

# Structural and functional effects of global invasion pressure on benthic marine communities—patterns, challenges and priorities

Anastasija Zaiko<sup>1,2</sup>  | Alice Cardecia<sup>3</sup>  | James T. Carlton<sup>4</sup> | Graeme F. Clark<sup>5</sup> | Joel C. Creed<sup>6</sup> | Ian Davidson<sup>1</sup> | Oliver Floerl<sup>1</sup> | Bella Galil<sup>7</sup> | Edwin Grosholz<sup>8</sup> | Grant A. Hopkins<sup>1</sup> | Emma L. Johnston<sup>5</sup> | Jonne Kotta<sup>9</sup> | Agnese Marchini<sup>3</sup>  | Henn Ojaveer<sup>10,11</sup> | Gregory Ruiz<sup>12</sup> | Thomas W. Therriault<sup>13</sup> | Graeme J. Inglis<sup>14</sup>

<sup>1</sup>Cawthron Institute, Nelson, New Zealand

<sup>2</sup>Sequench, Nelson, New Zealand

<sup>3</sup>Department of Earth and Environmental Sciences, University of Pavia, Pavia, Italy

<sup>4</sup>Ocean & Coastal Studies Program, Williams College-Mystic Seaport, Mystic, Connecticut, USA

<sup>5</sup>School of Life and Environmental Sciences, University of Sydney, Sydney, New South Wales, Australia

<sup>6</sup>Departamento de Ecologia, Instituto de Biologia Roberto Alcântara Gomes, Universidade do Estado do Rio de Janeiro, Rio de Janeiro, Brazil

<sup>7</sup>Steinhardt Museum of Natural History, Tel Aviv University, Tel Aviv, Israel

<sup>8</sup>Department of Environmental Science and Policy, University of California, Davis, California, USA

<sup>9</sup>Estonian Marine Institute, University of Tartu, Tallinn, Estonia

<sup>10</sup>National Institute of Aquatic Resources, Technical University of Denmark, Lyngby, Denmark

<sup>11</sup>Pärnu College, University of Tartu, Pärnu, Estonia

<sup>12</sup>Smithsonian Environmental Research Center, Edgewater, Maryland, USA

<sup>13</sup>Fisheries and Oceans Canada, Pacific Biological Station, Nanaimo, British Columbia, Canada

<sup>14</sup>National Institute of Water & Atmospheric Research Ltd (NIWA), Christchurch, New Zealand

## Correspondence

Anastasija Zaiko, Cawthron Institute, Private Bag 2, Nelson 7042, New Zealand.  
Email: [a.zaiko@sequench.co.nz](mailto:a.zaiko@sequench.co.nz)

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## Abstract

**Aim:** Retrospective (pre- vs. post-invasion) and cross-sectional comparisons of ecosystems exposed to high and low bioinvasion pressure, provide an alternative approach to evaluate shifts in biological communities associated with non-indigenous species (NIS) introductions. In this study, we aimed to examine general patterns of change in community composition, structure and function in six well-studied and globally distributed marine ecosystems that had documented histories of biological invasions.

**Location:** Global.

**Methods:** By considering a range of regional datasets and different sampling approaches, we evaluated trends within and among ecosystems by comparing paired measures of community and functional structure in either space or time.

**Results:** Our analyses revealed different patterns of structural and functional change at ecosystem scales, but direct comparisons across regions were hindered by

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confounding effects of study designs and other drivers of change. The most prominent shifts in community composition were observed in the retrospective studies, characterised by the greatest relative contribution of NIS. No uniform pattern of change in functional metrics was observed across study regions. However, functional evenness and dispersion showed a tendency to increase in systems under higher invasion pressure, refuting the hypothesis of selective accumulation of specific traits and functional homogenisation within ecosystems exposed to high invasion pressure.

**Main Conclusions:** Accumulation of NIS within broader communities can be a subtle process, with inherent spatial and temporal variability. Nonetheless, not only do species' proportional contributions to communities change over time in areas subjected to high bioinvasion pressure, but trait profiles can incrementally shift, which alters the original ecology of an area. Planned, long-term studies that incorporate a range of measures of environmental drivers and ecosystem response are crucial for better understanding of cumulative, community-level and ecosystem-scale change associated with biological invasions.

#### KEYWORDS

benthic communities, Biological invasions, cumulative effects, historical datasets, non-indigenous species, trait analysis

## 1 | INTRODUCTION

Biological invasions are a defining characteristic of global change and the Anthropocene epoch in general (Leroy et al., 2023; Lewis & Maslin, 2015; Ricciardi, 2007). Since the middle of the twentieth century, the number of species that have been detected outside their native historical range has increased dramatically across most of the world's terrestrial and aquatic ecosystems, in association with increased global trade and travel (Bailey et al., 2020; Early et al., 2016; Seebens et al., 2018). Over that period, research on the ecological and economic consequences of non-indigenous species (NIS) has increased correspondingly (IPBES, 2019; Pejchar & Mooney, 2009; Simberloff et al., 2013). Despite decades of research on bioinvasions, documenting new incursions and the consequences of many individual NIS (Carlton, 1999; Galil, 2018; Guy-Haim et al., 2018; Katsanevakis et al., 2014; Ruiz et al., 1997; Seebens et al., 2017), we still lack understanding of the chronic, cumulative impacts of multiple NIS on communities and ecosystems (Ojaveer & Kotta, 2015; Ruiz et al., 1999). Most of our understanding of invasion biology is at the population level, focused on a single NIS, a restricted geographical area and/or timeframe (Strayer et al., 2006; Watkins et al., 2021). There is a lack of standardised longer-term community data from the invaded environments, that can help us interpret how community assembly and ecosystem functions change over time in response to multiple invasions (Carlton, 2009). Impacts of marine NIS are known to vary from species-to-species and place-to-place, but most marine invasions have likely not reached equilibrium and the size of the invaded range for NIS is strongly associated with 'time since arrival' (Byers et al., 2015; Galil, 2021). Measuring and evaluating

this dynamism at the community or ecosystem level over reasonable timeframes would help reveal the extent to which invasions contribute to marine community change and to variation in ambient community effects, including ecosystem goods and services, of this global scale phenomenon.

A great deal of our current understanding of the impacts of individual marine NIS has been derived from: (i) *autecological studies*, producing one-off observational datasets of the ecological profile of a NIS (e.g. Firth et al., 2021; Lutz-Collins et al., 2009; Olenina et al., 2010; Orlova et al., 2004); (ii) *autecological/synecological experimental studies*, where interactions with native species and assemblages are deduced by manipulative experiments by adding, removing, altering abundance or using physical mimic models of natives or NIS (e.g. Atalah et al., 2019; Floerl et al., 2004; Giddens et al., 2014; Hollebone & Hay, 2008); and (iii) *presence-absence synecological studies*, usually observational and/or experimental comparisons within a site, when diversity, structure and function of the communities inside and outside the NIS-affected habitat are examined (e.g. Guilhem et al., 2020; Ross et al., 2006; Zaiko et al., 2009). However, to evaluate the chronic and cumulative effects of multiple invasions in the absence of genuine and consistent long-term datasets, *retrospective studies*, contrasting baseline (pre-invasion) to subsequent (post-invasion) data (e.g. Floerl et al., 2009; Forrest & Taylor, 2002; Steger et al., 2022); and *cross-sectional studies*, contrasting locations historically exposed to high propagule pressure and invader colonisation (e.g. due to proximity to a propagule source, Johnston et al., 2009) may offer greater insights (Strayer et al., 2006).

Trait-based analyses linking species abundances to a mixture of life history, morphological and behavioural characteristics of species

in a community (Bremner, 2008) may improve our understanding of community functioning among greatly varying locations at broad spatial scales (Statzner et al., 2001). Much of ecological theory predicts that species that share the same environment differ in their trait characteristics to reduce competition pressure and facilitate long-term coexistence (Pianka, 1978; Schoener, 1974). Recent mass invasions (Sax et al., 2007), however, have proved the apparent 'unsaturation' of communities indicating our generic lack of understanding on basic assembly rules of ecological systems. Successful settlement and further dispersal of non-indigenous species are determined by their ability to colonise and retain a niche in the environment (MacDougall et al., 2009). There exist many alternative views on how species traits and species invasiveness are related (Duncan & Williams, 2002; Marvier et al., 2004; Pires-Teixeira et al., 2021; Steger et al., 2022; Strauss et al., 2006). However, the combination and diversity of traits that determine successful establishment will only become apparent after the establishment of a permanent NIS population in a new region (Jiménez-Valverde et al., 2011).

Thus, the analyses of impacts of invasive species should not only focus on community diversity, but the functional trait diversity of the community and its relationship to ecosystem processes (Diaz & Cabido, 2001). Expansion or contraction of the functional space as a result of bioinvasion may signal substantial change in ecosystem functioning, susceptibility to further invasions, sustained biodiversity and provisioning of ecosystem services (Funk et al., 2008; Milanović et al., 2020; Wen et al., 2019).

In this study, we examine patterns of structural and functional community-level change in a range of well-studied marine ecosystems with documented histories of bioinvasion. We hypothesised that accumulation of NIS in ecosystems exposed to high bioinvasion pressure triggers structural divergence in the affected communities which in turn leads to functional changes. Specifically, we expect that in assemblages with higher exposure to NIS colonisation pressure: (i) substantial structural changes with higher relative NIS contributions will be observed (Bradley Bethany et al., 2019; Olenin et al., 2007); (ii) novel functions are likely to be introduced, thus more niche space will be occupied (Parker et al., 1999; Thomsen et al., 2011); (iii) the average functional dissimilarity among sites will decrease due to selective accumulation of certain species and traits across biological communities (McDowell & Byers, 2019; Smart et al., 2006). We evaluate trends within and among ecosystems by comparing paired measures of community and functional structure in either space or time. We acknowledge that these are not fully controlled measures since they can respond to both accumulation of NIS and other drivers of change, such as climate change, habitat loss, pollution, sedimentation or overfishing. By considering a range of regional datasets and different sampling approaches, we therefore test for concordance and robustness of any detected patterns to help build our understanding of ambient community change associated with globally observed levels of invasion pressure. This improved understanding can assist resource managers with justification and implementation of conservation strategies. Perhaps more importantly, it can also provide critical guidance for future global environmental reporting such as that undertaken by many nations to fulfil

their obligations under the Convention of Biological Diversity or other environmental commitments (Department of Conservation, 2019; Dobson, 2005; Lehtiniemi et al., 2015).

## 2 | METHODS

### 2.1 | Compilation of species datasets

Two workshops attended by 20 international marine invasion experts were held in 2016 (Australia) and 2018 (Argentina) to investigate the availability of temporal (long-term) and cross-sectional datasets for global coastal (marine and estuarine) locations associated with biological invasions. We identified six regions with extensive bay-scale datasets on native and non-indigenous benthic species assemblages, allowing paired comparisons in time (years to decades; retrospective datasets) or space (high vs. low proximity to hotspots of NIS introductions within a region; cross-sectional datasets) representing differences in bioinvasion pressure (Table 1). The magnitude of bioinvasion pressure was approximated by the extent of relevant drivers and mechanisms of environmental change (Oesterwind et al., 2016) that can lead to the accumulation of NIS. Assignment of the locations to a low- or high-pressure category was a case-by-case expert decision based on a qualitative assessment of indirect drivers likely contributing to the introduction and establishment of non-native species in an ecosystem (e.g. shipping intensity, mariculture activities, tourism and recreation). Where available, quantitative data sources were utilised to underpin those decisions. The selected ecosystems were as follows: (1) coastal waters of British Columbia, Canada (BC); (2) San Francisco Bay, USA (SF); (3) Ilha Grande Bay, Brazil (BR); (4) North-Eastern Baltic Sea, Estonia (BS); (5) estuaries of New South Wales, Australia (AU) and (6) Waitemata Harbour, New Zealand (NZ). These six regions are generally at mid- to higher-latitudes, except for one low-latitude BR. The ecosystems encompassed surveys of benthic communities: fouling assemblages (BC and AU), subtidal reefs (BR and BS) and soft-sediment benthos (SF, BS and NZ).

Two cross-sectional datasets (BC and AU; Table 1) used single-time designs (sensu Wiens & Parker 1995) in which multiple locations that have historically been subjected to high NIS colonisation pressure from shipping or other vectors (*high-pressure areas*) were contrasted with nearby reference locations in settings not adjacent to significant shipping ports and thus subjected to lower bioinvasion pressure (*low-pressure areas*) (Johnston et al., 2009; Ruiz et al., 2000). The high-pressure areas typically had major ports of entry for international vessels, whereas low-pressure ones were characterised by limited vessel movement (predominantly domestic). The locations were selected so that both high- and low-pressure areas featured similar environmental conditions (i.e. salinity, temperature regimes, habitat types). The other four regions (BR, SF, BS and NZ) provided data for paired contrasts of temporal datasets along the NIS accumulation curve, that is, a historic survey and similar or identical contemporary survey, with variation in the period of exposure to NIS (Table 1). For consistency with the cross-sectional studies, hereafter, these are referred to as *high-pressure* and

TABLE 1 Overview of the datasets considered in this study.

Ecosystem, region (type of data)	Low-pressure dataset	High-pressure dataset	Comments
BC: British Columbia coastal waters, Canada (cross-sectional)	<p><b>Year(s):</b> 2007–2011<sup>a</sup></p> <p><b>Study area(s):</b> 2 areas—Strait of Georgia and North Coast (small harbours)</p> <p><b>Purpose:</b> surveillance of the biofouling assemblages</p> <p><b>Habitat:</b> hard-substrate communities on artificial settlement plates</p> <p><b>Type of data:</b> semi-quantitative, dominance ranks summarised per sampling site (~10 plates per site)</p> <p><b>Nr. of samples:</b> 29</p> <p><b>Species nr.:</b> 172</p>	<p><b>Year(s):</b> 2007–2011<sup>a</sup></p> <p><b>Study area(s):</b> 2 areas—Strait of Georgia and North Coast (Vancouver Harbour and Port of Prince Rupert correspondingly)</p> <p><b>Purpose:</b> surveillance of the biofouling assemblages</p> <p><b>Habitat:</b> hard-substrate communities on artificial settlement plates</p> <p><b>Type of data:</b> semi-quantitative, dominance ranks summarised per sampling site (~10 plates per site)</p> <p><b>Nr. of samples:</b> 12</p> <p><b>Species nr.:</b> 113</p>	Low- and high-pressure datasets represent geographically separated areas with different proximity (relatively remote vs. close) to big international ports. Over the last decades these areas were subjected to incursion and subsequent spread of 21 benthic NIS and 10 cryptogenic species to a lesser or greater extent respectively.
AU: New South Wales estuaries, Australia (cross-sectional)	<p><b>Year(s):</b> 2009–2010<sup>b</sup></p> <p><b>Study area(s):</b> 5 areas (estuaries)—Broken Bay (BRO); The Clyde (Batemans Bay, CLY); Port Hacking (HAK); Karuah River (KAR); Wagonga Inlet (WAG)</p> <p><b>Purpose:</b> surveillance of the biofouling assemblages</p> <p><b>Habitat:</b> hard-substrate communities on artificial settlement plates</p> <p><b>Type of data:</b> quantitative, relative abundance averaged per sampling site—sum of primary (%) and secondary (%) cover (can exceed 100%)</p> <p><b>Nr. of samples:</b> 101</p> <p><b>Species nr.:</b> 28</p>	<p><b>Year(s):</b> 2009–2010<sup>b</sup></p> <p><b>Study area(s):</b> 5 areas (estuaries)—Botany Bay (BOT); Port Jackson (JAK); Port Kembla (KEM); Middle Harbour (MID); Newcastle (NEW)</p> <p><b>Purpose:</b> surveillance of the biofouling assemblages</p> <p><b>Habitat:</b> hard-substrate communities on artificial settlement plates</p> <p><b>Type of data:</b> quantitative, relative abundance averaged per sampling site—sum of primary (%) and secondary (%) cover (can exceed 100%)</p> <p><b>Nr. of samples:</b> 99</p> <p><b>Species nr.:</b> 29</p>	The high-pressure estuaries considered here are subject to a wide range of anthropogenic modification and shipping, with NIS previously recorded in these ecosystems. The low-pressure ones are relatively pristine, with low levels of contamination, urbanisation and industrialisation.
BR: Ilha Grande Bay, Brazil (retrospective)	<p><b>Year(s):</b> 2005–2006<sup>c</sup></p> <p><b>Study area(s):</b> 5 areas—Barreto, Crena, Enseada da Estrela, Guaxuma, Saco do Céu</p> <p><b>Purpose:</b> monitoring of the sun coral distribution</p> <p><b>Habitat:</b> rocky reefs, quadrat samples</p> <p><b>Type of data:</b> quantitative, % cover summarised per site</p> <p><b>Nr. of samples:</b> 75</p> <p><b>Species nr.:</b> 13</p>	<p><b>Year(s):</b> 2016<sup>d</sup></p> <p><b>Study area(s):</b> 5 areas—Barreto, Crena, Enseada da Estrela, Guaxuma, Saco do Céu</p> <p><b>Purpose:</b> monitoring of the sun coral distribution</p> <p><b>Habitat:</b> rocky reefs, quadrat samples</p> <p><b>Type of data:</b> quantitative, % cover summarised per site</p> <p><b>Nr. of samples:</b> 75</p> <p><b>Species nr.:</b> 19</p>	This timeframe covers the period of massive expansion of the two species of non-indigenous sun coral ( <i>Tubastraea coccinea</i> and <i>T. tagusensis</i> ) within the Ilha Grande Bay <sup>e,f</sup> .
SF: San Francisco Bay, USA (retrospective)	<p><b>Year(s):</b> 1987<sup>e</sup></p> <p><b>Study area(s):</b> 2 areas—Southern and Northern bay</p> <p><b>Purpose:</b> benthic macrofauna biodiversity assessment</p> <p><b>Habitat:</b> soft bottom, grab samples</p> <p><b>Type of data:</b> quantitative, counts</p> <p><b>Nr. of samples:</b> 30</p> <p><b>Species nr.:</b> 80</p>	<p><b>Year(s):</b> 2012<sup>h</sup></p> <p><b>Study area(s):</b> 2 areas—Southern and Northern bay</p> <p><b>Purpose:</b> monitoring of NIS in the soft-sediment marine communities</p> <p><b>Habitat:</b> soft bottom, grab samples</p> <p><b>Type of data:</b> quantitative, counts</p> <p><b>Nr. of samples:</b> 50</p> <p><b>Species nr.:</b> 56</p>	San Francisco Bay is a relatively young estuary geologically and one of the most highly invaded bays in the world with an average of one new introduction every 14 weeks between 1961 and 1995 <sup>i</sup> . New incursions of benthic and infauna species occurred over the 25-year span considered in this study.

TABLE 1 (Continued)

Ecosystem, region (type of data)	Low-pressure dataset	High-pressure dataset	Comments
BS: North-Eastern Baltic Sea, Estonia (retrospective)	<p><b>Year(s):</b> 1959–1967<sup>j</sup></p> <p><b>Study area(s):</b> 4 areas—Eastern Gotland Basin, Gulf of Riga, Väinameri (west-Estonian Archipelago Sea), Gulf of Finland</p> <p><b>Purpose:</b> benthic monitoring</p> <p><b>Habitat:</b> mixed bottom, grab samples</p> <p><b>Type of data:</b> quantitative, abundance (averaged from ~2 grabs per station)</p> <p><b>Nr. of samples:</b> 112</p> <p><b>Species nr.:</b> 36</p>	<p><b>Year(s):</b> 2006–2014<sup>j</sup></p> <p><b>Study area(s):</b> 4 areas—Eastern Gotland Basin, Gulf of Riga, Väinameri (west-Estonian Archipelago Sea), Gulf of Finland</p> <p><b>Purpose:</b> benthic monitoring</p> <p><b>Habitat:</b> mixed bottom, grab samples</p> <p><b>Type of data:</b> quantitative, abundance (averaged from ~3 grabs per station)</p> <p><b>Nr. of samples:</b> 118</p> <p><b>Species nr.:</b> 37</p>	<p>The Baltic Sea, a comparatively young and environmentally unstable ecosystem, is susceptible to immigration of novel biota, with greatly increased rate of human-mediated introductions in recent decades<sup>k</sup>. The study area comprises particularly high number of NIS<sup>l</sup>, with 24 of new benthic incursions recorded over the covered period<sup>m</sup></p>
NZ: Waitematā Harbour, North Island New Zealand (retrospective)	<p><b>Year(s):</b> 1930–1934<sup>n</sup></p> <p><b>Study area(s):</b> 3 areas across the harbour (A, B, E, see Powel (1937)<sup>n</sup> for details)</p> <p><b>Purpose:</b> benthic macrofauna biodiversity assessment</p> <p><b>Habitat:</b> soft bottom, dredge samples</p> <p><b>Type of data:</b> semi-quantitative, dominance ranks</p> <p><b>Nr. of samples:</b> 38</p> <p><b>Species nr.:</b> 67</p>	<p><b>Year(s):</b> 1993–1995<sup>o</sup></p> <p><b>Study area(s):</b> 5 areas representing distinct communities (B, E, AB, BE, ABE, see Hayward et al. (1997)<sup>o</sup> for details)</p> <p><b>Purpose:</b> assessment of faunal changes since Powell (1937) study</p> <p><b>Habitat:</b> soft bottom, dredge samples</p> <p><b>Type of data:</b> semi-quantitative, dominance ranks (summarised from 132 samples for 8 areas)</p> <p><b>Nr. of samples:</b> 8</p> <p><b>Species nr.:</b> 87</p>	<p>Waitematā Harbour is surrounded by New Zealand's largest city, Auckland, and has, historically, received the largest numbers of overseas ship visits of all New Zealand ports. It has a large number of NIS relative to other New Zealand ports<sup>p</sup>. Stations surveyed between 1926 and 1936<sup>n</sup> were re-sampled more than 60 years later<sup>o</sup></p>

<sup>a</sup>Gartner et al. (2016).

<sup>b</sup>Clark et al. (2015).

<sup>c</sup>Lages et al. (2011).

<sup>d</sup>Creed and Fleury (Projeto Coral-Sol, unpublished data).

<sup>e</sup>Creed et al. (2017).

<sup>f</sup>Silva et al. (2014).

<sup>g</sup>Schemel et al. (1988).

<sup>h</sup>Jimenez and Ruiz (2016).

<sup>i</sup>Cohen and Carlton (1998).

<sup>j</sup>Benthic monitoring data (unpublished).

<sup>k</sup>Olenin et al. (2017).

<sup>l</sup>Ojaveer et al. (2010).

<sup>m</sup>AquaNIS Editorial Board (2015).

<sup>n</sup>Powell (1937).

<sup>o</sup>Hayward et al. (1997).

<sup>p</sup>The Ministry for the Environment and Statistics New Zealand (2014).

low-pressure datasets respectively. We acknowledge that high-pressure and low-pressure is not a strict unambiguous dichotomy, as it is well-known that small estuaries and harbours lacking international shipping may be highly invaded, due to significant contribution of both intra-regional transport and the non-shipping vectors (Wasson et al., 2001; Zabin et al., 2014).

## 2.2 | Traits database

A set of species traits relevant to important ecosystem functions was identified and modalities for each trait category (representative of different types of benthic invertebrates) were defined by experts attending the two workshops and were guided by the approach

adopted in Marchini et al. (2008) (Table 2). Binary (0/1) trait information was compiled for all species in the datasets (only adult or benthic stages were considered for species with a complex life cycle). Where available, peer-reviewed scientific publications were used for the collation of trait data for each species. In all other cases,

available information was retrieved from relevant on-line databases (e.g. [www.corpi.ku.it/databases/aquanis/](http://www.corpi.ku.it/databases/aquanis/), <http://www.mollusca.co.nz/>, <https://www.marlin.ac.uk/>, <http://polytraits.lifewatchgreece.eu/>), grey literature and expert judgement (where no published information was available).

TABLE 2 Categories of species traits and their modalities considered in this study.

Traits	Modalities
Size <sup>a</sup>	<1 mm <sup>b</sup> 1–10 mm 11–100 mm >100 mm
Life form	Zoobenthos—animals living on or in the seabed Phytobenthos—algae and higher plants living on or in the seabed Demersal—animals living on or near seafloor, able to move about in water Parasite—an organism intimately associated/dependent on another living organism Symbiont—an organism living mutually with another species without harming it
Trophic position	Autotroph—an organism obtains metabolic energy from light by a photochemical process such as photosynthesis Mixotroph—an organism both autotrophic and heterotrophic Suspension Feeder—an organism feeds on particulate organic matter from the water column Deposit Feeder—an organism feeds on fragmented particulate organic matter from the substratum Omnivore—an organism feeds on a mixed diet including plant and animal material Herbivore specialist—a herbivore that feeds on specific type of plant material Herbivore generalist—a herbivore that feeds on a variety of different types of plant material Predator specialist—a predator that feeds on a specific type of animal prey Predator generalist—a predator that feeds on a specific type of animal prey (includes scavengers)
Mobility	Sessile encrusting—attached to substrate, cover with a crust or thin coating Sessile turfing—low growing erect or filiform organisms Sessile tubicolous—forms a structure/tube in which it lives Sessile reef-builder—forms consolidated biogenic habitat on the seabed or shore Sessile erect—upright in position or posture Swimmer—an organism capable of moving through the water by means of fins, limbs or appendages Crawler—an organism that moves along the substrate Burrower—an organism capable of digging in sediment/soft substrate Borer—an organism capable of penetrating a solid substrate by mechanical scraping or chemical dissolution
Body surface	Robust—heavily calcified or leathery, unlikely to be damaged by physical impacts Fragile—lightly calcified, easily damaged as a result of physical impact or pressure Rigid—chitinous endo- or exo-skeleton Soft—yields to the touch or pressure
Habitat modification <sup>c</sup>	Canopy—providing floating substrate by their living and dead tissues Matrix-forming—provide seafloor substrate by their living and dead tissues Substrate-modifying—modify physical/chemical properties of the habitat
Temperature tolerance	Wide range—tolerates wide range of temperatures Narrow range—tolerates temperatures typical for one climatic zone
Longevity	Short-lived—<2 years Long-lived—≥2 years

<sup>a</sup>Here we referred to the maximum body size of adult individuals.

<sup>b</sup>Species with an assigned size modality <1 mm were excluded for SF dataset, as different sieve sizes (0.5 and 1 mm) were used in the low-pressure and high-pressure datasets respectively.

<sup>c</sup>The habitat modification category was not considered for BC and AU datasets as it was considered irrelevant for settlement plate communities.

The trait categories included in the analyses were: body size, life form, trophic position, mobility, body surface, habitat modification (not considered in datasets from settlement plate communities), temperature tolerance and longevity. The overall traits table comprised information for 552 species (representing 19 phyla, 35 classes, 94 orders and 312 families) listed across all datasets analysed in this study. A number of traits initially considered for the analysis (position along the littoral-offshore gradient, substrate type, sociability, reproductive strategy, tolerance to pollution, eutrophication and hypoxia) were excluded in the course of database compilation due to lack of reliable and unambiguous information for many species (rate of unknowns ranging from 37 to 85% across all datasets). In the final list of traits, unknowns were allowed for 'longevity' and 'temperature tolerance' categories, but these did not exceed 5% of the overall dataset.

Additionally, a binary category that distinguished 'NIS' from 'other' species (combined category of native and cryptogenic species) within their respective study regions was included. A composite category 'Ecosystem engineer', representing the combination of size (>10mm), life form (zoobenthos or phytobenthos), habitat modification (canopy or matrix), body surface (robust, fragile or rigid) and longevity (long-lived) was also included in the analysis (except settlement plates [BC and AU] datasets). Unresolved taxa (family level and upwards) were excluded from the regional datasets and downstream analyses, as no reliable generalisations on biological traits could be made at that level. In total, nine taxa were removed across all datasets.

### 2.3 | Quality assurance and pre-processing of the datasets

The six datasets were groomed by removing inconsistencies in nomenclature (standardised against the WORMS <http://www.marinespecies.org> and ITIS <https://www.itis.gov> databases). For analyses where quantitative data were considered, community datasets were transformed into relative abundances (% of total community) and rank abundances. In the SF dataset, different sieve sizes (0.5 and 1mm) were used for sample processing in 1987 and 2012 respectively. To mitigate the potential bias introduced by this methodological inconsistency, the small-bodied meiofaunal species (e.g. cumaceans or ostracods) were removed from the datasets and not considered in the analyses.

After compilation of the traits database, the data were cross-checked for inconsistencies by comparing the trait profiles of closely related species (family level) and addressing any mismatches through additional literature searches and reviews. For quantitative traits analyses, a weighted traits matrix was created for each dataset and computed as a cross-product of binary traits data and transformed species data matrices. Non-quantitative comparisons between high- and low-pressure datasets within each region were made on occurrence of individual traits and trait profiles, which are the combination of traits expressed by individual species.

### 2.4 | Exploratory analyses of biological assemblages and traits space

Since the datasets did not meet the normality assumptions, non-parametric Kruskal–Wallis tests were used to identify significant differences in the relative abundance of NIS in low- and high-pressure datasets for each study region (see [Table 1](#)). For each global study region, structural (species data) and functional (traits data) shifts in species assemblages across the pressure (low vs. high) and spatial (study area) factors (see [Table 1](#)) were investigated using permutational multivariate analysis of variance (PERMANOVA) based on Bray–Curtis similarity matrices (species or weighted traits). PERMANOVA was performed using the *adonis2* function of the *vegan* package (Oksanen et al., 2019). A crossed-factor design (except for AU and NZ datasets, where 'area' was nested within the 'pressure' factor) with 999 permutations was applied. Hereafter, we refer to the 'area' factor as a geographical domain within the study region (i.e. an estuary, or a distinct part of a larger basin).

To visualise the multivariate structure of species and weighted traits data, principal component analysis (PCA) biplots were produced for each global study region using the *fviz\_pca\_biplot* function within the *factoextra* package (Kassambara & Mundt, 2017). The function *multipatt* of the package *indicpecies* (De Caceres & Legendre, 2009) was used to determine subsets of traits that were indicative of either low-pressure or high-pressure datasets. This approach allows determining indicator species (traits in our case) using an analysis of the relationship between the occurrence or abundance values from a set of sampled sites and the classification of the same sites into site groups, which may represent habitat types, community types, disturbance states, etc. The Indicator Value index measuring the association between a trait and a pressure-relevant group was calculated on the weighted traits matrix for each region. The statistical significance of this relationship was then tested using a permutation test, based on 999 permutations.

We used multidimensional indices of functional composition and diversity (FRic, FEve and FDis, [Table 3](#)) to compare changes in trait space among the temporal and spatial samples and explored the contributions of NIS to the changes. All functional diversity metrics were computed in the *FD* package (Laliberté & Legendre, 2010). Non-parametric Kruskal–Wallis tests were used to identify statistically significant differences in functional diversity metrics between high- and low-pressure datasets.

In addition to exploring the general functional diversity and describing the functional space using functional diversity metrics, we also considered 'trait profiles'—the full multidimensional combination of all trait modalities exhibited by a species or taxon (i.e. functional species). We assumed that shifts in the trait profiles of taxa represented in a community might have functional implications at ecosystem level. Therefore, to better understand the different levels of potential functional shift, we assessed the magnitude of overlap in both individual traits space and trait profiles for each ecosystem's low- and high-pressure datasets.

All analyses, calculations and visualisations were performed in R v.3.5 (R Core Team, 2014).

**TABLE 3** Components of functional diversity and functional diversity indices considered in this study to test for changes in community assembly along temporal and spatial gradients in relation to non-indigenous species effects.

Indices	Description	Calculation	Hypothesised change
Functional richness (FRic)	Measures the amount of functional space occupied by a species assemblage and is naturally positively correlated with the number of species present (the more species there are, the larger the functional space occupied when species traits are somewhat randomly distributed). However, two communities with the same number of species may have different FRic when functional traits of species are more closely clustered in one community than in the other <sup>a</sup> .	Calculates the volume of trait space with the convex hull volume, which represents the smallest convex hull that encloses all species. With a complex algorithm, the most extreme points (vertices) can be determined and the volume encompassed by these vertices is calculated. Not weighted by species abundance <sup>d</sup> .	<i>With accumulation of NIS, novel functions are likely to be introduced, thus the FRic will increase (more niche space is occupied).</i>
Functional evenness (FEve)	Measures whether mean species traits are distributed regularly within the occupied trait space, that is, with equal distances between nearest neighbours and equal abundances. A high FEve index usually means a very regular distribution of abundances among trait modalities; a low FEve index indicates clustered distribution, with some parts of the trait space poorly occupied and others densely populated <sup>b</sup> . FEve indices are used to indicate under- or overutilisation of resources, productivity and vulnerability to invasion <sup>c</sup> .	Uses the abundance-weighted distances between all species pairs to first calculate the minimum spanning tree (MST) that links all the species in a multidimensional trait space. The index then measures the consistency of the MST branch lengths (i.e. comparison with the optimal branch length distribution) <sup>d</sup> .	<i>In response to increasing invasion pressures, FEve will decrease in high-pressure systems due to selective accumulation of certain traits across biological communities (both in native and non-indigenous species).</i>
Functional dispersion (FDis)	Measures both functional richness and divergence. Elevated FDis should indicate niche complementarity enhancing species' occurrence probabilities and abundances, but also a predominance of extreme species <sup>a</sup> .	Estimated as the mean distance of all species to the weighted centroid of the community in the trait space <sup>e</sup> . When all species have equal abundances (e.g. presence-absence data), it is equivalent to the multivariate dispersion—average distance to the centroid <sup>f</sup> .	<i>Due to functional homogenisation, the average functional dissimilarity and consequently FDis will decrease.</i>

<sup>a</sup>Mason et al. (2013).

<sup>b</sup>Schleuter et al. (2010).

<sup>c</sup>Mason et al. (2005).

<sup>d</sup>Villéger et al. (2008).

<sup>e</sup>Laliberté and Legendre (2010).

<sup>f</sup>Anderson et al. (2006).

### 3 | RESULTS

#### 3.1 | Overview of patterns associated with biodiversity and traits distribution

The number of reported NIS varied across locations from 0 in the low-pressure NZ dataset (that is, no reported invasions in the 1920s–1930s era) to 26 in the high-pressure SF dataset. Significant differences in the average relative abundance of NIS between low- and high-pressure datasets were only detected in the SF and NZ studies, with both regions experiencing higher NIS contributions to abundance over time (Figure 1).

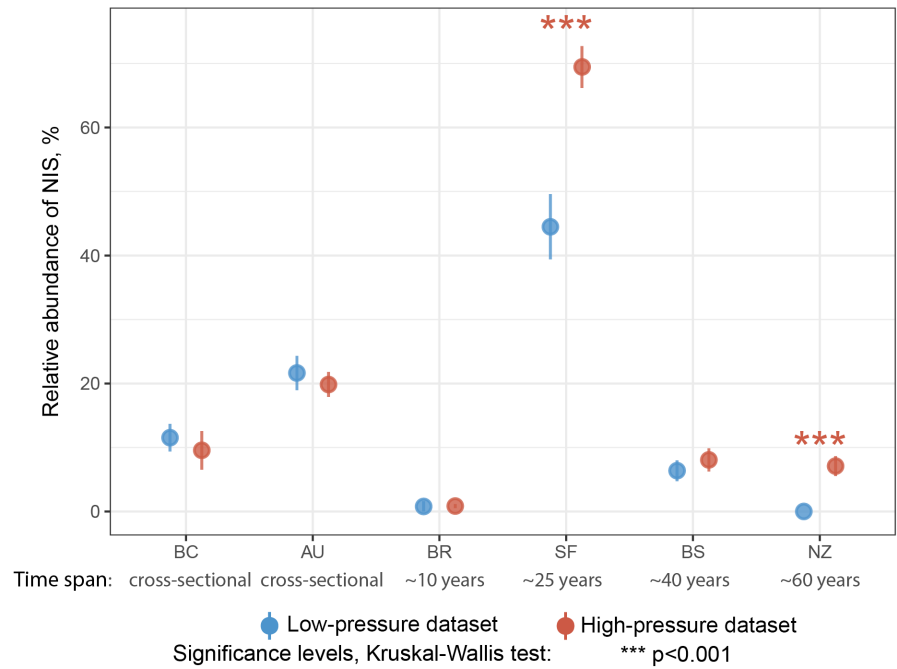
In most datasets, the structure of species assemblages was significantly affected by both the 'pressure' and 'area' (spatial) factors or their interaction term (Table 4). The exception was the NZ dataset, where there were only pressure-related differences. The functional structure

(weighted traits) of communities was also significantly affected by both main effects of the 'pressure' and 'area' factors or their interaction (except NZ where only 'pressure' had a significant effect, Table 5). However, the amount of unexplained variation (residual  $R^2$ ) was high (62%–91%) for all regions, habitats, species and traits datasets.

Overall, differences in species composition between groups were likely driven by dispersion of the data, rather than a shift in their centroids (Figure 2 and Figures S1–S6). For example, in the AU, BR and NZ datasets, high-pressure communities were structurally more variable compared to the low-pressure ones, reflected in plots that had much larger 'multivariate species space' (represented by dispersion of samples) for recent surveys compared to historic ones (Figure 2). The opposite pattern was detected for SF however, where compositional dispersion of the benthic community substantially contracted in the high-pressure dataset relative to the low-pressure one (Figure 2 and



**FIGURE 1** Averaged relative abundance (% of total community) of NIS across the analysed datasets. The error bars indicate standard deviation and asterisks highlight a significant difference as per Kruskal–Wallis tests.



**TABLE 4** Results of PERMANOVA for species data from six considered global coastal regions: British Columbia (BC), New South Wales Australia (AU), Ilha Grande Bay (Brazil), San Francisco Bay USA (SF), North-Eastern Baltic Sea (BS), Waitematā Harbour New Zealand (NZ).

Region	Factor	Df	Sum of squares	R <sup>2</sup>	F	p Value
BC	Pressure	1	0.518	.046	1.915	.04
	Area	1	0.729	.064	2.699	.005
	Pressure × Area	1	0.639	.056	2.363	.009
	Residual	35	9.464	.834		
AU	Pressure	1	2.736	.043	11.568	.001
	Area (Pressure)	8	17.485	.274	9.239	.001
	Residual	184	43.526	.683		
BR	Pressure	1	0.449	.013	2.398	.094
	Area	4	5.836	.169	7.799	.001
	Pressure × Area	4	1.986	.058	2.655	.009
	Residual	140	26.188	.759		
SF	Pressure	1	6.396	.246	28.051	.001
	Area	1	1.109	.043	4.865	.001
	Pressure × Area	1	1.176	.045	5.158	.001
	Residual	76	17.33	.666		
BS	Pressure	1	1.938	.027	6.642	.001
	Area	3	1.231	.017	1.406	.08
	Pressure × Area	3	2.543	.036	2.906	.001
	Residual	222	64.774	.919		
NZ	Pressure	1	1.601	.085	4.059	.001
	Area (Pressure)	6	2.169	.116	0.917	.749
	Residual	38	14.983	.799		

Note: Statistically significant effects ( $p < .05$ ) are bolded.

Figure S4). Across all regions, NIS were among the 10 species that contributed most to differentiating the principal components (highly correlating with one of two PCA main axes, Figures S1–S6) and generally

were associated with high-pressure samples. Only the SF dataset had major contributions of three NIS that correlated with low-pressure samples from the southern area (Figure S4).

TABLE 5 Results of PERMANOVA (computed by R function adonis2) for trait data from six considered datasets: British Columbia (BC), New South Wales Australia (AU), Ilha Grande Bay (Brazil), San Francisco Bay USA (SF), North-Eastern Baltic Sea (BS), Waitemata Harbour New Zealand (NZ).

Region	Factor	Df	Sum of squares	R <sup>2</sup>	F	p Value
BC	Pressure	1	0.021	.015	0.623	.634
	Area	1	0.08	.059	2.43	.058
	<b>Pressure × Area</b>	<b>1</b>	<b>0.09</b>	<b>.071</b>	<b>2.93</b>	<b>.033</b>
	Residual	35	1.175	.854		
AU	<b>Pressure</b>	<b>1</b>	<b>1.288</b>	<b>.043</b>	<b>12.740</b>	<b>.001</b>
	<b>Area(Pressure)</b>	<b>8</b>	<b>9.919</b>	<b>.333</b>	<b>12.269</b>	<b>.001</b>
	Residual	193	29.803	.624		
BR	Pressure	1	0.07	.006	0.995	.323
	<b>Area</b>	<b>4</b>	<b>1.498</b>	<b>.123</b>	<b>5.302</b>	<b>.001</b>
	<b>Pressure × Area</b>	<b>4</b>	<b>0.678</b>	<b>.056</b>	<b>2.399</b>	<b>.033</b>
	Residual	140	9.892	.815		
SF	<b>Pressure</b>	<b>1</b>	<b>0.971</b>	<b>.261</b>	<b>31.867</b>	<b>.001</b>
	<b>Area</b>	<b>1</b>	<b>0.331</b>	<b>.089</b>	<b>10.875</b>	<b>.001</b>
	<b>Pressure × Area</b>	<b>1</b>	<b>0.099</b>	<b>.027</b>	<b>3.279</b>	<b>.015</b>
	Residual	76	2.316	.623		
BS	<b>Pressure</b>	<b>1</b>	<b>0.539</b>	<b>.044</b>	<b>10.739</b>	<b>.001</b>
	Area	3	0.269	.022	1.79	.056
	<b>Pressure × Area</b>	<b>3</b>	<b>0.425</b>	<b>.034</b>	<b>2.825</b>	<b>.005</b>
	Residual	222	11.132	.900		
	<b>Pressure</b>	<b>1</b>	<b>0.153</b>	<b>.106</b>	<b>4.993</b>	<b>.003</b>
NZ	Area(Pressure)	6	0.129	.089	0.703	.692
	Residual	38	1.168	.805		

Note: Statistically significant effects ( $p < .05$ ) are highlighted in bold font.

Pressure-related changes in traits, where detected, were associated with shifts in centroids (multivariate mean) rather than dispersion, and this was most pronounced in the SF and NZ datasets (Figure 3 and Figures S4 and S6). There was substantial overlap of traits space in the four other datasets (Figure 3, Figure S1–S6). In fact, when looking into individual trait occurrence within each region, most (84%–100%) were shared between low-pressure and high-pressure datasets (Figure 4). Trait modalities unique to the low-pressure assemblages within a particular region were as follows: fragile 'body surface' (BR), parasite 'life form' (SF), borer 'mobility' (SF) and 'trophic positions' of predator specialist (BS) and herbivore specialist (NZ). Those found exclusively in the high-pressure datasets were: <1 mm 'size' (AU); sessile tubiculous 'mobility' (BS); encrusting 'mobility' and demersal 'life form' (SF); and sessile erect 'mobility', parasite 'life form', short-lived 'longevity' and NIS (NZ).

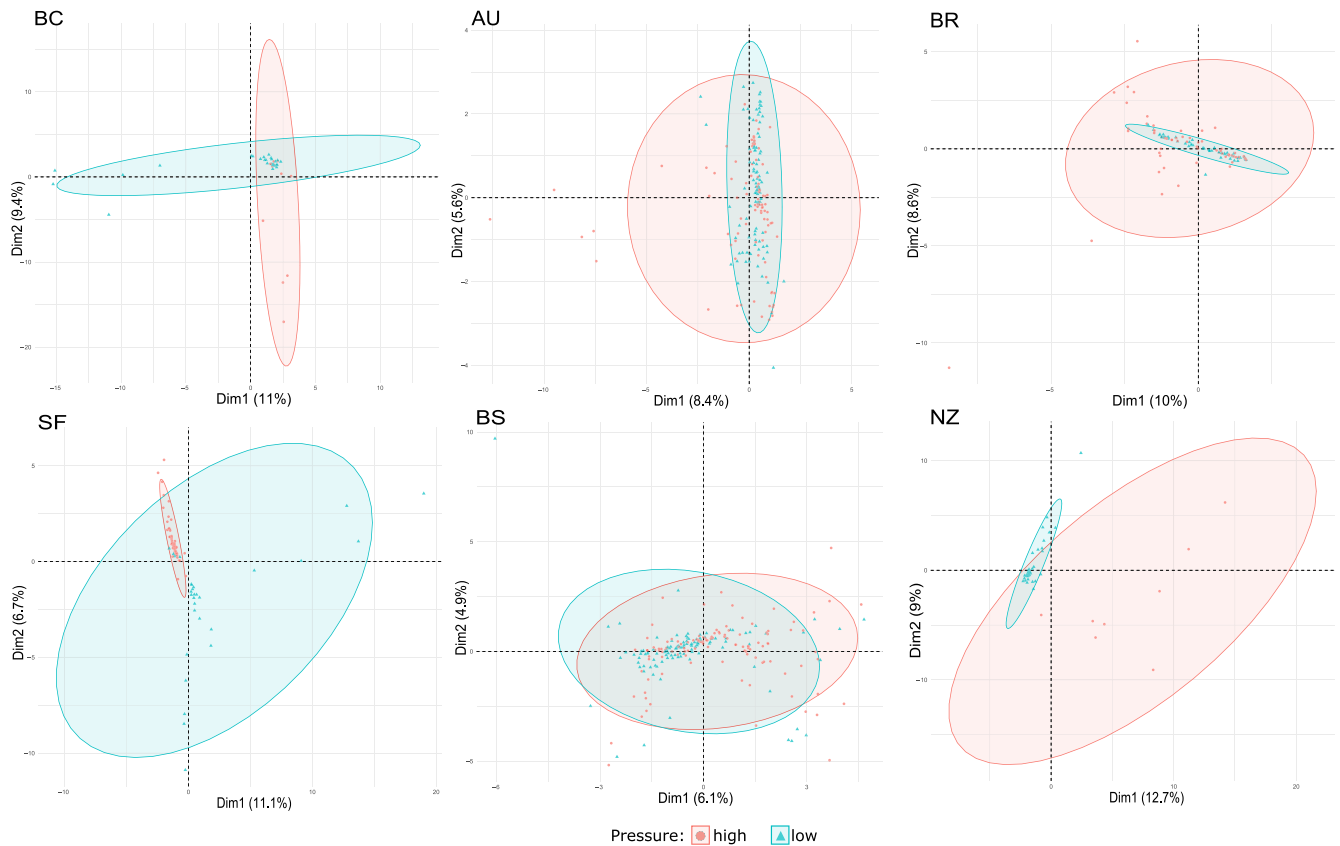
When considering the full combination of all trait modalities exhibited by a species or taxon ('trait profiles'), 10%–46% were unique for low-pressure samples and 15%–32%—for high-pressure samples (Figure 4). This suggests that while regional trait pools remained largely unchanged in the studied ecosystems, the representation of trait modalities in individual taxa shifted markedly between low- and high-pressure datasets. For example, in BC, 100% of individual traits were shared between low- and high-pressure datasets, but 76 (46%)

trait profiles (that occurred in 91 taxa) were reported exclusively in the low-pressure dataset (Figure 4).

Analysis of indicator traits revealed a higher number of trait modalities significantly associated with the high-pressure (35) than the low-pressure (26) datasets (Table 6). No general pattern emerged for trait occurrence or change in traits across regions and suites of indicator traits were region-specific. No significant indicator traits were detected for the BC and BR datasets, which is consistent with PCA results (see Figure S1, Figure S3). There were more traits significantly associated with low-pressure datasets in SF and BS, whereas high-pressure trait associations were more common in AU and NZ. NIS prevalence (the binary biogeographic trait) was only a statistically significant indicator in two high-pressure datasets (SF and NZ), where a significant increase in the relative abundance of NIS was also reported over the covered timeframe (Figure 1).

### 3.2 | Functional diversity

Functional diversity analysis returned differential responses in functional diversity metrics across regions (Figure 5). A significant increase in functional richness was only evident in AU and NZ datasets, while in SF it had substantially decreased. These results align with indicator



**FIGURE 2** Two-dimensional PCA visualisations of species composition from low-pressure and high-pressure datasets across all considered regions: BC—British Columbia coastal waters, Canada; AU—New South Wales estuaries, Australia; BR—Ilha Grande Bay, Brazil; SF—San Francisco Bay, USA; BS—North-Eastern Baltic Sea, Estonia; NZ—Waitematā Harbour, New Zealand (see Table 1 for details). The concentration ellipses cover 95% confidence interval for each group of samples.

trait associations in Table 4. Functional evenness and dispersion tended to increase across datasets (except BC), with significant change in SF (both evenness and dispersion), AU and NZ (dispersion only). Overall, the strongest shifts between low- and high-pressure datasets were detected in AU, SF and NZ, with no consistent effect for all three of these regions, and no significant changes apparent for the other three regions. SF and NZ had significant changes in NIS contributions to community abundance (Figure 2) but AU did not. The dispersion of species composition (in multivariate space) was higher in high-pressure datasets for all three regions (Figure 2) but shifts in centroids for species traits only occurred for SF and NZ (Figure 3). Indicator traits were more heavily associated with high-pressure datasets for AU and NZ, but were associated with the low-pressure dataset for SF (Table 4). SF had a loss of functional richness from low- to high-pressure datasets, while AU and NZ gained functional richness (Figure 5). Overall, out of the seven significant differences observed in functional diversity metrics, six were greater in the high-pressure datasets.

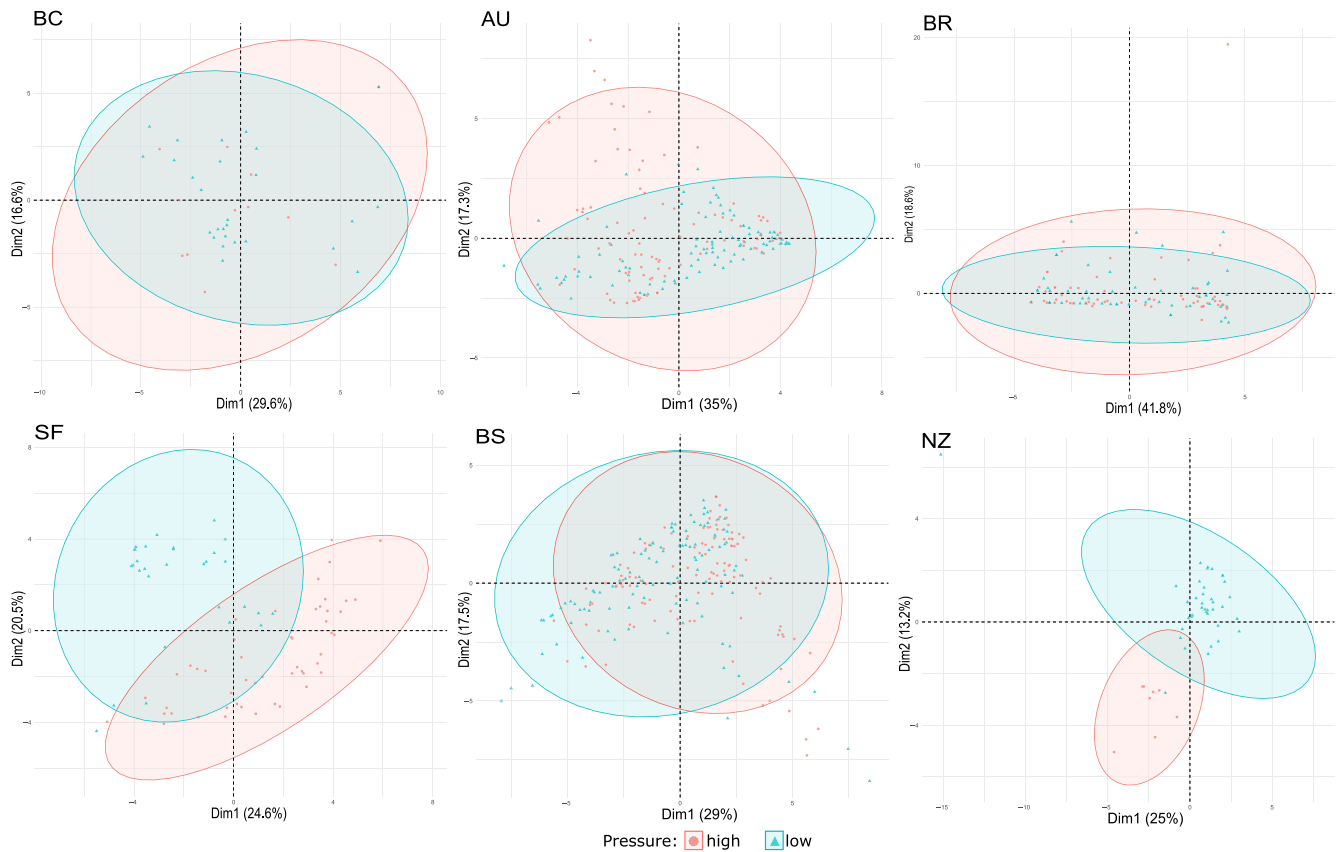
## 4 | DISCUSSION

Our study shows that the accumulation of NIS within broader communities can be a subtle process, with inherent spatial and temporal

variability that, nonetheless, can drive underlying shifts in community and ecosystem characteristics. Not only do species' proportional contributions to communities change over time in areas subjected to high bioinvasion pressure, but trait profiles can incrementally shift, which alters the original ecology of an area. A notable and somewhat unexpected finding was that the assumed bioinvasion pressure is not always unambiguously manifested in the available NIS accumulation data. This emphasises that NIS-focused surveys might not, by themselves, represent the community-level changes adequately and more holistic approaches are imperative to measure the long-term consequences of bioinvasions and other stressors for marine ecosystems and assess the bioinvasion-related status.

### 4.1 | Differential patterns of invasion-related change in community structure

Our analyses revealed that invasion-related change in communities was not consistent across the range of systems examined in this study. There are good reasons to expect community-level effects of NIS to be spatially and temporally variable (Bracewell et al., 2021; Clark & Johnston, 2011). Since human activity became a dominant force in global biotic exchange, the structural



**FIGURE 3** Two-dimensional PCA visualisations of species traits from low-pressure and high-pressure datasets across all considered regions: BC—British Columbia coastal waters, Canada; AU—New South Wales estuaries, Australia; BR—Ilha Grande Bay, Brazil; SF—San Francisco Bay, USA; BS—North-Eastern Baltic Sea, Estonia; NZ—Waitematā Harbour, New Zealand (see Table 1 for details). The concentration ellipses cover 95% confidence interval for each group of samples.

composition of assemblages changed through the successive introduction and establishment of NIS within local species pools as well as in response to other changes and stressors in receiving environments, including coastal hardening, maritime sprawl, pollution, commercial fishing and warming temperatures (Floerl et al., 2021; Hopkins et al., 2021; Occhipinti-Ambrogi, 2007). Significant time-lags in population development following introduction (Crooks & Soulé, 1996; Guastella et al., 2021), 'boom and bust' dynamics (Simberloff & Gibbons, 2004), seasonal (Schiel & Thompson, 2012) and interannual variation in recruitment (Crooks, 1996), perenniality (Thibaut et al., 2004) and facilitative effects of prior invasions (Grosholz, 2005; Zaiko et al., 2007) can all affect the outcome of NIS incursion and magnitude of manifested impact. Following ecosystems over long time periods (decades or longer, ideally) may enable detection of shifts in communities that proceed at a slower rate or involve time lags (Ojaveer et al., 2021). Therefore, we expected the retrospective studies to reflect changes in the regional species pool more reliably than the cross-sectional studies. Indeed, the most prominent shifts in community composition were observed in temporal SF and NZ datasets, with some contrasting patterns that were nonetheless characterised by the greatest relative contribution of NIS in the high-pressure dataset.

The pronounced changes in SF community structure were largely determined by high dimensional dispersion in low-pressure samples (Figure 3). This was driven mostly by differences in the relative contributions of three NIS (the polychaetes *Heteromastus filiformis* and *Streblospio benedicti*, and the bivalve *Mya arenaria*) in the southern basin (Nichols & Thompson, 1985; Robert, 1881). All three represent invasions that were established in the ecosystem well before the (historic) low-pressure dataset was acquired. It is likely that their long-term impact diminished over decades with ubiquitous spread of new NIS and accumulation of other anthropogenic pressures and environmental changes in the region, resulting in contracting variability between the north and south basins of the bay (Ely & Owens Viani, 2010). In contrast to SF, substantially higher dispersion was observed in the NZ high-pressure dataset compared to the low-pressure one. A significant shift in community composition was driven by two non-indigenous molluscs (*Theora lubrica* and *Limaria orientalis*), introduced into Waitematā Harbour in the 1970s (Hayward et al., 1997) with strong tolerance of sedimentation. It is likely that anthropogenic perturbations in the ecosystem over the last few decades, particularly sediment accumulation, have altered densities of large native bivalves and other functionally important benthic species, thus facilitating a shift in the prevalence of these NIS in muddy subtidal habitats



**FIGURE 4** Partitioning of the individual trait modalities (upper graph) and trait profiles (species-specific combination of all trait modalities, bottom graph) between low-pressure and high-pressure datasets from six regions: British Columbia (BC), New South Wales Australia (AU), Ilha Grande Bay Brazil (BR), San Francisco Bay USA (SF), North-Eastern Baltic Sea (BS), Waitemata Harbour New Zealand (NZ).

(Lohrer et al., 2008). The relatively long timelines between low- and high-pressure data collection, supported by published research on other environmental dynamics of these regions, provide context and an understanding of some underlying mechanisms for how invasions have progressed with other factors to shift community composition of these two systems (Atalah et al., 2019; Hayden et al., 2009; Jimenez et al., 2018; Kerr et al., 2016). In both cases, benthic community baselines appear to have shifted dramatically more than the other regions based on the current data.

NIS responding to environmental change as well as driving community shifts is an inevitable characteristic of chronic invasion effects (Bauer, 2012; Didham et al., 2005; MacDougall & Turkington, 2005; Vitousek et al., 1997). NIS can take advantage of human-induced impacts on ecosystems and homogenisation of habitats, potentially contributing further to the decline of native species and losses of ecosystem functions (Byers, 2002; Piola & Johnston, 2008). For instance, the Baltic Sea has faced a major increase in anthropogenic pressures and partly human-induced regime shifts that started before the historical (low-pressure) dataset was collected (Österblom et al., 2007). Therefore, the communities examined, already subjected to substantial environmental changes in the ecosystem, exhibited a rather smoothed response to the chronic effects of accumulation of NIS over the period spanned by the datasets (Hewitt et al., 2016). This highlights the difficulty or

impossibility of separating confounding factors from retrospective community analyses of invasions.

The BR community comparison had apparent shifts in dispersion of species and traits (Figures 3 and 4), as occurred in NZ, but no significant differences in relative NIS abundance (Figure 2) or functional diversity metrics (Figure 5), as were observed for the Baltic Sea. BR was considered a retrospective dataset but represents a comparatively short timeframe and primarily captures spread, rather than accumulation, of NIS in the region. The sampling in this system focused on range expansion of two sun coral species (Creed et al., 2017; Silva et al., 2014) and their possible interactions with—and effects on—native species. Although there did not appear to be major shifts or invasion-driven changes in traits, an overall expansion of community dispersion between low- and high-pressure sampling periods was noteworthy. This may be linked to the effect of *Tubastraea coccinea* on community structure in the high-pressure samples. It was noted previously by Guilhem et al. (2020), that an increase in sun coral cover in the invaded areas was associated with intensified turnover (i.e. higher spatial heterogeneity) of native species. This likely explains the increased dispersion in the high-pressure species data.

The cross-sectional studies considered here (AU, BC) are typical of single-time, post-impact studies that compare ecological assemblages at sites subject to a perturbation with sites that have not been exposed to the stressor ('Impact–Reference' designs) or which compare sites that have experienced different levels of exposure ('Gradient' designs; Eberhardt and Thomas, 1991; Wiens and Parker, 1995). In both cases, the presence of long-established NIS in the reference (low pressure) locations likely confounded comparison with high-pressure sites so that any invasion-related impacts are indistinguishable from other influences and local processes affecting community assembly (Davis et al., 2005). A related issue is that contemporary proxies of colonisation pressure, such as the numbers of vessel arrivals or recent ballast discharge volumes at a location, may fail to characterise historical patterns of invasion, since high-use environments may acquire NIS from other, uncharacterised pathways (Bailey et al., 2020; Ojaveer et al., 2018). The confounding effect of the pre-established NIS may partly explain comparable and even somewhat lower relative abundances of NIS in the high-pressure cross-sectional datasets (BC and AU). On the other hand, although caution was taken to include data for paired assessments only from the ecosystems with comparable environmental conditions (e.g. temperature and salinity ranges), we were unable to control for all possible biogeographical differences. For instance, the Pacific coast of Canada (represented by the Strait of Georgia dataset here) is by far more complex than the North Coast. This is most likely due to the environmental influence of the Fraser River but also likely reflects highly variable marine use (shipping, recreational boating, aquaculture, etc.) which might have an effect on the patterns observed in NIS and wider benthic communities. Still, both in BC and AU datasets, the pressure factor had a significant effect on variances in community composition, with major discrepancies between low- and high-pressure sites driven by NIS (Figure 2, Figures S1 and S2).

**TABLE 6** Trait modalities determined as significant ( $p < 0.05$ ) indicators of either low-pressure (blue cells) or high-pressure datasets (red cells) from six regions: British Columbia (BC), New South Wales Australia (AU), Ilha Grande Bay Brazil (BR), San Francisco Bay USA (SF), North-Eastern Baltic Sea (BS), Waitematā Harbour New Zealand (NZ).

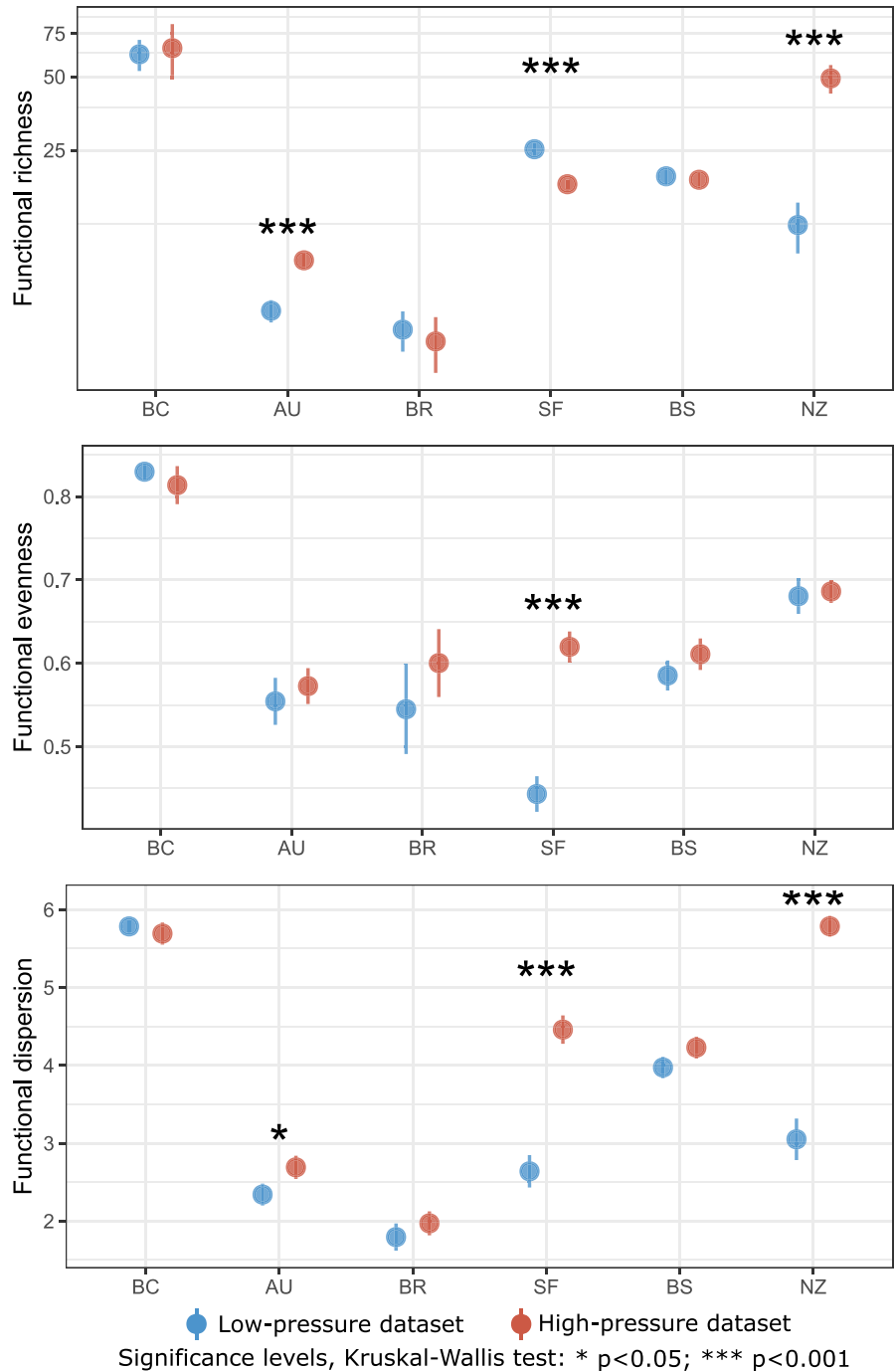
Modalities	BC	AU	BR	SF	BS	NZ	Traits
<1 mm							Size
1–10 mm				Blue		Red	
10–100 mm		Red		Blue			Life form
>100 mm		Blue		Blue		Red	
Zoobenthos		Red				Blue	Trophic position
Parasite				Blue		Red	
Suspension feeder		Red		Blue	Blue		Mobility
Deposit feeder		Red		Blue	Blue		
Omnivore				Red			Body surface
Herbivore generalist				Blue			
Predator specialist				Blue	Blue	Red	Habitat modification
Predator generalist				Red			
Sessile encrusting		Red					Temperature tolerance
Sessile turfing		Red		Blue			
Sessile tubiculous		Red		Red			Longevity
Sessile reef-builder		Red		Blue		Red	
Sessile erect							Additional
Swimmer				Blue	Blue	Red	
Crawler					Blue		Additional
Borer						Red	
Robust		Red			Red	Blue	Additional
Fragile		Blue				Red	
Rigid				Blue	Blue	Red	Additional
Soft		Red		Red			
Matrix-forming				Blue		Red	Additional
Substrate-modifying				Blue			
Wide range					Red		Additional
Narrow range		Red		Blue	Blue		
Short-lived		Red		Blue	Blue	Red	Additional
Long-lived				Red	Red	Red	
Engineer				Blue		Red	Additional
NIS				Red		Red	

#### 4.2 | Shifts in trait and functional make-up of benthic communities under invasion pressure

Our analyses revealed a significant effect of the invasion pressure factor on trait distribution within most of the regions examined (Table 5). NIS may bring new traits and novel functions to an ecosystem (Parker et al., 1999; Ruesink et al., 1995; Thomsen et al., 2011), increasing functional richness (as observed in e.g. AU and NZ datasets). Alternatively, regional ecosystems will likely favour invaders with similar characteristics to those of the recipient community, including NIS already present (Duncan & Williams, 2002). Thus, as colonisation pressure (sensu Lockwood et al., 2009) increases, the average functional dissimilarity among sites might decrease due to selective

accumulation of successful invaders (biotic homogenisation), replacement of native species, or prevalence of particular biological traits (Pires-Teixeira et al., 2021; Smart et al., 2006), without any apparent change in functional richness. Decreases in functional distinctiveness, in turn, can increase vulnerability to broadscale perturbations by synchronising local biological responses (Olden et al., 2004) and removing functional redundancy or community resilience, ultimately risking prolonged loss of diversity by restricting recolonisation capacity (Clavero & Garcia-Berthou, 2005). The SF dataset was the only one with a significant reduction in functional richness, which was combined with a significant increase in functional evenness (also unique to SF; Figure 5), suggesting a simplification of benthic communities with NIS playing a major role.

**FIGURE 5** Overview of three functional diversity metrics examined (see Table 3): mean values per region [British Columbia (BC), New South Wales Australia (AU), Ilha Grande Bay Brazil (BR), San Francisco Bay USA (SF), North-Eastern Baltic Sea (BS), Waitemata Harbour New Zealand (NZ)] and dataset (low-pressure vs. high-pressure) with error bars representing standard deviations. Asterisks indicate statistically significant change.



Contrary to our hypothesised increase in functional richness associated with elevated bioinvasion pressure, there was no uniform pattern across study regions. However, all three measures increased in high-pressure datasets in six of the seven detected significant differences and there was also a reasonable concordance in functional evenness and dispersion response to the pressure factor. Both measures showed a tendency to increase in the high-pressure datasets (except for BC), thus not supporting our hypothesised selective accumulation of certain traits and functional homogenisation in the invaded ecosystems (Table 3). Overall, no single observed trait shift was consistent among all regions—any changes were context-specific. However, across all

datasets, a substantial change in functional profiles (combinations of traits) within the largely overlapping functional space of individual traits was detected. It has been shown previously that the same environmental drivers define the ecological constitution of both native and NIS communities (Floerl et al., 2009; Pysek et al., 2020). However, certain combinations of traits might convey adaptive advantages for native species under increasing pressures and invasive success of NIS (Boltovskoy et al., 2021; Novoa et al., 2020; Nunez-Mir et al., 2019; Reichard & Hamilton, 1997). This could explain the phenomenon observed in our study and most profound in BC (Figure 5), where no individual trait was characteristic or distinctive to low- or high-pressure communities,

but trait profiles (the combination of traits within a species) were highly related to one or the other pressure state. The cumulative portrait for a unique functional species of BC changed from long-lived to short-lived species that were smaller in size with a lower signal for deposit-feeding (illustrated in Figure S2 for both low- and high-pressure locations). Such change, although quite subtle within a whole-community context, can lead to substantial shifts in ecosystem's functional characteristics and service provision. For example, cumulative effect of a small filtrator and a large deposit-feeder will not be equal to that of a small deposit-feeder and a large filtrator (although the traits remain the same for both cases). This means that species identity is important and functional changes should be considered and interpreted in conjunction with community structure assessments.

In contrast to other studied regions, there was a very large overlap in multivariate trait space between low- and high-pressure BS datasets. The Baltic Sea ecosystem is known for numerous strong spatial environmental gradients as well as multiple shifts in environmental conditions over recent and geological times (Österblom et al., 2007; Zettler et al., 2014). As a consequence, its communities primarily consist of very tolerant and opportunistic species, that is, traits that are often found among invasive species (Byers, 2002; Piola & Johnston, 2008). Although the Baltic Sea hosts a great number of non-indigenous species relative to its total species richness, invader traits were not unique to the 'trait space' of resident species, and thereby long-term changes in native communities were not as severe as in many other studied ecosystems.

### 4.3 | Further considerations for disentangling bioinvasion effects in the context of globally changing marine ecosystems

Comprehensive functional-taxonomic community characterisations are challenging and, in the context of our study, hindered by a lack of comparable, long term, whole-community datasets that capture invasion dynamics within a range of other drivers of change. Our results show that despite the exponential growth of bioinvasion studies over the last several decades (Ojaveer et al., 2021; Ruiz et al., 2000), we are still facing major challenges in quantifying and communicating the chronic, community- and ecosystem-scale effects of introduction for one of the best studied communities—macrozoobenthos—in our global marine environment.

The challenge ahead is to source historical datasets that are in a form that would lend themselves to contemporary comparison of functional change. This is likely to be difficult because many historical datasets were natural history-type inventories (focused on richness) that lacked measures of abundance, which is important for comparisons of structural composition. In parallel, there are emerging longer-term repeated-measures datasets of marine community dynamics that highlight the interacting roles of invasion and environmental perturbations in benthic systems (Chang et al., 2018;

Nygård et al., 2020; Philippe et al., 2017). In NIS-focused studies, native context is often lacking, resulting in disconnected records of native and non-indigenous biodiversity for the same time and place. Furthermore, in those datasets that are available and seemingly suitable for comparative analyses (including those considered in our study), a lack of concordance and consistency in data collection and reports impedes their consolidation and applicability for a large-scale synthesis, complicating interpretation of data. These hurdles only heighten the need for sourcing and unpacking historical information, foundational in ecology research (Swetnam et al., 1999) to develop our understanding of community baselines and invasion-related processes.

Other common challenges in bioinvasion ecology that can impede comparative functional traits analyses are (i) precise taxonomic identification or taxonomic bias (Ojaveer et al., 2021) and (ii) correctly assigning biogeographical status for all component species in a community (Carlton, 1996, 2009; Marchini & Cardeccia, 2017). Attention is needed to address changes in species nomenclature and designation that may have occurred between two sampling events separated by several decades. Although it is not uncommon for species within the same genus or family to share similar trait modalities (Grabowski et al., 2007), sometimes a misidentified species can bring a mistaken function in the dataset, especially within the traits related to trophic behaviour, environmental tolerance and life history, or when a NIS is incorrectly identified as a native species (Costello et al., 2021; Marchini & Cardeccia, 2017). Another impediment comes from our still limited knowledge of the natural history of many marine invertebrates and thus the difficulty in defining trait profiles and their shift across life-cycle stages for many marine organisms (Cardeccia et al., 2018), which limits both the accuracy and precision of functional traits analyses. It would be valuable to establish and estimate the uncertainty parameters of traits data (e.g. depending on the information source) if assessment of functional changes is implemented in routine bioinvasion management practices. This would also allow identifying the critical knowledge gaps across traits categories and taxonomic groups.

As well as addressing these challenges in near-future research, it is worth asking how to avoid these issues going forward such that mid- and late-century evaluations of current 'baselines' can proceed with fewer problems. Much more comprehensive surveys of coastal marine systems starting now might help interpreting changes associated with multiple anthropogenically driven pressures (including NIS introductions) as well as their interactions and identifying tipping points in the future. To better disentangle pressure-response relations, establishment of harmonised, ecosystem-based monitoring programmes is crucial (Lehtiniemi et al., 2015; Ojaveer et al., 2021). Comprehensive long-term observational and experimental datasets would allow robust quantification of NIS impacts, accounting for interannual and spatial variation, as well as other environmental and anthropogenic covariates (Cleland et al., 2004; Cusser et al., 2021). Greater transparency in dataset publication is already being implemented and will greatly improve access to raw datasets. Wider implementation of paired morphological and



genetic identification methods will also facilitate these investigations, along with globally harmonised species nomenclature linked to curated biological traits databases. Similarly, the concept of cryptogenic species (Carlton, 1996) is well established and can help avoid mischaracterisations of the native and non-native portions of communities when reconstructing invasion histories. Finally, a stronger awareness of shifting baselines and a determination to avoid overlooking base states has emerged recently in response to Anthropocene impacts and strengthened the field of historical ecology as a sub-discipline in its own right (Kittinger et al., 2015). Each of these components can give rise to more widespread generation of reliable and comparable large-scale community datasets globally (Lehtiniemi et al., 2015). This will undoubtedly facilitate our understanding of variation for the long-term consequences of global bioinvasion pressure at the ambient scale of regional marine ecosystems, and promote better management frameworks to address it (Ojaveer et al., 2021; Ruiz & Hewitt, 2002). Ultimately, this will help quantify the scale of change we might expect if we fail to develop effective barriers to the continued human-assisted spread of marine species.

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#### CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest for this study and the submitted manuscript.

#### PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.13838>.

#### DATA AVAILABILITY STATEMENT

No new data were generated in this study. All data sources are listed in the article/Supplementary Material, the raw datasets underlying the presented results are accessible at Zenodo <https://zenodo.org/record/8333424>.

#### ORCID

Anastasija Zaiko  <https://orcid.org/0000-0003-4037-1861>

Alice Cardecia  <https://orcid.org/0000-0002-5919-0887>

Agnese Marchini  <https://orcid.org/0000-0003-4580-0522>

#### REFERENCES

- Anderson, M. J., Ellingsen, K. E., & McArdle, B. H. (2006). Multivariate dispersion as a measure of beta diversity. *Ecology Letters*, 9, 683–693.
- AquaNIS Editorial Board. (2015). Information system on aquatic non-indigenous and cryptogenic species. World wide web electronic publication. [Www.Corpi.Ku.Lt/databases/aquanis](http://www.corpi.ku.lt/databases/aquanis). Version 2.36+. 2.36+. Retrieved from <http://www.corpi.ku.lt/databases/aquanis>
- Atalah, J., Floerl, O., Pochon, X., Townsend, M., Tait, L., & Lohrer, A. M. (2019). The introduced fanworm, *Sabella spallanzanii*, alters soft sediment macrofauna and bacterial communities. *Frontiers in Ecology and Evolution*, 7, 481. <https://doi.org/10.3389/fevo.2019.00481>
- Bailey, S. A., Brown, L., Campbell, M. L., Canning-Clode, J., Carlton, J. T., Castro, N., ... Zhan, A. (2020). Trends in the detection of aquatic non-indigenous species across global marine, estuarine and freshwater ecosystems: A 50-year perspective. *Diversity and Distributions*, 26(12), 1780–1797. <https://doi.org/10.1111/ddi.13167>
- Bauer, J. T. (2012). Invasive species: "Back-seat drivers" of ecosystem change? *Biological Invasions*, 14, 1295–1304.
- Boltovskoy, D., Correa, N. M., Burlakova, L. E., Karatayev, A. Y., Thuesen, E. V., Sylvester, F., & Paolucci, E. M. (2021). Traits and impacts of introduced species: A quantitative review of meta-analyses. *Hydrobiologia*, 848(9), 2225–2258. <https://doi.org/10.1007/s10750-020-04378-9>
- Bracewell, S. A., Dafforn, K. A., Lavender, J. T., Clark, G. F., & Johnston, E. L. (2021). Latitudinal variation in the diversity–disturbance relationship demonstrates the context dependence of disturbance impacts. *Global Ecology and Biogeography*, 30(7), 1389–1402. <https://doi.org/10.1111/geb.13305>
- Bradley Bethany, A., Laginhas Brittany, B., Whitlock, R., Allen Jenica, M., Bates Amanda, E., Bernatchez, G., Diez, J. M., Early, R., Lenoir, J., Vilà, M., & Sorte Cascade, J. B. (2019). Disentangling the abundance–impact relationship for invasive species. *Proceedings of the National Academy of Sciences of the United States of America*, 116(20), 9919–9924. <https://doi.org/10.1073/pnas.1818081116>
- Bremner, J. (2008). Species' traits and ecological functioning in marine conservation and management. *Journal of Experimental Marine Biology and Ecology*, 366(1), 37–47. <https://doi.org/10.1016/j.jembe.2008.07.007>
- Byers, J. E. (2002). Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes. *Oikos*, 97(3), 449–458. <https://doi.org/10.1034/j.1600-0706.2002.970316.x>
- Byers, J. E., Smith, R. S., Pringle, J. M., Clark, G. F., Gribben, P. E., Hewitt, C. L., Inglis, G. J., Johnston, E. L., Ruiz, G. M., Stachowicz, J. J., & Bishop, M. J. (2015). Invasion expansion: Time since introduction

- best predicts global ranges of marine invaders. *Scientific Reports*, 5(1), 12436. <https://doi.org/10.1038/srep12436>
- Cardecia, A., Marchini, A., Occhipinti-Ambrogi, A., Galil, B., Gollasch, S., Minchin, D., Naršćius, A., Olenin, S., & Ojaveer, H. (2018). Assessing biological invasions in european seas: Biological traits of the most widespread non-indigenous species. *Estuarine, Coastal and Shelf Science*, 201, 17–28.
- Carlton, J. T. (1996). Biological invasions and cryptogenic species. *Ecology*, 77(6), 1653–1655. <https://doi.org/10.2307/2265767>
- Carlton, J. T. (1999). The scale and ecological consequences of biological invasions in the world's oceans. In O. Sandlund, P. Schei, & Å. Viken (Eds.), *Invasive species and biodiversity management* (pp. 195–212). Kluwer Academic Publishers.
- Carlton, J. T. (2009). Deep invasion ecology and the assembly of communities in historical time. In *Biological invasions in marine ecosystems* (pp. 13–56). Springer.
- Chang, A. L., Brown, C. W., Crooks, J. A., & Ruiz, G. M. (2018). Dry and wet periods drive rapid shifts in community assembly in an estuarine ecosystem. *Global Change Biology*, 24(2), e627–e642. <https://doi.org/10.1111/gcb.13972>
- Clark, G. F., & Johnston, E. L. (2011). Temporal change in the diversity–invasibility relationship in the presence of a disturbance regime. *Ecology Letters*, 14(1), 52–57. <https://doi.org/10.1111/j.1461-0248.2010.01550.x>
- Clark, G. F., Kelaher, B. P., Dafforn, K. A., Coleman, M. A., Knott, N. A., Marzinelli, E. M., & Johnston, E. L. (2015). What does impacted look like? High diversity and abundance of epibiota in modified estuaries. *Environmental Pollution*, 196, 12–20. <https://doi.org/10.1016/j.envpol.2014.09.017>
- Clavero, M., & Garcia-Berthou, E. (2005). Invasive species are a leading cause of animal extinctions. *Trends in Ecology & Evolution*, 20(3), 110. <https://doi.org/10.1016/j.tree.2005.01.003>
- Cleland, E. E., Smith, M. D., Andelman, S. J., Bowles, C., Carney, K. M., Claire Horner-Devine, M., Drake, J. M., Emery, S. M., Gramling, J. M., & Vandermast, D. B. (2004). Invasion in space and time: Non-native species richness and relative abundance respond to interannual variation in productivity and diversity. *Ecology Letters*, 7(10), 947–957. <https://doi.org/10.1111/j.1461-0248.2004.00655.x>
- Cohen, A. N., & Carlton, J. T. (1998). Accelerating invasion rate in a highly invaded estuary. *Science*, 279(5350), 555–558.
- Costello, M. J., Dekeyser, S., Galil, B. S., Hutchings, P., Katsanevakis, S., Pagad, S., Robinson, T. B., Turon, X., Vandepitte, L., Vanhoorne, B., Verfaille, K., Willan, R. C., & Rius, M. (2021). Introducing the world register of introduced marine species (wrims). *Management of Biological Invasions*, 12(4), 792–811.
- Creed, J. C., Junqueira, A. O. R., Fleury, B. G., Mantellatto, M. C., & Oigman-Pszczol, S. S. (2017). The sun-coral project: The first social-environmental initiative to manage the biological invasion of *Tubastraea* spp. in Brazil. *Management of Biological Invasions*, 8(2), 181–195. <https://doi.org/10.3391/mbi.2017.8.2.06>
- Crooks, J. A. (1996). The population ecology of an exotic mussel, *Musculista senhousia*, in a southern california bay. *Estuaries*, 19, 42–50.
- Crooks, J. A., & Soulé, M. E. (1996). Lag times in population explosions of invasive species: Causes and implications.
- Cusser, S., Helms Iv, J., Bahlai, C. A., & Haddad, N. M. (2021). How long do population level field experiments need to be? Utilising data from the 40-year-old Iiter network. *Ecology Letters*, 24(5), 1103–1111. <https://doi.org/10.1111/ele.13710>
- Davis, M. A., Thompson, K., & Philip Grime, J. (2005). Invasibility: the local mechanism driving community assembly and species diversity. *Ecography*, 28(5), 696–704. <https://doi.org/10.1111/j.2005.0906-7590.04205.x>
- De Caceres, M., & Legendre, P. (2009). Associations between species and groups of sites: Indices and statistical inference. *Ecology*, 90(12), 3566–3574. <https://doi.org/10.1890/08-1823.1>
- Department of Conservation. (2019). New Zealand's sixth national report to the united nations convention on biological diversity. Reporting period: 2014–2018. Retrieved from Department of Conservation, Wellington, New Zealand.
- Diaz, S., & Cabido, M. (2001). Vive la différence: Plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, 16(11), 646–655. [https://doi.org/10.1016/S0169-5347\(01\)02283-2](https://doi.org/10.1016/S0169-5347(01)02283-2)
- Didham, R. K., Tylianakis, J. M., Hutchison, M. A., Ewers, R. M., & Gemmill, N. J. (2005). Are invasive species the drivers of ecological change? *Trends in Ecology & Evolution*, 20, 470–474.
- Dobson, A. (2005). Monitoring global rates of biodiversity change: Challenges that arise in meeting the convention on biological diversity (cbd) 2010 goals. *Philosophical Transactions of the Royal Society B*, 360(1454), 229–241. <https://doi.org/10.1098/rstb.2004.1603>
- Duncan, R. P., & Williams, P. A. (2002). Darwin's naturalization hypothesis challenged. *Nature*, 417(6889), 608–609. <https://doi.org/10.1038/417608a>
- Early, R., Bradley, B., Dukes, J., Lawler, J., Olden, J., Blumenthal, D., Gonzalez, P., Grosholz, E. D., Ibañez, I., Miller, L. P., Sorte, C. J. B., & Tatem, A. (2016). Global threats from invasive alien species in the twenty-first century and national response capacities. *Nature Communications*, 7(1), 12485. <https://doi.org/10.1038/ncomms12485>
- Eberhardt, L., & Thomas, J. (1991). Designing environmental field studies. *Ecological Monographs*, 61(1), 53–73.
- Ely, E., & Owens Viani, L. (2010). San francisco bay subtidal habitat goals report. Appendix 1–3: Anthropogenic impacts on san francisco bay and its subtidal habitat. Retrieved from State Coastal Conservancy: <http://www.sfbaysubtidal.org/PDFS/Appendix%20Anthropogenic%20Alterations.pdf>
- Firth, L. B., Duff, L., Gribben, P. E., & Knights, A. M. (2021). Do positive interactions between marine invaders increase likelihood of invasion into natural and artificial habitats? *Oikos*, 130(3), 453–463. <https://doi.org/10.1111/oik.07862>
- Floerl, O., Atalah, J., Bugnot, A. B., Chandler, M., Dafforn, K. A., Floerl, L., Zailko, A., & Major, R. (2021). A global model to forecast coastal hardening and mitigate associated socioecological risks. *Nature Sustainability*, 4, 1060–1067. <https://doi.org/10.1038/s41893-021-00780-w>
- Floerl, O., Inglis, G. J., & Gordon, D. P. (2009). Patterns of taxonomic diversity and relatedness among native and non-indigenous bryozoans. *Diversity and Distributions*, 15(3), 438–449. <https://doi.org/10.1111/j.1472-4642.2008.00553.x>
- Floerl, O., Pool, T. K., & Inglis, G. J. (2004). Positive interactions between nonindigenous species facilitate transport by human vectors. *Ecological Applications*, 14(6), 1724–1736.
- Forrest, B. M., & Taylor, M. D. J. B. I. (2002). Assessing invasion impact: Survey design considerations and implications for management of an invasive marine plant. *Biological Invasions*, 4(4), 375–386. <https://doi.org/10.1023/a:1023613428351>
- Funk, J. L., Cleland, E. E., Suding, K. N., & Zavaleta, E. S. (2008). Restoration through reassembly: Plant traits and invasion resistance. *Trends in Ecology & Evolution*, 23(12), 695–703. <https://doi.org/10.1016/j.tree.2008.07.013>
- Galil, B. S. (2018). Poisonous and venomous: Marine alien species in the mediterranean sea and human health. In G. Mazza & E. Tricarico (Eds.), *Invasive species and human health* (pp. 1–15). CABI. <https://doi.org/10.1079/9781786390981.0001>
- Galil, B. S. (2021). Non-indigenous species along the israeli mediterranean coast: Tally, policy, outlook. *Hydrobiologia*, 848(9), 2011–2029. <https://doi.org/10.1007/s10750-020-04420-w>
- Gartner, H. N., Murray, C. C., Frey, M. A., Nelson, J. C., Larson, K. J., Ruiz, G. M., & Therriault, T. W. (2016). Non-indigenous invertebrate species in the marine fouling communities of British Columbia, Canada. *BioInvasions Records: International Journal of Field Research*

- on *Biological Invasions*, 5(4), 205–212. <https://doi.org/10.3391/bir.2016.5.4.03>
- Giddens, J., Friedlander, A. M., Conklin, E., Wiggins, C., Stamoulis, K., & Donovan, M. K. (2014). Experimental removal of the invasive peacock hind (roi) *Cephalopholis argus*, in puakō, hawaii: Methods for assessing and managing marine invasive species. *Marine Ecology Progress Series*, 511, 209–221. <https://doi.org/10.3354/meps10919>
- Grabowski, M., Bacela, K., & Konopacka, A. (2007). How to be an invasive gammarid (Amphipoda: Gammaroidea)—comparison of life history traits. *Hydrobiologia*, 590, 75–84.
- Grosholz, E. D. (2005). Recent biological invasion may hasten invasional meltdown by accelerating historical introductions. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 1088–1091.
- Guastella, R., Marchini, A., Caruso, A., Evans, J., Cobiainchi, M., Cosentino, C., Langone, L., Lecci, R., & Mancin, N. (2021). Reconstructing bio-invasion dynamics through micropaleontologic analysis highlights the role of temperature change as a driver of alien foraminifera invasion. *Frontiers in Marine Science*, 8, 675807. <https://doi.org/10.3389/fmars.2021.675807>
- Guilhem, I. F., Masi, B. P., & Creed, J. C. (2020). Impact of invasive *Tubastraea* spp. (Cnidaria: Anthozoa) on the growth of the space dominating tropical rocky-shore zoantharian *Palythoa caribaeorum* (Duchassaing and Michelotti, 1860). *Aquatic Invasions*, 15(1), 98–113.
- Guy-Haim, T., Lyons, D. A., Kotta, J., Ojaveer, H., Queirós, A. M., Chatzinikolaou, E., ... Rilov, G. (2018). Diverse effects of invasive ecosystem engineers on marine biodiversity and ecosystem functions: A global review and meta-analysis. *Global Change Biology*, 24(3), 906–924. <https://doi.org/10.1111/gcb.14007>
- Hayden, B. J., Inglis, G. J., & Schiel, D. R. (2009). Marine invasions in New Zealand: A history of complex supply-side dynamics. In G. Rilov & J. A. Crooks (Eds.), *Biological invasions in marine ecosystems* (pp. 409–423). Springer-Verlag.
- Hayward, B. W., Stephenson, A. B., Morley, M., Riley, J. L., & Grenfell, H. R. (1997). Faunal changes in waitemata harbour sediments, 1930s–1990s. *Journal of the Royal Society of New Zealand*, 27(1), 1–20.
- Hewitt, J. E., Norkko, J., Kauppi, L., Villnäs, A., & Norkko, A. (2016). Species and functional trait turnover in response to broad-scale change and an invasive species. *Ecosphere*, 7(3), e01289. <https://doi.org/10.1002/ecs2.1289>
- Hollebone, A. L., & Hay, M. E. (2008). An invasive crab alters interaction webs in a marine community. *Biological Invasions*, 10(3), 347–358. <https://doi.org/10.1007/s10530-007-9134-9>
- Hopkins, G., Davidson, I., Georgiades, E., Floerl, O., Morrissey, D., & Cahill, P. (2021). Managing biofouling on submerged static artificial structures in the marine environment—Assessment of current and emerging approaches. *Frontiers in Marine Science*, 8, 759194. <https://doi.org/10.3389/fmars.2021.759194>
- IPBES. (2019). In S. Díaz, J. Settele, E. S. Brondízio, H. T. Ngo, M. Guèze, J. Agard, A. Arnet, P. Balvanera, K. A. Brauman, S. H. M. Butchart, K. M. A. Chan, I. A. Garibaldi, K. Ichii, J. Liu, S. M. Subramanian, G. F. Midgley, P. Miloslavich, Z. Molnár, D. Obura, ... C. N. Zayas (Eds.), *Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the intergovernmental science-policy platform on biodiversity and ecosystem services* (56). IPBES Secretariat.
- Jimenez, H., Keppel, E., Chang, A. L., & Ruiz, G. M. (2018). Invasions in marine communities: Contrasting species richness and community composition across habitats and salinity. *Estuaries and Coasts*, 41(2), 484–494. <https://doi.org/10.1007/s12237-017-0292-4>
- Jimenez, H., & Ruiz, G. M. (2016). Contribution of non-native species to soft-sediment marine community structure of san francisco bay, california. *Biological Invasions*, 18(7), 2007–2016. <https://doi.org/10.1007/s10530-016-1147-9>
- Jiménez-Valverde, A., Peterson, A. T., Soberón, J., Overton, J. M., Aragón, P., & Lobo, J. M. (2011). Use of niche models in invasive species risk assessments. *Biological Invasions*, 13(12), 2785–2797. <https://doi.org/10.1007/s10530-011-9963-4>
- Johnston, E. L., Piola, R. F., & Clark, G. F. (2009). The role of propagule pressure in invasion success. In G. Rilov & J. A. Crooks (Eds.), *Biological invasions in marine ecosystems: Ecological, management, and geographic perspectives* (pp. 133–151). Springer Berlin Heidelberg.
- Kassambara, A., & Mundt, F. (2017). Factoextra: Extract and visualize the results of multivariate data analyses. R package version 1.0.5. <https://CRAN.R-project.org/package=factoextra>
- Katsanevakis, S., Wallentinus, I., Zenetos, A., Leppakoski, E., Cinar, M. E., Öztürk, B., ... Cardoso, A. C. (2014). Impacts of invasive alien marine species on ecosystem services and biodiversity: A pan-european review. *Aquatic Invasions*, 9(4), 391–423.
- Kerr, D. W., Hogle, I. B., Ort, B. S., & Thornton, W. J. (2016). A review of 15 years of *Spartina* management in the San Francisco estuary. *Biological Invasions*, 18(8), 2247–2266. <https://doi.org/10.1007/s10530-016-1178-2>
- Kittinger, J. N., McClenachan, L., Gedan, K. B., & Blight, L. K. (2015). *Marine historical ecology in conservation: Applying the past to manage for the future*. University of California Press.
- Lages, B. G., Fleury, B. G., Menegola, C., & Creed, J. C. (2011). Change in tropical rocky shore communities due to an alien coral invasion. *Marine Ecology Progress Series*, 438, 85–96.
- Lablerté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91(1), 299–305. <https://doi.org/10.1890/08-2244.1>
- Lehtiniemi, M., Ojaveer, H., David, M., Galil, B., Gollasch, S., McKenzie, C., Minchin, D., Occhipinti-Ambrogia, A., Olenin, S., & Pederson, J. (2015). Dose of truth—monitoring marine non-indigenous species to serve legislative requirements. *Marine Policy*, 54, 26–35.
- Leroy, B., Bellard, C., Dias, M. S., Hugué, B., Jézéquel, C., Leprieux, F., Oberdorff, T., Robuchon, M., & Tedesco, P. A. (2023). Major shifts in biogeographic regions of freshwater fishes as evidence of the Anthropocene epoch. *Science Advances*, 9(46), eadi5502. <https://doi.org/10.1126/sciadv.adi5502>
- Lewis, S., & Maslin, M. (2015). Defining the anthropocene. *Nature*, 519, 171–180.
- Lockwood, J., Cassey, P., & Blackburn, T. (2009). The more you introduce the more you get: The role of colonization pressure and propagule pressure in invasion ecology. *Diversity and Distributions*, 15(5), 904–910. <https://doi.org/10.1111/j.1472-4642.2009.00594.x>
- Lohrer, A. M., Townsend, M., Morrison, M., & Hewitt, J. (2008). Change in the benthic assemblages of the waitemata harbour: Invasion risk as a function of community structure. Biosecurity New Zealand Technical Paper No: 2008/17, 56.
- Lutz-Collins, V., Ramsay, A., Quijón, P. A., & Davidson, J. (2009). Invasive tunicates fouling mussel lines: Evidence of their impact on native tunicates and other epifaunal invertebrates. *Aquatic Invasions*, 4(1), 213–220.
- MacDougall, A. S., Gilbert, B., & Levine, J. M. (2009). Plant invasions and the niche. *Journal of Ecology*, 97(4), 609–615. <https://doi.org/10.1111/j.1365-2745.2009.01514.x>
- MacDougall, A. S., & Turkington, R. (2005). Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology*, 86, 42–55.
- Marchini, A., & Cardeccia, A. (2017). Alien amphipods in a sea of troubles: Cryptogenic species, unresolved taxonomy and overlooked introductions. *Marine Biology*, 164(4), 69. <https://doi.org/10.1007/s00227-017-3093-1>
- Marchini, A., Munari, C., & Mistri, M. (2008). Functions and ecological status of eight Italian lagoons examined using biological traits analysis (bta). *Marine Pollution Bulletin*, 56(6), 1076–1085. <https://doi.org/10.1016/j.marpolbul.2008.03.027>

- Marvier, M., Kareiva, P., & Neubert, M. G. (2004). Habitat destruction, fragmentation, and disturbance promote invasion by habitat generalists in a multispecies metapopulation. *Risk Analysis*, 24(4), 869–878. <https://doi.org/10.1111/j.0272-4332.2004.00485.x>
- Mason, N. W. H., de Bello, F., Moullot, D., Pavoine, S., & Dray, S. (2013). A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. *Journal of Vegetation Science*, 24(5), 794–806. <https://doi.org/10.1111/jvs.12013>
- Mason, N. W. H., Moullot, D., Lee, W. G., & Wilson, J. B. (2005). Functional richness, functional evenness and functional divergence: The primary components of functional diversity. *Oikos*, 111(1), 112–118. <https://doi.org/10.1111/j.0030-1299.2005.13886.x>
- McDowell, W. G., & Byers, J. E. (2019). High abundance of an invasive species gives it an outsized ecological role. *Freshwater Biology*, 64(3), 577–586. <https://doi.org/10.1111/fwb.13243>
- Milanović, M., Knapp, S., Pyšek, P., & Kühn, I. (2020). Linking traits of invasive plants with ecosystem services and disservices. *Ecosystem Services*, 42, 101072. <https://doi.org/10.1016/j.ecoser.2020.101072>
- Nichols, F. H., & Thompson, J. K. (1985). Persistence of an introduced mudflat community in south San Francisco Bay, California. *Marine Ecology Progress Series*, 24(1/2), 83–97.
- Novoa, A., Richardson, D. M., Pyšek, P., Meyerson, L. A., Bacher, S., Canavan, S., Catford, J. A., Čuda, J., Essl, F., Foxcroft, L. C., Genovesi, P., Hirsch, H., Hui, C., Jackson, M. C., Kueffer, C., Le Roux, J. J., Measey, J., Mohanty, N. P., Moodley, D., ... Wilson, J. R. U. (2020). Invasion syndromes: A systematic approach for predicting biological invasions and facilitating effective management. *Biological Invasions*, 22(5), 1801–1820. <https://doi.org/10.1007/s10530-020-02220-w>
- Nunez-Mir, G. C., Guo, Q., Rejmánek, M., Iannone Iii, B. V., & Fei, S. (2019). Predicting invasiveness of exotic woody species using a traits-based framework. *Ecology*, 100(10), e02797. <https://doi.org/10.1002/ecy.2797>
- Nygård, H., Lindegarth, M., Darr, A., Dinesen, G. E., Eigaard, O. R., & Lips, I. (2020). Developing benthic monitoring programmes to support precise and representative status assessments: A case study from the baltic sea. *Environmental Monitoring and Assessment*, 192(12), 795. <https://doi.org/10.1007/s10661-020-08764-7>
- Occhipinti-Ambrogi, A. (2007). Global change and marine communities: Alien species and climate change. *Marine Pollution Bulletin*, 55(7), 342–352. <https://doi.org/10.1016/j.marpolbul.2006.11.014>
- Oesterwind, D., Rau, A., & Zaiko, A. (2016). Drivers and pressures—Untangling the terms commonly used in marine science and policy. *Journal of Environmental Management*, 181, 8–15.
- Ojaveer, H., Galil, B. S., Carlton, J. T., Alleway, H., Gouletquer, P., Lehtiniemi, M., Marchini, A., Miller, W., Occhipinti-Ambrogi, A., Peharda, M., Ruiz, G. M., Williams, S. L., & Zaiko, A. (2018). Historical baselines in marine bioinvasions: Implications for policy and management. *PLoS ONE*, 13(8), e0202383. <https://doi.org/10.1371/journal.pone.0202383>
- Ojaveer, H., Jaanus, A., MacKenzie, B. R., Martin, G., Olenin, S., Radziejewska, T., Telesh, I., Zettler, M. L., & Zaiko, A. (2010). Status of biodiversity in the baltic sea. *PLoS ONE*, 5(9), e12467.
- Ojaveer, H., & Kotta, J. (2015). Ecosystem impacts of the widespread non-indigenous species in the baltic sea: Literature survey evidences major limitations in knowledge. *Biological Invasions*, 19, 799–813.
- Ojaveer, H., Kotta, J., Outinen, O., Einberg, H., Zaiko, A., & Lehtiniemi, M. (2021). Meta-analysis on the ecological impacts of widely spread non-indigenous species in the Baltic sea. *Science of the Total Environment*, 786, 147375. <https://doi.org/10.1016/j.scitotenv.2021.147375>
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., ... Wagner, H. (2019). Vegan: Community ecology package. R Package Version 2.5-5. <https://CRAN.R-project.org/package=vegan>
- Olden, J. D., Poff, N. L., Douglas, M. R., Douglas, M. E., & Fausch, K. D. (2004). Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology & Evolution*, 19, 18–24.
- Olenin, S., Gollasch, S., Lehtiniemi, M., Sapota, M., & Zaiko, A. (2017). Biological invasions. In P. Snoeijs-Leijonmalm, H. Schubert, & T. Radziejewska (Eds.), *Biological oceanography of the Baltic sea* (pp. 193–232). Springer Science+Business Media.
- Olenin, S., Minchin, D., & Daunys, D. (2007). Assessment of biopollution in aquatic ecosystems. *Marine Pollution Bulletin*, 55(7), 379–394. <https://doi.org/10.1016/j.marpolbul.2007.01.010>
- Olenina, I., Wasmund, N., Hajdu, S., Jurgensone, I., Gromisz, S., Kownacka, J., Toming, K., Vaiciūtė, D., & Olenin, S. (2010). Assessing impacts of invasive phytoplankton: The Baltic sea case. *Marine Pollution Bulletin*, 60, 1691–1700.
- Orlova, M., Golubkov, S., Kalinina, L., & Ignatieva, N. (2004). Dreissena polymorpha (Bivalvia: Dreissenidae) in the neva estuary (eastern gulf of Finland, Baltic sea): Is it a biofilter or source for pollution? *Marine Pollution Bulletin*, 49(3), 196–205. <https://doi.org/10.1016/j.marpolbul.2004.02.008>
- Österblom, H., Hansson, S., Larsson, U., Hjerne, O., Wuff, F., Elmgren, R., & Folke, C. (2007). Human-induced trophic cascades and ecological regime shifts in the Baltic sea. *Ecosystems*, 10, 877–889.
- Parker, I. M., Simberloff, D., Lonsdale, W. M., Goodell, K., Wonham, M., Kareiva, P. M., Kareiva, P. M., Williamson, M. H., Von Holle, B., Moyle, P. B., Byers, J. E., & Goldwasser, L. J. B. I. (1999). Impact: Toward a framework for understanding the ecological effects of invaders. *Biological Invasions*, 1(1), 3–19. <https://doi.org/10.1023/a:1010034312781>
- Pejchar, L., & Mooney, H. (2009). Invasive species, ecosystem services and human well-being. *Trends in Ecology & Evolution*, 24(9), 497–504. <https://doi.org/10.1016/j.tree.2009.03.016>
- Philippe, A., Plumejeaud-Perreau, C., Jourde, J., Pineau, P., Lachaussee, N., Joyeux, E., Corre, F., Delaporte, P., & Bocher, P. (2017). Building a database for long-term monitoring of benthic macrofauna in the pertuis-charentais (2004–2014). *Biodiversity Data Journal*, 5, e10288. <https://doi.org/10.3897/BDJ.5.e10288>
- Pianka, E. R. (1978). *Evolutionary ecology*. Harper & Row.
- Piola, R. F., & Johnston, E. L. (2008). Pollution reduces native diversity and increases invader dominance in marine hard-substrate communities. *Diversity and Distributions*, 14(2), 329–342. <https://doi.org/10.1111/j.1472-4642.2007.00430.x>
- Pires-Teixeira, L. M., Neres-Lima, V., & Creed, J. C. (2021). How do biological and functional diversity change in invaded tropical marine rocky reef communities? *Diversity*, 13(8), 353.
- Powell, A. W. B. (1937). Animal communities of the sea-bottom in auckland and manukau harbours. *Transactions of the Royal Society of New Zealand*, 66, 354–401.
- Pyšek, P., Bacher, S., Kühn, I., Novoa, A., Catford, J. A., Hulme, P. E., Pergl, J., Richardson, D. M., Wilson, J. R. U., & Blackburn, T. M. (2020). Macroecological framework for invasive aliens (mafia): Disentangling large-scale context dependence in biological invasions. *NeoBiota*, 62, 407–461.
- R Core Team. (2014). R: A language and environment for statistical computing. Retrieved from <http://www.R-project.org>
- Reichard, S. H., & Hamilton, C. W. (1997). Predicting invasions of woody plants introduced into north america. *Conservation Biology*, 11(1), 193–203.
- Ricciardi, A. (2007). Are modern biological invasions an unprecedented form of global change? *Conservation Biology*, 21(2), 329–336. <https://doi.org/10.1111/j.1523-1739.2006.00615.x>
- Robert, E. C. S. (1881). *Mya arenaria* in San Francisco Bay. *The American Naturalist*, 15(5), 362–366.
- Ross, D. J., Johnson, C. R., & Hewitt, C. L. (2006). Abundance of the introduced seastar, *Asterias amurensis*, and spatial variability in soft sediment assemblages in SE Tasmania: Clear correlations but complex interpretation. *Estuarine, Coastal and Shelf Science*, 67(4), 695–707. <https://doi.org/10.1016/j.ecss.2005.11.038>
- Ruesink, J. L., Parker, I. M., Groom, M. J., & Kareiva, P. M. (1995). Reducing the risks of nonindigenous species introductions. *Bioscience*, 45(7), 465–477. <https://doi.org/10.2307/1312790>

- Ruiz, G. M., Carlton, J. T., Grosholz, E., & Hines, A. (1997). Global invasions of marine and estuarine habitats by non-indigenous species: Mechanisms, extent, and consequences. *American Zoologist*, 37, 621–632.
- Ruiz, G. M., Fofonoff, P., Hines, A. H., & Grosholz, E. D. (1999). Non-indigenous species as stressors in estuarine and marine communities. *Assessing Invasion Impacts and Interactions*, 44(3part2), 950–972. [https://doi.org/10.4319/lo.1999.44.3\\_part\\_2.0950](https://doi.org/10.4319/lo.1999.44.3_part_2.0950)
- Ruiz, G. M., Fofonoff, P. W., Carlton, J. T., Wonham, M. J., & Hines, A. H. (2000). Invasion of coastal marine communities in North America: Apparent patterns, processes, and biases. *Annual Review of Ecology and Systematics*, 31(1), 481–531. <https://doi.org/10.1146/annurev.ecolsys.31.1.481>
- Ruiz, G. M., & Hewitt, C. L. (2002). Toward understanding patterns of coastal marine invasions: A prospectus. In E. Leppäkoski, S. Gollasch, & S. Olenin (Eds.), *Invasive aquatic species of Europe. Distribution, impacts and management* (pp. 529–547). Springer Netherlands.
- Sax, D. F., Stachowicz, J. J., Brown, J. H., Bruno, J. F., Dawson, M. N., Gaines, S. D., Grosberg, R. K., Hastings, A., Holt, R. D., Mayfield, M. M., O'Connor, M. I., & Rice, W. R. (2007). Ecological and evolutionary insights from species invasions. *Trends in Ecology & Evolution*, 22(9), 465–471. <https://doi.org/10.1016/j.tree.2007.06.009>
- Schemel, L. E., Ota, A. Y., Harmon, J. G., Shay, J. M., & Adorador, R. N. (1988). *Benthic macrofauna and ancillary data for San Francisco Bay, California, March to November 1987*. U.S. Geological Survey. Retrieved from Sacramento, California.
- Schiel, D. R., & Thompson, G. A. (2012). Demography and population biology of the invasive kelp *Undaria pinnatifida* on shallow reefs in southern New Zealand. *Journal of Experimental Marine Biology and Ecology*, 434–435, 25–33.
- Schleuter, D., Daufresne, M., Massol, F., & Argillier, C. (2010). A user's guide to functional diversity indices. *Ecological Monographs*, 80(3), 469–484. <https://doi.org/10.1890/08-2225.1>
- Schoener, T. W. (1974). Resource partitioning in ecological communities. *Science*, 185(4145), 27–39.
- Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., Pagad, S., Pyšek, P., van Kleunen, M., Winter, M., Ansong, M., Arianoutsou, M., Bacher, S., Blasius, B., Brockerhoff, E. G., Brundu, G., Capinha, C., Causton, C. E., Celesti-Gradow, L., ... Essl, F. (2018). Global rise in emerging alien species results from increased accessibility of new source pools. *Proceedings of the National Academy of Sciences of the United States of America*, 115(10), E2264–E2273. <https://doi.org/10.1073/pnas.1719429115>
- Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., Pagad, S., Pyšek, P., Winter, M., Arianoutsou, M., Bacher, S., Blasius, B., Brundu, G., Capinha, C., Celesti-Gradow, L., Dawson, W., Dullinger, S., & Essl, F. (2017). No saturation in the accumulation of alien species worldwide. *Nature Communications*, 8, 14435. <https://doi.org/10.1038/ncomms14435>
- Silva, A. G., Paula, A. F., Fleury, B. G., & Creed, J. C. (2014). Eleven years of range expansion of two invasive corals (*tubastraea coccinea* and *tubastraea tagusensis*) through the southwest atlantic (Brazil). *Estuarine, Coastal and Shelf Science*, 141, 9–16.
- Simberloff, D., & Gibbons, L. (2004). Now you see them, now you don't—population crashes of established introduced species. *Biological Invasions*, 6(2), 161–172.
- Simberloff, D., Martin, J.-L., Genovesi, P., Maris, V., Wardle, D., Aronson, J., ... Vilà, M. (2013). Impacts of biological invasions: What's what and the way forward. *Trends in Ecology & Evolution*, 28(1), 58–66. <https://doi.org/10.1016/j.tree.2012.07.013>
- Smart, S. M., Thompson, K., Marrs, R. H., Le Duc, M. G., Maskell, L. C., & Firbank, L. G. (2006). Biotic homogenization and changes in species diversity across human-modified ecosystems. *Proceedings of the Biological Sciences*, 273(1601), 2659–2665. <https://doi.org/10.1098/rspb.2006.3630>
- Statzner, B., Bis, B., Dolédec, S., & Usseglio-Polatera, P. (2001). Perspectives for biomonitoring at large spatial scales: A unified measure for the functional composition of invertebrate communities in European running waters. *Basic and Applied Ecology*, 2(1), 73–85. <https://doi.org/10.1078/1439-1791-00039>
- Steger, J., Bošnjak, M., Belmaker, J., Galil, B. S., Zuschin, M., & Albano, P. G. (2022). Non-indigenous molluscs in the eastern mediterranean have distinct traits and cannot replace historic ecosystem functioning. *Global Ecology and Biogeography*, 31(1), 89–102. <https://doi.org/10.1111/geb.13415>
- Strauss, S. Y., Webb, C. O., & Salamin, N. (2006). Exotic taxa less related to native species are more invasive. *Biological Sciences*, 103(15), 5841–5845. <https://doi.org/10.1073/pnas.0508073103>
- Strayer, D. L., Eviner, V. T., Jeschke, J. M., & Pace, M. L. (2006). Understanding the long-term effects of species invasions. *Trends in Ecology & Evolution*, 21(11), 645–651. <https://doi.org/10.1016/j.tree.2006.07.007>
- Swetnam, T. W., Allen, C. D., & Betancourt, J. L. (1999). Applied historical ecology: Using the past to manage for the future. *Ecological Applications*, 9(4), 1189–1206. [https://doi.org/10.1890/1051-0761\(1999\)009\[1189:AHEUTP\]2.0.CO;2](https://doi.org/10.1890/1051-0761(1999)009[1189:AHEUTP]2.0.CO;2)
- The Ministry for the Environment and Statistics New Zealand. (2014). New Zealand's environment reporting series: Marine pests in ports. Retrieved from <https://data.mfe.govt.nz/table/52521-marine-pests-in-ports-2014/>
- Thibaut, T., Meinesz, A., & Coquillard, P. (2004). Biomass seasonality of *Caulerpa taxifolia* in the mediterranean sea. *Aquatic Botany*, 80(4), 291–297.
- Thomsen, M. S., Wernberg, T., Olden, J. D., Griffin, J. N., & Silliman, B. R. (2011). A framework to study the context-dependent impacts of marine invasions. *Journal of Experimental Marine Biology and Ecology*, 400(1), 322–327. <https://doi.org/10.1016/j.jembe.2011.02.033>
- Villéger, S., Mason, N. W. H., & Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, 89(8), 2290–2301. <https://doi.org/10.1890/07-1206.1>
- Vitousek, P. M., D'Antonio, C. M., Loope, L. L., Rejmanek, M., & Westbrooks, R. G. (1997). Introduced species: A significant component of human-caused global change. *New Zealand Journal of Ecology*, 21(1), 1–16.
- Wasson, K., Zabin, C. J., Bedinger, L., Cristina Diaz, M., & Pearse, J. S. (2001). Biological invasions of estuaries without international shipping: The importance of intraregional transport. *Biological Conservation*, 102(2), 143–153. [https://doi.org/10.1016/S0006-3207\(01\)00098-2](https://doi.org/10.1016/S0006-3207(01)00098-2)
- Watkins, H. V., Yan, H. F., Dunic, J. C., & Côté, I. M. (2021). Research biases create overrepresented “poster children” of marine invasion ecology. *Conservation Letters*, 14(3), e12802. <https://doi.org/10.1111/conl.12802>
- Wen, Z., Zheng, H., Smith, J. R., Zhao, H., Liu, L., & Ouyang, Z. (2019). Functional diversity overrides community-weighted mean traits in linking land-use intensity to hydrological ecosystem services. *Science of the Total Environment*, 682, 583–590. <https://doi.org/10.1016/j.scitotenv.2019.05.160>
- Wiens, J., & Parker, K. (1995). Analyzing the effects of accidental environmental impacts: approaches and assumptions. *Ecological Applications*, 5(4), 1069–1083.
- Zabin, C. J., Ashton, G. V., Brown, C. W., Davidson, I. C., Sytsma, M. D., & Ruiz, G. M. (2014). Small boats provide connectivity for nonindigenous marine species between a highly invaded international port and nearby coastal harbors. *Management of Biological Invasions*, 5(2), 97–112.
- Zaiko, A., Daunys, D., & Olenin, S. (2009). Habitat engineering by the invasive zebra mussel *Dreissena polymorpha* (pallas) in a boreal coastal lagoon: Impact on biodiversity. *Helgoland Marine Research*, 63(1), 85–94.
- Zaiko, A., Olenin, S., Daunys, D., & Nalepa, T. F. (2007). Vulnerability of benthic habitats to the aquatic invasive species. *Biological Invasions*, 9, 703–714.

Zettler, M. L., Karlsson, A., Kontula, T., Gruszka, P., Laine, A. O., Herkul, K., Schiele, K. S., Maximov, A., & Haldin, J. (2014). Biodiversity gradient in the baltic sea: A comprehensive inventory of macrozoobenthos data. *Helgoland Marine Research*, 68, 49–57.

#### AUTHOR BIOGRAPHY

**Anastasija Zaiko** is a research scientist at Cawthron Institute and Sequench Ltd. with a broad expertise in aquatic ecology, development and application of molecular tools for monitoring and surveillance. Interests and expertise of the group of authors include invasion ecology, marine ecology, conservation biology and/or evolution, focusing on a variety of taxa from freshwater fishes to marine phytoplankton. The authors conduct research on patterns, mechanisms, and consequences of species introductions to aquatic environments, assessment and management of risks associated with non-indigenous species, development and implementation of biosecurity practices.

#### SUPPORTING INFORMATION

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

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