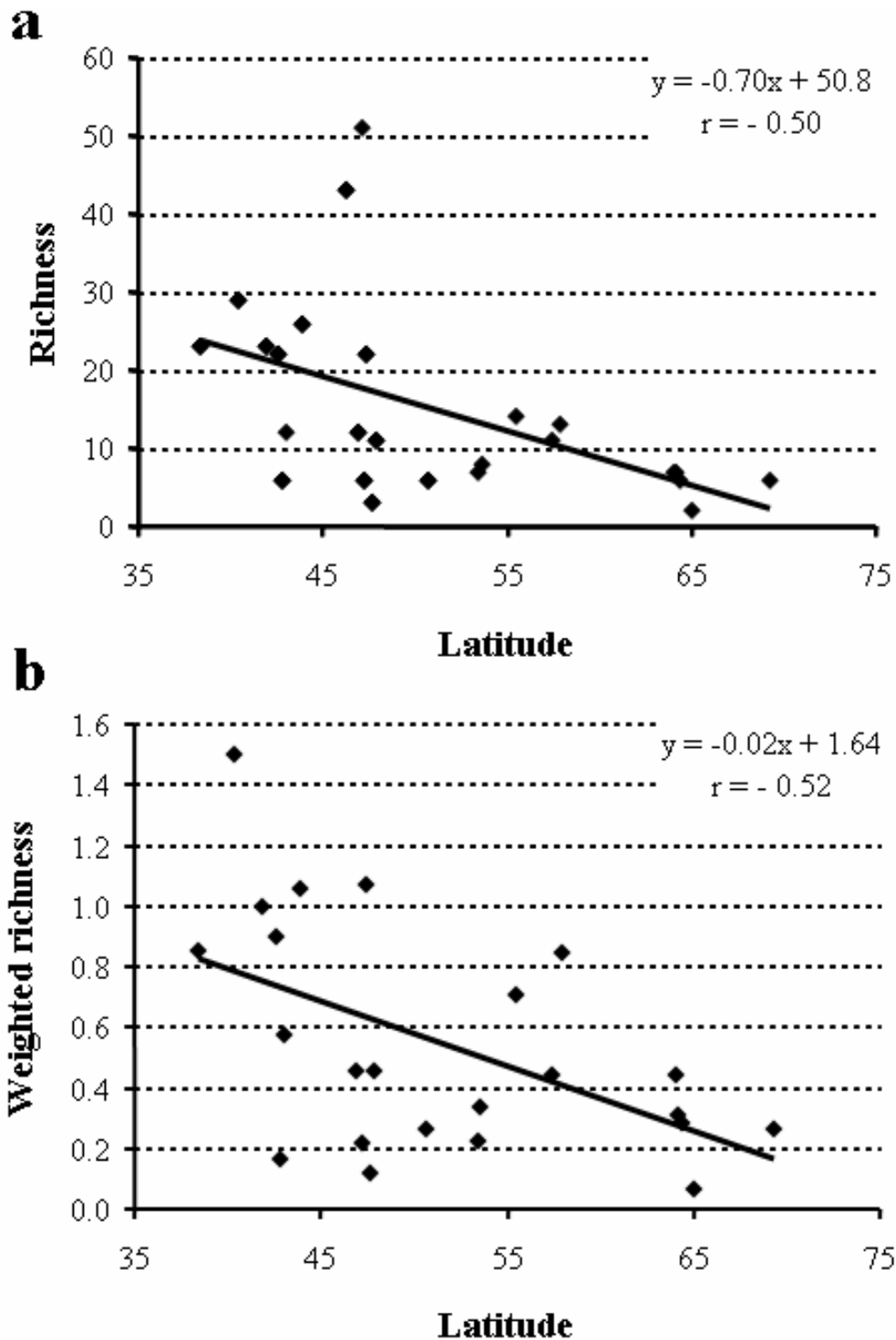


Figure 1: Map of the 25 European biogeographical areas, redrawn after Illies (1978). Shaded areas represent the number of endemics.

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

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

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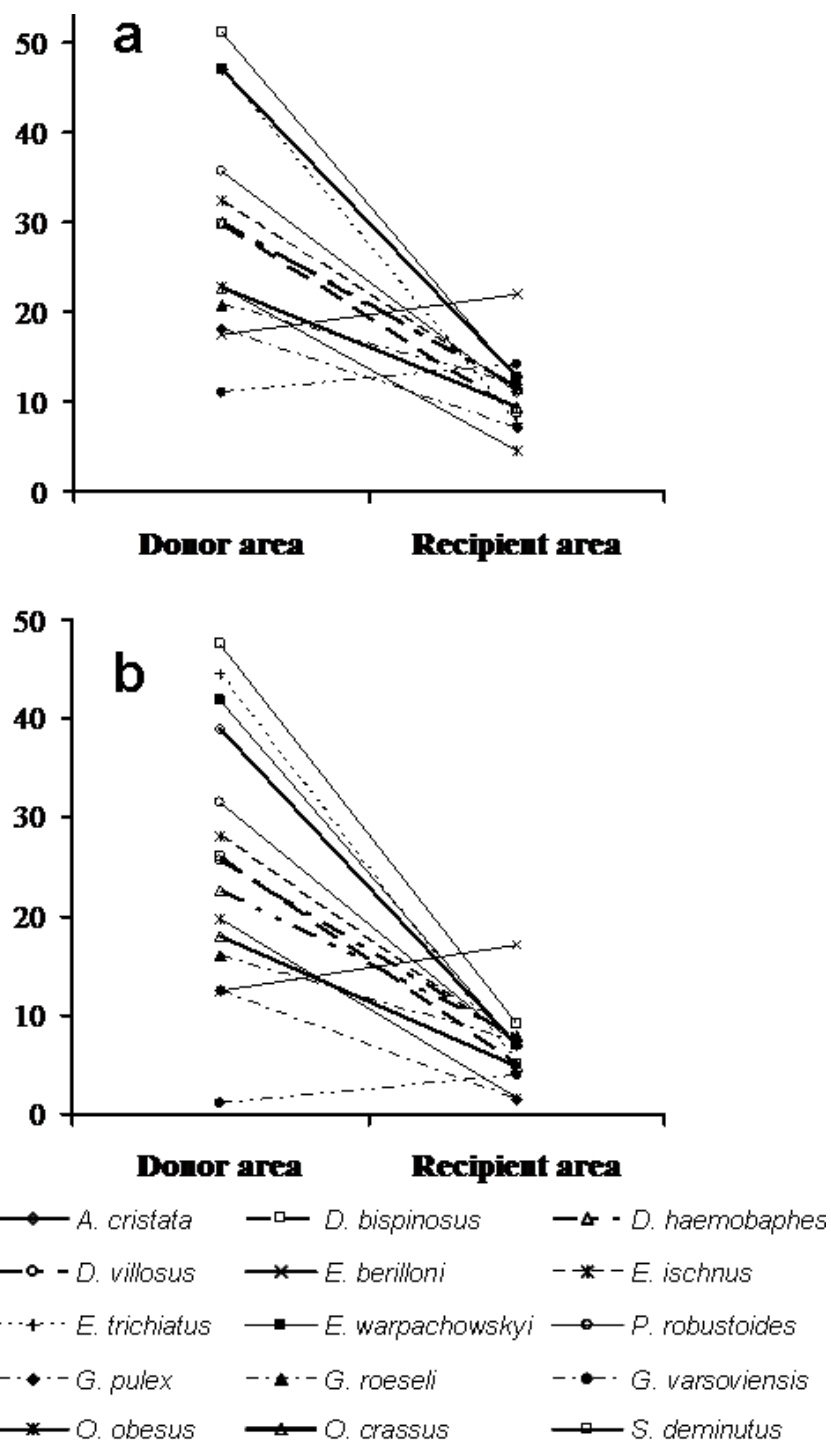
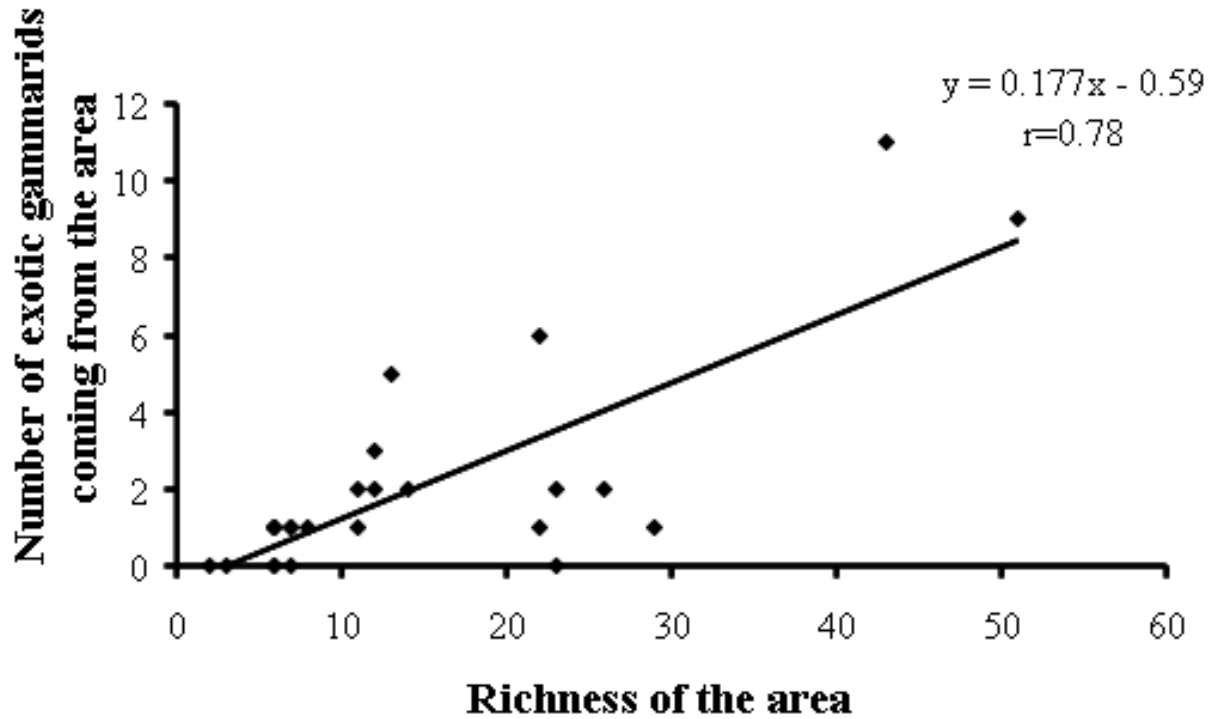


Figure 3: Relationship linking the total number of gammarid species in an area to the number of exotic gammarid species coming from this area.



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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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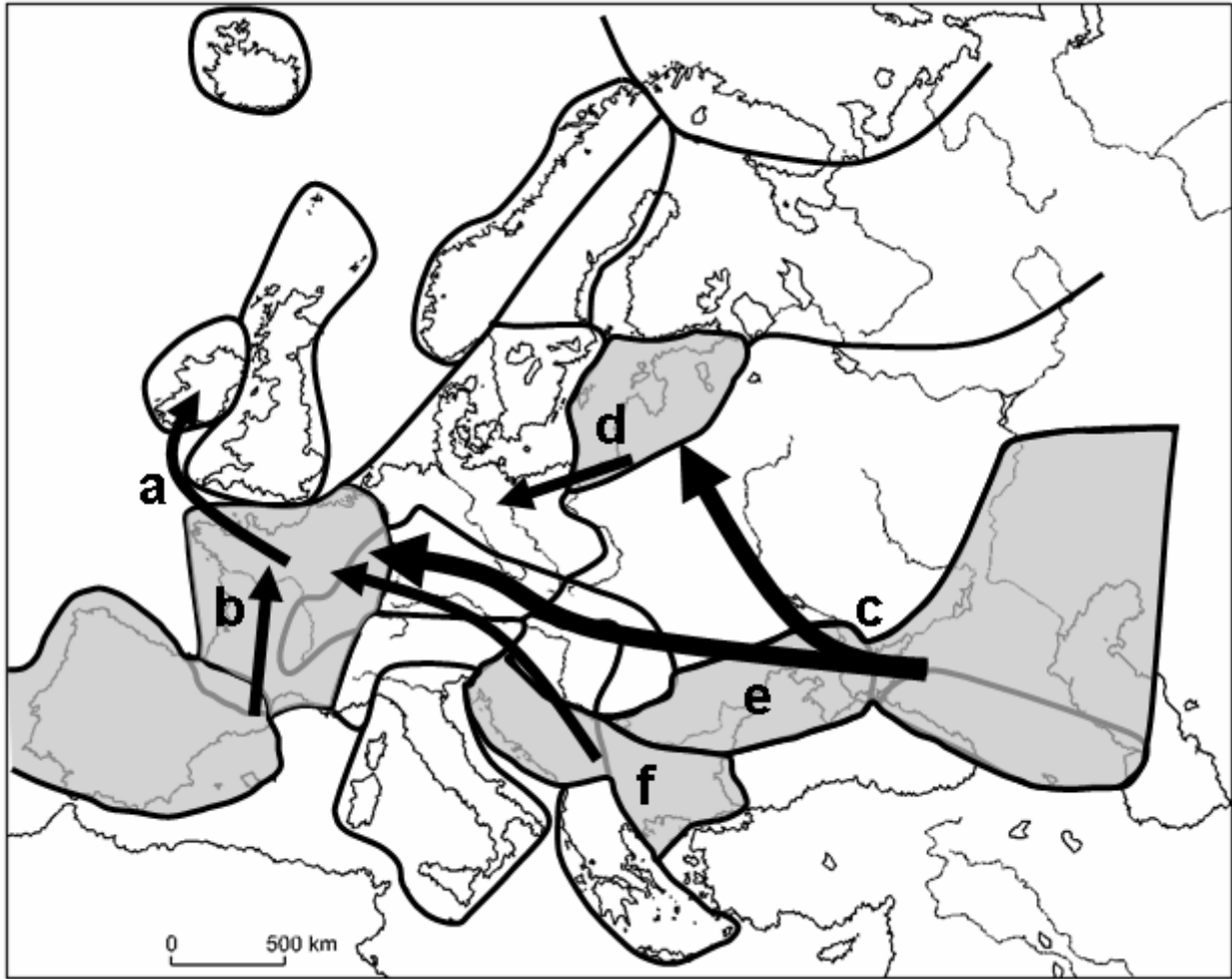


Figure 5: Main flux of gammarid species in Europe according to a bibliographic review (see text for references and Barnard and Barnard 1983 for species authorities).

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

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