






Research Article

Disentangling the effects of abiotic and biotic processes on non-indigenous species dominance

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Abstract

Relatively little attention has been paid to the underlying mechanisms determining the dominance of non-indigenous species (NIS) once established, despite being regarded as a proxy of invasion success and potential impacts in recipient communities. To bridge this knowledge gap, here we evaluate the potential direct and indirect effects of community filters on the dominance of two widespread NIS in the Baltic Sea: *Marenzelleria* spp. and the round goby (*Neogobius melanostomus*) within their corresponding communities. We applied a structural equation modelling approach to assess the direct and indirect effects amongst multiple abiotic and biotic variables on the relative biomass (as proxy of dominance) of NIS. The biotic variables represented the taxonomic- and functional diversity of the recipient communities, as well as the trait similarity between NIS and native species. We observed a comparable influence of abiotic and biotic drivers on the dominance of both NIS, with biotic variables having a somewhat stronger overall direct effect. Specifically, the dominance of both NIS was similarly affected negatively by the richness and positively by the evenness of the native communities. However, we also detected that both NIS might need different ecological strategies to become dominant in their recipient communities, which underwent similar assembly processes. Such strategies were partly highlighted by the different degrees of trait similarity between each NIS and their respective co-occurring native species. A better understanding of the underlying processes affecting NIS dominance is of high relevance to mitigate potential impacts of NIS once established. Furthermore, the provided approach could be further applied to unveil the potential strategies that NIS might follow in other regions and ecosystem types.

Key words: Benthos, biological invasions, coastal fish, community assembly rules, dominance, functional distinctiveness, functional ecology, SEM, traits



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Introduction

The spread of non-indigenous species (NIS) pose a major threat to biodiversity and the integrity of ecosystems worldwide (IPBES 2023). The global spread of NIS is mostly driven by human activities linked to increasing trade and transport (Seebens et al. 2021). While only a minimal fraction of NIS become naturalised and further invasive (Blackburn et al. 2011; IPBES 2023), the global impacts of NIS establishment in marine communities are predominantly negative (Anton et al. 2019) and often intensified by anthropogenic pressures (Gerald et al. 2020). However, at more local scales, the effects of NIS on ecosystem structure and functioning can

also be innocuous or even positive (Thomsen et al. 2014; Vivó-Pons et al. 2020). Hence, the effect and potential impacts of NIS on native communities is likely to be highly scale-, context- and species-dependent (Guy-Haim et al. 2018).

The establishment of NIS has been shown to be influenced by the same community assembly processes structuring the composition of native communities (Gallien et al. 2014; Pearson et al. 2018). Communities exposed to a strong environmental filtering (e.g. extreme temperatures) tend to harbour functionally similar species with a limited set of physiological, morphological or behavioural characteristics (i.e. traits), which NIS may also display in order to cope with the environmental conditions (Cleland 2011; El-Barougy et al. 2020). Conversely, in communities mainly shaped by biotic interactions (e.g. limiting similarity), NIS might need to display more dissimilar traits or strategies compared to natives in order to limit niche overlap and avoid competitive exclusion (Mathakutha et al. 2019; Xu et al. 2022). As evident from the abovementioned studies, considerable effort has been dedicated to understand NIS establishment (Richardson and Pyšek 2012; Gallien and Carboni 2017). However, relatively little attention has been paid to the underlying mechanisms determining the dominance of NIS once established (Lundholm and Larson 2004). This lack of knowledge is critical since NIS dominance is regarded as a key proxy of invasion success (Crall et al. 2006) and may provide information about the magnitude of potential impacts on recipient communities (Bradley et al. 2019; Cadotte 2023). Hence, a better understanding of the multiple processes affecting NIS dominance is essential to evaluate potential risks of already established NIS to become hazardous in the future (Richardson and Pyšek 2012).

Here, we aim to bridge this knowledge gap by providing one of the first comprehensive assessments of the main drivers of NIS dominance in recipient communities by integrating existing community assembly theory (Pearson et al. 2018) with the functional similarity between NIS and co-occurring species. As model organisms, we performed a comparative analysis on two widespread and well-known NIS in European waters and beyond: the benthic polychaete worm *Marenzelleria* spp. (Mesnil, 1896); (Blank et al. 2008) and the demersal fish round goby (*Neogobius melanostomus*; Pallas, 1814). We conducted the analysis in the Baltic Sea region, where both species are currently well established. The Baltic Sea provides an illustrative case study area as it is highly susceptible to the arrival and establishment of NIS from both marine and limnetic origin (Paavola et al. 2005) and currently contains > 100 recorded NIS, many of which form self-sustaining populations (Ojaveer et al. 2017).

The first report of the *Marenzelleria* species complex in the Baltic Sea was in 1985, probably introduced through ballast water from North America (Bastrop et al. 1997; Blank et al. 2008). Subsequently, it spread and established throughout the entire Baltic Sea (Blank et al. 2008; Maximov 2011), often reaching high densities (Delefosse et al. 2012). *Marenzelleria* is regarded as an ecosystem engineer species, as it has been documented to change sediment and nutrient dynamics of recipient areas together with other multifaceted impacts on native communities (Delefosse et al. 2012; Kauppi et al. 2018). The round goby is native to the Ponto-Caspian region and was first recorded in the Gulf of Gdansk in 1990 (Skóra and Stolarski 1993). This NIS has been spreading throughout several regions within the Baltic Sea, being established in many coastal areas (Puntilla-Dodd et al. 2018). Round goby attains very high population densities partly due to a wide tolerance to environmental conditions and high reproductive turnover rate (Behrens et al.

2017; Kruze et al. 2023). To date, the overall impacts of round goby’s establishment are assumed ecosystem- and context specific (Hirsch et al. 2016), yet it has been shown to decimate local invertebrate populations (van Deurs et al. 2021; Wallin-Kihlberg et al. 2023) and compete with native species due to overlapping dietary preferences (Karlson et al. 2007).

To evaluate the potential direct and indirect effects of both abiotic and biotic community filters on the dominance of both NIS, we applied a structural equation modelling (SEM) approach (Shipley 2009) using high-resolution monitoring data on species biomass and environmental conditions as input. SEM has previously been used to study the associated impacts of NIS (Britton-Simmons 2004) and the mechanisms behind their establishment success (Xu et al. 2022); but, to date, not to assess the main processes affecting their dominance once established. More specifically, we aimed to analyse how environmental conditions and biotic variables, reflected by key taxonomic and functional community metrics, as well as the degree of niche (trait) overlap between NIS and native species, determine the dominance of NIS. This overall aim was achieved by pursuing the following research questions and their associated hypotheses (Fig. 1):

- Q1: What are the effects and relative importance of abiotic and biotic drivers on NIS dominance?
- Q2: Are the responses to drivers similar or different between NIS?
- Q3: To what extent does trait similarity and niche overlap with native species determine the dominance of NIS?

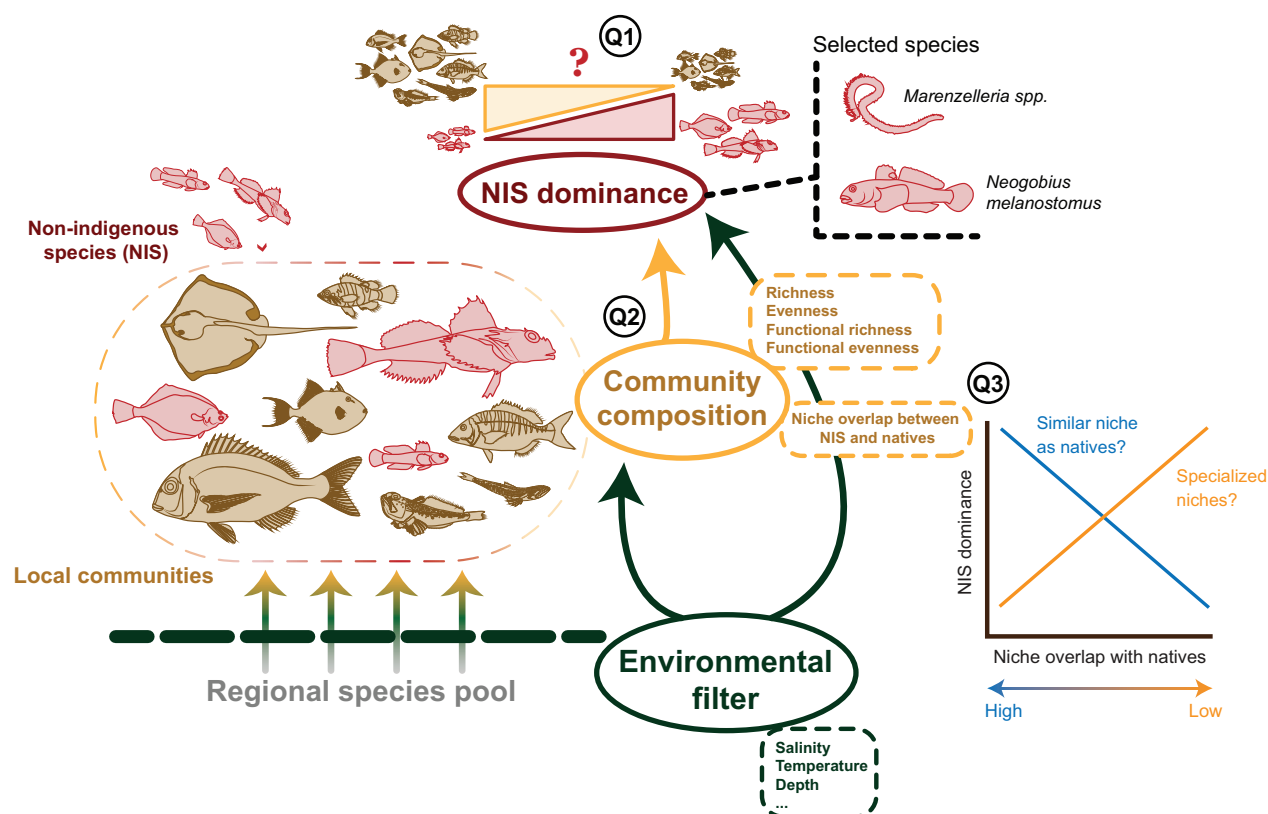


Figure 1. Conceptual figure summarising the key assembly processes acting on community composition and NIS dominance along with the three main questions and selected species.

Community assembly theory predicts that the environment is more important in shaping communities across larger spatial scales, while biotic interactions gain relevance at more local scales (Zobel et al. 1998; Pearson et al. 2018). Given the fine spatial resolution of the analysis (i.e. by sample unit), we therefore expect that the biotic drivers have a greater influence than the abiotic ones in determining NIS dominance (Q1). Furthermore, we assume that the benthic invertebrate and fish communities are subjected through analogous environmental filtering processes and that the dominance of both NIS will respond similarly to the community attributes (i.e. richness and evenness of species and traits; Q2). Finally, we expect that the NIS will adopt different strategies depending on the degree of niche overlap with their corresponding native species (Q3).

Materials and methods

Data collection

We collected available monitoring data on *Marenzelleria* and round goby, as well as the co-occurring native benthic invertebrates and fish species throughout the study area. For *Marenzelleria* and the native benthic invertebrates, wet weight was obtained from the Swedish Ocean Archive (<https://sharkweb.smhi.se>), containing a total of 3534 unique sampling events from 1993 to 2020 covering the Baltic Sea from the Bothnian Bay in the north-east, to the south-western Baltic Sea (Fig. 2A). Only grab samples were included with approximately 0.1 m² area sieved through a 1-mm meshed net. Wet weight was converted to ash-free dry weight (AFDW), with conversion factors obtained from Rumohr et al. (1987) and Gogina et al. (2022). For round goby and the co-occurring fish species, data on wet weight (g) per unit effort (WPUE) was obtained from the Swedish national and regional monitoring programme (<https://www.slu.se/en/departments/aquatic-resources/1/databases/database-for-coastal-fish-kul/>). The data comprised 14 locations sampled from 2005 to 2021, covering most parts of the *Marenzelleria* programme, from the Bothnian Sea in the NE to the south-western Baltic Sea, with a total of 735 sampled communities (Fig. 2B). Two gear types, Nordic coastal multi-mesh gillnets or sets of nets, were used in the selected monitoring locations (see Suppl. material 1: appendix S1 for details). To avoid the inclusion of highly sporadic species, we retained all species representing 99.5% of the total species occurrences in each dataset. This led to a final selection of 173 benthic invertebrates and 27 coastal fish species.

In addition to the monitoring data, we collected available trait information for all species representing the fundamental ecological processes of feeding, growth, reproduction, survival and behaviour following existing trait-based descriptions of marine organisms (Törnroos and Bonsdorff 2012; Litchman et al. 2013). For benthic invertebrates, 10 traits with 56 different trait categories or modalities were selected: size, adult life span, reproductive type, developmental mechanism, environmental position, living habits, feeding habits, mobility, movement method and bioturbation ability (Suppl. material 1: table S1, appendix S1). For coastal fishes, 11 traits with 37 different modalities were selected: habitat switching, parental care, territorial behaviour, diet, temperature preference, development mode, pharyngeal bones, habitat, fin type, body type and length class (Suppl. material 1: table S1, appendix S1).

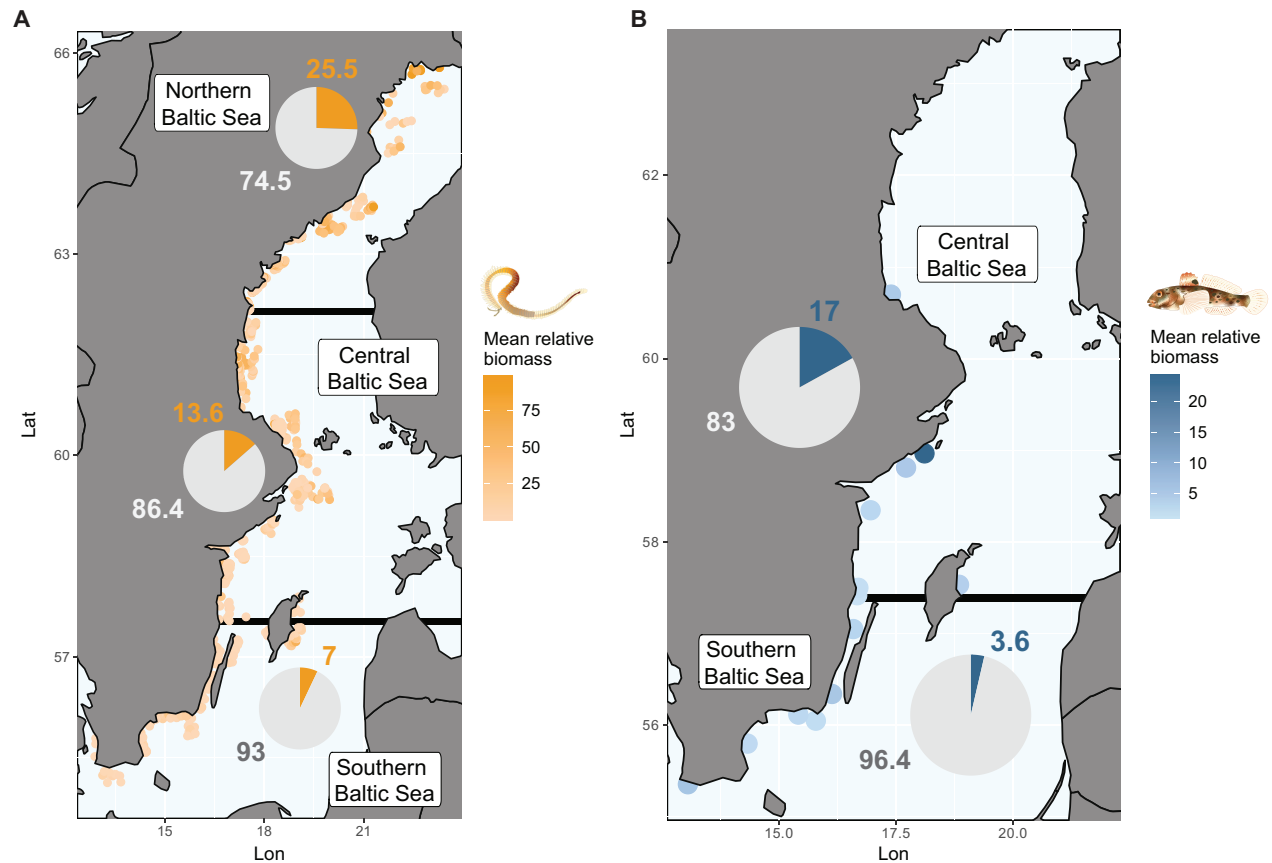


Figure 2. Mean relative biomass of *Marenzelleria* (A) and round goby (B) at each sampling location. The pie plots illustrate the percentage of total biomass corresponding to NIS (coloured) or native species (grey) in each region.

Biotic variables

On the basis of the data, the relative biomass of NIS compared to the native species at each sample unit was used to represent NIS dominance. Furthermore, to examine potential biotic factors affecting dominance of NIS, we computed several community metrics representing the taxonomic and functional richness and evenness in each sampled community. For species evenness, we used Pielou's Index (J), based on the specific measure of biomass of species at each unique sampling event. Functional richness (FRic) was measured as the minimum amount of functional space (convex hull) filled by all the species in a community (Villéger et al. 2008). Functional evenness (FEve) corresponds to how evenly the species biomass is distributed in the functional space (Villéger et al. 2008). Evenness was calculated with the function *diversity* from the *vegan* package (Dixon 2003) and FRic and FEve were calculated with the function *dbFD* from the *FD* package (Laliberte and Legendre 2010).

To assess the potential individual strategies of NIS in their recipient communities, we further included the functional distinctiveness metric as a predictor. This metric reflects the degree of niche differentiation between species given by their traits, measured as the mean functional distances from one species to all the others within the same community (Violle et al. 2017). If applied to biological invasions, functional distinctiveness provides information about the strategy that a certain NIS could be following in the recipient communities, in relation to how the individual trait expression might be favouring that NIS over the native community

(Vivó-Pons et al. 2023a). We estimated the functional distances between species needed to compute distinctiveness with the function *compute_dist_matrix* from the *funrar* package (Grenié et al. 2017). Further details about the distinctiveness calculation can be found in the Suppl. material 1: appendix S1.

Environmental variables

Spatial differences in salinity and bottom oxygen concentrations, as well as temperature and depth have been shown to influence the structure and composition of benthic invertebrates and fish communities in the Baltic Sea (Gogina et al. 2016; Pecuchet et al. 2016). Hence, we included these four environmental factors as potential predictors in the analysis of NIS dominance for both *Marenzelleria* and round goby. For round goby, we also included chlorophyll A and coastal exposure as environmental predictors since both variables have been regarded to be more relevant in communities from shallower areas in the Baltic Sea (Frelat et al. 2018; Kraufvelin et al. 2018). We did not include these factors for *Marenzelleria*, since this NIS was sampled over a pronounced depth gradient (0–240 m).

Additionally, we computed the standard deviation for the set of environmental predictors by year (*Marenzelleria*), month (round goby) and location to represent the variability and seasonality of environmental conditions. To test for potential multi-collinearity amongst predictor variables, we performed a variance inflation factor (VIF) analysis. Based on the VIF results, we removed bottom temperature variation from *Marenzelleria* (VIF > 5; Suppl. material 1: fig. S2) and species richness from the round goby analysis (VIF > 10; Suppl. material 1: fig. S2). More details about the sources and processing of the environmental data are found in the Suppl. material 1: appendix S1.

Statistical analysis

To assess multiple relationships between NIS dominance and the set of environmental and biotic variables, we used a structural equation modelling (SEM) framework, based on linear mixed models. We first developed a SEM with links considered only between NIS dominance and biotic variables and between biotic variables and environmental drivers separately. After evaluating model fits (Suppl. material 1: appendix 2), we developed a final model where we added all significant direct paths between environmental predictors and NIS dominance identified as missing in the initial setup. We fitted the final SEM for each NIS on the basis of the following setup:

$$\begin{aligned} \text{NIS relative biomass} = & a + \beta_1 (\text{NIS functional distinctiveness}) + \beta_2 (\text{Richness}) + \beta_3 \\ & (\text{Evenness}) + \beta_4 (\text{Functional richness}) + \beta_5 (\text{Functional evenness}) + \beta_6 \\ & (\text{Environmental predictor 1}) + \dots + \beta_N (\text{Environmental predictor N}) + \\ & d(\text{Year}) + e \dots n(\text{Random effects}) + \varepsilon \end{aligned}$$

where α and β reflect the intercept and regression coefficients for each predictor (N) on NIS relative biomass (as a response) and ε the residual error term. We also tested for non-linear relationships by adding a second term for each predictor variable x that reflected the quadratic effect: $(x - \text{mean}(x))^2$ (Maureaud et al. 2019). This term was only retained in the final SEM if both the quadratic and non-quadratic

term were significant. Additionally, we transformed NIS relative biomass, richness and FRic using a natural logarithm. To account for potential temporal effects of repeated measures over time, all models contained a random effect d for year, as well specific random factors to account for other potential biases, such as the type of gear or the sampling location (Suppl. material 1: appendix 2). We tested each model for spatial autocorrelation and selected the best covariance structure (if applicable) using Akaike Information Criteria (AIC). Please note that the same considerations were taken when fitting the separate regression models for each biotic variable, with the environmental variables as predictors and with non-causal links between biotic variables that are correlated. Further details about the initial SEM tests, data exploration, the model setup and formulation can be found in the Suppl. material 1: appendix 2. The linear mixed models were performed using the *lme* function from the *nlme* package (Pinheiro et al. 2017). The SEMs were performed using the package *piecewiseSEM* (Lefcheck 2016). All analyses were conducted in R version 4.1.0.

After model fit and validation, we compared the strength and relative importance of environmental and biotic predictors by summarising the standardised coefficients of all the significant direct and indirect effects on NIS dominance. We estimated indirect effects of environmental variables by multiplying the path coefficients from any environmental variable by the path coefficient of any biotic variable that showed a significant link with NIS dominance. We also estimated the overall effect of environment and biotic variables on NIS dominance by obtaining the absolute sum of all the direct effects within each group.

Results

Overall, both SEMs demonstrate pronounced direct links between the environmental and biotic variables, including dominance (Fig. 3A, B) and indirect effects on NIS dominance channelled through the biotic variables (Fig. 4C, D). Taken together, both SEMs show a slightly higher relative importance of biotic versus environmental variables as direct drivers of NIS dominance, indicated by the higher absolute sum of standardised coefficients (i.e. direct joint effects) across variables within each group (Fig. 4E).

NIS dominance in both SEMs was positively related to species evenness (Fig. 3), but the effect was somewhat stronger for *Marenzelleria* (Fig. 4A). The significant non-linear effect indicates that *Marenzelleria*'s dominance decreases in highly evenly distributed communities. Furthermore, the dominance of *Marenzelleria* and round goby was negatively related to species richness and FRic, respectively (Fig. 3; Fig. 4B, C). Regarding distinctiveness, we found a negative relationship for round goby dominance, whereas a weak positive, but non-significant relationship for *Marenzelleria* (Fig. 3B, Suppl. material 1: table S2). This indicates that round goby is more dominant when it co-occurs with functionally similar species (Fig. 4D). No significant effects were detected for FEve on NIS dominance in the SEMs.

Amongst the set of environmental predictors, the dominance of *Marenzelleria* showed strong positive and negative (non-linear) links with depth and bottom salinity, respectively (Figs 3A, 5E, F). Weaker relationships were found with bottom temperature (negative) and bottom oxygen variation (positive) (Figs 3A, 5G, H). For round goby, we found strong and negative relationships between dominance, bottom temperature and bottom oxygen concentration (Figs 3B, 5G, I).

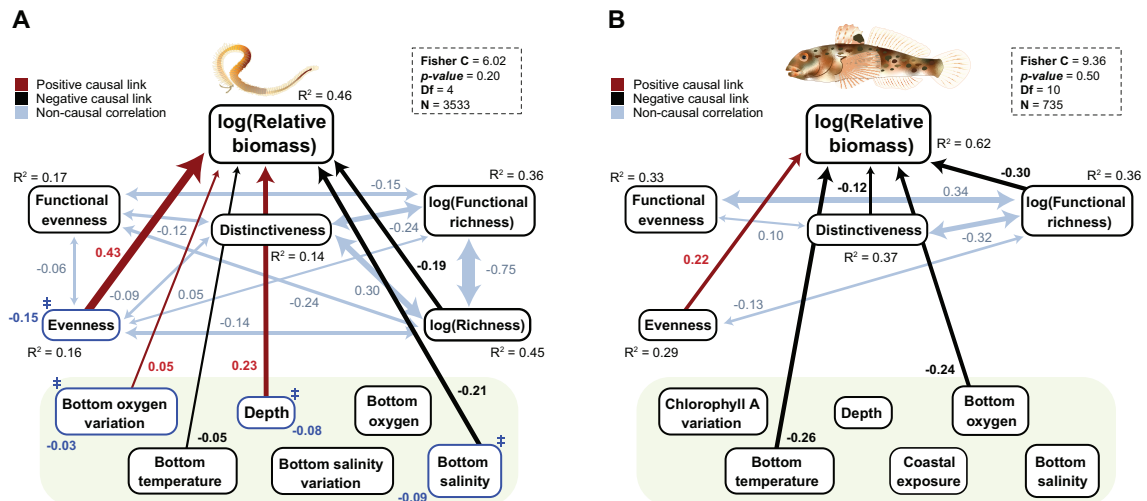


Figure 3. SEM structures for *Marenzelleria* (A) and round goby (B) dominance showing the direct and indirect links between abiotic and biotic variables. Blue boxes indicate a significant quadratic effect of the corresponding predictor. The values next to the arrows show the standardised coefficients. Non-causal correlations are expressed as light blue arrows. Fisher’s C test parameters and corresponding p-value (i.e. goodness-of-fit) of each SEM structure are shown in the dashed box. The coefficient of determination (R^2) is shown for each biotic variable and NIS dominance. The direct links between abiotic and biotic variables are shown in Fig. 4A, B.

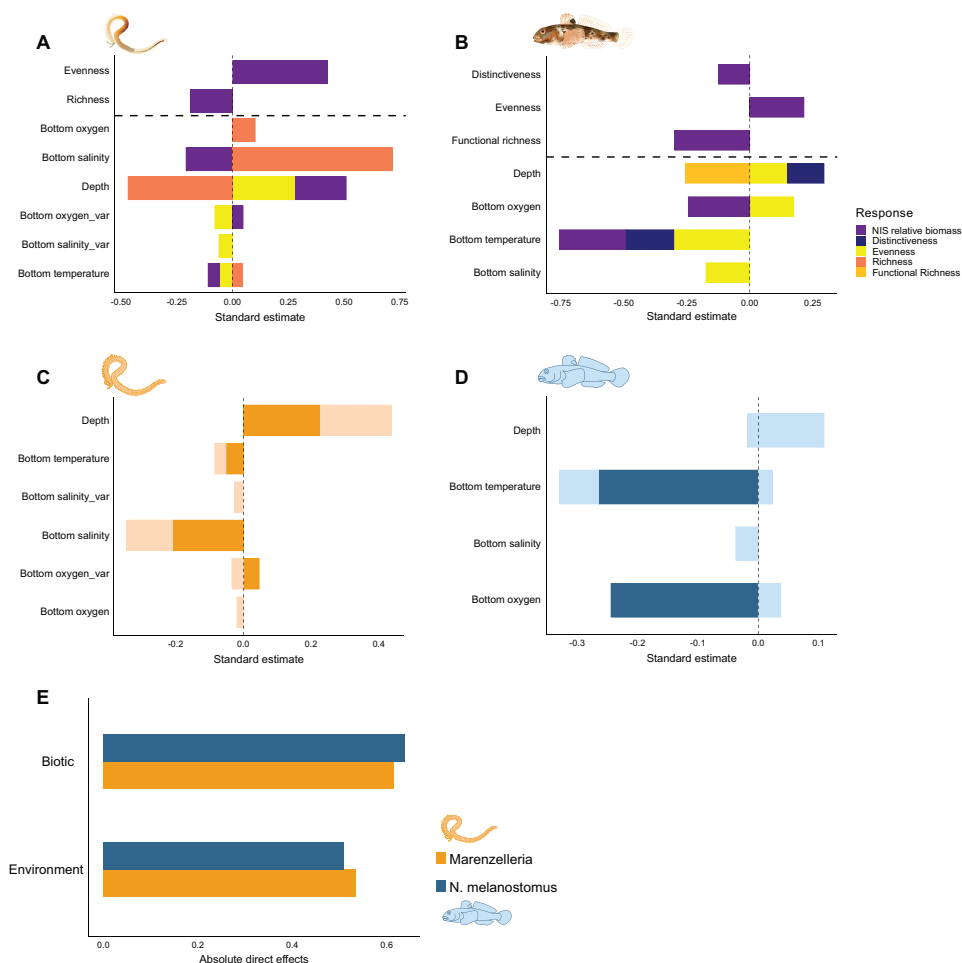


Figure 4. Direct significant effects of the environment on biotic variables and relative biomass on *Marenzelleria* (A) and round goby (B). Direct (darker colour) and indirect effects (lighter colour) from environmental variables on the relative biomass of *Marenzelleria* (C) and round goby (D). Cumulative absolute direct effects from both environmental and biotic variables on NIS relative biomass (E).

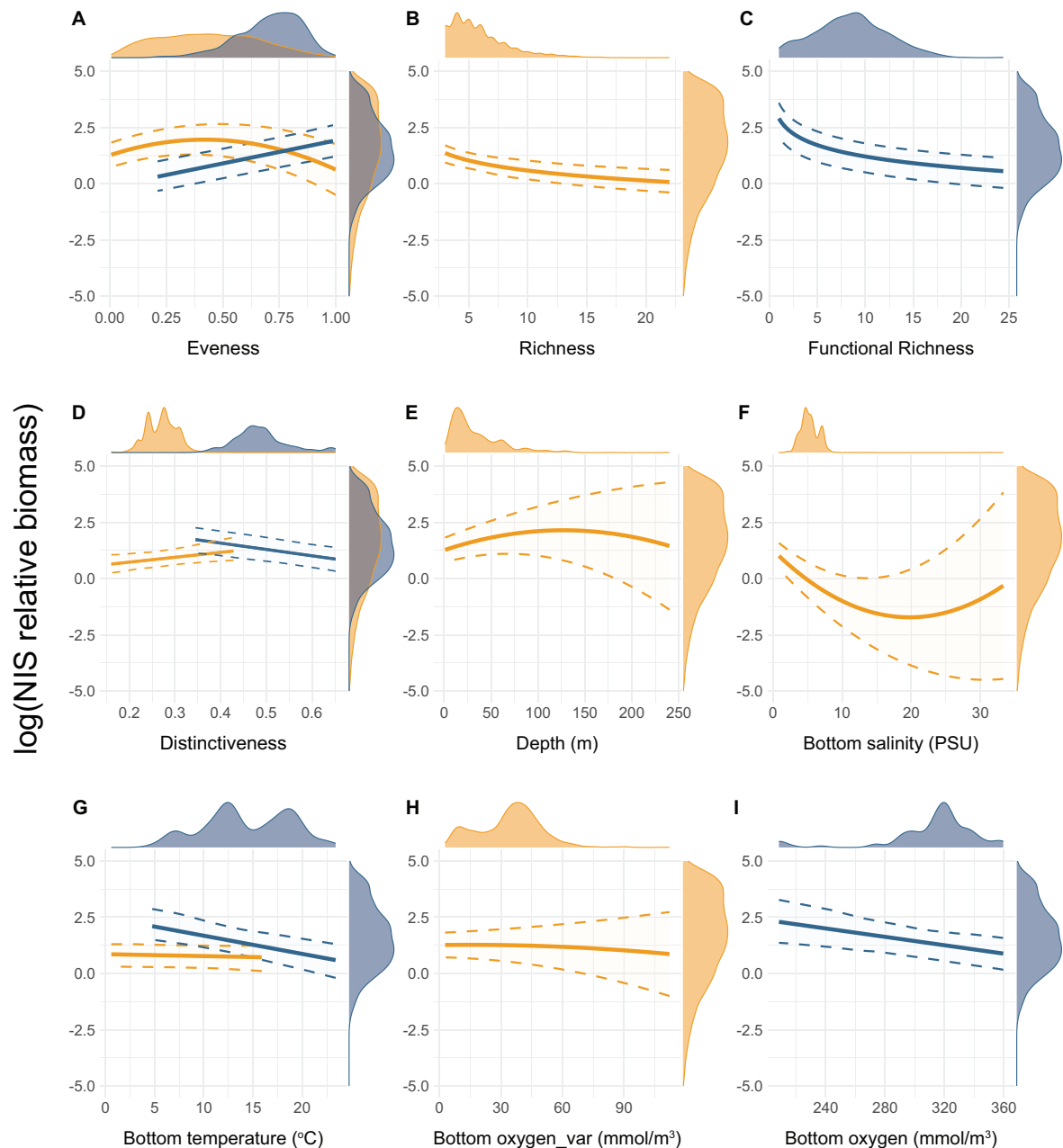


Figure 5. Partial effects plot from all significant variables (A–I) illustrating their effects on the relative biomass of *Marenzelleria* (orange) and round goby (blue). Panel D included the non-significant relationship between distinctiveness and NIS dominance for *Marenzelleria* to illustrate the opposite direction of both trends. The y-axis in each plot represents the change of NIS relative biomass values in function of each variable, with its entire range of values represented in the x-axis.

The most important direct predictors affecting richness and evenness in both communities were depth and salinity for *Marenzelleria* along with bottom temperature for round goby (Fig. 4A, B). Additionally, depth and salinity showed large indirect effects on *Marenzelleria*'s dominance (Fig. 4C). For round goby, depth and bottom temperature had a pronounced indirect effect on dominance (Fig. 4D).

Marenzelleria's dominance was reasonably well explained by the environmental and biotic variables ($r^2 = 46\%$) (Fig. 3A). Environmental variables also explain a considerable proportion of the variance in two of the biotic variables, FRic ($r^2 = 36\%$) and richness ($r^2 = 45\%$), while distinctiveness ($r^2 = 14\%$), evenness

($r^2 = 16\%$) and FEve ($r^2 = 17\%$) were less well explained (Fig. 3A). For round goby, the dominance was well explained by both the environment and biotic variables ($r^2 = 63\%$). The biotic variables show a more moderate degree of explained variance; distinctiveness ($r^2 = 37\%$), FRic ($r^2 = 36\%$), FEve ($r^2 = 33\%$) and evenness ($r^2 = 29\%$) (Fig. 3B). The final SEM structures for both NIS showed a favourable goodness-of-fit (Fisher's test with $p > 0.1$) after including several links between NIS dominance and the environmental variables deemed missing in the initial runs (Suppl. material 1: appendix 2, table S2).

Discussion

Our findings indicate a comparable direct influence of environmental conditions and biotic factors on the dominance of NIS, with biotic variables exerting a slightly stronger overall effect. These outcomes emphasise the importance of biotic drivers (i.e. potential biotic interactions) as small-scale community assembly processes, although biotic interactions are also relevant beyond local extents (Wiens 2011; Wisz et al. 2013). Such results conform with previous works (Zobel et al. 1998; Paine et al. 2011; Gaüzère et al. 2023) and support our initial hypothesis. In addition, we observed that environmental filtering processes play a dual role in defining NIS dominance. The abiotic variables indirectly influenced the dominance of NIS by shaping the structure and composition of local communities, but also by determining suitable conditions for NIS to become dominant.

The biotic attributes from the host community showed a similar influence on NIS dominance in both SEMs, in line with our second hypothesis. More specifically, the observed negative relationship with richness suggests that a higher number of native species or functional groups, present at a given sampled location, may provide some sort of biotic resistance towards both NIS (Elton 1958). Indeed, previous studies have shown that richer communities in species, functions or both, tend to hinder the establishment of NIS, as well as their subsequent expansion and impacts (Kennedy et al. 2002; Santamaría et al. 2021; Delavaux et al. 2023). The underlying mechanisms are likely due to increased competition and predation from native species affecting population numbers of NIS through lower growth, reproduction and survival (Kimbrow et al. 2013). In addition to richness, the positive effect of evenness, demonstrated in both SEMs, indicates that NIS may have a higher chance of becoming dominant if the biomasses are more equally distributed amongst native species, compared to a situation where the biomass is skewed towards one or a few taxa. Whether this implies that the success of NIS may be lower in the presence of a highly competitive or locally better adapted native species (i.e. highly dominant) is unclear and merit further study.

Amongst the environmental variables considered in the SEMs, only depth and bottom temperature had strong and similar effects on richness and evenness in both communities. This corroborates previous studies on the role of both depth and temperature as primary factors structuring marine communities in the Baltic Sea (Olenin 1997; Gogina et al. 2016) and in marine systems elsewhere (Zintzen et al. 2017; Beukhof et al. 2019). In addition to depth and temperature, salinity also impacted the richness and evenness, especially for benthic invertebrates, thus supporting previous findings on the role of salinity structuring the diversity and composition of marine organisms in the Baltic Sea (Törnroos et al. 2015; Gogina et al. 2016; Pecuchet et al. 2016). Although the dominance of both NIS and

the attributes of their associated communities show generally similar responses to several biotic and abiotic drivers, we observed that both NIS can follow different strategies in order to become dominant, as shown by their corresponding relationships with distinctiveness. More specifically, our findings show a higher dominance of round goby when co-existing with functionally similar species, indicating that it might be a good competitor despite native species occupying a similar niche. In the Baltic Sea, round goby has been found to compete with flounder (*Platichthys flesus*) and juvenile cods (*Gadhus morhua*) due to overlapping dietary preferences (Karlson et al. 2007; Ericsson et al. 2021). The apparent success of round goby, even in the presence of competitors, could be due to its aggressive behaviour (Dubs and Corkum 1996; Balshine et al. 2005), coupled with a high degree of territoriality and offspring protection (Vivó-Pons et al. 2023b), which might provide an adaptive advantage for round goby compared to native species, thus limiting the inter-specific competition for resources. Likewise, round goby has also been shown to tolerate a wide range of environmental conditions, specifically for temperature, oxygen and salinity (Christensen et al. 2021; Puntilla-Dodd et al. 2021). This broader environmental tolerance could help with increasing the dominance of round gobies under suboptimal conditions, such as low temperatures or hypoxia. For example, oxygen-poor waters may act as physiological refuges where round gobies would not overlap with predators such as Northern pike (*Esox lucius*) or Atlantic cod (Herlevi et al. 2023), as these species appear to largely avoid hypoxic areas (Neuenfeldt 2002; Yamanaka 2013).

While no significant effect of distinctiveness was found for *Marenzelleria*, the observed negative effect of species richness may provide additional insight. It has been observed that *Marenzelleria* has the potential to displace or strongly compete with other native species (Kotta and Ólafsson 2003; Delefosse et al. 2012). However, this NIS can be outperformed in some cases (Kotta et al. 2004) and several of *Marenzelleria*'s colonisation events occurred only after a mass mortality event of a potential competitor, the native amphipod *Monoporeia affinis* (Maximov 2011). These results may suggest that *Marenzelleria* performs better in the absence of functionally similar species, likely benefitting from a unique or more specialised niche to become dominant. Such a specialised niche may be further evidenced by the positive direct effect of depth on *Marenzelleria*'s dominance. Deeper waters in the Baltic Sea are often characterised by hypoxic conditions (Jovanovic et al. 2014; Carstensen and Conley 2019). Although such conditions are not optimal for *Marenzelleria*, it can withstand fluctuating oxygen conditions or even anoxic events (Schiedek et al. 1997) thanks to its unique pumping behaviour ensuring access to oxygen more efficiently than native species (Jovanovic et al. 2014). This behaviour may help to explain the higher relative biomass of *Marenzelleria* in deeper areas, facing variable oxygen conditions with frequent hypoxia or anoxia. Similarly, the higher dominance of *Marenzelleria* in low-saline areas could be due to its remarkable tolerance to low salinities by both larvae and adult life-stages (Bochert 1997; Stigzelius et al. 1997).

In conclusion, our results show that local-scale biotic drivers together with the environment constitute key determinants of both NIS dominance in recipient communities. These findings highlight that biotic interactions may play a fundamental role in community assembly at small spatial scales (Wisz et al. 2013). However, biotic interactions are often overlooked in studies about the potential future impacts or distribution of NIS, as the influence of environmental variables and

other anthropogenic impacts receive most attention (Geraldi et al. 2020; Bennett et al. 2021; Lindegren et al. 2022). Our findings demonstrate that the diversity and composition of native communities have the potential to control NIS populations (Levine et al. 2004; Santamaría et al. 2021; Delavaux et al. 2023), since the outcomes of interactions with natives (i.e. competition, predation, facilitation) may ultimately define NIS success (Richardson and Pyšek 2012). Finally, the approach used in this study provides a broadly applicable framework to address the potential drivers and community assembly processes influencing NIS dominance in other regions or ecosystem types. In that sense, improved knowledge on where, under what conditions and within which communities NIS can be more successful can enhance spatial management actions directed to address biological invasions (Lodge et al. 2016; Buchadas et al. 2017). Especially at an early stage, fostering preventive actions to keep NIS from becoming invasive and harmful to the overall structure and functioning of ecosystems (Richardson and Pyšek 2012).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

A.V.P. and M.L. conceived the ideas and designed methodology; A.V.P., D.vD. and M.L. conducted the main research with contributions of C.J. and L.F.; A.V.P. analysed the data with contributions of M.L., D.vD. and L.F.; A.V.P. and M.L. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data availability

The data and R code used in this study are publicly available in Dryad (<https://doi.org/10.5061/dryad.4f4qrfjkr>) and GitHub (https://github.com/ToniVP/NIS_dominance).

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Supplementary material 1

Supplementary information

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Data type: docx

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