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# Habitat type drives the distribution of non-indigenous species in fouling communities regardless of associated maritime traffic

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## Abstract

**Aim:** Biological invasions and changes in land and sea use are among the five major causes of global biodiversity decline. Shipping and ocean sprawl (multiplication of artificial structures at the expense of natural habitats) are considered as the major forces responsible for marine invasions and biotic homogenization. And yet, there is little evidence of their interplay at multiple spatial scales. Here, we aimed to examine this interaction and the extent to which the type of artificial habitat alters the distribution of native and non-indigenous biodiversity.

**Location:** Southeast Pacific—Central Chilean coastline.

**Methods:** Settlement plates were deployed upon two types of artificial habitats (floating and non-floating hard substrates) at a total of ten study sites, exposed to either international or local traffic. After colonization periods of 3 and 13 months, plates were retrieved to determine their associated fouling sessile assemblages at an early and late stage of development, respectively. Putative confounding factors (temperature, metal concentrations) were taken into account.

**Results:** While traffic type had no detectable effect, there were strong differences in community structure between habitats, consistent across the study region. These differences were driven by non-indigenous species which contributed to 58% and 40% of the community structure in floating habitats after 3 and 13 months, respectively—roughly 10 times greater than in their non-floating counterparts. Assemblages on floating structures also displayed a lower decline in similarity with increasing distance between sampling units, being thus more homogenous than non-floating habitats at the regional scale.

**Main conclusions:** With the absence of international traffic effect, the colonization success by non-indigenous species appears to be mainly habitat-dependent and driven by local propagules. Floating structures not only provide specific niches but characteristics shared with major introduction and dispersal vectors (notably hulls), and in turn constitute important corridors to invasions and drivers of biotic homogenization at multiple scales.

KEYWORDS
artificial structures, biotic homogenization, colonization pressure, corridors, ecological filters, niche opportunity, predation, propagule pressure, SE Pacific

## 1 | INTRODUCTION

Biodiversity is declining at an unprecedented rate, over multiple spatial scales, in response notably to climate change, pollution, direct exploitation of biota, changes in land and sea use, and bioinvasions (Catford, Bode, & Tilman, 2018; IPBES, 2019; Nowakowski, Frishkoff, Thompson, Smith, & Todd, 2018; Pecl et al., 2017). Biological invasions are among the most pervasive changes in the Anthropocene (Anton et al., 2019; Chan et al., 2019; Simberloff et al., 2013): the number of emerging non-indigenous species (NIS) rose particularly over the last five decades along with the intensification and multiplication of dispersal pathways (sensu Lockwood, Hoopes, & Marchetti, 2013; Sardain, Sardain, & Leung, 2019; Seebens et al., 2018; Wilson, Dormontt, Prentis, Lowe, & Richardson, 2009). Human-mediated species introductions redefine biogeographic boundaries (e.g. Wallace realms, Elton, 1958) and contribute substantially to biotic homogenization at multiple spatial scales (Capinha, Essl, Seebens, Moser, & Pereira, 2015; McKinney & Lockwood, 2005). In this context, there are urgent needs to determine the ecological and evolutionary mechanisms promoting the establishment and spread of NIS in order to help building up appropriate management and conservation strategies from local habitats to landscapes (Caselle, Davis, & Marks, 2018; Fitzgerald, Tobler, & Winemiller, 2016; Fridley & Sax, 2014; Kalusová et al., 2017).

Habitat invasibility is expected to depend on the interplay among habitat attributes (e.g. environmental conditions, resource level and heterogeneity), the invader traits and dispersal limitations, as well as interactions with the recipient communities (Byers, 2002; Davis, Grime, & Thompson, 2000; Fridley et al., 2007; Pyšek et al., 2015). Anthropogenic activities are susceptible to alter each of these aspects. Of particular concerns are alterations to biodiversity with respect to the biotic resistance paradigm which predicts that the probability of NIS establishment at the local scale diminishes as the interactions with native species increase (Elton, 1958; Lockwood et al., 2013). This paradigm may partially explain why many NIS are usually more frequent in disturbed and/or less diverse artificial (semi-natural to human-made) habitats, than in their natural counterparts, across all ecosystems (e.g. Chytrý et al., 2008; Fitzgerald et al., 2016; Mineur et al., 2012). In addition, artificial habitats present attributes (see above) hardly found in the wild, and in turn constitute unique ecological filters for community assembly, through which a series of traits from the local pool of species and incomers are selected (Aronson et al., 2016; Bulleri & Chapman, 2010; Johnston, Dafforn, Clark, Rius Viladomiu, & Floerl, 2017; Nowakowski et al., 2018). The same is true for transport vectors which constitute transition habitats for hitchhiking species, at multiple stages of their life cycle (Briski et al., 2018). In this context, it can be hypothesized that invasibility would be exacerbated in artificial habitats showing environmental similarities with transport vectors. In the marine realm for instance, fouling taxa with traits favouring colonization of floating vectors (e.g. hulls and marine debris) may be more likely to invade similar niches, namely floating artificial habitats (e.g. floating pontoons, buoys and aquaculture lines), as compared to fixed (e.g. pilings and seawalls) ones (Dafforn, Johnston, & Glasby, 2009; Johnston et al., 2017). The more the suite of ecological filters acting on community assembly in a given habitat tend to be similar with increasing spatial scales, the more it will be prone to biotic homogenization (Aronson et al., 2016; Nowakowski et al., 2018).

Because habitat invasibility is expected to depend partly on dispersal limitations, both the colonization pressure (number of species introduced) and the propagule pressure (number of individuals of a given species) are key determinants (Fridley et al., 2007; Lockwood, Cassey, & Blackburn, 2009; but see Nuñez, Moretti, & Simberloff, 2011). Insights about the relative importance of dispersal limitations over habitat resistance have come from small-scale experiments in which propagule pressure can be relatively easily manipulated for a single species (Clark & Johnston, 2009; Von Holle & Simberloff, 2005). Manipulating and measuring both propagule and colonization pressures, even at local scales, are however challenging and subject to bias (Clarke Murray, Pakhomov, & Therriault, 2011; Leclerc et al., 2018; Stachowicz & Byrnes, 2006; Sylvester et al., 2011). Indirect methods are thus often necessary. The use of semi-quantitative proxies (e.g. human population size and distance to the nearest conurbation) has been proven particularly efficient to determine the most relevant drivers of invasiveness among terrestrial habitats (Aikio, Duncan, & Hulme, 2012; Chytrý et al., 2008; Pyšek et al., 2015). Likewise, shipping traffic across locations could give insights into colonization and propagule pressures (Sardain et al., 2019; Seebens, Schwartz, Schupp, & Blasius, 2016), which can be hypothesized to be lower in local than international ports—the latter being fuelled by a higher diversity of putative dispersal pathways (e.g. interoceanic and intercontinental maritime routes) and vectors (hulls, ballasts). In that context, it is worth noting that recent progress in risk assessment of marine bioinvasions came from modelling using global shipping movements and environmental conditions which could filter specific taxa or traits (Sardain et al., 2019; Seebens et al., 2016). Whether shipping traffic could produce contrasting patterns among habitats and across diversity gradients is however still an open question.

In a way similar to landscape urbanization in the terrestrial realm, "ocean sprawl" (i.e. multiplication of artificial structures along natural shores) is recognized as a major threat to marine biodiversity and ecosystem functioning (Bishop et al., 2017; Bulleri & Chapman, 2010; Duarte et al., 2012). Because ocean sprawl affects the connectivity of both natives and NIS (Bishop et al., 2017; Dafforn, 2017), there are urgent needs to compare the invasibility of habitats at multiple spatial scales. The present study aimed to determine whether

invasion patterns and processes vary with associated maritime traffic, and across different types of artificial habitats. To this end, we deployed settlement plates within a series of study sites in Central Chile, a region of increasing invasion risks (Sardain et al., 2019) although still poorly examined. We predicted that community development would differ between habitats, owing to contrasting suites of ecological filters. Likewise, we hypothesized that maritime traffic would influence both the colonization and propagule pressures and in turn affect the diversity and abundance of NIS settled on the plates. We further predicted an interaction between traffic and habitat categories, hence revealing whether the resistance mechanisms conferred by each habitat are vulnerable to colonization and propagule pressures.

## 2 | METHODS

### 2.1 | Sampling design

The study was performed along approximately 100 km of coastline in the Biobío region (Chile) between March 2017–April 2018. Within the region, a total of ten marine sites (average salinity S > 30) were selected (Figure 1, Table S1): these sites belong to eight localities (ports), wherein diverse types of artificial substrata (habitats) were found, either floating (e.g. buoys and lines) or non-floating (e.g. pilings and rocks) substrata. These localities were characterized by two different categories of shipping traffic, namely international versus local (Table S1). In the study region, international traffic is concentrated within three Bays, namely Coronel, San Vicente and Concepción (Figure 1), the latter being hedged by three international ports and the regional naval base of the Chilean Armada (DIRECTEMAR). In 2016, between 39 and 427 foreign commercial ships, mainly originating from Asia, South America, North America, Europe and Australasia, along with 20–217 national ships, made stopover in the study international ports (Table S1). These ships are released from any regulation on biofouling and barely controlled for ballast water, for which a national legal procedure is undergoing revision since 2002 (Leclerc et al., 2018). During the same year, ten fishing crafts (3.5–18 m length) have moored in local ($n$ = 10–107) and international ports (64–162) (Table S1).

Biodiversity and community structure were determined following the deployment of settlement plates. By using standardized substrata, we controlled for the substrate type per se and resource availability (Davis et al., 2000), here bare surface, which is independent of inherent properties of the studied habitats. A series of plates (black polypropylene, 150 × 150 mm) were deployed vertically upon two experimental units, made of plastic fence (mesh 25 × 25 mm) and PVC tubes (diameter 25 mm) in two plots separated by 20–50 m within each port at ca. – 4 m depth (Figure 1). Depending on the site (i.e. available substratum), experimental units were either attached to non-floating (i.e. concrete/steel pilings or large rocks) or floating (i.e. buoys or floating longlines) substrates at the closest distance possible of targeted traffic (cf., details in Table S1). Plates were designed to measure colonization following 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 (eight per plot) were deployed per site on each occasion. After 3 and 13 months, eight plates (four at random per plot) were retrieved using polypropylene rubble bags (mesh < 0.5 mm) and then stored (for up to 4 hr) within a tank filled with seawater until processing in the laboratory.

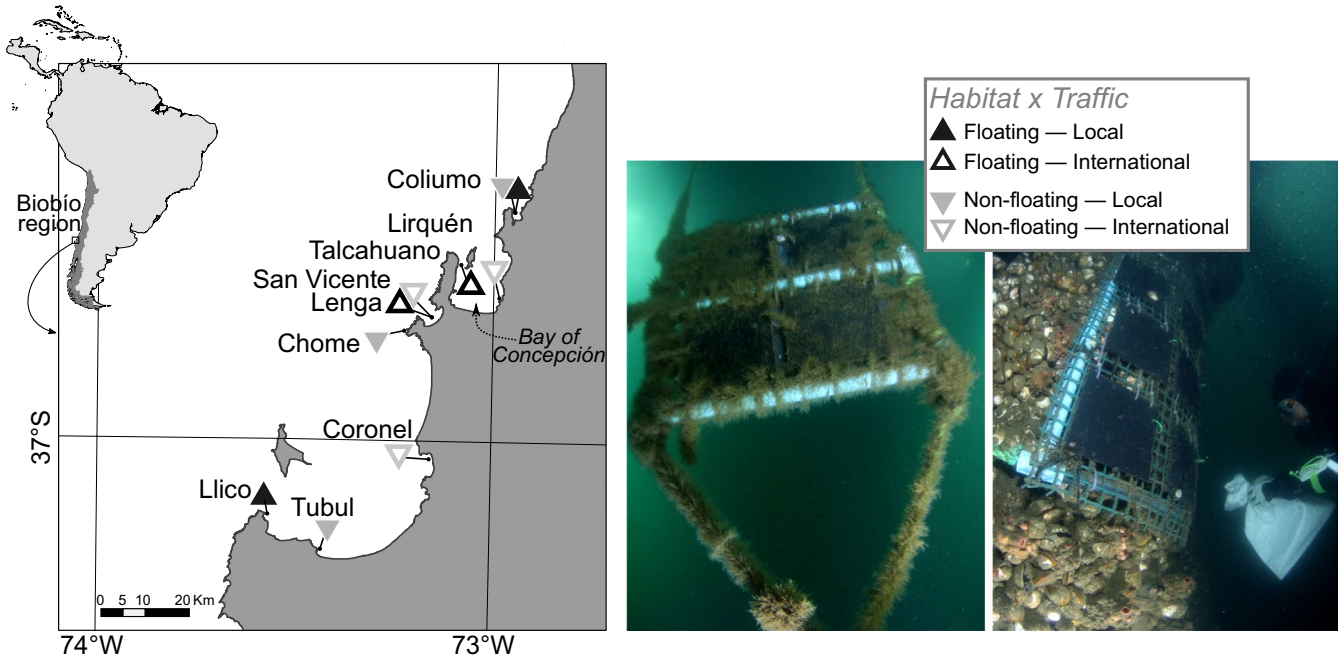


**FIGURE 1** Location of the study sites along the Bíobio region with corresponding habitat (floating vs. non-floating, photographs are courtesy of Mauricio Altamirano) and traffic (international vs. local) categories

## 2.2 | Data collection

### 2.2.1 | Environmental parameters

Environmental conditions at each site were assessed from a series of parameters: incident light, temperature, sediment pH, sediment organic matter content and concentration of different metals. Temperature (°C) and illuminance (Lum $ft^{-2}$) were measured in situ at 10-min intervals between March–June 2017 using data loggers (onset HOBO® data loggers Pendant Temp-Light, Onset Computer Corporation) deployed within each locality (international and local ports). Because of biofouling growing on the data loggers, light data gathered more than 4 weeks after panel deployment were not considered. Sediment parameters were determined from superficial sediment (first cm) samples ($n$ = 3–4) collected below experimental units in June 2017 and stored at −20°C until analyses. In the laboratory, sediment samples were lyophilized and pulverized. The pH was measured in 1:2.5 sediment to water ratio using an electrode. The organic matter content (%OM) was determined after calcination at ca. 550°C. Metal contents were determined using total reflection X-ray fluorescence analysis (Towett, Shepherd, & Cadisch, 2013, details provided in Leclerc et al., 2018 and Table S2).

### 2.2.2 | Diversity and community structure

In the laboratory, plates were removed from their bags, cleared from cable tiles and left with all remaining bag contents in seawater tanks until sessile fauna returned to their natural, untense state. Sessile taxa (mostly fauna, see Results) were identified under a dissecting microscope, and their abundances were assessed using percentage cover. To avoid edge effects in their distribution, a 15 mm perimeter was excluded from analysis, giving a 120 × 120 mm working area. Within the working area, species cover was estimated under 100 random intersection points out of 169 created between 13 × 13 evenly spaced (by 10 mm) lengths of string. Any species identified out of these intersection points was given a cover of 0.5%. Using the same procedure, cover was also determined for bare surface, grazing marks and organism remains (e.g. empty tubes or barnacle plates), hereafter referred as "abiotic variables" (though indirectly related to biotic processes). Species layering was taken into account; therefore, the total cover frequently exceeded 100%. All sessile specimens were identified at the lowest taxonomic level possible (generally species) by the same observer (JCL) and occasionally verified by external experts (see acknowledgements). Throughout the survey, voucher specimens were collected, dissected when appropriate and preserved in 95% ethanol in order to fill in the local reference collection (for further morphological and/or molecular examination). When appropriate, some specimens were maintained in isolated tanks with bubbling air stone and filled with seawater at ambient temperature until they developed diagnostic size and/or characteristics. Molecular barcoding (using COI) was also employed whenever necessary and possible to confirm species identification (e.g. *Mytilus galloprovincialis*, *Lissoclinum perforatum*). The identified specimens were categorized as "native," "non-indigenous," "cryptogenic" or "unassigned" according to the literature (e.g. Galea, 2007; Moyano, 1983; Turon, Canete, Sellanes, Rocha, & Lopez-Legentil, 2016) and public databases (EASIN, WORMS/WRIMS, Pagad, Hayes, Katsanevakis, & Costello, 2016). It is noteworthy that the cryptogenic species, from unknown/uncertain origin (sensu Carlton, 1996), found in this study displayed a cosmopolitan distribution and were potentially non-indigenous to the study area. When appropriate, taxa were also sorted according to their main function within the food web (carnivores, suspension–deposit feeders, herbivores).

## 2.3 | Statistical analyses

### 2.3.1 | Environmental variables

Patterns in abiotic conditions across localities were explored using a principal component analysis (PCA), based on normalized data. Data related to sediment conditions (pH, %OM, metal concentrations) were replicated ($n$ = 3–4 per sites) and all included as active variables in the PCA. All samples were given the same values for light and temperature (average and range over deployment period); therefore, these data were included as supplementary (i.e. illustrative or inactive) variables (Lê, Josse, & Husson, 2008). Environmental patterns were also examined with a two-way design using a permutational multivariate analysis of variance (PERMANOVA, Anderson, 2001), with 4,999 permutations. Factors were "maritime traffic" (hereafter "traffic," fixed, two levels: international and local) and "site" (random, nested within traffic). Sediments could not be sampled in two sites (Table S2), within which experimental units were deployed along floating structures (Talcahuano, Lenga); therefore, habitat type was not considered in this analysis. PERMANOVA was based on a Euclidean distance matrix generated from normalized data of the active variables of the PCA.

### 2.3.2 | Biota

Patterns in species richness, abundance and community structure of sessile taxa colonizing the experimental plates were examined with a four-way design using PERMANOVAs with 4,999 permutations. Factors were "traffic" (fixed, two levels: international and local ports), "habitat" (fixed, two levels: floating and non-floating), age of the settlement plate at the time of collection ("age," fixed, two levels: 3 and 13 months) and "site" (random, nested within "traffic × habitat"). One experimental unit was lost over the course of the experiment, therefore the corresponding term (plot) was not included in analyses, yet between 4–8 replicate plates were available for each combination of Site (Traffic × Habitat) × Age. The same model was also applied to test whether the abundance (cover and, when possible, number of individuals) of each non-indigenous taxon differed among levels of the main factors and

their interaction. Univariate analyses were based on Euclidian distance matrices, whereas multivariate analyses were based on Bray–Curtis similarity matrices generated from either raw or transformed data. In order to down weight the importance of most abundant species (and homogenize multivariate dispersion), multivariate data were always log-transformed. The homogeneity in univariate or multivariate dispersion was checked among the levels of the lowest interaction term Site (Traffic × Habitat) × Age using PERMDISP (Anderson, Gorley, & Clarke, 2008). No transformation allowed homoscedasticity to be achieved in univariate data, except in a few cases (see. Table S4–S6). Given the balance of the design and the large number of samples, univariate PERMANOVAs (analogous to ANOVAs) were considered robust enough to cope with this issue and were run on untransformed data (Underwood, 1997). As for multivariate data, samples were also ordinated using principal coordinate (PCO) analyses 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. Likewise, the variables (taxa and abiotic variables) contributing to the dissimilarity among the levels of the factors of interest were analysed using similarity percentage (SIMPER) analyses. All these statistical analyses were performed either on all variables combined (including unassigned taxa as well as abiotic data in the case of community structure) or separately for native taxa, non-indigenous and cryptogenic species (Thomsen, Wernberg, South, & Schiel, 2016). By analysing subcomponent of communities separately, Bray–Curtis similarity could not always be computed because of the presence of empty samples (e.g. plates not colonized by NIS): corresponding pairs of samples were thus removed from analyses (see degree of freedom in PERMANOVA results, Tables S3-S5).

We further compared the variations in beta diversity between habitats. To this end, we determined the decline in Jaccard similarity and Bray–Curtis similarity coefficients (McKinney & Lockwood, 2005), computed from presence–absence and log-transformed cover matrices (abiotic variables excluded), respectively, with increasing linear distance between independent pairs of samples (randomization procedure described in Figure S3) in both habitat types. The procedure was carried using 3- and 13-month-old plates, separately. After examining the residual versus fitted value plot and the Q-Q plot, trends in similarity declines across spatial scales were compared between habitats using an analysis of covariance (ANCOVA) with "habitat" as categorical factor and log10-transformed distance between sampling units as covariate.

Community analyses (including PCO, SIMPER and PERMDISP) and all PERMANOVAs were performed using PRIMER 7 (Clarke & Warwick, 2001), whereas PCA and ANCOVAs were conducted using R environment (Lê et al., 2008; R Development Core Team, 2014).

## 3 | RESULTS

A total of 78 taxa, dominated by sessile fauna (68 taxa), were identified on the plates across all sites and sampling times (Table S3). Thirteen taxa were non-indigenous and 12 cryptogenic.

### 3.1 | Contrasting effects of the maritime traffic on abiotic and biotic variables

The environmental conditions differed among sites (PERMANOVA: site (traffic): $F_{6,17} = 4.79$, $p < .001$) and maritime traffic categories (traffic: $F_{1,17} = 3.41$, $p = .012$, Axis 1 on PCA, Figure S1). As compared to local ports, international ports were generally characterized by greater metal concentrations (except Hg) and lower incident light (inactive variable along Axis 1). There were however some overlaps among sites, as exemplified by similar metal concentrations or light level at the docks of Coliumo (local), Lirquén and San Vicente (international). According to the PCA, an important part of the remaining

**TABLE 1** Summary of PERMANOVA tests for differences in richness, cover and community structure among levels of the main factors (traffic, habitat, age and site) and their interactions

| | | Richness | | | | Cover | | | | Community structure | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Source | *df* | All | Nat. | Cry. | NIS | All | Nat. | Cry. | NIS | All | Nat. | Cry. | NIS |
| Traffic (T) | 1 | .677 | .857 | .554 | .239 | .534 | .986 | .674 | .310 | .594 | .367 | .247 | .374 |
| Habitat (H) | 1 | **.027** | .651 | .726 | **.019** | .068 | .878 | .851 | **.041** | **.030** | .337 | .214 | **.009** |
| Age (A) | 1 | .265 | **.003** | .292 | .680 | **.003** | **.004** | .344 | .370 | **.005** | **.007** | .199 | **.037** |
| H × T | 1 | .972 | .360 | .978 | .540 | .283 | .196 | .517 | .924 | .572 | .310 | .374 | .489 |
| T × A | 1 | .886 | .705 | .308 | .361 | .780 | .393 | .673 | .060 | .282 | .146 | .111 | .481 |
| H × A | 1 | .523 | .310 | .320 | .631 | .994 | .592 | .986 | .574 | .081 | .120 | .298 | .318 |
| Site (H × T) = S | 6 | **<.001** | **<.001** | **<.001** | **<.001** | **<.001** | **<.001** | **<.001** | **<.001** | **<.001** | **<.001** | **<.001** | **<.001** |
| H × T × A | 1 | .977 | .440 | .415 | .218 | .094 | .518 | .050 | .140 | .623 | .181 | .620 | .631 |
| S (H × T) × A | 5 | **<.001** | **<.001** | **<.001** | **<.001** | **<.001** | **<.001** | **.024** | **<.001** | **<.001** | **<.001** | **<.001** | **<.001** |

*Note:* Only *p*-values are given and highlighted in bold when significant at $p < .05$. Tests are presented for all, native (Nat.), cryptogenic (Cry.) and non-indigenous (NIS) taxa, separately. Detailed tests (incl. transformations and PERMDISP) are given in Tables S2-S4.

variation in abiotic conditions (Axis 2, 23.5%) was actually most likely explained by regional oceanography: as compared to other localities, higher temperature, organic matter and pH in sediments were consistently measured in the Bay of Arauco (i.e. in Llico, Tubul and Coronel, Figure S1).

Conversely, no effect of the maritime traffic could be detected on the associated biota for any of the general response variables investigated (richness, abundance, community structure) regardless of the type of substratum and the age of panel assemblage (Table 1, Figure 2, Figure S2). Overall (Table S3), similar numbers of NIS and cryptogenic taxa were identified in local (10 and 12, respectively) and international ports (11 and 10, respectively). Only a few species were observed in a single category of port, and most of them were recorded at one site only (Table S3).

Similarly, no effect of the maritime traffic could be detected on the abundance of each NIS, with however one exception: a significant interaction Habitat × Traffic ($F_{1,159}$ = 68.39, $p$ < .001) was found for the numerical abundance of the introduced tunicate *Ciona robusta*. The abundance of *Ciona robusta* did not vary between traffic categories in non-floating habitats (pairwise test, $t$ = 0.98, $p$ = .398), whereas 52-fold as many individuals was observed on floating substrata in international than in local ports ($t$ = 6.94, $p$ = .024). With any of the other response variables tested, no interaction between the traffic category and habitat type was observed.

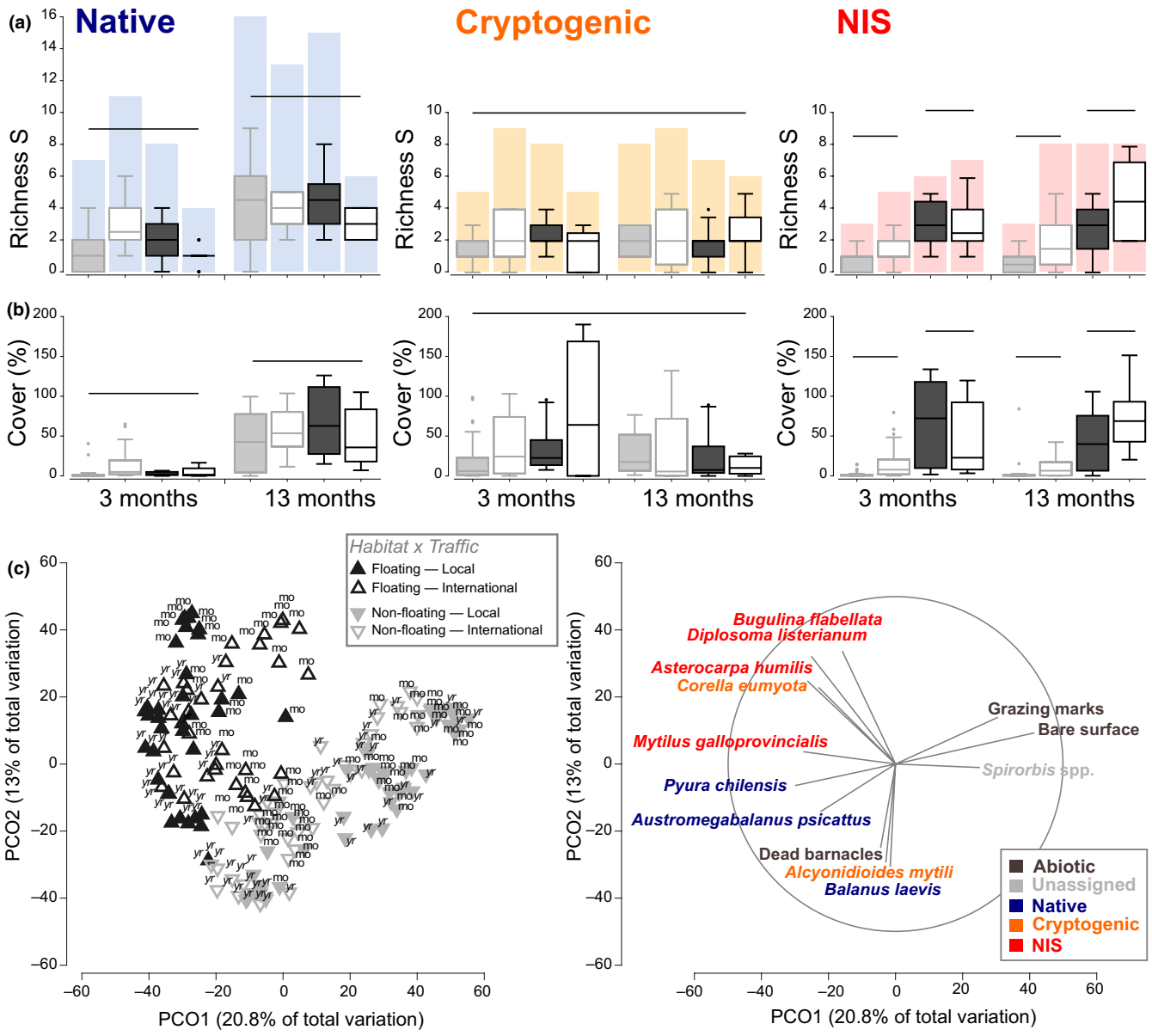


**FIGURE 2** Richness (a) and abundances (b) of native, cryptogenic and non-indigenous taxa, and community structure (c, principal coordinate analysis) compared between habitat types (floating, non-floating) and maritime traffic categories (international, local) across study sites, after 3 and 13 months (labelled "mo" and "*yr*," respectively, in the PCA left panel in c). Horizontal lines overhanging the bars regroup values that do not differ significantly following pairwise tests. Backward coloured bars indicate cumulative richness values across all replicates and sites, for each category. Vector plots of variables correlated with the PCO axes ($r$ > .5) are indicated in the bottom right panel

### 3.2 | Taxon-dependent effects of the habitat type on community diversity and structure

Regardless of the maritime traffic associated with each study site, there were important differences in diversity and community structure between the two types of habitats investigated (Figures 2,3, Figure S2, Table 1). Upon experimental plates, the fouling assemblage was on average 35.3% richer, for a total cover 71.3% marginally greater, on floating than non-floating substrata (Table 1, Figure S2).

Neither native nor cryptogenic species displayed differences between habitats, conversely to NIS. Comparing floating and non-floating habitats, differences in richness and cover were mainly driven by non-indigenous species (Figure 2, Table 1). On average, there were three times as many NIS upon floating compared with non-floating substrata (Figure 2a). In addition, NIS occupied about sevenfold as much of the panel surface (Figure 2b). This assessment is further supported by analyses on community structure. Both the PCO and the PERMANOVA clearly distinguished assemblages established in floating versus non-floating habitats, across the study region (Figure 2c, Table 1). Again, only the non-indigenous component of these assemblages displayed significant differences between habitats (Table 1). Diverse NIS contributed substantially to

**TABLE 2** Results of SIMPER analyses based on Bray–Curtis similarity among treatments (floating and habitat) after 3 and 13 months of assemblage development

| | | 3 months | | | | 13 months | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Abundance | | $\bar{\delta}$ = 90.4 | | Abundance | | $\bar{\delta}$ = 87.3 | |
| Taxon/other variables | Phylum | Floating | Fixed | $\bar{\delta}_i$% | $\bar{\delta}_i$:SD | Floating | Fixed | $\bar{\delta}_i$% | $\bar{\delta}_i$:SD |
| Abiotic variables | | | | | | | | | |
| Bare surface | – | **0.7** | **2.4** | **7.7** | **1.3** | **0.3** | **1.9** | **5.0** | **1.2** |
| Grazing marks | – | – | **1.2** | **4.6** | **0.6** | **< 0.1** | **0.8** | **2.3** | **0.6** |
| Dead barnacles | Art | < 0.1 | 0.2 | 0.6 | 0.6 | **0.5** | **1.1** | **3.2** | **1.0** |
| NIS | | | | | | | | | |
| *Bougainvillia muscus* | Cni | **0.5** | **0.4** | **2.8** | **0.8** | **0.4** | **0.5** | **1.9** | **0.7** |
| *Bugulina flabellata* | Bry | **2.0** | **0.1** | **7.4** | **1.2** | 0.6 | 0.1 | 1.4 | 0.6 |
| *Exochella* sp. nov. | Bry | **0.5** | **0.1** | **2.2** | **0.6** | 0.1 | 0.6 | 1.5 | 0.6 |
| *Mytilus galloprovincialis* | Mol | – | – | 0.0 | – | **2.5** | **0.1** | **6.7** | **1.7** |
| *Asterocarpa humilis* | Cho | **0.9** | – | **3.2** | **0.7** | **1.3** | – | **3.4** | **1.0** |
| *Ciona robusta* | Cho | **0.7** | – | **2.5** | **0.7** | **0.8** | **0.1** | **2.1** | **0.6** |
| *Diplosoma listerianum* | Cho | **2.3** | **<0.1** | **8.5** | **1.3** | **1.6** | – | **4.2** | **1.2** |
| Cryptogenic species | | | | | | | | | |
| *Amphisbetia operculata* | Cni | – | 0.2 | 0.7 | 0.4 | **0.2** | **0.8** | **2.3** | **0.6** |
| *Clytia linearis* | Cni | – | 0.5 | 1.8 | 0.5 | **0.6** | **0.3** | **2.2** | **0.7** |
| *Coryne eximia* | Cni | **1.1** | **0.7** | **5.2** | **0.7** | <0.1 | <0.1 | 0.2 | 0.3 |
| *Obelia dichotoma* | Cni | **0.9** | **0.7** | **4.9** | **0.8** | **0.9** | **0.1** | **2.5** | **0.7** |
| *Alcyonidioides mytili* | Bry | – | 0.3 | 1.3 | 0.4 | **< 0.1** | **1.2** | **3.0** | **0.7** |
| *Amathia* cf. *gracilis* | Bry | **1.3** | **0.3** | **5.2** | **0.7** | **0.6** | **0.5** | **2.3** | **0.8** |
| *Corella eumyota* | Mol | **0.9** | **0.0** | **3.2** | **0.8** | **0.7** | **<0.1** | **1.8** | **0.9** |
| Native species | | | | | | | | | |
| *Austromegabalanus psittacus* | Art | 0.3 | 0.3 | 1.5 | 0.8 | **1.9** | **0.7** | **5.1** | **1.1** |
| *Balanus laevis* | Art | – | 0.5 | 1.6 | 0.6 | **0.4** | **2.0** | **5.2** | **1.1** |
| *Crepipatella fecunda* | Mol | 0.1 | 0.3 | 1.1 | 0.8 | **0.7** | **1.1** | **3.1** | **1.1** |
| *Semimytilus algosus* | Mol | < 0.1 | 0.5 | 1.9 | 0.5 | **0.6** | **0.8** | **3.0** | **0.7** |
| *Pyura chilensis* | Cho | 0.3 | 0.4 | 2.0 | 0.8 | **2.6** | **0.4** | **6.4** | **1.5** |
| Unassigned | | | | | | | | | |
| Amphipod tubes | Art | **1.3** | **<0.1** | **5.0** | **0.7** | **1.0** | **0.5** | **2.9** | **0.9** |
| *Spirorbis* sp. | Ann | **< 0.1** | **1.0** | **4.1** | **0.6** | <0.1 | 0.5 | 1.5 | 0.6 |

*Note:* The average dissimilarity ($\bar{\delta}$) is indicated for each analysis. Average abundances were log-transformed. Values in bold indicate that the corresponding variable (or taxa) contributed to pairwise dissimilarity at a cut-off level of 70%. Variables found above this cut-off level are not presented. Variable type, status and phylum (Ann: Annelida, Mol: Mollusca, Art: Arthropoda, Cni: Cnidaria, Bry: Bryozoa, Cho: Chordata) are indicated.

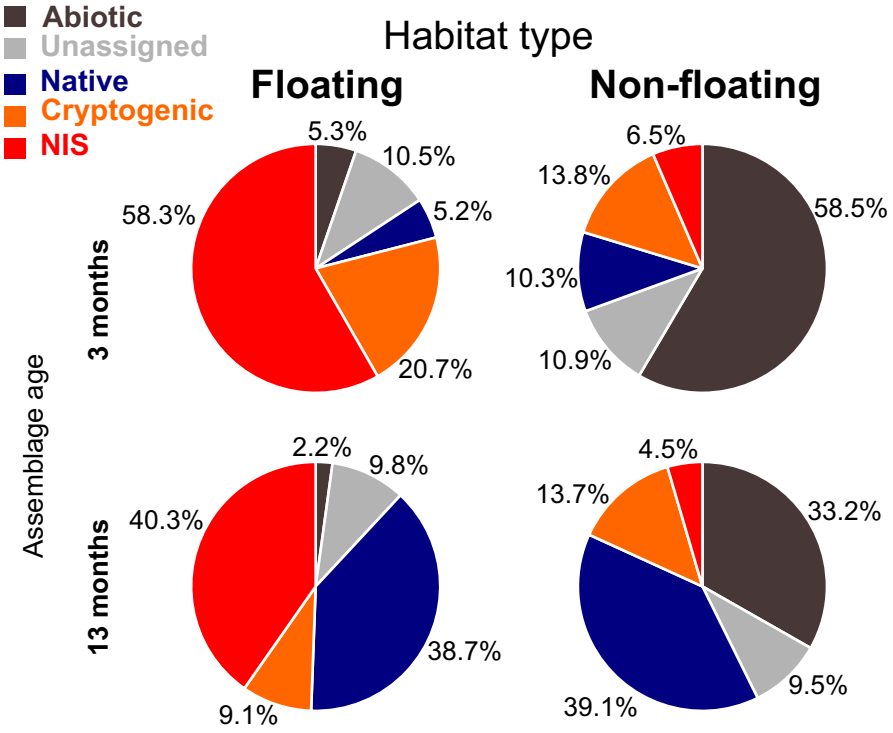


**FIGURE 3** Cumulative contribution of all taxa and abiotic variables (e.g. bare surface and grazing marks) to the within-group similarity (SIMPER) of assemblages in floating versus non-floating habitats, after 3 (S = 31.0) and 13 months (S = 24.1)

the overall community structure according to their correlations with the PCO axes (Figure 2c), as detailed below.

### 3.3 | Taxa responsible for differences between habitats

Differences between habitats were further analysed using SIMPER. The factors "age" and "site" were frequently found significant and consistently presented significant interactions regardless of the response variable (Table 1). Indeed, the community structure changed over succession in every site. SIMPER analyses among levels of the factor "habitat," albeit not interacting with "age," were thus run separately for 3- and 13-month-old assemblages (Table 2, Figure 3).

After 3 months, non-indigenous and cryptogenic species were jointly responsible for >80% of the contribution to the similarity among floating assemblages (58.3% and 20.7%, respectively, Figure 3). Of these taxa, colonial and solitary ascidians (e.g. *Diplosoma listerianum*, *Ciona robusta*, *Asterocarpa humilis* and *Corella eumyota*), bryozoans (e.g. *Bugulina flabelatta* and *Amathia* cf. *gracilis*) and hydrozoans (e.g. *Coryne eximia*) were the main contributors to the dissimilarities between habitats (Table 2). The similarity among non-floating assemblages and their dissimilarity with floating ones were mainly due to abiotic variables (58.5% contribution), such as bare surface and grazing marks (Table 2, see also Figure 2c, Figure S2).

After 13 months, an important increase in the contribution of native taxa (3.8–7.4 fold change) was observed in the two study habitats, some of which were also contributing to the dissimilarity between the habitats. For instance, among native barnacles, *Austromegabalanus psicattus* and *Balanus laevis* were more abundant within floating and non-floating assemblages, respectively (Table 2). At the same time, the contribution of all NIS to the community structure decreased by 30.1% on floating structures and some of the NIS that largely contributed to the dissimilarities between habitats after 3 months became less important after 13 months (e.g. *Bugulina flabelatta*, Table 2). In contrast, others arose, such as *Mytilus galloprovincialis* which successfully colonized all floating sites, but was virtually absent from assemblages developed on non-floating substrates (Table 2).

### 3.4 | Stronger decrease in community similarity in non-floating habitat across scales

Whether considering presence–absence or quantitative data in the two study habitats, a clear decline in community similarity with geographic distance was captured at the scale of the study (Figure 4). According to the ANCOVAs, a significant interaction between the categorical factor (habitat) and covariate (geographical distance) was detected for both the Jaccard ($F_{1,73}$ = 8.564, $p$ = .004) and the Bray–Curtis ($F_{1,73}$ = 5.689, $p$ = .019) similarity coefficients, indicating different slopes between habitats (Figure 4). The rate of decline was stronger in non-floating than in floating habitat, with diverging similarity values towards the regional scale as shown by the confidence intervals in Figure 4. This pattern indicates higher biotic homogenization in floating habitat at the scale of the study.

## 4 | DISCUSSION

Our results partly support our working hypotheses. Firstly, as predicted, community diversity and structure differ between habitats. Interestingly, this pattern is mainly driven by NIS and

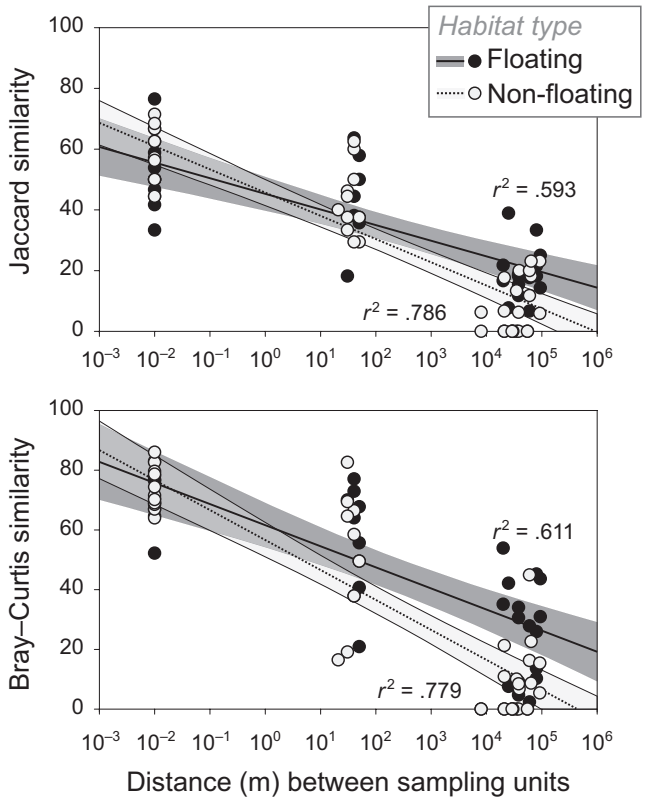


**FIGURE 4** Decline in Jaccard similarity (top) and Bray–Curtis similarity (bottom) coefficients (with 95% CI and $r^2$), computed from presence–absence and log-transformed cover matrices (abiotic variables excluded), respectively, with increasing distance (linear coastline, m, $\log_{10}$-scale) between pairs of samples (randomization procedure described in Figure S3) in the two study habitats

is consistent across the study region. Regardless of the type of maritime traffic, our results reveal a remarkable susceptibility to invasion and to biotic homogenization of floating structures—compared with their non-floating counterparts—at both early and later stages of community development. Secondly, conversely to our expectations, neither the type of maritime traffic nor its interaction with habitat has an influence at the community level (for any response variable, except one NIS: *Ciona robusta*), suggesting that the combined colonization and propagule pressures of all NIS varied poorly across maritime traffic categories (international vs. local).

Theory predicts that habitats are not equally prone to invasion for a given immigration rate (Davis et al., 2000; Lockwood et al., 2013). This prediction is empirically supported in terrestrial ecosystems by work at broad scales which used proxies of combined colonization and propagule pressures, such as human population or distance to the nearest conurbation (Aikio et al., 2012; Chytrý et al., 2008; Pyšek et al., 2015). Here, we used settlement plates to compare whether habitat invasibility varied between two categories of ports, associated with international versus local maritime traffic. As pointed out above, we observed an interaction between habitat type and traffic category in one case: *Ciona robusta* colonized plates in greater abundances in international than in local ports, upon floating substrata only. This non-indigenous tunicate is a common hitchhiker of ship hulls, and the abundance of its recruits is likely to give a proxy of its associated propagule pressure (Lockwood et al., 2009; Zhan, Briski, Bock, Ghabooli, & MacIsaac, 2016). With a limited scope, the case of *C. robusta* supports the hypothesis that marine habitats are not equally affected by propagule pressure (see also Simkanin, Davidson, Therriault, Jamieson, & Dower, 2017 for an experimental manipulation of propagule pressure of one NIS at a local scale). However, besides this specific example, and albeit various NIS observed in our study, no other NIS displayed varying distribution (incl. on plates) according to the maritime traffic. This confirms the results from Leclerc et al. (2018), who did not observe differences in NIS establishment and contribution to community structure (including on established assemblages) between international and local ports. Above this preliminary study in the region, we herein controlled for habitat type and thus can conclude with confidence that the overall propagule and colonization pressures (i.e. encompassing all NIS) were not directly related to the traffic type. In order to explain this overall pattern, Leclerc et al. (2018) proposed several hypotheses and notably revealed important similarities in the relative abundance of most taxa (incl. NIS) on settlement plates and surrounding assemblages on artificial substrata. The propagule pressure associated with each NIS and their contribution to colonization pressure may thus rather reflect spread processes of a mixture of founding and well-established populations (Blackburn et al., 2011; Seebens et al., 2019).

Whereas the individual contributions of these NIS to the propagule pool have likely integrated the influence of maritime traffic of each site, their introduction and invasion history is more intricate to unravel (Schwindt & Bortolus, 2017; Seebens et al., 2019). Colonization of and spread across artificial habitats are influenced by a combination of human-mediated and natural dispersals. In seemingly "open" marine systems, the relative influence of both types of dispersal is however expected to differ according to pelagic dispersal duration, with a putative larger influence of human-mediated dispersal for species characterized by short-lived dispersal stage. This expectation has been supported by genetic studies of short dispersers, such as the tunicate *Ciona intestinalis* (Hudson, Viard, Roby, & Rius, 2016) or the Pacific kelp *Undaria pinnatifida* (Guzinski, Ballenghien, Daguin-Thiébaut, Lévêque, & Viard, 2018): in marinas, these species display chaotic genetic structure at regional scale, which is best explained by the role of shipping than natural dispersal. The influence of human-mediated dispersal may however be less important in marine invertebrates displaying larval stage lasting typically 3–5 weeks in the water column (e.g. molluscs; Shanks, 2009). Dispersal traits may thus be key determinants of colonization and propagule pressure at local scales. Considering them, the complex and dynamic network of transport vectors and pathways (including physical corridors) altering connectivity in marine systems (Bishop et al., 2017; Sardain et al., 2019) constitutes a major challenge for characterizing habitat invasibility at multiple spatial scales.

Whether an introduced species can successfully establish self-sustaining populations depends on the match between its phenotypic traits (e.g. size, growth rare, metabolic requirements, feeding and reproductive strategies) and recipient habitat properties (e.g. resource levels, community and abiotic conditions; Fridley & Sax, 2014; Lockwood et al., 2013; Pyšek et al., 2015). Here, we show that regardless of the type of maritime traffic, marine artificial habitats are not equally prone to NIS spread and to biotic homogenization at regional scale (Figure 4). Ocean sprawl is of particular concern for biodiversity conservation and invasion risks because artificial structures cannot represent surrogate habitat for the diversity and ecosystem functioning of neighbouring rocky reefs (Bishop et al., 2017; Chapman & Underwood, 2011). Our results suggest that some particular artificial habitats, here non-floating ones, such as piling or rocks, may be "better" surrogates than others (Dafforn et al., 2009). Despite drastic differences in orientation, substrate type and habitat heterogeneity in comparison with natural rocky reefs (e.g. Firth et al., 2016), piling and seawalls are influenced by a series of stress gradients, along which species assembly follows general rules (Bulleri & Chapman, 2010; Connell, 1961; Jones & Kain, 1967). Even after 13 months, we observed an important contribution of abiotic variables, such as bare space and grazing marks on settlement plates deployed upon pilings, suggesting that fouling assemblages were structured by habitat-specific properties. A series of exclusion experiments performed within four of the local and international ports herein studied showed that predation was particularly strong upon NIS settling on pilings, and could be a major driver of biotic resistance within non-floating artificial habitats, both locally and regionally (Leclerc et al., 2019). Leclerc et al. (2019) also showed that consumptive biotic resistance was dependent on the diversity of predators. Floating structures (e.g. pontoons, buoys and farms) are poorly connected to the bottom and may therefore be within reach of less abundant and diversified predators than their non-floating counterparts intimately associated with the bottom (Dumont, Gaymer, & Thiel, 2011; Rogers, Byrnes, & Stachowicz, 2016). Among other candidate stressors altered within such artificial structures (Dafforn et al., 2009; Holloway & Connell, 2002; Johnston et al., 2017), biotic interactions with recipient communities could therefore be a major filter determining community and NIS assembly—and thus beta diversity (Chase, Biro, Ryberg, & Smith, 2009, our study)—in marine urban habitats.

The habitat legacy concept predicts that traits allowing a species to colonize habitats in its native range influence its ability to successfully overcome ecological filters in its introduced range (Fridley & Sax, 2014; Pyšek et al., 2015). This concept has recently proven pivotal in explaining invasion patterns in terrestrial and freshwater habitats (Fitzgerald et al., 2016; Kalusová et al., 2017), but tend to be overlooked in marine systems. For centuries (Carlton & Hodder, 1995), humans have deployed floating structures (including ship hulls, buoys, pontoons, aquaculture facilities and marine debris) and thus created novel niche opportunities above virtually all types of coastal habitats (and associated species pools)—a phenomenon still expanding (Mineur et al., 2012; Moser et al., 2016). Regardless of the biotic and abiotic processes influencing species assembly on floating substrata (Bravo et al., 2011; Holloway & Connell, 2002; Thiel & Gutow, 2005a; Wahl, 1989), these structures may have promoted the invasive behaviour of cosmopolitan fouling invaders, by selecting a series of characteristic traits (Aronson et al., 2016; Bishop et al., 2013; Gérard, Bierne, Borsa, Chenuil, & Féral, 2008; Pyšek et al., 2015; Zhan et al., 2016), as mirrored by the abundance of many of them in our floating sites. For instance, in its putative native range (New Zealand), *Asterocarpa humilis* is abundant in diverse habitats from intertidal undersides of rocks to rock walls up to 30 m across natural shores and harbours (Brewin, 1948, 1956), but has been particularly successful in colonizing floating artificial substrata (ship hulls, floating docks and aquaculture nets; Bishop et al., 2013; Lambert, Lambert, & Waaland, 1996 and references therein). Likewise, mussel aquaculture mainly relies on the use of suspended ropes attached to floating rafts and longlines (Beaumont, Gjedrem, & Moran, 2007; Díaz, Sobenes, & Machino, 2019). In order to cultivate *Mytilus galloprovincilis*, this practice has dramatically expanded in the Mediterranean since the 1950s (Beaumont et al., 2007) and may thus have had a pivotal role in its recent invasions worldwide (Gérard et al., 2008). Irrespective of the vast array of putative vectors of primary and secondary introductions of marine NIS, floating habitats may have constituted a major corridor to their spread from and within their native to introduced ranges.

Floating, rafting or moving substrata have likely played an important role in shaping marine biogeography, but until the Anthropocene, they were composed by relatively rare, small-sized, ephemeral and highly disturbed items (e.g. wood, kelp and pumice; Thiel & Gutow, 2005b). Floating habitats are now blooming pervasively across diverse and abundant artificial structures comparatively massive, less disturbed and built up with perennial materials (Dafforn et al., 2015; Mineur et al., 2012; Moser et al., 2016). At large scales, the diversity and asynchronous deployment of these floating structures under the influence of multiple local stressors possibly create a mosaic of successional stages and in turn may allow for the coexistence of diverse species (including NIS) displaying a range of opportunistic to more perennial strategies (Connell, 1978; Leclerc, 2018; Sousa, 1979). At the regional scale herein studied, the overall contribution of NIS to community structure on floating structures remained substantial (>40%, Figure 3) between 3–13 months. While this contribution varied among NIS, we did not observe any sign of replacement of early successional species that have been flourishing after 3 months (Table 2). We rather sampled a larger number of NIS (combined richness, Figure 2) after 13 months. In that context, it is worth noting that our results indicate that *M. galloprovincialis* (absent after 3 months) successfully colonized and became a dominant species (after 13 months) on floating plates already heavily fouled (after 3 months), across all study sites. These results suggest that invasional meltdown could be important on floating structures of the region, although testing

for this effect would require further studies of community assembly (Bulleri, Bruno, & Benedetti-Cecchi, 2008; Leclerc & Viard, 2018; Sax et al., 2007; Simberloff & Von Holle, 1999; Stachowicz & Byrnes, 2006).

At a regional scale, our study demonstrates that the distribution and colonization of marine NIS vary among habitats, regardless of associated type of maritime traffic. More specifically, we show that floating artificial habitats are particularly prone to NIS colonization, likely due to long-standing selection processes concomitant to the worldwide expansion of shipping and aquaculture. Following a strict terminology (Lockwood et al., 2013; Wilson et al., 2009), the floating function is shared by both transport vectors and dispersal pathways, through the creation of corridors, all constituting a complex suite of micro-habitats (Coutts, Moore, & Hewitt, 2003; Holloway & Connell, 2002). To some extent, our results support Connell's (2000) point that floating structures are poor surrogates of the fundamental processes of natural shores. In a changing world where they are expanding at unprecedented rate, applied and invasion ecologists are encouraged to reinforce the current body of knowledge on the functioning and connectivity within and among these habitats at multiple spatial scales (Johnston, Hedge, & Mayer-Pinto, 2015; Lavender, Dafforn, Bishop, & Johnston, 2017a, 2017b), not only to improve risk models (Sardain et al., 2019; Seebens et al., 2016) and spatial planning (Bishop et al., 2017; Dafforn, 2017), but also to efficiently estimate the rate of biotic homogenization due to ocean sprawl.

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## DATA AVAILABILITY STATEMENT

Most of the data are provided in the supplementary material associated with the manuscript. Further detailed data will be made publicly available in the Dryad repository (https://doi.org/10.5061/dryad.8gtht76jg, submitted).

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## BIOSKETCH

**Jean-Charles Leclerc** is a community ecologist who recently completed his post-doctoral project dealing with the processes influencing marine invasions in Chile. His current research interests are related to the ecological mechanisms allowing specific habitats or ecosystems to resist environmental changes in the Anthropocene.

Author contributions: JCL, FV and AB conceived the working hypotheses and study design. JCL led sample collection and processing and conducted the taxonomic analyses. EGS and JNH conducted chemical analyses and KPA and FS assisted with barcoding. JCL analysed the data and led the writing, with substantial contributions from FV to the first draft. All authors critically edited the manuscript drafts.

## SUPPORTING INFORMATION

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

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