Specialization among amphipods: the invasive *Gammarus tigrinus* has narrower niche space compared to native gammarids

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Abstract.   Human-mediated invasions of nonindigenous species are modifying global biodiversity. Despite significant interest in the topic, niche separation and specialization of invasive and closely related native sympatric species are not well understood. It is expected that combined use of various methods may reveal different aspects of niche space and provide stronger evidence for niche partitioning as compared to a single method. We applied the species marginality index (OMI) and species distribution modeling (SDM) in the northern Baltic Proper to determine (1) if environmental niche spaces at habitat scale differ between taxonomically and functionally closely related invasive and native gammarid species, and (2) whether the observed pattern relates to the species distribution overlap. Both methods agreed in notably narrower and more segregated realized niche of invasive *Gammarus tigrinus* compared to the studied native gammarids. Among native species, the distribution of *G. zaddachi* overlapped the most with *G. tigrinus*. Our results confirm that widespread colonization does not require a wide niche of the colonizer, but may rather be a function of other biological traits and/or the saturation of the recipient ecosystem. The niche divergence and wider environmental niche space of native species are likely to safeguard their existence in habitats less suitable for *G. tigrinus*.

Key words: Baltic Sea; environmental niche space; *Gammarus tigrinus*; habitat specialization; nonindigenous species; species distribution modeling.

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INTRODUCTION

Invasions of nonindigenous species (NIS) are considered among the most serious threats to global biodiversity (Costello et al. 2010). When establishing in the recipient ecosystem, NIS may cause significant, unpredictable and irreversible changes to abiotic and biotic environment as well as result in severe economic damage in a variety of waterbodies worldwide (e.g., Carlton 1996, Vitousek et al. 1997, Sala et al. 2000). Despite of their importance, the knowledge on the extent to which NIS actually affect biodiversity and species co-existence is still vague (Gurevitch and Padilla 2004, McGill et al. 2015).

Much of ecological theory predicts that species differ in their niches. It has been speculated that sympatric populations of taxonomically closely related species rely on niche separation to reduce competition pressure that, in turn, facilitates long term co-existence (Schoener 1974, Pianka 1978, Fenchel and Kolding 1979, Kolding 1981). The outcome of this niche difference is that species limit their own populations more than they limit others or that niche separation causes intraspecific effects to be more negative than interspecific effects (Chesson 2000). However, there exists an alternative theory that all species are identical in their fitness and in their effects on one another, thus the primary driver of population dynamics

is random variation in births, deaths, and dispersal (Bell 2000, Hubbell 2001). Based on this theory, high diversity can occur if extinction rates are slow enough to be balanced by speciation.

Surprisingly, very few studies have successfully quantified the importance of either mechanism (functional difference among species vs. demographic stochasticity and dispersal limitation) for maintaining the diversity we observe in natural communities. Though, classic views of community saturation have been challenged by recent mass invasions (Sax et al. 2007), and the apparent "unsaturation" of communities may indicate our lack of knowledge on basic assembly rules of ecological systems. Many alternative views have been developed in order to take the first steps toward a generic theory of how species niche space and species invasiveness are related. Some authors have shown that successful invaders are expected to have broad environmental tolerance or a wide environmental niche space (Marvier et al. 2004). Even more, mass invasions have provided evidence that invasive species can adapt to the recipient environment and quickly widen their niche space (Dlugosch and Parker 2008), possibly due to the lack of enemies in the recipient environment (Callaway and Ridenour 2004). Other authors have shown that coexistence is supported by niche differentiation and only those invasive species that are different from natives are able to establish successfully (Strauss et al. 2006). Such niche separation between invasive and native species has been confirmed over a few environmental gradients (e.g., Priddis et al. 2009) and the widening of niche in this context may indicate niche separation to secure co-existence. However, there is also a diametrically opposing view that invaders that are more similar to native species should be more likely to establish as their trait characteristics allow them to succeed in the recipient environment (Duncan and Williams 2002). This has also been shown in many empirical examples (Bruno et al. 2005).

To date, studies comparing multidimensional niche overlaps of invasive and native guild members are almost lacking. It is expected though that increasing the dimensionality of models will guide us closer to ecological reality and enable a better understanding of the mechanisms and consequences of environmental change (Clark et al. 2007). Niche width is also an important concept in conservation biology, as habitat specialization has been considered an important determinant of species vulnerability to global changes, and worldwide decline in specialist species has been noticed (Clavel et al. 2011). Nevertheless, niche width has received limited attention in invasion studies (Evangelista et al. 2008).

The Baltic Sea is heavily trafficked and in terms of salinity it resembles estuarine conditions of many of the world's ports. The high dispersal connectivity for estuarine NIS between the Baltic Sea and potential donor regions yields high rates of invasion (Leppäkoski et al. 2002*a*). However, the Baltic Sea is still a relatively species-poor ecosystem due to its geological youth, and therefore represents an excellent model system to study different aspects of species invasions, including relationships with native congenerics and the recipient environment (Leppäkoski et al. 2002*b*). Several nonindigenous amphipods have been recorded in the northern Baltic Sea in recent years (Herkül et al. 2006*a*, 2009). Six sympatric species of the crustacean amphipod genus *Gammarus* are found in these brackish waters. Among them are five native gammarids: *G. zaddachi* Sexton, *G. salinus* Spooner, *G. oceanicus* Segerstråle, *G. duebeni* Liljeborg, and *G. locusta* (Linnaeus), and an invasive species *G. tigrinus* Sexton that originates from North America. *G. tigrinus* was found for the first time in the northern Baltic Sea in 2003 and its range has been continuously expanding (Grabowski et al. 2006, Herkül et al. 2006*b*, Paavola et al. 2008, Kotta et al. 2013). A notable decrease in the diversity and density of native amphipods has been observed concurrent with the invasion of *G. tigrinus* in the region (Grabowski et al. 2006, Jänes et al. 2015).

Approaches for estimating environmental niche are mainly based on either ordination methods or species distribution models (SDM) (Broennimann et al. 2012). Species distribution models (SDM) are numerical methods that relate observations of species occurrences or abundances to environmental variables (Elith and Leathwick 2009). These relationships are further used to predict species distribution across different spatial and/or temporal scales (Elith and Leathwick 2009). Unlike in the case of simple plotting of species occurrences on a map, modeled distribution maps enable assessment of (1) surface area of habitats, (2) distribution of spe-

cies in areas that were not sampled or sampled sparsely, and (3) spatial overlap of distributions of different species. In contrast, ordinations enable assessment of niche in multidimensional environmental space by constructing synthetic axes from measured environmental variables (e.g., principal component analysis, canonical correspondence analysis, outlying mean index; ter Braak and Verdonschot 1995, Dolédec et al. 2000). We used both approaches in this study to address the environmental niche separation in the case of gammarids in the northern Baltic Proper. Applying both approaches yields a more robust insight into the potential niche separation among species than applying only one approach (Broennimann et al. 2012). We are not aware of any previous studies that combine these approaches to clarify the possible niche separation between taxonomically closely related native and invasive species. To this end, improved knowledge about the connection of species distribution maps with multidimensional niche space would be a highly rewarding approach.

In this study, we asked why *G. tigrinus* is a successful invader in the north-eastern Baltic Sea, and if this could be explained by similar or divergent niche breadth when compared to native gammarids. Specifically, we addressed the following research questions by applying multivariate ordination and species distribution modeling:

(1) Do environmental niche spaces differentiate between taxonomically and functionally closely related sympatric species?
(2) Does similarity in niche space result in species distribution overlap?
(3) Are there any particular differences in the niche width and segregation between invasive and native species? Does the invasive species have wider or narrower environmental niche?

Methods

Study area

Abiotic environment.—The Baltic Sea is a tideless and brackish water body. This study was conducted in the coastal water of western Estonia, northern Baltic Proper (Fig. 1). The area is characterized by complex topography with numerous islands, islets, bays, and peninsulas. Most of the study area is very shallow with water depths seldom exceeding 25 m. Strong gradients of wave exposure and salinity exist in the area. The sea areas west of the islands Saaremaa and Hiiumaa are exposed to the open Baltic Proper and have a wave fetch of hundreds of kilometers. In contrast, the inner reaches of the bays of the mainland (e.g., Matsalu and Haapsalu bays, see Fig. 1) are very sheltered both by the mainland and by islands. Similar to wave exposure, the salinity gradient generally follows an east-west direction. Salinity reaches 7 in the westernmost study area while it falls to almost 0 in the inner parts of bays with riverine inflow in the eastern study area. Hard limestone substrate and granite boulders dominate in the most exposed areas. Different combinations of mixed sediments comprised of sand, gravel, and pebbles can be found in the mid-range of the exposure gradient. Fine sand and mud dominates in the most sheltered bays. Scattered single boulders or boulder fields can be found throughout the area in shallow waters. Regardless of the relatively small spatial extent of the study area, important environmental gradients (depth, salinity, wave exposure, seabed sediments) were well represented because of the high heterogeneity of the area that encompasses the Gulfs of Finland and Riga, the Baltic Proper, and the West Estonian Archipelago Sea.

Benthic communities.—Variability in the abiotic environment is also reflected in the structure of macrobenthic communities. Species of marine origin dominate in the areas of medium and high salinity while freshwater species dominate in the eastern bays with riverine inflow. Among algal species, the brown alga *Fucus vesiculosus* and the red alga *Furcellaria lumbricalis* are the most important perennial species on hard substrates. *F. vesiculosus* usually grows in depth of 1–4 m, whereas *F. lumbricalis* inhabits deeper areas (>4 m). Several annual and perennial filamentous green, brown, and red algae like *Ulva intestinalis*, *Cladophora glomerata*, *Pilayella littoralis*, *Ceramium tenuicorne*, *Polysiphonia* spp are very common. Many species of vascular plants are common on soft substrate: *Zostera marina*, *Stuckenia pectinata*, *Potamogeton perfoliatus*, *Zannichellia palustris*, *Myriophyllum spicatum*, *Ruppia maritima*. Charo-
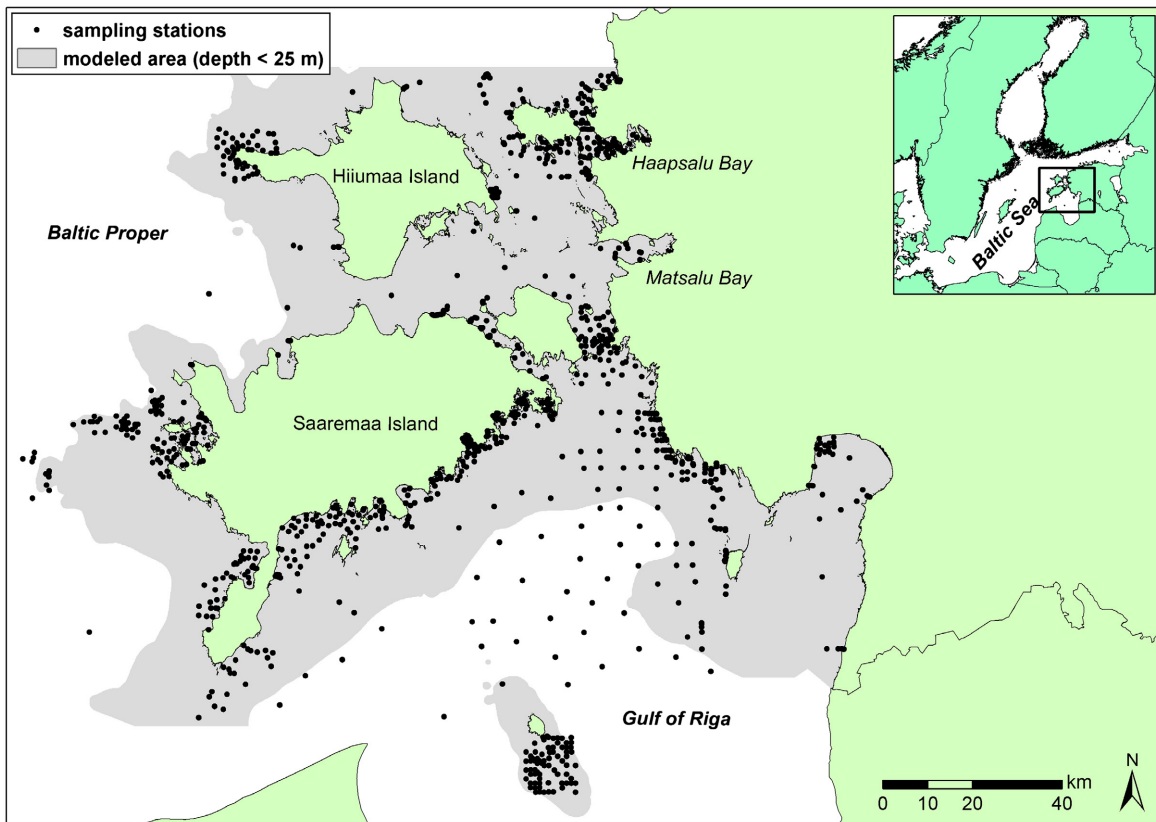
Fig. 1.   Study area and locations of sampling sites.

phytes (*Chara* spp., *Tolypella nidifica*) are common on sandy and muddy sediments in the shallow waters of the most sheltered bays. Extensive growth of ephemeral filamentous algae and formation of drift algal mats as a result of eutrophication are common phenomena in the area (Kotta et al. 2008).

Among the invertebrates, the bivalve *Mytilus trossulus* and the barnacle *Amphibalanus improvisus* prevail on hard bottoms. Gammarid amphipods, idoteid isopods, the snails *Peringia ulvae*, *Radix balthica*, and *Theodoxus fluviatilis* are common in vegetated areas. Common infaunal species in soft sediments are the bivalves *Macoma balthica* and *Cerastoderma glaucum* and polychaetes *Hediste diversicolor* and *Marenzelleria neglecta*. Various insect larvae inhabit shallow coastal areas with low salinity.

All five species of native gammarids are present in the study area but *G. duebeni* and *G. locusta* are very rare in benthic samples compared to the other native species (*G. salinus*, *G. oceanicus*,

G. zaddachi) and the nonindigenous *G. tigrinus*. Therefore, only *G. salinus*, *G. oceanicus*, *G. zaddachi*, and *G. tigrinus* were included in this study. The nonindigenous *G. tigrinus* has been common in the study area since 2006 (Herkül et al. 2009).

Benthic sampling

The macrobenthos database of the Estonian Marine Institute, University of Tartu was used as a data source on the distribution of gammarids and key phytobenthic species. Only quantitative samples from the period of 2005–2012 were used. Data were averaged when several samples were collected from the same sampling station. Samples from soft bottoms were predominantly collected using Ekman type or Van Veen type bottom grab samplers. Samples from hard substrate were collected by divers by harvesting all material inside a 20 × 20 cm metal frame. Samples were sieved through a 0.25 mm mesh and all retained material was

stored deep frozen (−18°C) until analysis. In the laboratory, all samples were sorted under a binocular microscope (20–40× magnification). All macrobenthic organisms were identified to species level except for oligochaetes, chironomids, and juveniles of gammarid amphipods (length <5 mm). Sampling and analysis followed the guidelines developed for the HELCOM COMBINE program (HELCOM 2015). The locations of sampling sites (n = 1329) are shown in Fig. 1.

Environmental niche analysis

Niche breadth and separation of habitat niche between gammarid species was assessed using analysis of outlying mean index (OMI). OMI, or species marginality, measures the distance between the mean habitat conditions used by the species (niche center), and the mean habitat conditions of the sampling area (Dolédec et al. 2000). The higher the value of the OMI index of a species, the higher is its habitat specialization. OMI analysis is a multivariate coinertia analysis that unlike canonical correspondence analysis (CCA) and redundancy analysis (RDA), can handle nonunimodal and nonlinear species–environment relationships. Compared to the traditional multivariate methods, CCA and RDA, OMI gives a more even weight to all sampling units even if they exhibit a low number of species or individuals. Thus, OMI more adequately captures the multivariate environmental space represented by sampling units (Dolédec et al. 2000). The package "ade4" (Dray and Dufour 2007) was used for running OMI analysis in the statistical software R 2.15.1 (R Core Team 2012). Occurrence (i.e., presence-absence) data of gammarids was used as a species matrix input (n = 1329). A permutation test with 9999 permutations was used to calculate the statistical significance of the values of OMI of each gammarid species. The environmental niche space of gammarid species was visualized based on a principal component analysis (PCA) ordination of sampling sites on two synthetic axes and by drawing a convex hull over the points where a given species was present. Five percent of species occurrences that were most distant from niche center were considered as outliers and were excluded when drawing the border of niche space.

Abiotic and biotic georeferenced environmental data was used for environmental niche analysis. The abiotic environmental variables included different bathymetrical (depth, slope of seabed), topographic (distance to land), hydrodynamic (wave exposure), geological (seabed substrate), and physico-chemical (temperature, salinity, transparency, ice conditions) variables. The biotic variables included chlorophyll content and modeled probability of occurrence of key phytobenthic species (*Fucus vesiculosus*, *Furcellaria lumbricalis*, and charophytes). Altogether 20 environmental variables were used that were all available as raster layers in a geographical information system (grid size 50–200 m). The full list of variables with additional information (data source) is presented in Table 1.

Species distribution models (SDM)

The same environmental variables were used in the SDMs as in the OMI analysis. The spatial distribution (probability of occurrence) of all studied gammarid species was modeled. Several candidate models were built for each species using the following algorithms: generalized additive models (GAM), random forests (RF), and boosted regression trees (BRT); descriptions of the algorithms are given below. The candidate model with the best predictive performance was chosen to produce the final distribution maps. All distribution modeling exercises were done in the statistical software R 2.15.1 (R Core Team 2012). During modeling, 80% of the input data was randomly selected and used as model training data while 20% of the data was reserved for validation. The predictive performance of the candidate models was validated by calculating the area under the receiver operating curve (AUC, Fielding and Bell 1997). Following Hosmer and Lemeshow (2000), AUC values over 0.9 indicate excellent, 0.8–0.9 very good, 0.7–0.8 satisfactory, and below 0.7 poor discriminative ability. The algorithm that produced models with the highest AUC value over all the studied species was then used to build final models for all species using 100% of the input data. The approach of selecting a single best-performing algorithm to produce the final models for all species was chosen in order to get comparable distribution predictions and to achieve a more balanced interpretation of

Table 1. Variables used in the environmental niche analysis and species distribution models. Five variables with the highest importance in the final random forest (RF) models are indicated for each gammarid species (higher rank indicates higher importance).

		Five variables with the highest importance in RF models			
Variable	Source†	*G. oceanicus*	*G. salinus*	*G. zaddachi*	*G. tigrinus*
Depth	a	4	4	2	1
Average depth in 500 m radius	a		5	3	2
Average depth in 2000 m radius	a				4
Slope of seabed	a				
Slope of seabed in 500 m radius	a	3		5	
Slope of seabed in 2000 m radius	a				
Distance to land	b				
Distance to 20 m depth isoline	b				
Proportion of soft sediment (modeled)	b	1	2	1	
Salinity	b	5			
Wave exposure	c				
Chlorophyll a content based on satellite imagery; average over 2009–2010	b				
Water transparency estimated as attenuation coefficient based on satellite imagery; average over 2010–2012	b				5
Water temperature based on satellite imagery; average over 2009–2010	b				
Number of ice days per year; average over 2009–2011	d				
Ice coverage; average over 2009–2011	d				
Ice thickness; average over 2009–2011	d				
Probability of occurrence of *Furcellaria lumbricalis* (modeled)	b		3		
Probability of occurrence of *Fucus vesiculosus* (modeled)	b	2	1	4	
Probability of occurrence of charophytes (modeled)	b				3

† Data sources: a – Bathymetric raster, developed at the Estonian Marine Institute. b – Databases of the Estonian Marine Institute. c – Wave exposure calculations for the Estonian coast (Nikolopoulos and Isæus 2008). d – Finnish Meteorological Institute.

differences in distributions. The distribution predictions were produced with 100 m grid size over a depth zone of 0-25 m (Fig. 1). The depth limitation was set because gammarid amphipods very rarely inhabit areas of greater depth.

Generalized additive models (GAM) are a semiparametric extension of generalized linear models that enables the user to fit complex non-linear relationships and handle different types of error distributions (Hastie and Tibshirani 1990). Due to these characteristics, GAM has been one of the most widely used methods for SDM (Elith et al. 2006). The package "mgcv" was used for building GAMs (Wood 2006). The models were built using penalized regression splines as the smoothing function, binomial error distribution, and automatic calculation of smoothing parameters. The maximum degree of freedom was set

to four for each variable. At first, single predictor models were built. Predictors were then added into the final model in the decreasing order of explained deviances of single variable models.

Random forests (RF) is a machine learning method that generates a large number of regression trees, each calibrated on a bootstrap sample of the original data (Breiman 2001). Each node is split using a subset of randomly selected predictors and the tree is grown to the largest possible extent without pruning. For predicting the value of a new data point, the data are run through each of the trees in the forest and each tree provides a value. The model prediction is then calculated as the average value over the predictions of all the trees in the forest (Breiman 2001). The package "party" (Hothorn et al. 2006) was used to run RF models in R. Two parameters must be set in RF models: the number of predictor variables to

be randomly selected at each node (*mtry*) and the number of trees in a forest (*ntree*). *mtry* was set to one-third of the number of predictor variables as suggested by Liaw and Wiener (2002). *ntree* was set to 1000 as 500 trees usually yield stable results (Liaw and Wiener 2002). The importance of predictor variables was assessed by using the AUC-based permutation (*n* = 1000) routine (Janitza et al. 2012) in the package "party" (Hothorn et al. 2006).

Boosted regression trees (BRT) is an ensemble method that combines the strength of two algorithms: regression trees and boosting (Elith et al. 2008). Regression trees are good at selecting relevant predictor variables and can model interactions. Boosting enables building of a large number of trees in a way that each successive tree adds small modifications in parts of the model space to fit the data better (Friedman et al. 2000). The algorithm keeps adding trees until finding the optimal number of trees that minimizes the predictive deviance of a model. The predictive performance of BRT has been shown to be superior to most other modeling methods (Elith et al. 2006, Revermann et al. 2012). The BRT modeling was performed using packages "gbm" (Ridgeway 2012) and "dismo" (Hijmans et al. 2012). Important parameters in building BRT models are learning rate, tree complexity, and bag fraction (Elith et al. 2008). Learning rate determines the contribution of each tree to the growing model and tree complexity defines the depth of interactions allowed in a model. Bag fraction determines the proportion of data to be selected randomly at each iteration. Different combinations of these parameters may yield variable predictive performance but generally a lower learning rate and inclusion of interactions gives better results. For each species, two groups of BRT models were built that had tree complexity of 1 and 5, respectively. A tree complexity of 1 fits a model without interactions between predictors while a tree complexity of 5 fits a model with up to five-way interactions. In both groups, models with learning rates of 0.0001, 0.0005, 0.001, 0.005, 0.01, 0.05, and 0.1 were built. The bag fraction was set at 0.5 which is the recommended default value for presence–absence models (Elith et al. 2008). This design resulted in 14 models for each species.

Schoener's D was used to assess the overlaps of distributions of gammarid species based on the results of SDMs. There are many metrics for measuring the distribution overlap but Schoener's D was chosen because of its simplicity, long history of use and good performance (Warren et al. 2008, Rödder and Engler 2011). Schoener's D varies between zero and one. Zero indicates no overlap while one indicates full distribution overlap between species.

RESULTS

Environmental niche analysis

According to OMI analysis, *G. salinus* had the largest environmental niche space followed by *G. zaddachi*, *G. oceanicus*, and *G. tigrinus*. The niche space of invasive *G. tigrinus* was notably smaller than that of the native species *G. salinus* and *G. zaddachi* (Fig. 2). The centers of niche positions of native species almost coincided while that of *G. tigrinus* laid notably farther apart (Fig. 2). Based on the values of OMI, *G. tigrinus* had the highest habitat specialization among the studied gammarid species, whereas *G. salinus* had the lowest specialization (Fig. 2). OMI values of all species were statistically significant ($P < 0.001$).

Species distribution models (SDMs)

The predictive accuracy of models was very high, as the AUC values of all models exceeded 0.8. GAM showed somewhat lower accuracy than BRT and RF, whereas the AUC values of BRT and RF were very similar (Table 2). Among the models of native species, RF had the highest AUC values. BRT was only fractionally better than RF in the case of *G. tigrinus*. As RF produced the best models among three of four species and gave essentially equally good result in the case of one species, RF was chosen as the method for modeling the spatial distribution of gammarid species. In the final RF models, depth was among five most important predictor variables for each gammarid species. In addition to depth, modeled distributions of macrophytes proved to have high importance in predicting the distribution of gammarids (Table 1).

The predicted distributions clearly differed between gammarid species in terms of both the distribution area and distribution pattern (Fig. 3). Based on SDMs, *G. salinus* had the most extensive distribution area. The distribution
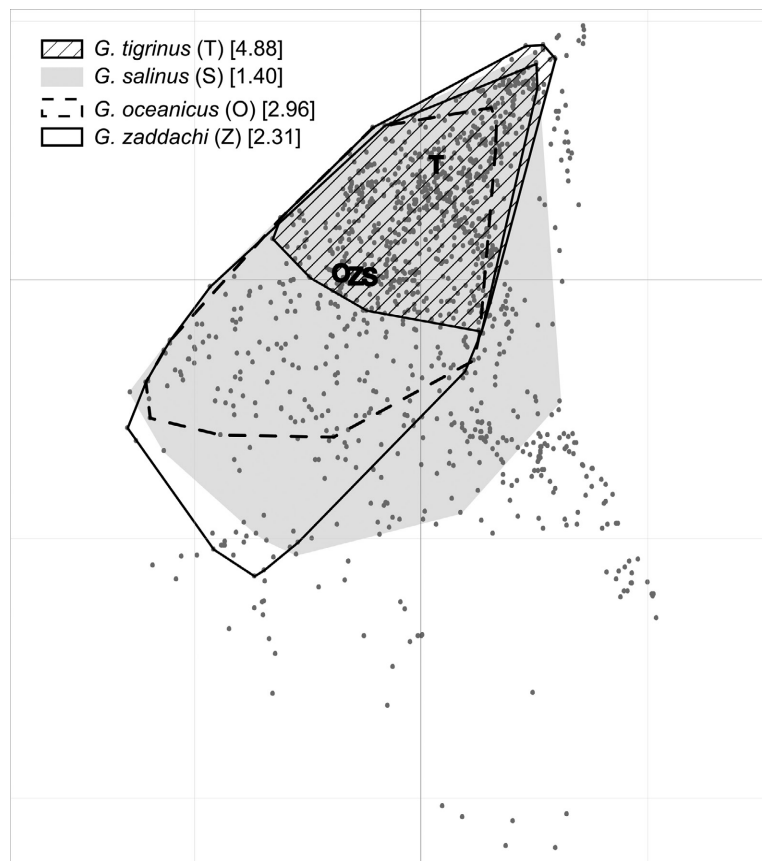
Fig. 2. Environmental niche characteristics of the studied gammarid species based on PCA ordination of the values of environmental variables in sampling sites. Dots represent sampling sites, polygons represent the realized niche breadths, and letters on the plot indicate the centers of niche spaces of the species. The values of OMI are shown in square brackets.

Table 2. AUC values of species distribution models.

Species	GAM	BRT	RF
G. tigrinus	0.884	0.898	0.896
G. oceanicus	0.824	0.847	0.857
G. salinus	0.816	0.858	0.865
G. zaddachi	0.815	0.821	0.829

Notes: GAM – generalized additive model, BRT – boosted regression trees, RF – random forest. Higher AUC value indicates better performance of model. RF was chosen to model the spatial distribution of all gammarid species based on the best overall performance.

pattern of the invasive *G. tigrinus* clearly distinguished from the distributions of the native gammarids: the probability of occurrence of *G. tigrinus* was highest in sheltered bays where the probability of occurrence of native species was very low (Fig. 3).

Based on the SDMs, the overlap of distribution was larger among native species than between *G. tigrinus* and native species (Table 3). Among distribution overlaps between native species and invasive *G. tigrinus*, Schoener's D scores suggest that the overlap was largest between *G. zaddachi* and *G. tigrinus* and smallest between *G. oceanicus* and *G. tigrinus*.

DISCUSSION

Our data showed that invasive species may have narrower environmental niche space than native species in a particular area, with the invasive *Gammarus tigrinus* being more specialized than any of the native gammarid species. The difference in the values of OMI was more than three-fold between the most specialized
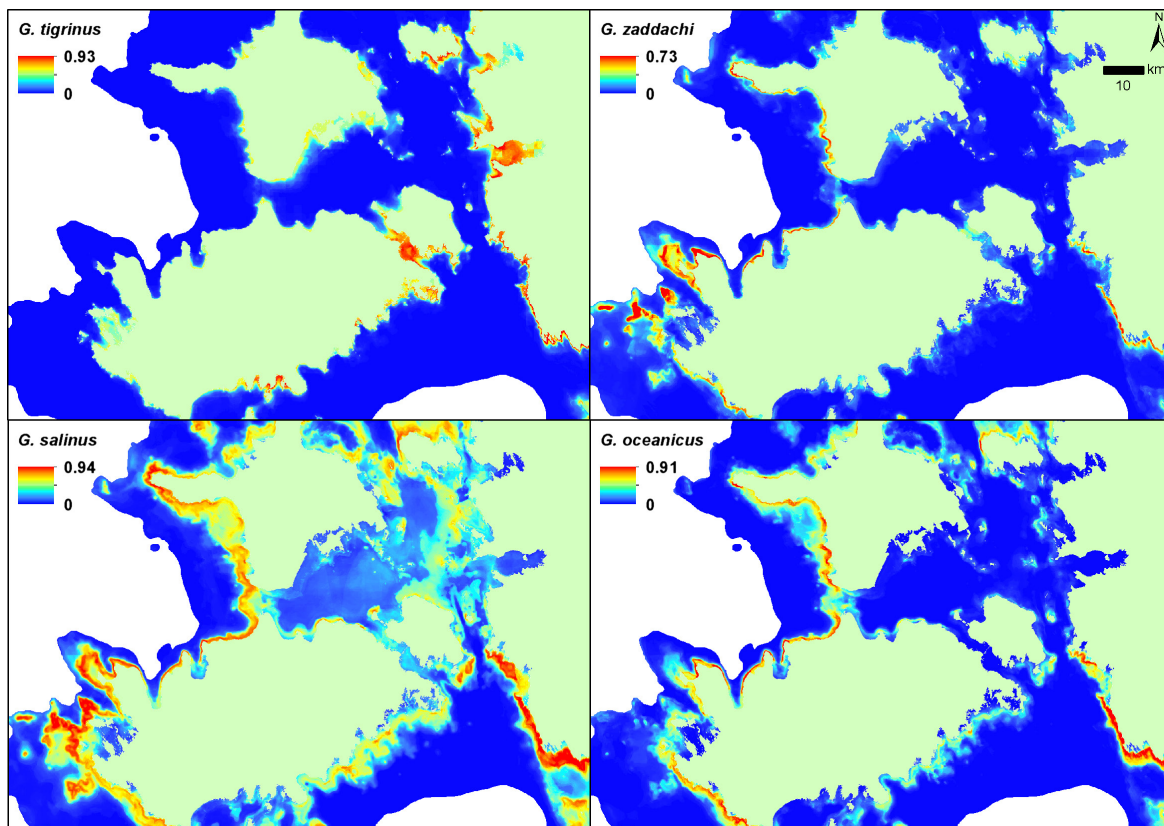
Fig. 3. Modeled distributions of the studied gammarid species. The color gradient indicates the probability of occurrence of a given species. The central part of the study area is zoomed in for easier comparison.

Table 3. Schoener's D values between modeled distributions of gammarid species. Higher value indicates larger overlap of distributions.

	G. tigrinus	G. oceanicus	G. salinus
G. oceanicus	0.277		
G. salinus	0.265	0.670	
G. zaddachi	0.380	0.596	0.526

species, *G. tigrinus*, and the least specialized species, *G. salinus*. In addition to higher specialization, the centroid of the niche of the nonindigenous species departed strongly from all the other species, indicating niche segregation. Our results suggest that successful nonindigenous species do not necessarily have to be habitat generalists and species with narrow niche space may become a pest species. This also suggests that high similarity in environmental niche space between native and invasive

species may reduce the success of invading species (Callaway et al. 2004, Vivanco et al. 2004). Therefore, the degree of segregation in environmental niche space between an invader and native community may provide a predictive tool for invasiveness as shown for the phylogenetic relatedness in terrestrial habitat (Strauss et al. 2006). There exist two potential mechanisms explaining the observed segregation in environmental niche space between invasive and native species. First, species that highly overlap within their niche space should not coexist because they highly overlap in resource use (Fargione et al. 2003). Second, natural enemies (e.g., parasites or predators) are expected to switch to close relatives of their host and/or prey more easily than to distantly related taxa. Consequently, larger differences in environmental niche space between native and invasive species result in more complete release of invasive species from enemies (Strong et al.

1984). For the gammarid amphipod perspective, a direct competitive inhibition of *G. tigrinus* by natives of their own functional guild is not likely as *G. tigrinus* has been experimentally shown to be competitively superior over natives (Orav-Kotta et al. 2009). However, indiscriminate predation on juveniles by all gammarid species is very strong in the study area (Jänes et al. 2015) and weakening of such predation gives the invasive species a clear advantage.

Earlier studies have demonstrated that *G. tigrinus* is rather euryoecious in its native distribution range (Steele and Steele 1972, Bousfield 1973) as well as more tolerant toward some physical and chemical factors like salinity, hypoxia, and thermal stress compared to other gammarids in Europe (Grabowski et al. 2006, Lenz et al. 2011, Sareyka et al. 2011). Nevertheless, the environmental space occupied by the invasive species was significantly narrower compared to the native species in the eastern Baltic Sea. This leads to another important implication of this study: wider tolerance limits do not necessarily translate to wider occupied niche of an invasive species in an area subject to invasion.

There may be several reasons why the invasive gammarid has narrower habitat niche compared to local species. One plausible explanation may be preadaptation of the invasive species to warmer and more sheltered habitats that have emerged in the Baltic Sea during postglacial period but are under-occupied by the native Baltic species. The native fauna of the contemporary Baltic Sea is assembled by the most euryoecious species from the Arctic and northern Atlantic faunal groups (Segerstråle 1957). Thus, the native gammarids are probably more tolerant to low water temperatures characteristic to the eastern Baltic Sea with the exception of the shallowest bays. Contrastingly, for *G. tigrinus* several experiments have confirmed tolerance to high temperatures and optimal developmental temperatures as high as 25 °C (Savage 1982, Lenz et al. 2011). The other possible explanation for the narrower niche may be lower genetic diversity of the species in the invasive range due to recent bottleneck effects (Lee 2002). However, the Baltic population of *G. tigrinus* is characterized by high genetic diversity resulting from an invasion history combining separate invasion events from distinct source populations (Kelly et al. 2006).

In addition to the named reasons, it is probable that the new species is still expanding its distribution in the study area. In the case of *G. tigrinus* and the spatial scale of this study, range expansion may not necessarily result from time-consuming distribution strategies as has been shown for several terrestrial species (Svenning and Skov 2004), as the Eastern European populations of *G. tigrinus* have displayed fast spatial expansion in new areas at scales comparable to the extent of our study area (Pinkster et al. 1977, Kotta et al. 2013). Further range expansion may rather result from rapid evolutionary postinvasion responses to new environments (Lee 2002), and in such case, future niche changes may be expected.

The relatively narrower niche of an invasive species compared to sympatric congeners seemingly contradicts several previous studies that found larger niche in invaders (Scott and Panetta 1993, Goodwin et al. 1999, Sultan 2001) or an enlargement of niche presumably due to invader's successful escape from biotic suppressors (Callaway and Ridenour 2004). However, the spatial scale of niche studies must be considered before drawing conclusions. The spatial extent of our study area was about 200 km while the whole extent of the European range of *G. tigrinus* is more than one order of magnitude larger covering also freshwater populations (Kelly et al. 2006). Therefore, a local pattern of niche breadth does not necessarily coincide with the regional or global pattern, and analysis on the scale of the whole invasive range of *G. tigrinus* would have possibly revealed a notably larger niche space.

Both ordination and distribution modeling showed partial overlap of the niches of *G. tigrinus* and native gammarids. This indicates that no complete competitive exclusion exists among the studied sympatric species. This may be a product of large temporal variability in the Baltic Sea environment represented by many stochastic disturbances at multiple spatial and temporal scales with abiotic disturbance enabling the coexistence of species (Roxburgh et al. 2004). Previous experimental evidence suggests that there is no strong interference competition among adult individuals of gammarid species in the northern Baltic Sea (Kotta et al. 2011), although adult predation on juvenile gammarids has been observed in all of the studied species (Jänes et al. 2015). Contrast-

ingly, there are cases from European fresh waters where superior intraguild predators *G. duebeni* or *Dikerogammarus villosus* may outcompete *G. tigrinus* in certain habitats resulting in a strict habitat segregation (MacNeil and Prenter 2000, MacNeil et al. 2008). The width of the realized niche of an invader in a new geographic range most likely results from an interplay between available niche space and biotic interactions with resident species within the framework of this particular niche space.

Our results indicate that *G. tigrinus* is not occupying a new niche totally devoid of other gammarids in the northern Baltic Sea, although its environmental preferences clearly distinguish it from all the native species. An addition of a species with differing preferences may, however, lead to competitive dominance and accordingly high densities of the newcomer at environmental combinations favored distinctly by it. This seems to be the case in the Baltic Sea, as *G. tigrinus* has been reported to dominate in several areas with native gammarid species present at very low numbers (Packalén et al. 2008, Herkül et al. 2009, Kotta et al. 2013). In areas of niche overlap, microhabitat segregation is the likely cause for density patterns, as has also been shown for native gammarids with highly overlapping niches (Korpinen and Westerbom 2010).

The spatial resolution of the used environmental data sets was generally in a magnitude of 100 m. Higher resolution of environmental data may very likely reveal stronger niche separation between the studied species. Environmental variability in a submeter spatial scale can be driving micro-habitat selection in small-sized invertebrates (Platvoet et al. 2009). However, due to practical reasons such a small-scale variability can seldom be recorded during standard benthos sampling and neither can environmental GIS-layers achieve that high spatial resolution. Specially targeted field work is needed to record very small-scale environmental variability, and the results of such detailed data collection may likely reveal stronger niche separation between the species than this study.

The species distribution models (SDMs) produced predictions with high accuracy and thus proved to be useful for comparing the distribution of gammarid species. The high prediction accuracy can be explained by several reasons: (1) the input data set of the presence and absence of gammarid species was very representative including thousands of records and covering all important environmental gradients; (2) modern modeling algorithms like RF and BRT have proved to produce highly accurate predictions (e.g., Elith et al. 2006, Lindegarth et al. 2014); (3) the elaborate set of environmental variables (including biotic predictors) for model building reflected well the heterogeneity and natural gradients of the study area.

Most studies on species distribution modeling have focused only on abiotic drivers of species distribution (Zimmermann et al. 2010). However, inclusion of biotic predictors like competitors or facilitators, may increase the predictive power of models (Araújo and Luoto 2007, Pellissier et al. 2010). In this study, the distributions of key phytobenthic species were highly important predictors in distribution models of gammarids: the probability of occurrence of *Fucus vesiculosus*, *Furcellaria lumbricalis*, and charophytes were among the top four predictors in the models of every gammarid species (Table 1). This proves that available species distribution maps can be a rewarding input for species distribution modeling. Charophytes grow on soft sediments in the most sheltered bays. *F. vesiculosus* and *F. lumbricalis* grow on hard substrate but in different depths and wave exposure levels. Based on the importance of predictor variables in SDMs, *G. tigrinus* is most related to charophytes and native gammarids to *F. vesiculosus* and *F. lumbricalis* indicating habitat separation between the invasive and native species. The included three key macrophytes may have caused the exclusion or decreased importance of abiotic variables like wave exposure from SDMs in this study because the distribution of different plant groups reflect certain gradients in many abiotic drivers like depth, wave exposure, substrate, and salinity. However, compared to the cumulative and interactive effects of abiotic variables, the distribution of vegetation showed higher predictive power. This indicates that the modeled biotic variables (vegetation in this study) carry additional information compared to the sum of effects of underlying abiotic variables.

Modeled distribution maps (Fig. 3) enabled assessment of the spatial aspect of niche over-

lap between gammarid species in the study area. Based on the pairwise comparisons of distribution overlap (Schoener's D), the distribution of *G. tigrinus* had the smallest overlap with all the other species. This result complied well with the analysis of niche specialization (OMI values) which indicated that *G. tigrinus* has the highest habitat specialization. Among native gammarids, the distribution of *G. zaddachi* had the largest overlap with *G. tigrinus* and this clearly indicates that *G. zaddachi* is the most affected by the competitive and predation pressure by *G. tigrinus*. Compared to OMI analysis, the modeled distributions reflect the actual geographic dimensions where biological interactions take place. The geographic nature of SDM and SDM-based analyses makes the approach easily comprehendible in a management point of view.

Tolerance to stress is sometimes considered less important for invasiveness than reproduction following the r-selection strategy (McMahon 2002). Our study suggests that tolerance does not necessarily convert to wider environmental niche or distribution in the invaded range. Instead, larger tolerance of invasive species compared to local species along some environmental gradient may translate to niche and habitat segregation in the invaded range. However, the situation is far from static (Simberloff 2014), and not only are the species evolving but also the available niche space is constantly transforming in geographic space. Warming climate prospects may change the amount of available niche space for both native and non-native co-occurring species and accelerate changes in the arrangement of occupied niches (Williams and Jackson 2007), with probable retraction of niches of more cold-adapted resident species like *G. zaddachi* and possible protrusion of invaders favored by or more tolerant to warmer conditions.

Conclusions

The distribution and niche assessment of NIS by combining spatial modeling and multivariate ordination in this study proved to be a highly relevant approach to reveal patterns of invasion process. Environmental niche analysis (OMI) offers complementary information about biotic patterns in available environmental space compared to more traditional species distribution

modeling. The occupied niche space of the nonindigenous gammarid *G. tigrinus* was narrower than those of native gammarids. Also, niche centers of the native species almost coincided while the one of *G. tigrinus* was situated notably apart. This differentiation was also well reflected in the modeled distributions: the highest probability of occurrence of *G. tigrinus* was spatially restricted to shallow and sheltered areas that are predominantly warmer and of lower salinity. These findings indicate that the success of the invasion of *G. tigrinus* has been facilitated by specific habitats in the recipient area that are highly suitable for the species due to favorable preadaptations. Considering intraguild interactions, the invasion of *G. tigrinus* may have the strongest effect on *G. zaddachi*, as the distribution overlap between these two congeners is the largest. However, the observed niche divergence and wider realized niche of the native species are likely to aid survival in habitats less suitable for *G. tigrinus*. Our study reminds that wide environmental tolerance of a species does not necessarily result in a wide realized niche in the course of an invasion process. Our results also suggest that colonization success and wide distribution do not necessarily require a broad environmental niche of the colonizer, but may instead rely on the saturation of the recipient ecosystem and the novelty of the preadaptations of the colonizer: an ability to optimally utilize previously under-occupied environmental niche can support the apparent luck of the draw. Despite the decline in specialist species worldwide (Clavel et al. 2011), anthropogenic introductions may thus regionally increase the proportion of relatively specialized taxa.

Acknowledgments

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