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A trait-based approach to assess niche overlap and functional distinctiveness between non-indigenous and native species

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Abstract

Our understanding of the community assembly processes acting on non-indigenous species (NIS), as well as the relationship with native species is limited, especially in marine ecosystems. To overcome this knowledge gap we here develop a trait-based approach based on the functional distinctiveness metric to assess niche overlap between NIS and native species, using high-resolution data on benthic invertebrate communities in the Baltic Sea. Our results show that NIS retain a certain degree of similarity with native species, but display one or a few singular unique traits (e.g., bioturbation ability). Furthermore, we demonstrate that community assembly processes, including both environmental filtering and limiting similarity affect NIS establishment, but that their effects may be highly context dependent, as illustrated by pronounced spatial patterns in distinctiveness. Finally, our trait-based approach provides a generic framework applicable to other areas and organisms, to better understand and address biological invasions.

KEYWORDS

Baltic Sea, benthos, biological invasions, functional distinctiveness, trait-based approach, traits

INTRODUCTION

The introduction and spread of non-indigenous species (NIS) pose a major threat to biodiversity and the structure and functioning of ecosystems worldwide (Bax et al., 2003; IPBES, 2023). While the global impact of NIS on marine systems is negative (Anton et al., 2019), their effects on native communities vary widely depending on the context (Guy-Haim et al., 2018; Thomsen et al., 2013; Viana et al., 2019; Vivó-Pons et al., 2020). This diversity of responses is mirrored in the broad range of definitions of NIS, reflecting whether NIS established self-sustaining populations, presented no harm or serious negative effects (Blackburn et al., 2011; Lockwood et al., 2007; Richardson et al., 2000). It is clear that the potential impacts of NIS depend on the identity of the actual NIS as well as on the environmental conditions and composition of native communities (Didham et al., 2005; Geraldi et al., 2020; Thomsen et al., 2014).

NIS establishment, the structure, and composition of communities are shaped by several community assembly processes (Gallien et al., 2015; Kraft et al., 2015; Zobel, 1997). If a community is strongly environmentally filtered, NIS should be limited by the same conditions as natives and therefore present similar traits or life-history strategies (Cornwell et al., 2006; Gallien et al., 2014). Conversely, in communities shaped mostly by competition (e.g. limiting similarity), species tend to be different; thus, a functionally dissimilar NIS might be established (Gallien et al., 2014). However, native species can present biotic resistance (Elton, 1958), which may limit or even completely exclude NIS in recipient communities owing to both competition and predation (Cebrian et al., 2011; Skein et al., 2021). Biotic resistance depends on the community composition and functionality, as more diverse communities show a greater variety of responses (Santamaría et al., 2021; Tilman, 2004). Therefore, understanding the underlying assembly processes acting on

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communities and the degree of niche overlap between NIS and native species is key to expanding our knowledge about biological invasions and improving our management actions to mitigate their consequences (Gallien et al., 2015).

Trait-based studies provide a mechanistic approach to advance our understanding of the underlying processes affecting community structure and function (Mcgill et al., 2006; Violle et al., 2007). Within invasion ecology, trait-based approaches to assess niche overlap between NIS and native species are largely needed (Gallien & Carboni, 2017). This is because traits, rather than taxonomic identities, can help to elucidate the biotic interactions and functional roles of co-occurring species, including NIS (Belmaker et al., 2013; Elleouet et al., 2014; Quell et al., 2021; Xu et al., 2022). Herein, we propose a trait-based framework to facilitate the study of how NIS, independent of their invasion stage (Blackburn et al., 2011), are related to other co-occurring species and the environment, both at large (regional) and fine (local) spatial scales (Figure 1). Combining different spatial scales is recommended to reveal the underlying mechanisms that influence NIS and native coexistence (Gallien & Carboni, 2017; Thuiller et al., 2010), as species interactions tend to be stronger at local scales, potentially driving biotic resistance to invasion (Byers & Noonburg, 2003; Maron & Marler, 2007). We used the functional distinctiveness index as a primary metric of niche differentiation, which reflects the mean functional distance of a single species from all others present in a given community (Violle et al., 2017). This metric has not been used within a formal framework to address NIS and biotic invasions in general, but recently gained considerable attention in ecology (Gaüzère et al., 2023;

Munoz et al., 2023). For example, to assess the current threats of functionally unique species involved in key ecosystem processes (Coulon et al., 2023; Loiseau et al., 2020; Murgier et al., 2021) or to detect the competitive performance of individuals within the same species (Mahaut et al., 2023). Functional distinctiveness offers a precise measure of functional dissimilarity for each single species within a community, thus providing greater resolution compared to other metrics also based on species dissimilarities, but which only allow comparisons between communities as a whole (Mammola et al., 2021). When applied to invasion ecology this metric can enable the comparison between the functional positions of one or several NIS relative to native species, which can be extended across multiple communities and spatial scales.

As an illustrative case study, we tested our proposed framework on benthic invertebrate communities in the Baltic Sea (Figure 2). This large semi-enclosed sea contains >130 recorded NIS, many of which display self-sustaining populations and affect native species in many ways (Leppäkoski et al., 2002; Ojaveer et al., 2021; Ojaveer et al., 2017). The combination of brackish water conditions (Voipio, 1981), the naturally low biodiversity (Gogina et al., 2016; Törnroos et al., 2015) together with previous anthropogenic disturbances (e.g. pollution or warming) make the Baltic Sea highly susceptible to the arrival and establishment of NIS from both marine and limnetic origin (Paavola et al., 2005; Reusch et al., 2018). Although numerous studies have been conducted on NIS in the region (Jaspers et al., 2021; Ojaveer et al., 2010, 2021; Paavola et al., 2005), little is known about the underlying processes determining their establishment or the degree of niche overlap with native species across spatial scales.

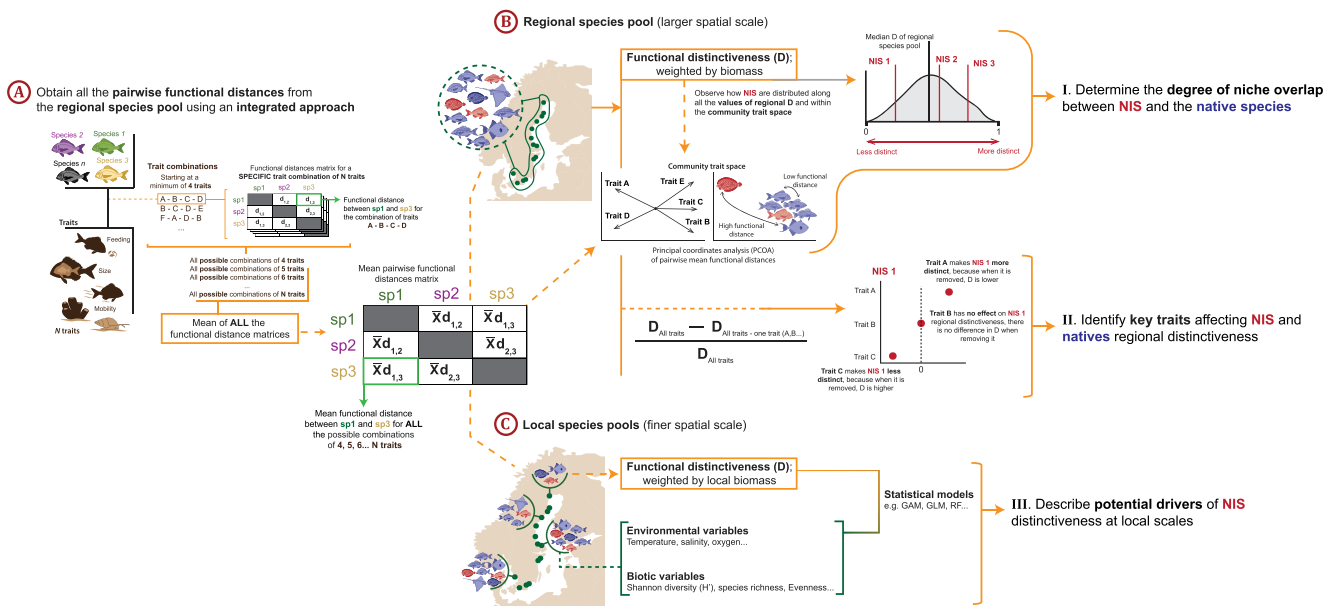


FIGURE 1 Conceptual figure of the proposed trait-based framework showing the different steps of the analysis, as well as the input data and the derived outputs (I–III) fitting the three overall research questions of the study.

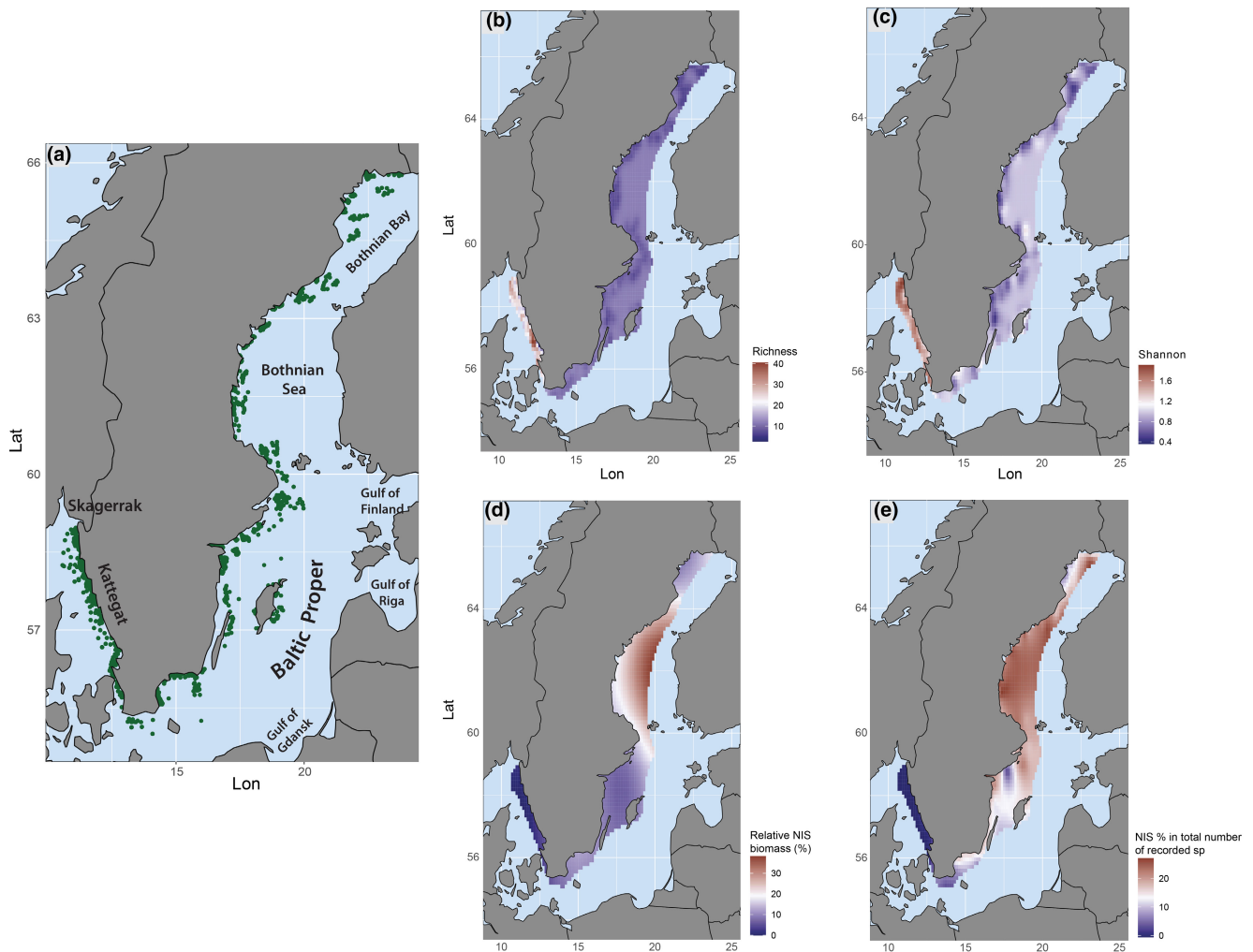


FIGURE 2 Map of the study area including positions of all sampled locations (a). Total species richness (b) and diversity (Shannon H' ; c); relative biomass of NIS (d) and percent of NIS relative to the total number of recorded species (e). Linear interpolation (ordinary kriging) was used to visualize spatial patterns in each metric (b–e).

To address these knowledge gaps, we aimed to answer the following research questions:

1. Are NIS functionally similar or distinct from the native species present in the regional species pool?
2. Which traits make NIS functionally similar or dissimilar to the native species?
3. What are the key drivers and assembly rules that affect the functional distinctiveness of the NIS at fine spatial scales?

MATERIALS AND METHODS

Data collection

Data on species abundance and wet weight of benthic invertebrates from soft substrates along the Swedish coastline were obtained from the Swedish Ocean Archive (<https://sharkweb.smhi.se>). The monitoring programs comprised 1349 stations sampled from 2005 to

2020 from Bothnian Bay to Skagerrak, leading to a total of 7118 unique sampling events (Figure 2a). Only grab samples with approximately 0.1 m^2 area sieved through a 1-mm sieve were included. Wet weight was converted to ash-free dry weight (AFDW), which is the most relevant measure of biomass (Gogina et al., 2022). The conversion factors were obtained from Gogina et al. (2022) for all taxa, except *Ostracoda*, which were extracted from Rumohr et al. (1987). To avoid the inclusion of highly sporadic species, all species representing 99.5% of the total species occurrences were selected, resulting in a total of 189 species. Bivalves were the most common group, representing 57% of the total biomass, followed by brittle stars (*Ophiuroidea*, 18%) and polychaete worms (Polychaeta, 11%) (Figure S1, Table S1). To identify the NIS, we relied on the available classification of NIS in the region (AquaNIS; <https://www.corpi.ku.lt/databases/index.php/aquanis/>). Among these species, five were identified as NIS: *Marenzelleria* spp., *Streblospio benedicti*, *Polydora cornuta* (class: *Polychaeta*), *Mya arenaria* (class: *Bivalvia*) and

Potamopyrgus antipodarum (class: *Gastropoda*). The species complex *Marenzelleria* spp. consists of three highly similar species that are distinguishable only via genetic techniques (Blank et al., 2008). Therefore, the taxa were represented at the genus level. NIS represented only 3.6% of the total biomass, with *Marenzelleria* being the most dominant and widespread species, representing 80.2% of the NIS biomass with more than 3000 occurrences. In contrast, the other NIS were not as widespread (all of them with less than 1500 occurrences combined) and represented only a very small fraction of the NIS biomass (<2%; Figure S1), with the exception of *M. arenaria* (18.6%; Figure S1).

Trait data collection

To broadly characterize the ecology of the species, 10 morphological, physiological and behavioural traits were selected: size, adult life span, reproductive type, developmental mechanism, environmental position, living habits, feeding habits, mobility, movement method and bioturbation ability (Table 1). The selected set of traits and their associated modalities aimed to represent the fundamental processes of feeding, growth, reproduction and survival following existing trait-based descriptions of marine organisms (Litchman et al., 2013; Törnroos & Bonsdorff, 2012). Trait information was obtained from online trait data portals, including WoRMS (World Register of Marine Species; <https://www.marinespecies.org/>), MARLIN (<https://www.marlin.ac.uk/biotic/>), Polytraits (<http://polytraits.lifewatchgreece.eu/>), as well as from literature and other peer-reviewed sources (Garcia, 2010). If missing, trait information was supplemented with expert knowledge following the procedure used in Törnroos et al. (2015, 2019) and Törnroos and Bonsdorff (2012). For traits classified as multi-choice nominal, a score of 1 was assigned to the trait modality expressed by a species, whereas non-expressed modalities were scored as 0. Ordinal traits, according to the values of the different modalities, were ranked from 1 to the maximum number of categories (i.e. from 1 to 5 for size and adult lifespan, as both traits had five modalities each) (Table 1). From the selected 189 species, complete trait information was found for 173 species (91.5%), which formed the final selection.

Step I: Evaluation of the degree of niche overlap between NIS and native species at a regional scale

To determine the degree of niche overlap between NIS and the native species present in the regional pool, we applied the functional distinctiveness metric (D) by Violle et al. (2017) using the following equation:

$$D_i = \frac{\sum_{j=1; j \neq i}^N d_{ij}}{\sum_{j=1; j \neq i}^N N - 1} \quad (1)$$

where d_{ij} is the functional distance between species i and j and N is the number of species in the community. This metric can also be weighted based on the relative importance of species,

$$D_i = \frac{\sum_{j=1; j \neq i}^N d_{ij} \times Ab_j}{\sum_{j=1; j \neq i}^N Ab_j} \quad (2)$$

where Ab_j accounts for the relative importance of species j based on either biomass (e.g. AFDW) or the number of individuals. Consequently, abundant species with common traits lead to low values of D , whereas rare species with uncommon traits lead to a high value of D . The functional distance between each pair of species (d_{ij}) was obtained from Gower's general coefficient of dissimilarity (Gower, 1971) that assigns equal weights between traits with different classes (i.e. numerical, categorical, or ordinal) (Pavoine et al., 2009). However, to avoid potential biases owing to one or a few traits having a disproportional effect on functional distances and distinctiveness, we performed an integrated process to compare the outcomes for multiple combinations of randomly selected traits (Coulon et al., 2023; Figure 1). As a sensitivity test, we first estimated and compared the functional distances and associated distinctiveness for all possible combinations of four, six and eight traits (Figure S2a–c). Then, we started with all combinations of four traits (here considered as a minimum to characterize niche differences between species) and sequentially added one trait until reaching the maximum number of available traits (i.e. 10). This integrated process resulted in 848 matrices for all the multiple trait combinations. These were then summarized into a mean functional distance matrix containing all pairwise distances (d_{ij}) between species (Figure 1a). From this overall mean functional distance matrix, different values of functional distinctiveness were calculated at both the regional and local scales. To test the sensitivity of the values to different weightings, we also included a formal comparison between the values of regional distinctiveness weighted by abundance, biomass (AFDW) or non-weighted. Finally, we performed a principal coordinate analysis (PCoA) on the overall pairwise dissimilarity matrix (Belmaker et al., 2013). This was done to compare the degree of functional similarity in the trait space between the NIS and native species present in the regional species pool. A specific decile was assigned to each species based on its distinctiveness value to classify them into functionally common or distinct species. Hence, the 1st decile accounted for functionally common species (low distinctiveness), whereas the 10th decile accounted for the most functionally distinct species. Functional distances were computed using the function `compute_dist_matrix` from the `funrar` package

TABLE 1 List of traits and modalities included with their explanation.

Traits	Nature of the trait	Categories (<i>n</i> =56)	Frequency (% of species having that category)	Explanation
Size	Ordinal	0–10 mm	16	
		11–20 mm	20	
		21–50 mm	25	
		51–100 mm	27	
		>100 mm	13	
Adult life span	Ordinal	<1 year	12	
		1–3 years	45	
		3–6 years	29	
		6–10 years	5	
Reproductive type	Multi-choice nominal	Semelparous-Monotelic	14	Species that reproduce once then dying
		Iteroparous-Polytelic	72	Species that breeds several times (episodic or over an extended period)
		Semi-continuous	19	Species with a short life time that breeds semi-continuously over their lifetime
Developmental mechanism	Multi-choice nominal	Fragmentation/Fission	2	Species with an asexual developmental, includes fragmentation, fission, and budding
		Direct	36	Species that have a benthic direct development of individuals with adult appearance
		Lecitotrophic	31	Species with pelagic larvae nourished on internal resources
		Planktotrophic	49	Species with pelagic larvae feeding on material captured from the plankton
		Ovoviviparous	1	Embryo(s) develop in persistent membranes and hatch within the maternal body. No nutrition is derived from the mother
Environmental position	Multi-choice nominal	Infaua deep	11	Living within the substrate, deeper than 5 cm
		Infaua middle	73	Living within the substrate, between 2–5 cm
		Infaua top	77	Living within the top 2 cm of the substrate
		Interface	2	Living half in and half out of the sediment
		Epibenthic	26	Living on the surface of the substrate
		Benthopelagic	3	Living in the water column but (primarily/ occasionally) feeds on the bottom
		Epilithic	1	Living in the surface of rock or other hard inorganic substrata
Living habits	Multi-choice nominal	Epifaunal	2	Living on the surface of other organisms
		Attached	2	Adherent to a substratum temporarily or permanently (95% of the adult life time)
		Tube dweller	24	Builds and dwells in tube(s)
		Burrow dweller	40	Builds and dwells in burrow(s)
		Crevic dweller	4	Builds and dwells in crevic(s)
		Case builder	1	Builds and dwells in case(s)
		Free	55	Free living in or on sediment or in water column
Parasite/commensal	2	Lives parasitic or associated with others		

(Continues)

TABLE 1 (Continued)

Traits	Nature of the trait	Categories (<i>n</i> =56)	Frequency (% of species having that category)	Explanation
Feeding habit	Multi-choice nominal	Suspension/filter feeder	36	Obtaining food by actively or passively sweeping or holding out a filter
		Deposit-feeder	69	Can feed either on the sediment surface or on the sub-surface with or without an active selection of particles
		Predator	31	Feeds on live prey, active predation
		Scavenger	14	Feeds on dead animal or plant material
		Herbivore	5	Feeds on plant material
		Miner/Borer	0	Obtaining food through mining or boring in e.g. woody material
		Parasite	2	Obtaining food from another animal
		Grazer	1	Obtaining food by rasping benthic algae or sessile animals from inorganic particles, the substratum or the surface of macroalgal fronds and blades
Mobility	Multi-choice nominal	Sessile	2	Temporary or permanently (more than 90% of adult life)
		Semi-motile	37	
		Motile	64	
Movement method	Multi-choice nominal	No movement	1	
		Swimmer	21	An organism that moves through the water column via movements of its fins, legs or appendages, via undulatory movements of the body or via jet propulsion
		Crawler	40	An organism that moves along on the substratum via movements of its legs, appendages or muscles
		Rafter/Drifter/Byssus	8	An organism whose movement is dependent on wind or water currents
		Tube-builder	20	
		Burrower	72	An organism that lives or moves in a burrow
		Temporary attachment	2	Attached to a substratum but capable of movement across (or through) it
Bioturbation	Multi-choice nominal	No transport	21	
		Diffusive mixing	62	Vertical diffusive transport (e.g. reworking, excavation)
		Surface deposition	24	Surface deposition or particles (e.g. defecation or egestion)
		Conveyor belt transport	8	Translocation of sediment within the sediment from deeper parts to top of sediment
		Reverse conveyor belt transport	18	Subduction of particles from surface to some depths

(Grenié et al., 2017) in R software, version 4.1.0 (R Core Team, 2021).

Step II: Identification of key traits affecting NIS regional distinctiveness

To assess the effect of each trait on functional distinctiveness, we calculated the difference between the

distinctiveness values for each species based on all traits ($D_{i,T}$) and the values when each individual trait was removed from the analysis ($D_{i,T-t}$). We then divided the difference by regional distinctiveness, including all traits ($D_{i,T}$) as follows:

$$\text{Effect of trait}_t \text{ on } D_i = \frac{D_{i,T} - D_{i,T-t}}{D_{i,T}} \times 100 \quad (3)$$

Thus, the relative importance of each trait was expressed as the percentage of variation in regional distinctiveness, where a positive or negative value implied that a specific trait, if excluded, made a given species more or less distinct than all other species, respectively. This calculation was repeated for all the traits, with one trait removed at a time.

Step III: Patterns and drivers of NIS functional distinctiveness at a local scale

To assess the patterns and drivers of NIS distinctiveness on a fine spatial scale, we extracted the functional distances between all species present at each unique sampling event from the overall pairwise matrix of mean functional distances (Figure 1c). These distances were combined with the corresponding species biomass to compute the local D of each individual NIS compared to the native species present (Equation 2). To visualize spatial patterns in local distinctiveness, we computed the mean D of all NIS for each site where NIS was present, as well as the mean D for only the native species and then interpolated the values throughout the study area using ordinary kriging (see Appendix S1, Table S4). Please note that the derived maps were only used for visualization and not for the subsequent analysis.

We applied a multi-model approach using generalized additive mixed models (GAMMs) to test which variables drive NIS local distinctiveness. GAMMs were selected because they provide a useful tool for examining nonlinear relationships while allowing the inclusion of random effects (Wood, 2017; Zuur et al., 2009). To reflect the potential effect of environmental filtering on the local distinctiveness of the NIS, we extracted the monthly median-specific values of bottom salinity, temperature and dissolved oxygen for each unique sampling event (Figure S4). Data were derived from the ice-ocean model NEMO-Nordic (<https://doi.org/10.48670/moi-00013>) available from the Copernicus Marine Service (<https://marine.copernicus.eu/>). Depth measured in situ for each sampling location was included as an additional environmental variable (Figure S4c). To reflect potential biotic effects, we estimated species richness and the Shannon diversity index (H') based on the number of species and their relative biomass in each sample (Figure 2b,c). These were selected to represent assembly processes affecting limiting similarity (e.g. competition), acting through both the number and evenness of species. All variables had a variance inflation factor of <2.5 , thus discarding any possibility of multicollinearity between predictors.

To account for imbalance in the number of observations between NIS, we resampled the data according to a value lower than the least observed species (i.e. *P. cornuta* with <50 occurrences). This was done to avoid statistical relationships being biased by the most

abundant species and therefore detect key drivers of local distinctiveness across NIS. Hence, we obtained random subsets of 40 observations for each NIS and fitted a joint model using species and site as random effects. This process was repeated 400 times to assess the range of outcomes across multiple bootstraps. To determine whether the explanatory variables had an overall effect on distinctiveness, we estimated the proportion of the total number of models in which the variables had significant effects. Furthermore, the general relationship between distinctiveness and each predictor was obtained by estimating a smooth line that summarized the common patterns from all the individual models. GAMMs were additionally fitted for each NIS to detect the species-specific effects of the environmental and biotic drivers on their distinctiveness (Figure S5, Table S5). Further details regarding the model setup and formulation are provided in the Supplementary Material (Appendix S2). All statistical analyses were conducted using the R software, version 4.1.0 (R Core Team, 2021) and the package *mgcv* (Wood, 2017).

RESULTS

Step I: Niche overlap between NIS and native species at a regional scale

The distribution of distinctiveness values for all species present in the regional pool was quite narrow when non-weighted or weighted by the mean abundance of species (Figure 3a). In contrast, when weighted by AFDW, the distribution was wider and covered a broad range of values (Figure 3a). The median regional distinctiveness weighted by AFDW was similar for natives (0.23) and NIS (0.27) (see Table S1 for each species). However, all NIS, except *M. arenaria*, showed higher values than the median for the entire regional species pool (Figure 3b).

The first two axes of the trait space explained 35.6% and 19.9% of the total variability between species. The two less distinct NIS (*Marenzelleria* and *M. arenaria*) were found closer to the most functionally common species (defined by the 1st decile; Figure 3c). These species were aggregated (Figure 3c) and were mostly defined by trait categories commonly shared between species in the regional pool (Figure 3d, Table 1; Table S2), for instance, having an iteroparous reproductive type (shared by 72% of species), a planktotrophic developmental mechanism (71%), as well as being burrowers (72%), living in the top (77%) or middle (73%) part of the substrate. In contrast, the other NIS (*P. cornuta*, and *S. benedicti*) were located close to functionally distinct species, while *P. antipodarum* was classified as one of the most distinct species in the regional pool (defined by the 10th decile). Those species were less aggregated, occupied a broad area in the trait space (Figure 3c) and were defined by uncommon trait

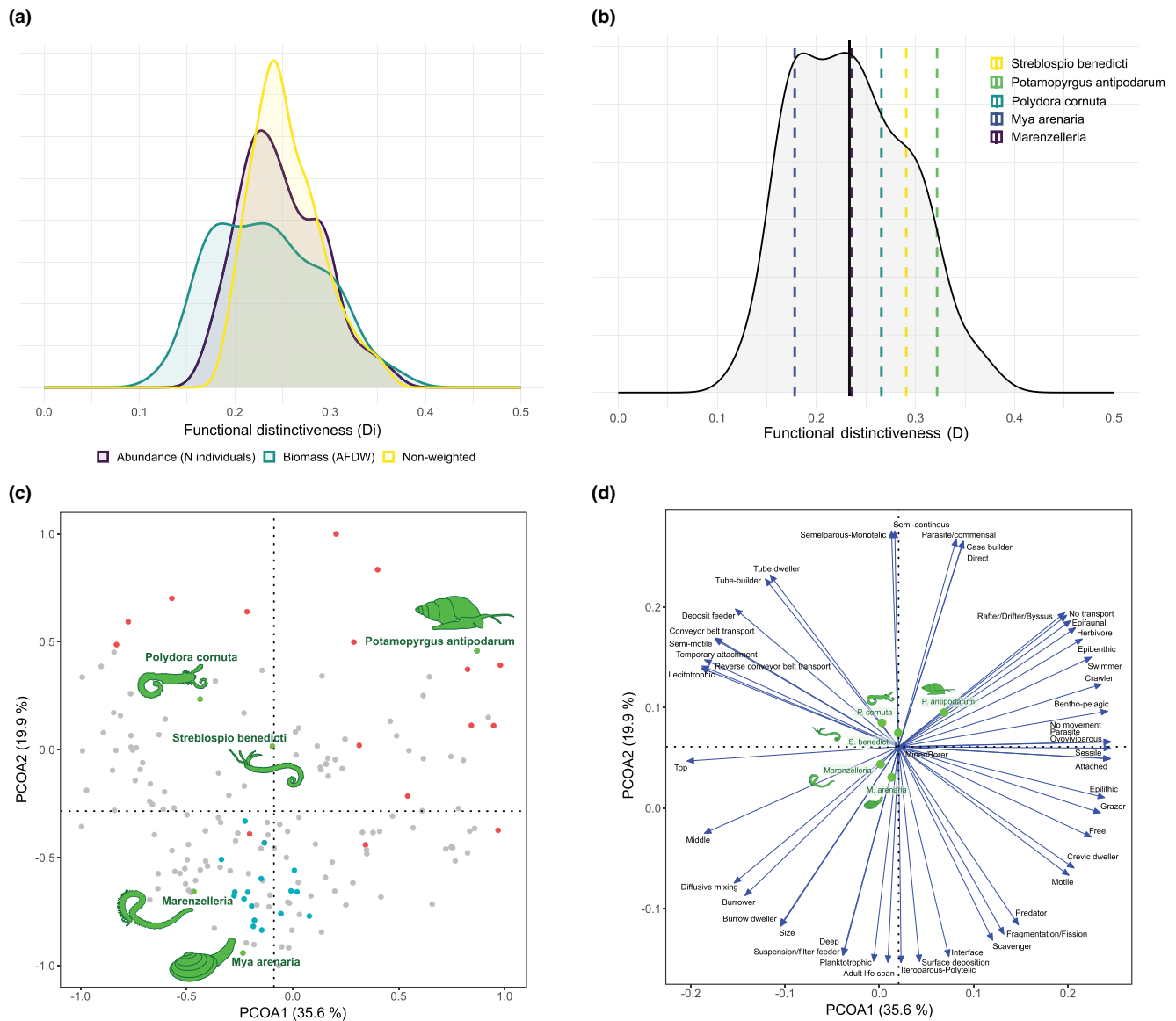


FIGURE 3 Distribution of D values for all species in the regional species pool according to different weightings (a). Position of NIS along the distribution of biomass-weighted D values from the regional species pool (b). The black vertical line indicates the median value of distinctiveness across species. Community trait space given by a PCOA of functional distances between all species in the regional species pool (c). Green dots indicate the position of NIS. Red dots indicate the position of species classified as being the most distinct, while blue dots define species classified as most similar compared to the rest of the community. (d) A biplot of trait vectors and loadings showing which traits are influencing the position of each species in the PCOA.

modalities (Figure 3d, Table 1; Table S2), including being semi-motile (37%), semelparous (14%) or tube-dwelling organisms (24%) not transporting any sediment (21%).

Step II: Key traits affecting NIS regional distinctiveness

The relative influence of each trait on the regional distinctiveness demonstrated that bioturbation had the highest overall positive effect on NIS (10.2%), whereas living habits had the most negative effect (−6.7%) (Figure 4). Notably, the median effect of bioturbation on NIS distinctiveness was higher than that of bioturbation

on natives. This indicates that the presence of certain uncommon modalities for bioturbation in the regional species pool make NIS more distinct than the native species. This was particularly evident for *Marenzelleria* and *M. arenaria*, which demonstrated the highest positive effects for bioturbation among the set of NIS (18% and 15%, respectively). These values rank *Marenzelleria* and *M. arenaria* as the 4th and 14th species in the entire regional pool ($N=173$), respectively, with the highest increase in distinctiveness for bioturbation. A similar result was also observed for mobility, where *S. benedicti* and *P. cornuta* demonstrated modalities contributing to positive effects (−10%) compared to negative effects for the other NIS and native species for this trait.

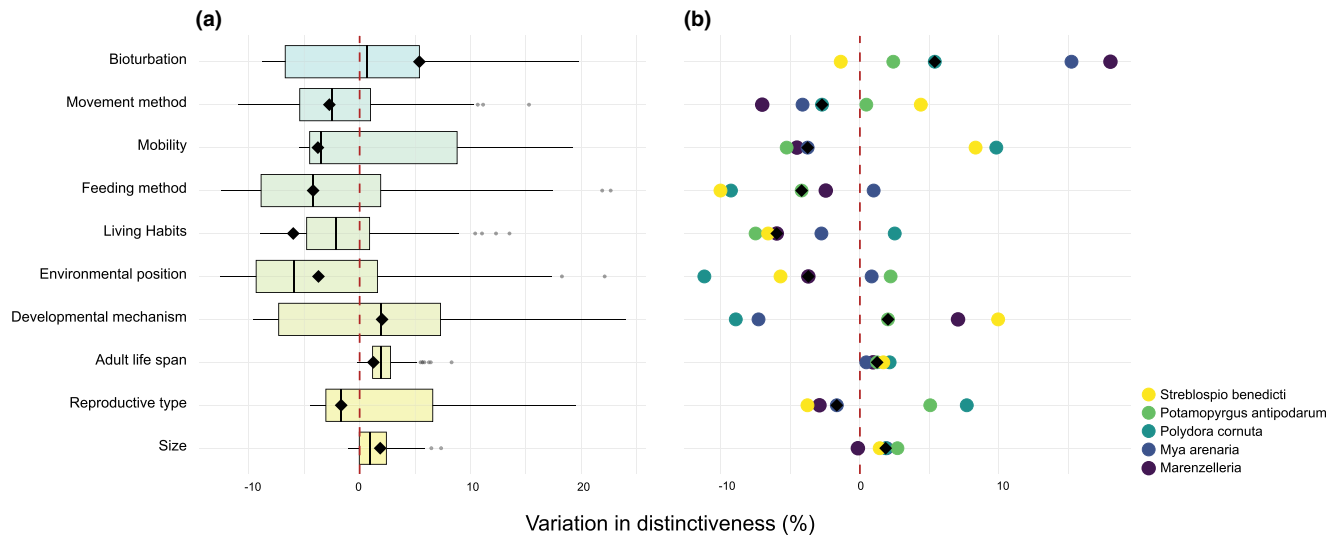


FIGURE 4 Effect of traits on species functional distinctiveness, shown as the percentage change in overall distinctiveness if excluding each individual trait in the calculations. Results are shown when using either the whole regional species pool (a), or only NIS (b). The black diamonds in both panels indicate the median effect for all NIS.

Step III: Patterns and drivers of NIS functional distinctiveness at a local scale

The overall distinctiveness of NIS was highest in the central and Northern Baltic Sea (Figure 5a; Figure S3). Similarly, the natives demonstrated the highest distinctiveness in the Bothnian Bay and the lowest distinctiveness on the west coast along Skagerrak and Kattegat (Figure 5b). Among the selected model predictors, Shannon, depth and bottom salinity had a significant effect on the local distinctiveness of NIS in >50% of models (Figure 5c). The remaining predictors did not demonstrate consistent and overall significant effects across all models (Table S3; Figure 5c). The overall trends in the fitted relationships between NIS distinctiveness versus salinity and depth showed similar positive relationships (Figure 5d). Conversely, we observed an overall negative relationship with Shannon's diversity index (Figure 5d). The random factors (*Species* and *Station*) were significant across models (100% and 97.7%, respectively), indicating a strong context and species dependence of this metric at fine local scales (Table S3).

DISCUSSION

Our trait-based framework showed that the set of NIS considered in this study were generally not fundamentally different from native species, at least when considering the entire regional species pool. Although four of the five NIS displayed higher values of distinctiveness than the median for the whole species pool, the two most widespread NIS with the highest biomass, *Marenzelleria* and *M. arenaria*, showed values close to or even below the median of the whole community. The different degrees of regional distinctiveness between NIS were also

evident from the community trait space, where the three most distinct NIS (*P. antipodarum*, *P. cornuta* and *S. benedictii*) were relatively close to the native species classified as being the most distinct, whereas *Marenzelleria* and *M. arenaria* were associated with the most functionally common species. This indicates that regardless of their level of distinctiveness, the NIS may share, or at least partially overlap with the niches of the native species.

In contrast, some NIS displayed differences in terms of individual trait modalities. Overall, the key trait distinguishing NIS from the native species was mainly bioturbation and to a lesser degree, size. This partially conforms to the findings of Quell et al. (2021), who demonstrated that large bodies, long lifespans, and singular burial behaviour were the most common traits among benthic NIS in Western Europe. In our study, the two most widespread NIS (*Marenzelleria* and *M. arenaria*) displayed the two largest modalities for size (51–100 mm and >100 mm, respectively), had long lifespans (3–6 and 6–10 years, respectively), and were both burrowing species (Table S2). Although both species can be found living in the top and middle parts of the substrate, they can also live in deeper layers, resulting in a combination of traits shared by only eight species in the regional pool (Table S2). Although Quell et al. (2021) did not specifically consider bioturbation, it is directly influenced by burrowing behaviour (Harvey et al., 2019). This was particularly notable for *Marenzelleria*, showing the 4th highest increase in distinctiveness for bioturbation, likely due to displaying the two least common trait modalities, namely conveyor and reverse conveyor belt transport (Table 1; Table S2). *Marenzelleria* can enhance bioturbation and exchange of solutes between sediment and bottom water (Bonaglia et al., 2013; Kauppi et al., 2018). Although the large-scale consequences of

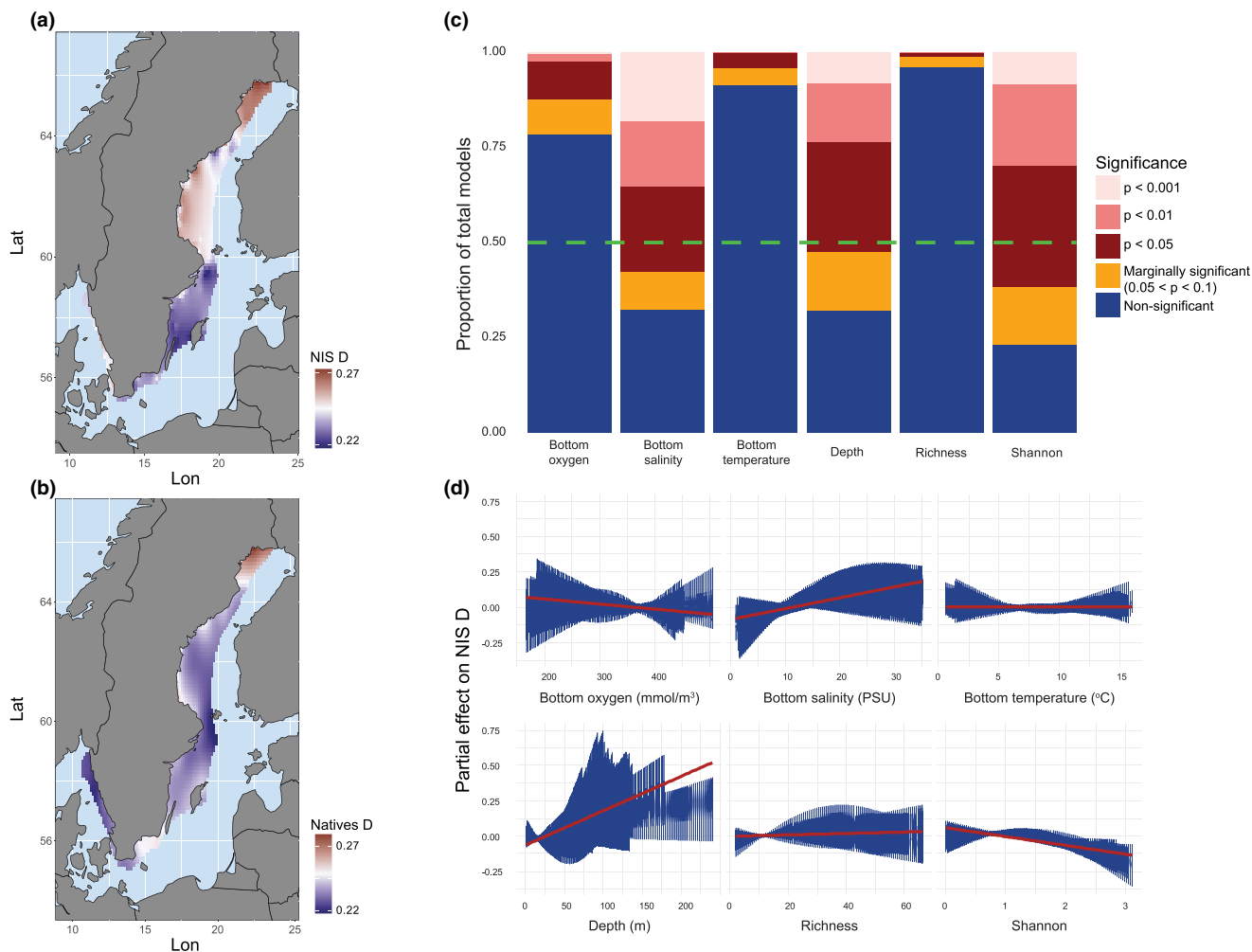


FIGURE 5 Spatial patterns of mean functional distinctiveness among the native species (a), as well as between NIS and the native species in each local community (b). Proportion of individual models with the effect of each variable on distinctiveness (c). The red colour scale accounts for models where p -value < 0.05 ; lighter red accounts for a lower p -value. Orange accounts for marginal significant effects ($0.05 < p < 0.1$) and in blue are shown the amount of models where the variable showed no effects. (d) Combination of all the individual models' partial effect of each variable on NIS distinctiveness (blue shades), including the overall trend line (red).

Marezzelleria are unknown, this unique trait may potentially contribute or add a new ecosystem function that did not exist before (Didžiulis, 2006; Sandman et al., 2018). Taken together, our results support previous terrestrial and freshwater studies demonstrating that NIS may be successfully established by displaying only one or a few singular traits, allowing them to colonize new or partly vacant niches while retaining a certain degree of similarity with the natives (Cleland, 2011; El-Barougy et al., 2020; Xu et al., 2022), thus being able to cope with the existing environmental pressure (Gallien et al., 2014).

While we show a rather moderate degree of functional distinctiveness of NIS compared to the regional species pool, we observed pronounced spatial differences in the level of local distinctiveness. Among the candidate factors explaining this variability, bottom salinity and depth showed the strongest effects. A marked salinity effect has also been observed for fish,

where the pronounced Baltic Sea salinity gradient is regarded as the primary driver influencing diversity and community composition (Pecuchet et al., 2016). Specifically, brackish conditions strongly limit the types of species and traits needed for survival, resulting in less species and low functional richness (Ojaveer et al., 2010; Törnroos et al., 2015). Therefore, as both natives and NIS experience strong environmental filtering, low functional distinctiveness emerge due to a limited variety of species and traits (MacArthur & Levins, 1967; Zobel, 1997). The spatial patterns of distinctiveness follow a 'transition zone' between the marine and freshwater communities (Paavola et al., 2005; Remane, 1934). Such transition areas are known to be functional hotspots as they tend to be functionally diverse because species from different environments may co-exist at their edges of tolerance (Darr et al., 2014; Törnroos et al., 2015). The opposite cases of *P. antipodarum* and *Marezzelleria* can be used to

elucidate the changes in distinctiveness that occur in functional hotspots (Figures S3c,d and S5b,e). *P. antipodarum* is native to freshwater in New Zealand but can also adapt to saline conditions (Hoy et al., 2012), in contrast to *Marezzelleria*, native from North America and able to withstand oligohaline conditions (Stigzelius et al., 1997). Hence, under low-salinity conditions, both species co-occur with more freshwater-like species, whereas as salinity increases marine species appear, being functionally similar to *Marezzelleria* and dissimilar to *P. antipodarum*.

Depth appears as a primary structuring factor for marine communities, also in the Baltic Sea, where benthic communities experience substantial changes with depth (Beukhof et al., 2019; Gogina et al., 2016; Olenin, 1997). In our study, the organisms were primarily shallow-water species occurring at a depth of 0–50 m (Strasser, 1998; Figure S6). However, a few species can occur at considerably greater depths, if adapted to withstand the deep-water hypoxia (Carstensen & Conley, 2019; Koop et al., 1990). This is particularly the case for *Marezzelleria*, which has a unique pumping behaviour that ensures access to oxygen, allowing it to tolerate hypoxia better than native species (Fritzsche, 1997; Jovanovic et al., 2014). Hence, the positive relationship between depth and local distinctiveness of the NIS can largely be explained by the unique ability and occurrence of *Marezzelleria* at great depths (Figure S6b). Furthermore, this reflects the role of depth as an environmental filter determining community composition and the presence of NIS in marine ecosystems, similar to the effects of altitude on land (Li et al., 2023; Steinbauer et al., 2017).

Among the biotic variables considered, we detected a negative relationship between the Shannon diversity index and NIS local distinctiveness, but no overall effect of species richness. The latter may be due to the pronounced gradient in both salinity and the number of species in the area (Ojaveer et al., 2010; Törnroos et al., 2015) which may mask an overall effect of richness, despite significant individual level effects for some of the NIS (Figure S5). Regardless of whether there are many or few species in the local pool highly uneven communities can be found at small spatial scales (Hillebrand et al., 2008). Under such conditions, where the most dominant species limits the presence and abundance of other functionally similar species, NIS distinctiveness might be high if displaying different trait combinations than the most dominant native species. Conversely, in equally rich but even local communities (i.e. high Shannon values), it is generally assumed that most of the niches are occupied (Hillebrand et al., 2008). Native species that occupy these niches could display a great variety of responses towards newly arrived species, which could result in a low establishment success for NIS (Kimbrow et al., 2013; Maron & Marler, 2007). Therefore, lower values of

distinctiveness in more even communities could be associated with a scenario where the NIS needs to retain a certain degree of similarity, likely as a result of environmental filtering but at the same time needs to display some degree of dissimilarity to not be outcompeted by natives in case niche is occupied (Gallien et al., 2014). In terms of competition, some of the NIS found in our study area, notably *M. arenaria* and *P. antipodarum*, have been present for a long time and are considered as completely naturalized. Hence, the potential impacts from their past introductions may be difficult to quantify (Jensen, 2010a, 2010b; Strasser, 1998). However, if they colonize new areas, they may interact with and affect native species (Kerans et al., 2005; Obolewski & Piesik, 2005), for instance through competition, which has been shown to occur following the introduction of *Marezzelleria* (Kotta et al., 2001). Hence, a better understanding of the traits and potential niche overlap between NIS and native species may allow for an exploratory assessment of the potential vulnerabilities and impacts of NIS on recipient communities.

We are aware that our framework represents a simplification of complex processes regulating the establishment of NIS. Such complexity must be integrated within a functional approach using appropriate metrics together with other issued considerations (Gallien et al., 2014; Gallien & Carboni, 2017; Thuiller et al., 2010). Functional distinctiveness reflects niche differentiation between a specific NIS and other co-occurring species, known as the alpha niche concept (Ackerly & Cornwell, 2007). Implementation of this concept to biological invasions is strongly recommended to study how the trait expression of a given NIS could influence its establishment, by exploiting unique resources or displaying singular behaviour (Stubbs & Wilson, 2004; Thuiller et al., 2010). Unlike other available metrics also related to the alpha niche concept (e.g. distance to the most abundant native species [DMANS] or distance to the nearest native species [DNNS]) (Thuiller et al., 2010), functional distinctiveness allows to address invasions from a community perspective, because NIS will coexist and interact with all present species; not only with the most abundant (DMANS) or functionally similar species (DNNS). Additionally, functional distinctiveness appears as a suitable metric to assess the type of community filtering at work, as it represents the functional distance of an invader towards the rest of the species (Gallien et al., 2014) that can also be weighted by the relative abundance (MDNS and WMDNS; Thuiller et al., 2010). To this end, we encourage further research on biological invasion to apply functional distinctiveness to other case studies (Gallien & Carboni, 2017; Strayer, 2012). Some possible applications could be related to the effects of local distinctiveness in NIS dominance, determining changes in community functions (see Viana et al., 2019), as well as detecting possible

signs of competition, trophic interactions, or facilitation (Altieri et al., 2010; Elo et al., 2021; Marjankangas et al., 2021), potentially through, combining our approach with new community modelling techniques (Ovaskainen et al., 2017).

In conclusion, the trait-based approach used in this study allowed us to better describe and understand the relationship and degree of niche overlap between NIS and native species, as well as the potential underlying assembly rules determining the establishment of NIS. The developed framework is generic and therefore applicable to other aquatic or terrestrial case studies where NIS are found and where data on their traits and abundances (or biomass) are available. Furthermore, it may inform management and conservation actions targeting NIS, for instance by identifying habitats and sites that are particularly sensitive and vulnerable to biotic invasions (i.e. given by the trait composition of the native communities and their potential niche overlap with potential invaders). Such knowledge can feed into existing risk assessment tools that address biotic invasions (Lodge et al., 2016) to better prioritize spatial management actions. To this end, we support the idea of Murgier et al. (2021) to consider functional distinctiveness within management and conservation, especially regarding biotic invasion and its impacts on native communities worldwide.

AUTHOR CONTRIBUTIONS

Antoni Vivó-Pons and Martin Lindegren conceived the ideas and designed methodology; Mats Blomqvist and Anna Törnroos collected the data with contributions of Antoni Vivó-Pons; Antoni Vivó-Pons analysed the data with contributions of Martin Lindegren, Mats Blomqvist and Anna Törnroos; Antoni Vivó-Pons and Martin Lindegren 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 STATEMENT

The data and R code used in this study are publicly available in Dryad (<https://doi.org/10.5061/dryad.4mw6m90gn>) and GitHub (https://github.com/ToniVP/NIS_distinctiveness).

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SUPPORTING INFORMATION

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