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Distribution of functionally distinct native and non-indigenous species within marine urban habitats

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Abstract

Aim: Trait-based approaches are powerful to examine the processes associated with biological invasions. Functional comparison among native and non-indigenous species (NIS) can notably infer whether novel assemblages result from neutral or niche-based assembly rules. Applying such a framework to biofouling communities, our study aimed to elucidate their distributions within two marine urban habitats (namely floating vs. nonfloating habitats).

Location: Southeast Pacific—Central Chilean coastline.

Methods: Here, we examined the distribution of 12 functional traits in fouling communities established on settlement plates, after 3 and 13 months of deployment in the two habitats and across ports in Central Chile. Based upon previously described differences of assemblages and NIS contribution across habitats, we hypothesized that nonindigenous, cryptogenic and native taxon pools would be functionally distinct (and trait biased), and that functional diversity and structure would vary across habitats and successional stages.

Results: Our results show, as anticipated, that nonindigenous (13 taxa), cryptogenic (12) and native (18) taxon pools are functionally distinct, though overlapping in the trait space. Non-indigenous species are rather related to colonizing traits, while native species are more related to competitive traits. Only one widespread NIS was functionally similar to the late successional and most competitive native species, including taxa elsewhere invasives. Despite differences in taxonomic composition between habitats, we did not observe functional differences between them. In contrast, temporal variations across colonization stages were detected along with an increased contribution in large and long-lived taxa, together with site-specific trajectories.

Main Conclusions: We conclude that the functional distinctness among nonindigenous, cryptogenic and native taxa occupying artificial habitats in ports reflects niche-based processes. Site-specific trajectories indicate that scale-dependent assembly processes, such as dispersal and species interactions, are at play.

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KEYWORDS

artificial structures, community assembly, limiting similarity, SE Pacific, sessile assemblages, trait-based approach

1 | INTRODUCTION

Trait-based approaches can provide valuable insights into the ecological and evolutionary processes associated with biological invasions (Daly et al., 2023; Pearson, Ortega, Eren, & Hierro, 2018; Van Kleunen, Dawson, et al., 2010; Villéger et al., 2014). Variations in functional traits have long been recognized as major determinants of multiple stages of biological invasion processes (Catford et al., 2019; Elton, 1958; MacArthur & Levins, 1967; Van Kleunen, Dawson, et al., 2010). Subsequent investigations have questioned what makes non-indigenous species (NIS) invasive (invasiveness) and/or what makes communities susceptible to establishment, spread and potential impacts (invasibility), either supporting or opposing diverse hypotheses (Brown & Barney, 2021; Daly et al., 2023).

Much research effort has been made in looking for traits associated with the invasiveness of introduced species (Pyšek & Richardson, 2008; van Kleunen, Weber, & Fischer, 2010). This can be done by comparing trait composition and/or values among invasive vs. noninvasive introduced species, although further comparisons with native groups can be particularly insightful (Hufbauer & Torchin, 2008). Such approaches have for instance helped to infer greater propensity of invasive than noninvasive plants for traits associated with performance in a given environment (physiology, leaf-area allocation, shoot allocation, growth rate, size and fitness; van Kleunen, Weber, & Fischer, 2010). The application of a framework similar to that proposed by van Kleunen, Weber, and Fischer (2010) has rarely been attempted in marine systems. Using the modalities of nine potential traits, Cardeccia et al. (2018) sought functional distinction among the most widespread marine NIS in European seas and a subset of these species, classified by the authors as putatively 'impact-causing'. Although traits conferring high dispersal ability, high reproductive rate and ecological versatility appeared common in all 68 taxa studied, the two groups of NIS could not be discriminated. In these systems, further research and comparative work are encouraged.

Examining functional traits within local communities can also help understanding assembly rules among native and non-indigenous species, in particular if they follow random (or neutral) vs. deterministic rules (cf. invasibility). Such an approach can help addressing mechanisms associated with the limiting similarity concept, which considers coexistence or reduction in interspecific competition within communities as driven by functional distinctness or distinct niche occupancy and resource partitioning among species (Fargione et al., 2003; MacArthur & Levins, 1967; Price & Pärtel, 2013). This concept is intimately linked to the biotic resistance hypothesis of Elton (1958). Although the limiting similarity concept has received some support in plant communities, it seems not generalisable to all types of plants (e.g. forbs vs. grass) and to all assemblages types

(natural vs. experimental; Price & Pärtel, 2013). Besides mechanisms that may explain deviation to this rule at a local scale (e.g. fluctuating resources, productivity; Davis et al., 2000), the different stages of the biological invasion process (from pretransport to range expansion; Blackburn et al., 2011) are critical to consider. In addition, filters such as biotic interactions, propagule pressure and disturbances, interplaying at local scales, also interact with neutral and nonrandom processes operating at regional to global scales (e.g. natural vs. aided dispersal; Brown & Barney, 2021), such as anthropogenic drivers of changes (e.g. climate change, species extirpation and habitat modification; Pyšek et al., 2020). These interactions can lead to modification, including trait-biased homogenization of community composition across multiple spatial scales, and may cascade upon associated functions (McKinney, 2006; Olden et al., 2004; Villéger et al., 2014).

The complex interactions among such processes can be illustrated by the concomitant alteration of natural habitats and expansion of marine artificial infrastructures embedded within an ever-growing network of propagule transport (e.g. via the maritime traffic; Carlton, 1996; Johnston et al., 2017). Marine built infrastructures and disturbances liberate surface available to colonization by fouling communities. Depending on the local disturbance regime, these surfaces can exacerbate colonization of opportunist and stress-resistant taxa (Johnston et al., 2017). Regardless of their status as nonindigenous versus native species locally, many of these taxa may be widely distributed and conspicuous in ports (Darling & Carlton, 2018). The interactions between artificialization and transport networks make these taxa great candidates to disperse upon novel surfaces (ship hulls, anthropogenic marine debris) owing to their local abundances (propagule pressure) but also to traits allowing them to overcome the stresses associated with the transport-destination continuum. There is mounting evidence that trait selection operates during the transport stage (Briski et al., 2018), as illustrated by tolerance to the multiple environmental stressors that the transported propagules must overcome during their journey but also in the environments where they are introduced, such as ports (cf. Johnston et al., 2017 for review). This includes variation in temperature (Cardenas et al., 2020; Gauff et al., 2022), salinity (Dafforn et al., 2009; Mcknight et al., 2017) and contaminants (Piola & Johnston, 2008). In that context, the identification of functional distinctness or trait biases within communities (e.g., among NIS and natives) may help to identify environmental filters that have operated during several stages of the invasion process (cf. trait biases in exotic plants or birds; González-Lagos et al., 2021; Pearson, Ortega, Villarreal, et al., 2018), but also to give hints into future candidates to invasions. Analysing traits of species transported by tsunami marine debris, Miller et al. (2018) observed differences among species with known vs. no prior invasion histories, with broader habitat

breadth and environmental tolerance in the first group. Importantly, the authors identified a broad subset of taxa with no known invasion history that were functionally similar to known invaders commonly associated with anthropogenic transport vectors. Although promising, trait-based comparisons of marine NIS to natives are, to our knowledge, still rare and focus on the values of specific traits (e.g. trophic; Mcknight et al., 2017; environmental tolerance; Bates et al., 2013) or to trait modalities in focal group (amphipods; Cuthbert et al., 2020; macroalgae; Nyberg & Wallentinus, 2005) or habitat (aquaculture facilities, Piló et al., 2021). Because NIS and natives can present distinct functional responses to local or regional filters (López & Freestone, 2021), trait-based approaches may further improve our understanding of the assembly processes linking habitat modifications to biological invasions.

In this study, we examined the distribution of functional traits within fouling communities associated with marine urban habitats across 10 ports in Central Chile. We worked upon community data from Leclerc, Viard, González-Sepúlveda, et al. (2020) who identified contrasting diversity, structure, and contributions of nonindigenous, cryptogenic, and native taxon pools within two types of artificial habitats. As hypothesized elsewhere (e.g. Giachetti et al., 2020; Glasby, 2001; Hawk & Johnson, 2022), the overrepresentation of NIS within one of these habitats (floating infrastructures) could be explained by specific assembly processes (strong environmental and weak species interaction filters), some of which being akin to those operating during the transport stage (e.g. on hulls). Considering contrasting distributions and co-occurrence histories, we thus explore the presence of trait biases among taxon pools within communities. Within fouling communities, such bias could for instance be expected if traits conferring high efficiency in exploiting free resources and stress tolerance are overrepresented in NIS, at the expense of their competitive abilities and predator defences. We further tested whether interhabitat differences in taxonomic composition mirrored contrasting functional diversity and structure across successional stages. In particular, we predicted a trait bias between floating and nonfloating habitats consistent with the high contribution of NIS in the floating habitat, along with an increasing contribution of long-lived and more competitive taxa with the age of studied assemblages.

2 | METHODS

2.1 | Study design and data set overview

The species data set used in this study comes from Leclerc, Viard, González-Sepúlveda, et al. (2020). These authors examined the diversity and community structure of 3- and 13-months chronosequences of fouling assemblages. Briefly, the study was carried out along approximately 100km of coastline in the Biobío region (Chile) between March 2017 and April 2018. In each of 10 ports, nested within 4 days (Figure S1), either nonfloating (e.g. pilings; rocks) or floating (buoys and lines) habitats were found. Nonfloating habitats

are usually in direct contact with the benthos while floating habitats remain in the water column with a weaker, less prominent link to the benthos.

The experiment consisted of the deployment of a series of 15×15cm black polypropylene settlement plates, arranged in an experimental unit (i.e. a structure held by PVC tubes). The plates were used to have a standardized substrate and new available surface area, which is a main limiting resource (Davis et al., 2000), to be colonized by sessile and mobile taxa. In each of the study sites, unit-bearing plates were attached to the available substrate in two plots separated by 20–50m, and at approximately 3m to 4m depth. Plates were designed to measure colonization after settlement; therefore, biofouling in place was removed from the surface (piling, rock) upon which experimental units were deployed at the time of installation. A total of 16 plates (8 per plot) were deployed per site on each occasion. After 3 and 13 months, eight plates (four randomly selected per plot) were collected by scuba diving. In the laboratory, sessile taxa (mainly fauna) settled on plates were identified, at the lowest taxonomic level possible (or morphotypes depending on available information) under a dissecting microscope and their abundances were assessed using cover (estimated at 100 intersection points in an area of 12×12cm). The identified specimens were categorized as 'native', 'nonindigenous', 'cryptogenic' (i.e. uncertain origin sensu Carlton, 1996) or 'unassigned' according to the literature and public databases. The cryptogenic species found in this study displayed a cosmopolitan distribution, most likely resulting from historical anthropogenic dispersal (i.e. neocosmopolitan; Darling & Carlton, 2018) and were most likely nonindigenous to the study area (Bailey et al., 2020; Leclerc et al., 2018). The unassigned category was used for specimens for which the taxonomic resolution and/or available information were insufficient.

2.2 | Categorisation of functional traits

Taxa were classified according to 12 functional traits related to their life history, behaviour, defence and resource acquisition (Martini et al., 2021). All categorical, these functional traits were subdivided into different modalities as proposed by, for example Bremner et al. (2003), López and Freestone (2021, and references therein). Following up on the work by Figueroa et al. (2021), life history traits were extracted from online sources (e.g. MarLIN, BIOTIC, WORMS), bibliographic sources, and field observations. Each trait was categorized into three to five modalities (e.g. the trait 'Larval development' was given three modalities: pelagic planktotrophic, pelagic lecithotrophic or direct benthic) obtaining a total of 12 traits and 50 modalities of traits, as detailed in Table S1. The affinity of each taxon with the modalities of each trait was assigned on a scale from 0 to 4, so that the 'total affinity' of each trait equalled 4 (Boyé et al., 2019; Cardecchia et al., 2018; Chevenet et al., 1994). This fuzzy coding allows a taxon to display modalities of a trait to different degrees, and is compatible with the highly flexible distance-based framework adopted in

our study (see next section; Laliberté & Legendre, 2010; Villéger et al., 2008). When information about a particular trait in a taxon could not be obtained, the affinity value of a similar taxon within its taxonomic group (genus or family, whichever closest available) was used as a proxy; however, only whenever variations of the trait within the taxonomic group chosen had not been reported (Figuroa et al., 2021). Otherwise, an equal affinity value was assigned for all modalities of that trait for the taxon.

2.3 | Functional diversity and statistical analyses

Four pools of taxa were considered, namely 'native', 'non-indigenous', 'cryptogenic' (and unassigned) taxa. To determine whether the four pools are functionally distinct in the study area, all taxa were mapped in the functional space, according to their functional dissimilarities, using a Gower Log_{10} -modified dissimilarity index yielded from the taxon-by-trait matrix (Villéger et al., 2008). Based upon these dissimilarities, a one-way permutational multivariate analysis of variance (PERMANOVA, Anderson et al., 2008) associated with a PERMDISP test was then used to check whether the position and the dispersion, respectively, of the status-taxon pools within the functional space varied among groups. Because these tests are based on permutations ($\times 4999$), both of them are especially well-suited to address this question, the null hypothesis herein being that any status could have been associated to any one of the taxa taken randomly. Taxa were also ordinated in the functional space using a principal coordinate analysis (PCoA, or PCO) to support PERMANOVA results.

Because our data set comprises a large number of unassigned taxa ($S=30$), we addressed to what extent a reassignment of these taxa (e.g. should further information be obtained in the future) to any assigned group (NIS, native or cryptogenic) could change the outcomes of our analyses. To this end, we first simulated three extreme scenarios in which we reassigned the whole set of unassigned taxa as either native species, NIS or cryptogenic species, then ran again the PERMANOVAs and PERMDISPs. Second, we simulated a series of random reassignment of individual taxa to the three classes by iterations (4999 iterations) and extracted the p -value from each of the corresponding PERMANOVAs and PERMDISPs. The density distributions of these p -values were latter checked in order to determine the proportion of consistent vs. inconsistent outcomes in our analyses depending on the positions of unassigned taxa in the trait space.

We then tested whether differences in taxonomic composition (community structure) of 3- and 13-month assemblages among habitats translate in the functional space. This question was visually addressed after transposing individual taxa contributions to the within-group community structure (SIMPER; cf. methods and results in Leclerc, Viard, González-Sepúlveda, et al., 2020) upon their individual coordinates on the PCoA described above. Before any comparison of functional diversity and structure, this step was deemed useful to further hint at functional distinctness versus redundancy

between taxa and processes at play in community assembly among habitats (Mouillot et al., 2013).

To further investigate whether functional diversity and structure in 3- and 13-month assemblages differ among habitats, we used the frameworks of Villéger et al. (2008) and Laliberté and Legendre (2010). Four functional diversity indices were retained based on their complementarity, namely the functional richness (F_{Ric} , which gives an estimate of the niche space occupied by a given assemblage, regardless of taxon abundances), the functional evenness (F_{Eve} , which reveals the regularity of taxon abundances within the functional space), the functional divergence (F_{Div} , which gives the mean abundance-weighted deviation of taxa to their mean distance to the centre of gravity of the functional space, regardless of its size), and the functional dispersion (F_{Dis} , which gives the abundance-weighted mean distance of taxa to their abundance-weighted centroid in the functional space). Either taxon-by-trait matrix, sample-by-taxon matrix or both were used in the calculation of these indices. These two matrices were also used to calculate all community-level-weighted means (CWMs) of trait modalities. Community-level-weighted means yielded our sample-by-trait matrix which allowed us to compare the multivariate functional structure among factor levels. Patterns in functional diversity (for each index) and structure of the taxa colonizing the experimental plates were examined in a five-way design using PERMANOVAs with 4999 permutations. Factors were habitat ('habitat', fixed, 2 levels: floating and nonfloating), age of the settlement plate at the time of collection ('age', fixed, 2 levels: 3 and 13 months), 'bay' (random, four levels), 'site' (random, nested within 'habitat' \times 'bay') and 'plot' (i.e. experimental unit, random, nested within site). A unit was lost over the course of the experiment, therefore, the interaction term 'age' \times 'plot' was not included in the analyses, but between 4 and 8 replicate plates were available for each combination of 'age' \times 'site'. The homogeneity in univariate or multivariate dispersion was checked among the levels of the interaction term among fixed factors, that is Habitat \times Age using PERMDISP (Anderson et al., 2008). When assumption of homoscedasticity was not met after any transformation of univariate data, the analysis was conducted on untransformed data following Underwood (1997) and a more conservative level of significance ($\alpha=0.01$) was taken into account. For multivariate data, samples were also ordinated using principal coordinate analyses (PCoA) to support PERMANOVA results (Anderson et al., 2008). When appropriate, PERMANOVAs were followed by pairwise comparisons, and p -values were estimated using the Monte Carlo procedure. In order to check for the putative influence of unassigned taxa in these functional variations across habitats and assemblage ages, the same analyses on functional diversity and structure were computed on separate data sets in which we randomly dropped either 0, 6, 12, 18, 24 or all 30 unassigned taxa off. We also checked the spatiotemporal variations in richness of unassigned (but also native, native, cryptogenic and nonindigenous) taxa, using the same statistical model described above (which differs from the model used by Leclerc, Viard, González-Sepúlveda, et al., 2020).

Data analyses were performed using PRIMER 7 (Anderson et al., 2008) and the packages 'FD' (Laliberté et al., 2014) 'ade4'

(Chessel et al., 2009), 'vegan' (Oksanen et al., 2022), and 'ggplot2' (Wickham et al., 2016) from the R environment (R Development Core Team, 2020). The open-source software Inkscape was used to amend the figures.

3 | RESULTS

3.1 | Nonindigenous and native taxa pools in the study area are functionally distinct

Leclerc, Viard, González-Sepúlveda, et al. (2020) identified 78 taxa on the plates across all sites and successional stages, including 13 non-indigenous and 12 cryptogenic taxa. On the basis of available traits, taxa did not appear to distribute randomly within the functional space (Figure 1a,b, Figure S2). Depending on their status, the taxa differed in their average functional position (PERMANOVA, Pseudo- $F_{3,73}=3.42$, $p_{mc}<.001$) and dispersion (PERMDISP, $F_{3,73}=10.05$, $p_{MC}<.001$), or in turn a combination of both. Pairwise tests further indicated that cryptogenic and non-indigenous taxa were functionally similar to each other, whereas they both differed from natives in their multivariate position and dispersion.

Most nonindigenous (and cryptogenic taxa) did actually resemble to only a portion of native taxa when conferring to the trait variation explained by the first axis of the PCoA (30.6% of total variation, Figure 1a). These differences involve diverse life history traits notably related with attachment, mobility, larval dispersal and longevity (Figure 1b). For example, a single NIS (*Mytilus galloprovincialis*) have the potential to live up to more than 5 years, while eight native species display this potential. Along its second axis (19.4% of total variation), the PCoA further discriminates taxa according to their reproductive mode, dispersal but also trophic and defence traits. For example, there is a continuum of structural defence from the bottom to the top on axis 2, ranking seaweeds, tunicates, hydrozoans, bryozoans, barnacles, and molluscs.

Overall, similar outcomes would be found should all the taxa be either reassigned as native species (PERMANOVA: Pseudo- $F_{2,74}=2.76$, $p_{mc}=.001$; PERMDISP, $F_{2,74}=12.62$, $p_{mc}<.001$), cryptogenic species (Pseudo- $F_{2,74}=2.96$, $p_{mc}=.003$; $F_{2,74}=16.89$, $p_{mc}<.001$) or NIS (Pseudo- $F_{2,74}=3.25$, $p_{mc}<.001$; $F_{2,74}=6.76$, $P_{MC}=.006$). Pairwise differences among natives and NIS are maintained in all of these cases, although being marginal in multivariate dispersion when all unassigned taxa are reassigned as natives (NIS vs. natives: $p=.068$). In any case, native and cryptogenic species differ in their functional position and dispersion. Upon random individual reassignment of unassigned taxa to one of the assigned groups, the multivariate position among groups varies significantly in 83.5% of the cases and marginally (at $\alpha=0.07$) in 99.9% of the cases, with p -values ranging from 0.006 to 0.065 (1st to 99th percentiles, Figure S5). The multivariate dispersion among groups varies significantly and marginally in 83.8% and 85.0% of the cases, respectively, with P -values ranging from 0.001 to 0.096. In either analysis, the

distribution is not unimodal (Figure S5) and a series of tests including the extreme simulations presented above indicate that p -values above $\alpha=0.05$ are obtained when reassignments fill in the trait space in all three categories.

3.2 | Functional variations in time but not between habitats

Spatiotemporal community patterns in taxonomic composition can be transposed into the functional space considering the individual taxa contributions to the within-group similarity (SIMPER). When exploring temporal change between 3 (Figure 1c,d) and 13 months (Figure 1e,f), this approach illustrates in both habitats an increasing contribution of taxa distributed along the right portion of the PCoA, notably associated with longer life duration and dispersal potential—most of them being natives (with the aforementioned exception of *M. galloprovincialis* contributing to 21% of within-group similarity in the floating habitat after 13 months, Figure 1e). In addition, a temporal signal was detected for F_{RiC} (increasing significantly by about 85% between 3 and 13 months, Figure 2a; quality of $F_{RiC}=0.44$) and functional structure (marginally changing at the chosen α : $p=.011$, Figure 3a). This last change is perceptible along the first axis of the corresponding PCoA (28.9% variation, Figure 3a,b) illustrating some shifts in life history strategies, such as reproduction and attachment, but also a marked increase in the contribution of large and long-lived taxa in older assemblages.

Overall, the contribution of nonindigenous and cryptogenic taxa was generally higher in the floating habitat (Figure 1c,e) than in the nonfloating habitat (Figure 1d,f). It was not explained by the same taxa among habitats: important contributions of tree-like bryozoans, vine hydrozoans and tunicates were observed in the floating habitat, while a further contribution of chitinous to calcareous crust-bryozoans was observed in the nonfloating habitat. However, no functional differences between habitats could be detected (Table 1), either in the general composition structure (Figure 3a,b) or associated indices (Figure 2a–d). Overall, these results were consistent, if not strengthened (cf. mean square and p -values) when 0, 6, 12, 18, 24 or 30 unassigned taxa were dropped off of the data set (Figure S6, Table S4). Even F_{RiC} , which unlike the other indices, is dependent on the taxonomic richness, displayed consistent spatiotemporal variations. Noteworthy, neither the taxonomic richness nor the cover of unassigned taxa varied among habitats (Figure S5, Tables S2 and S3), unlike those of NIS. Along with the native richness, the unassigned taxa richness increased consistently with the age of the assemblage (Table S2). With age, the unassigned taxa cover varied however inconsistently across study sites (Table S3).

We further note that the second axis (23.2%) of the PCoA describing functional structure (Figure 3a,b) is not associated with any of the main factors but rather illustrates contrasting contribution in growth forms and types of defence against predator if any, among diverse spatial units (plot, site) regardless of the age of chronosequences.

Functional patterns within the taxon pool

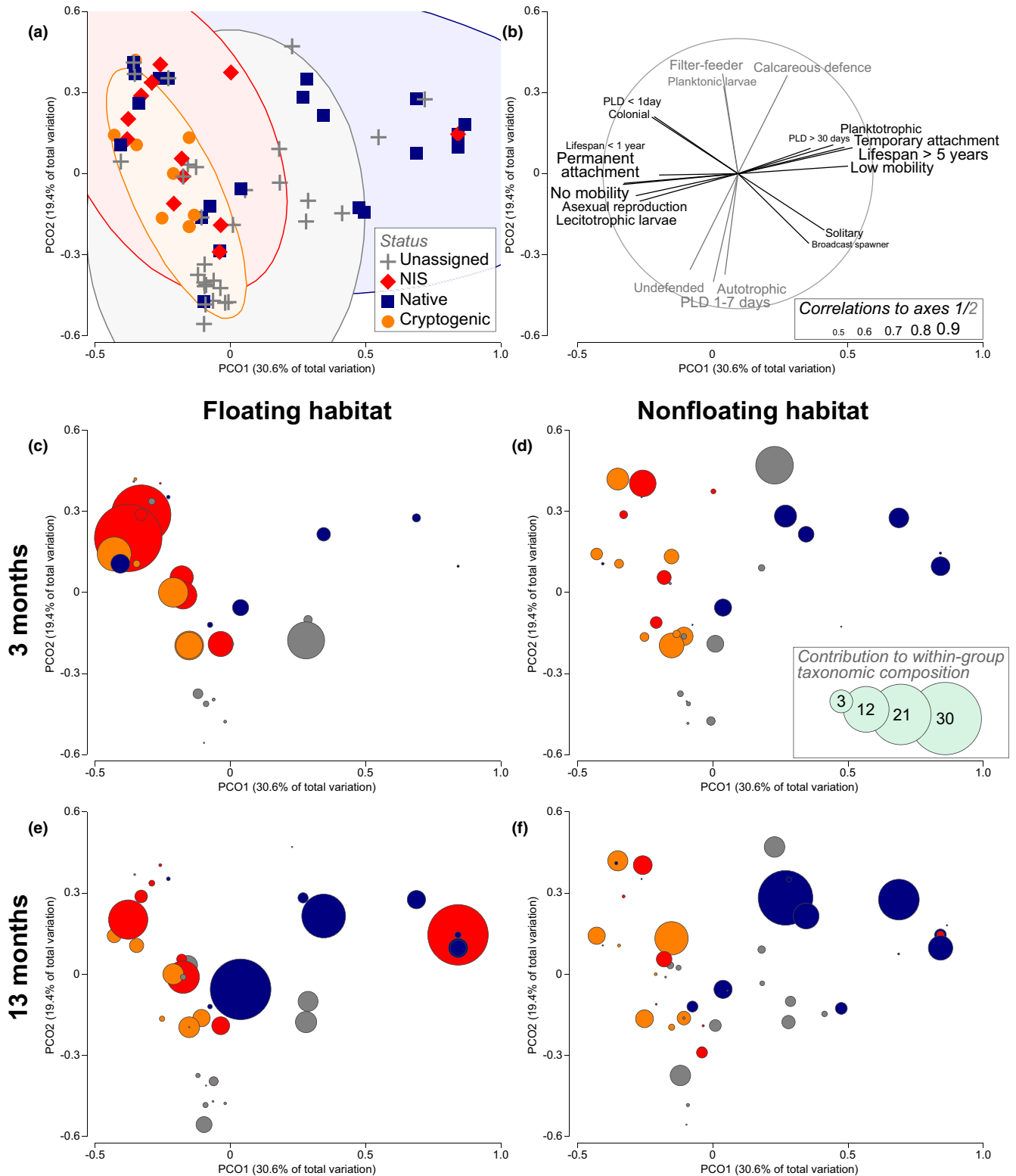
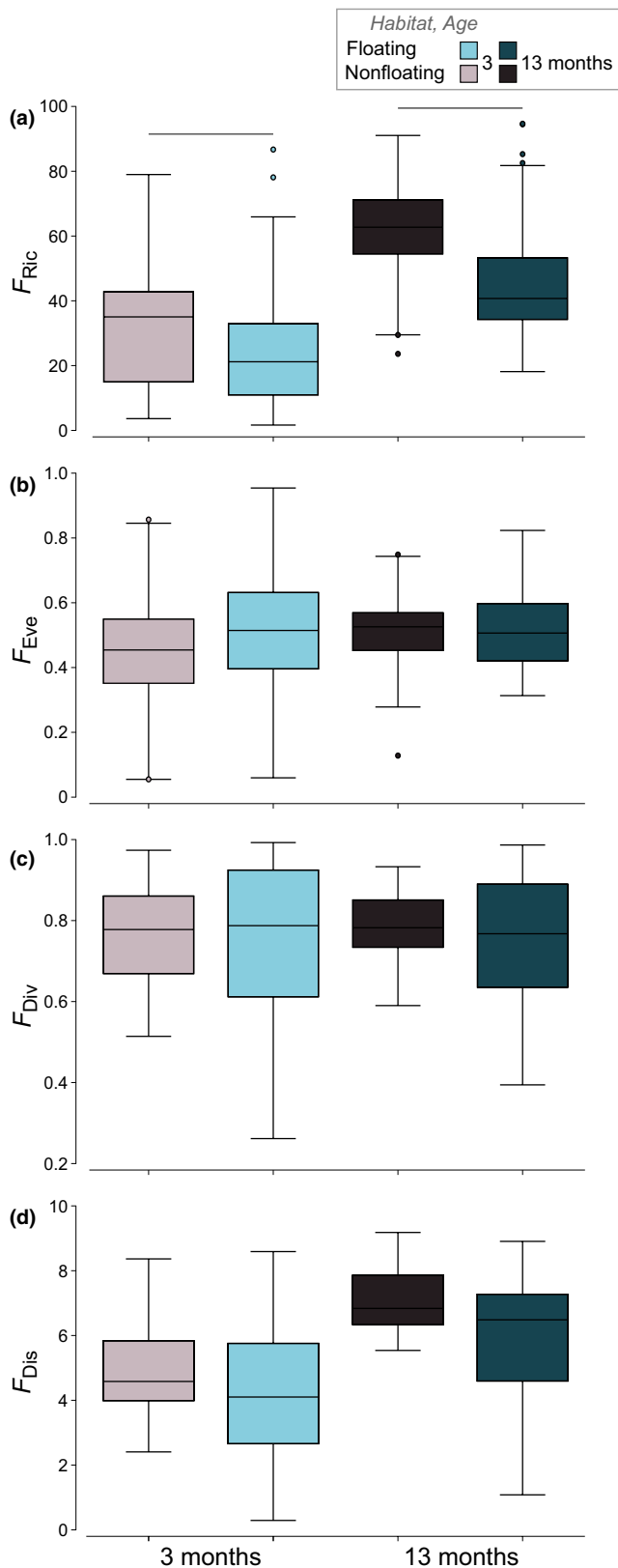


FIGURE 1 Distribution of the study taxa in the functional space, herein characterized by the first two axes of a principal coordinate analysis (50% of the total variation). Taxa are separated according to their status (native, nonindigenous, cryptogenic and unassigned) in the study area, with within group-confidences depicted by backward ellipses (a, see Figure S1 for a more detailed description of the full extent of the ellipses). Vector plots of variables correlated with the PCoA axes ($r > .5$) are indicated in the top right panel (b). Bubble plots of taxa contributions to the community structure within each habitat \times age combinations are indicated in the functional space depicted in the other panels (c–f).



3.3 | Inconsistencies in temporal trajectories of the functional structure across sites

Significant interactions between age and site were observed for most response variables (Table 1), namely functional richness (F_{Ric} ,

FIGURE 2 Mean functional richness (F_{Ric} , a), functional evenness (F_{Eve} , b), functional divergence (F_{Div} , c) and functional dispersion (F_{Dis} , d) on 3- and 13-months old-plates deployed within floating and nonfloating habitats (Detailed data across all sites are given in Figure S4). Around the median (horizontal line), the box plots show the quartiles, the 95% confidence intervals (whiskers) and the outliers. Horizontal lines overhanging the bars regroup values that do not differ significantly after pairwise tests.

with pairwise variations consistent with the main effect, Figure S4a), functional divergence (F_{Div} , Figure S4c), functional dispersion (F_{Dis} , Figure S4d), and functional structure (Figure 3c). For instance, out of the 10 study sites, F_{Dis} significantly increased in seven sites, whereas it significantly decreased in two of them (Figure S4d) without any patterns across habitat types. Besides PERMANOVA results, this inconsistency is generally well-reflected in the variability in temporal trajectories of centroids across sites (Figure 3c).

4 | DISCUSSION

Overall, our results show that nonindigenous and native taxa pools in the study area are functionally distinct, with most NIS resembling only a portion of native taxa. In spite of contrasting distribution and contribution of nonindigenous and native taxa to community structure across floating and nonfloating habitats, we did not observe functional differences among habitats for any of the response variables based on available trait data. Some temporal variations across colonization stages could however be detected with specific trajectories across sites, likely explained by contrasting assembly processes operating at various spatial scales.

4.1 | The pools of nonindigenous and native taxa are functionally distinct, but the devil is in the details

Using the whole set of trait modalities available, we were able to describe the entire pools of native vs. nonindigenous and cryptogenic taxa as functionally distinct. Without ruling neutral processes out (Brown & Barney, 2021; Fargione et al., 2003), this result indicates that these novel assemblages are governed to some extent by niche-based processes. Generally robust to most random and non-random reassignments of individual unassigned taxa to these pools (Figure S3), this difference in the trait space was detected for both the multivariate position and dispersion. Such combination calls for caution in interpretation, as among group-differences in dispersion influence tests on position (Anderson et al., 2008), hence the importance of examining ordinations in tandem. Considering the first two axes of the PCoA (half of the total variation, Figure 1a), there is indeed important overlap of these taxon pools in the trait space without conspicuous outliers. This first suggests that none of the introduced taxa may have delivered novel function to the studied habitats and may rather be redundant. Since these artificial habitats

Functional composition among habitats across age treatments

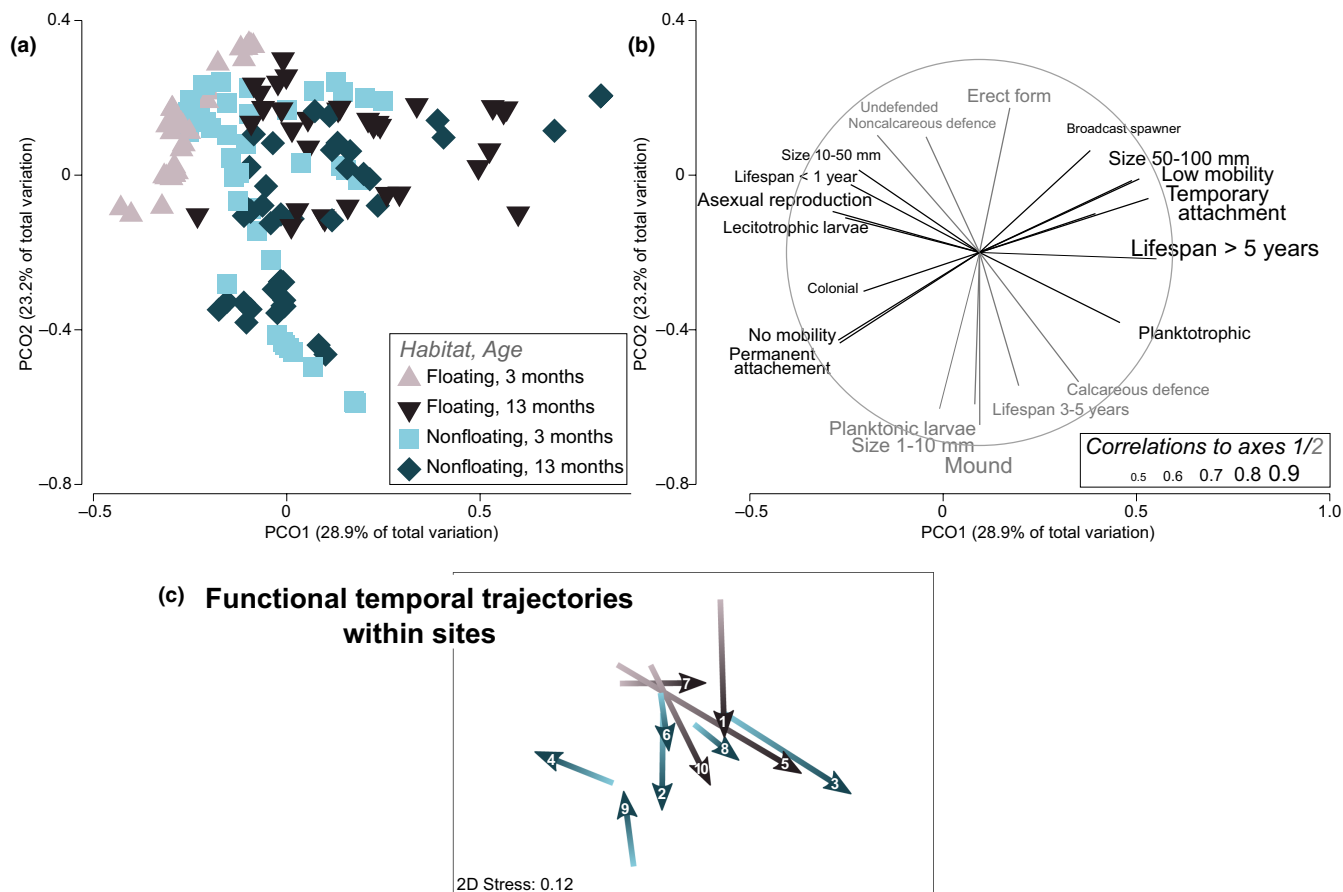


FIGURE 3 Variation of functional composition on plates among habitats across age treatments (52.1% of total variation first two axes of the principal coordinate analysis, a). Vector plots of variables correlated with the PCoA axes ($r > .5$) are indicated in the top right panel (b). Temporal trajectories in functional composition are indicated for each site (1: Llico, 2: Tubul, 3: Coronel, 4: Chome, 5: Lenga, 6: San Vicente, 7: Talcahuano, 8: Lirquén, 9: Coliumo dock, 10: Coliumo aquaculture facilities) by arrows connecting 3 and 13 months centroid values.

are themselves novel, there may be, however, little point to further interpret this result in terms of 'impact' for local functioning unless these taxa are drivers of community assembly and disturbances (Catford et al., 2012; Mouillot et al., 2013), and this may not be captured by the traits considered here. The second outcome of this analysis is that the distribution of neocosmopolitans (i.e. non-native and cryptogenic taxa) in the trait space is rather nested within that of natives, the latter being functionally more diversified.

4.2 | Most neocosmopolitans appear as opportunistic taxa

Multiple succession trials and disturbance experiments of fouling communities in the study region suggested that most of the neocosmopolitans are opportunistic, stress-tolerant or both (Leclerc et al., 2021; Leclerc, Viard, González-Sepúlveda, et al., 2020). By analysing their traits, the present study confirms this hypothesis and provides further elements to disentangle associated mechanisms. Most of the early colonizers were indeed permanently attached, short lived (<1 year), colonial and/or with the ability of vegetative

growth and reproduction, essential to the colonization of empty patches (Hiebert et al., 2019; Valdivia et al., 2005). Such fouling organisms are notably grouped by some authors as vines and runners (through stolonial expansion, Greene & Schoener, 1982).

Noteworthy, however, most of these taxa are likely limited in their natural dispersal abilities (e.g. hydroid propagules dispersing over a few meters in a few minutes, Shanks, 2009), displaying lecithotrophic larvae and pelagic larval duration of up to 24 h. At first glance, this can affect their colonization potential. However, natural dispersal limitations may be compensated with overlooked and worth scrutinizing traits (e.g. reproductive output) and more importantly by anthropogenically aided dispersal as stowaways—a pathway which is not really questioned regarding these neocosmopolitan taxa (cf. Bailey et al., 2020; Massé et al., 2023 for reviews).

Overall, neocosmopolitan taxa showed an overrepresentation of traits conferring high efficiency in exploiting free resource and a low rank in the competitive hierarchy (cf. competition-colonization trade-off), which is akin to trait biases within introduced (and naturalized) plants (Catford et al., 2012; Pearson, Ortega, Villarreal, et al., 2018) and birds (González-Lagos et al., 2021; McKinney, 2006) in several regions worldwide. These biases are generally attributed

TABLE 1 Summary of PERMANOVA tests for differences in functional richness (F_{Ric}), functional evenness (F_{Eve}), functional divergence (F_{Div}), functional dispersion (F_{Dis}) and functional structure (F_{Struct}) among levels of the main factors (habitat, age, bay and site) and their interactions.

PERMDISP	F_{Ric}	F_{Eve}	F_{Div}	F_{Dis}	F_{Struct}						
$F_{3,152}$	1.17	5.36	12.77	5.81	3.7						
p	.352	.001	<.001	<.001	.026						
Pairwise	(F3 ≠ F13) = (NF3 ≠ NF13)		(F3 ≠ NF3) ≠ ^m (F13 ≠ NF13)	(F3 ≠ ^m NF3) = (F13 ≠ NF13)	(F3 ≠ ^m NF3) = (F13 ≠ NF13)						
PERMANOVA											
Source	df	MS	p_{MC}	MS	p_{MC}	MS	p_{MC}	MS	p_{MC}	MS	p_{MC}
Habitat (H)	1	4025.40	.294	0.02	.448	0.03	.421	49.38	.152	2.80	.103
Age (A)	1	24137.00	.004	0.06	.326	0.00	.956	108.22	.133	2.93	.011
Bay (B)	3	1239.10	.580	0.03	.787	0.10	.836	17.96	.787	1.63	.736
H × A	1	379.22	.530	0.04	.618	0.01	.769	2.01	.699	1.50	.260
H × B	3	2443.50	.389	0.03	.804	0.03	.969	14.45	.837	1.24	.864
A × B	3	457.84	.802	0.05	.233	0.19	.426	24.63	.522	0.61	.560
Site (H × B) = S	2	1272.00	.005	0.07	.053	0.31	.001	43.06	.001	1.95	<.001
H × A × B	3	740.00	.700	0.13	.103	0.09	.662	10.65	.752	1.05	.214
Plot (S (H × B))	10	148.03	.790	0.02	.593	0.02	.361	2.86	.070	0.12	<.001
A × S (H × B)	2	1175.00	.008	0.01	.562	0.12	.001	20.31	<.001	0.55	<.001
Res	126	236.77		0.02		0.01		1.59		0.06	

Note: p -values are highlighted in bold when significant at $p < .01$. PERMDISP results and pairwise tests are summarized for the combined factors habitat (F and NF stand for floating and nonfloating habitats, respectively) and age. ^mmarginal difference at $\alpha = 0.07$.

to the legacy of species association with human-made and disturbed habitats embedded in dispersal networks (Pearson, Ortega, Eren, & Hierro, 2018; Pyšek et al., 2015). As such, and although this may be counter-intuitive on a first sight (Price & Pärtel, 2013), our findings are not in contradiction with the limiting similarity concept (MacArthur & Levins, 1967): the mechanisms of biotic resistance involving functional similarity (notably through competition) are indeed undermined by disturbance (Elton, 1958) as demonstrated with our model community (Leclerc et al., 2021). Importantly, our model community is also composed of multiple foundation species and prone to complex epibioses involving neutral to positive interactions, which also affect its invasibility (Bulleri et al., 2008; Leclerc & Viard, 2018). Considering traits associated with these interactions could be valuable for future research, and this may alleviate applications of the limiting similarity concept in conservation and restoration planning (Catford et al., 2012; Funk et al., 2008).

4.3 | A few neocosmopolitans can however be major competitors

While traits permitting to exploit free resource help colonizing disturbed habitats, traits conferring efficiency to hold on to this resource may promote species persistence as well as putative impacts in recipient communities (Catford et al., 2019; Price & Pärtel, 2013). These abilities are common in widespread sessile marine invaders, such as seagrasses, seaweeds and bivalves, which have the potential for ecosystem-level disruptions (habitat modification, resource

use, and nutrient cycling, Thomsen et al., 2014). Among them, mussels are textbook cases of 'perfect' hitchhikers, colonizers and competitors (Bertolini et al., 2019; Cardenas et al., 2020). These abilities are notably highlighted in our study by traits associated with long pelagic larval duration, life span and post-settlement mobility, (cf. extreme dots on the right side of PCoA axis 1, Figure 1a), which are attributes of one non-indigenous (*Mytilus galloprovincialis*) but also four native mussels. It is noteworthy that one native mussel (*Semimytilus patagonicus*, formerly *S. algosus*), which proliferates along highly disturbed port pilings (JCL pers. obs.) and is common across floating substrates, including ship hulls (Bigatti et al., 2014; Leclerc, J.-C. & Pinochet, J., Fouling invertebrates upon commercial ships arriving in Concepción, Chile, unpublished data), has also successfully invaded SW Africa shores following its (likely aided) introduction (de Greef et al., 2013). Besides NIS-natives comparisons, there is much to learn from functional comparisons among native groups, as they can give both fundamental and applied hints into either historical or impending invasions (Miller et al., 2018; Van Kleunen, Dawson, et al., 2010).

4.4 | Singularities in temporal changes across sites overcome habitat differences

Considering known differences in taxonomic composition among floating vs. nonfloating habitats in the region (Leclerc, Viard, González-Sepúlveda, et al., 2020) and elsewhere (e.g., Glasby, 2001; Hawk & Johnson, 2022), the absence of overall

difference in functional diversity and composition between habitats was an unexpected result (but see Figueroa et al., 2021 at smaller spatiotemporal scale). Since these taxonomic differences were mostly driven by NIS, the nested structure of NIS pool within the native trait space, however, can explain this finding. It can indeed be hypothesized that the sessile assemblages colonizing the two types of habitats are functionally redundant, regardless of the origin of the taxa composing them (Byrnes & Stachowicz, 2009). However, because there is mounting evidence for distinct assembly processes between these habitats, some of the present results should be taken with caution. For instance, using percentage cover, which is usual in such comparative study (e.g., Glasby, 2001; Hawk & Johnson, 2022), rather than biomass (Perkol-Finkel et al., 2006) to characterize species contribution to community structure may have constrained data dispersion in the trait space. In addition, the breadth of available information regarding all traits was unequal across all taxa—a common issue with marine taxa (e.g. Miller et al., 2018). Also, a majority of taxa could not be identified at the species level. To overcome these two limitations, we chose to include all taxa even those with partial trait data, thanks to the fuzzy coding approach. In comparison to well-known taxa shortlisting (e.g. Boyé et al., 2019; López & Freestone, 2021), this choice has arguably decreased our ability to discriminate groups of samples, but we considered it more parsimonious. Comparing outcomes of existing approaches in different settings should provide important guidance for future research, although this is beyond the scope of this study. Noteworthy, the simulations herein performed after dropping off varying number of unassigned taxa suggest that the conclusions obtained from our analyses are robust to the lack of taxonomic resolution, and the resulting lack of assignment for some taxa. These results indicate that unassigned taxa are poor contributors to the functional diversity structure of the studied communities, whether this is due to the limited information on their traits, to their consistent richness and cover across habitats, and/or to the flexible distance-based framework herein considered (Laliberté & Legendre, 2010; Villéger et al., 2008). Of the complementary functional indices used, three (F_{Eve} , F_{Div} and F_{Dis}) are independent of the taxonomic richness and at least two (F_{Ric} and F_{Div}) are unaffected when a taxon is split into two taxa (say following taxonomic revision) with the same total abundance and the same trait values. Should available information differ among the two taxa though, improved taxonomic resolution would unarguably enhance their discrimination in the trait space and can only be advocated for future studies.

In contrast to the lack of habitat effects, we were able to identify conspicuous temporal effects with site-specific trajectories. This complexity most likely reflects local assembly processes, some of which previously described in the region, including for instance spatiotemporal dynamics in abiotic environment (Atkinson et al., 2002), in dispersal (Figueroa et al., 2021), propagule supplies and settlement (Leclerc et al., 2018) and in species interactions (Leclerc, Viard, & Brante, 2020). In particular, plot- or site-specific filtering associated with predation over assembly may be reflected by trade-offs

in growth forms and types of defence, among others, in the functional structure (second axis in PCoA, Figure 3b). Along with others (Boyé et al., 2019; López & Freestone, 2022), our results encourage further development of trait-based approaches to explore assembly processes at varying scales.

5 | CONCLUSIONS

Using a trait-based approach with fouling communities, we were able to detect functional differences among non-indigenous and native taxa but also among assemblages at different successional stages. In both cases, these differences were attributable to life-history trade-offs (notably linked with competitive hierarchy) that are relevant to explore assembly rules, comprising neutral and niche-based processes, in such model communities. Although these findings cannot be generalized to the broad diversity of taxa voyaging with anthropogenic vectors (and which requires dedicated policy and management), they imply that the management of biological invasions can hardly be dissociated from conservation and disturbance mitigation in putative recipient habitats. In spite of contrasting taxonomic compositions across different artificial habitats, no difference in their functional diversity and structure was however detected at the regional scale of our study. This unexpected result may be attributable to complex interplay of assembly processes (including dispersal, facilitation, and predation) at several spatial scales, as suggested by the diversity of temporal trajectories in functional structure observed across sites. Echoing several recent opinions and review pieces (Martini et al., 2021; Vranken et al., 2022), these results generally encourage concerted efforts among marine scientists to expand trait databases and further research on functional responses of organisms and communities. Beyond fundamental knowledge, these efforts can have important implications into conservation and restoration planning.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All taxonomic and abundance data are provided at: [10.5061/dryad.8gtht76jg](https://doi.org/10.5061/dryad.8gtht76jg). Trait data have been made available at: [10.5281/zenodo.7750497](https://doi.org/10.5281/zenodo.7750497). Further details are given in the supplementary material associated with the manuscript and available from the corresponding authors upon reasonable request.

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BIOSKETCH

Jean-Charles Leclerc is a community ecologist, interested in examining the natural and human-mediated processes affecting the diversity, structure, functioning and stability of marine habitats and associated communities. His current research focusses on the interactions among communities across natural and urban seascapes, at multiple scales.

Author contributions: Jean-Charles Leclerc, Frédérique Viard and Antonio Brante conceived the working hypotheses and study design. Jean-Charles Leclerc led sample collection and processing and conducted the taxonomic analyses. Naili Nashira Figueroa led the literature research on functional traits, which were checked by Jean-Charles Leclerc and Frédérique Viard. Jean-Charles Leclerc analysed the data and led the writing. All authors critically edited manuscript drafts.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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