



Testing differences of marine non-indigenous species diversity across Macaronesia using a standardised approach

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ABSTRACT

The introduction of non-indigenous species (NIS) induces severe impacts on marine biodiversity and ecosystems. Macaronesia is an ecologically relevant region where several NIS were detected recently. For the first time, a standard experimental approach was designed to examine biofouling assemblages and investigate NIS across the region. In this context, sessile biofouling assemblages were examined in four recreational marinas in all the Macaronesian archipelagos from 2018 to 2020: the Azores, Madeira, Canary Islands, and Cabo Verde. We hypothesised that NIS numbers, abundance, and recruitment differed in each location due to abiotic and biotic features. From the Azores (higher latitudes) to Cabo Verde (lower latitudes), NIS recruitment and percentage cover decreased following a partial latitude gradient. The present study unveiled 25 NIS, with new records for the Azores (two cryptogenic species), Canary Islands (one NIS and two cryptogenic species), and Cabo Verde (three NIS and three cryptogenic species). The present research represents a pioneer and relevant step in advancing our current understanding of marine biological invasions in Macaronesia, employing a standard and low-cost approach.

1. Introduction

In recent decades, human-induced changes have influenced species distribution, abundance, and diversity in the world's marine ecosystems (Carlton, 2000; Storch et al., 2022; Tuomainen and Candolin, 2011). Pollution, habitat destruction, overfishing, global climate change and

the introduction of non-indigenous species (NIS) are among the most significant anthropogenic impacts on marine biodiversity and ecosystems (Albano et al., 2021; Carlton, 2000; Cepic et al., 2022; Kelly et al., 2020).

Since nautical navigation began, people have accidentally or deliberately transported an array of organisms (Bax et al., 2003). Wooden

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sailing ships were often heavily covered with fouling organisms with dozens of associated species in dry ballast and the anchor chain (Carlton, 1999a). For example, barnacles are well-known ship-fouling organisms worldwide, and human-mediated translocations over the past several centuries influenced their current distribution (Carlton et al., 2011). Unsurprisingly, several other species have today a cosmopolitan distribution due to human-induced introductions (Bax et al., 2003; Carlton, 1999b; Carlton et al., 2011; Wares et al., 2022). Marine invasions are, therefore, not just a process that happened in the distant past. The dispersion of marine species beyond their natural biogeographical limits is promoted and facilitated by several human activities. In this context, several introduction vectors such as shipping, aquaculture, live bait trade, marine debris and aquarium trade are known to play a major role in introducing NIS on a global scale (Carlton et al., 2017; Chainho et al., 2015; Harrower et al., 2018). For example, maritime traffic (shipping and recreational navigation) has been identified as the most relevant NIS introduction vector in the marine realm through ballast water and hull fouling (Bailey et al., 2020; Davidson and Simkanin, 2012; Godwin, 2003). Indeed, hull fouling on recreational vessels is essential in primary and secondary introductions (Canning-Clode et al., 2013; Castro et al., 2022b; Ferrario et al., 2017; Zabin et al., 2014). Luckily, most of these transported species are unable to survive (Gollasch et al., 2000) to the conditions applied during the voyage (e.g. physical impact (i.e. waves collision), speed, trip duration, and fluctuations in environmental conditions) (Chan et al., 2016; Davidson et al., 2018). For other species, the abiotic conditions at the destination, mainly harbours and marinas, are unsuitable (Afonso et al., 2020; Barry et al., 2008; Keller et al., 2011). Even when conditions are appropriate, most organisms fail to establish, and of those that do establish, most fail to spread and become invasive (Sakai et al., 2001). The success of biological invasions is mainly determined by environmental conditions but also by several biotic processes at the neighbourhood scale that strongly influence this stage (e.g. competition, predation, disease, parasitism and species attributes; Castro et al., 2021; Papacostas and Freestone, 2019; Ruiz et al., 2000). Ecologists have theorised that communities with higher species richness offer more biotic resistance against biological invasions by maintaining high levels of predation pressure or increasing competition for resources (Freestone et al., 2013; Gestoso et al., 2017). New experimental evidence has supported the hypothesis that biotic interactions strengthen toward lower latitudes, reporting stronger predation intensity (Freestone et al., 2021). In addition, a recent study using standardised experiments that spanned 115° of latitude across 36 sites confirmed higher predation and more substantial impacts on benthic communities near the equator, verifying that these tendencies were more related to water temperature than latitude, i.e. stronger interactions occur at warmer tropical waters (Ashton et al., 2022).

Over the years, islands have been used as “ports of call” facilities for ancient explorers, and these ecosystems were subject to change (Castro et al., 2020). Consequently, marine infrastructures were constructed to accommodate maritime traffic (Castro et al., 2020; Kölzsch and Blasius, 2011) and parallel to artificial structures to protect coastal human populations (Aguilera, 2018; Airoidi et al., 2015; Moschella et al., 2005). These ocean sprawls resulted in NIS hotspots (Castro et al., 2022b, 2021; Gestoso et al., 2017), also providing a double role as “stepping-stone” structures or hubs in which some species can thrive and disperse to nearby coastal zones and ultimately to entire regions (Afonso et al., 2020; Png-Gonzalez et al., 2021). Thus, as hotspots, marinas and ports are also considered focal points for early detection of unwanted NIS, crucial for containment, treatment, potential eradication and effective management of these species (Anderson, 2005b; Marraffini et al., 2017). A common and straightforward approach to examining ecological patterns in marine biofouling assemblages is the deployment of settlement plates in docks and marinas (Ashton et al., 2022; Marraffini et al., 2017; Papacostas and Freestone, 2019). This methodology has been implemented in several global regions as a cost-effective approach to monitor NIS (e.g. Ashton et al., 2022; Canning-Clode et al., 2013; Gittenberger

et al., 2010; Tait et al., 2016).

The Macaronesia region is located in the Northeast Atlantic Ocean and comprises the volcanic archipelagos of the Azores, Madeira, Canary Islands and Cabo Verde. These island systems’ distance from the European or African continents varies from 95 to 1600 km (Aranda et al., 2014), and water depths beyond 1300–1500 m divide these archipelagos from the nearby mainland and other plausible natural species sources regions, such as neighbouring archipelagos or shallow sea-mounts (Freitas et al., 2019).

Marine biological invasions in Macaronesia were first explored at the archipelago level (Canning-Clode et al., 2013; Cardigos et al., 2006; Freitas and Castro, 2005; Freitas and Wirtz, 2019; Micael et al., 2014; Pajuelo et al., 2016; Triay-Portela et al., 2015). More recently, Castro et al. (2022a) examined marine invasions in the region by conducting an extensive literature review and statistical analysis. However, in situ experimental studies on marine NIS were restricted to a local scale on each sub-archipelago (Ferrario et al., 2020; Gestoso et al., 2018; Monteiro, 2012; Vaz-Pinto et al., 2013), and to the best of our knowledge, no study has ever attempted to assess NIS numbers and patterns in Macaronesia using a standardised experimental approach.

In this context, the present study represents the first attempt to examine the marine bioinvasions of Macaronesia at a higher resolution. For this purpose, a standardised experimental approach was designed to examine sessile biofouling assemblages and investigate NIS in four recreational marinas in each of the four Macaronesian archipelagos from 2018 to 2020: We hypothesised that there are differences in NIS numbers, abundance and recruitment in the different locations due to abiotic (i.e. temperature/latitude differences) and biotic features (i.e. more species richness more competition for resources and therefore higher biotic resistance).

2. Material and methods

2.1. Study sites

Four recreational marinas were chosen for the present study, one in each archipelago. Site selection was determined by accessibility and the highest propagule pressure available for each archipelago (i.e. being the most or one of the most visited marinas in each archipelago). Thus, from high to low latitude, we selected in the Azores, Ponta Delgada Marina in São Miguel Island (640 berths; www.portosdosacores.pt/marinas/marina-ponta-delgada); in Madeira archipelago, Quinta do Lorde Marina in Madeira Island (200 berths, www.navigo.com/port/marina-quinta-do-lorde-marina/1732); in the Canary Islands, Puerto Deportivo Marina Tenerife in Tenerife Island (220 berths, <https://www.puertosedetenerife.org/marinas/marina-tenerife/>); and finally in Cabo Verde, Mindelo Marina in São Vicente Island (140 berths; www.marinaminidelo.cv/english/marinaminidelo.html) (Fig. 1).

2.2. Experimental design

A total of 30 experimental units, consisting of 14 × 14 × 0.3 cm PVC plates, were suspended underneath random floating fingers at 1 m depth within each selected marina, totalising 120 experimental units throughout the Macaronesian region. This method was adapted from Canning-Clode et al. (2013) and later improved by Ramalhosa et al. (2014) and is a common method for NIS monitoring in port environments (e.g. Marraffini et al., 2017; Ramalhosa et al., 2019; Tamburini et al., 2021). At each Marina, a set of 30 PVC plates was deployed at the beginning of the experiment (Time 0 = T0 – January 2018). Five plates were retrieved during each sampling event (T1 to T5) and replaced every sampling occasion to get a temporal recruitment cycle of young assemblages (hereafter referred to as “young plates”) (Fig. 2). The other five plates were retrieved and sampled after continuous submersion to monitor the development of mature assemblages (hereafter referred to as “mature plates”) from T2 to T5 (Fig. 2). This procedure ensured

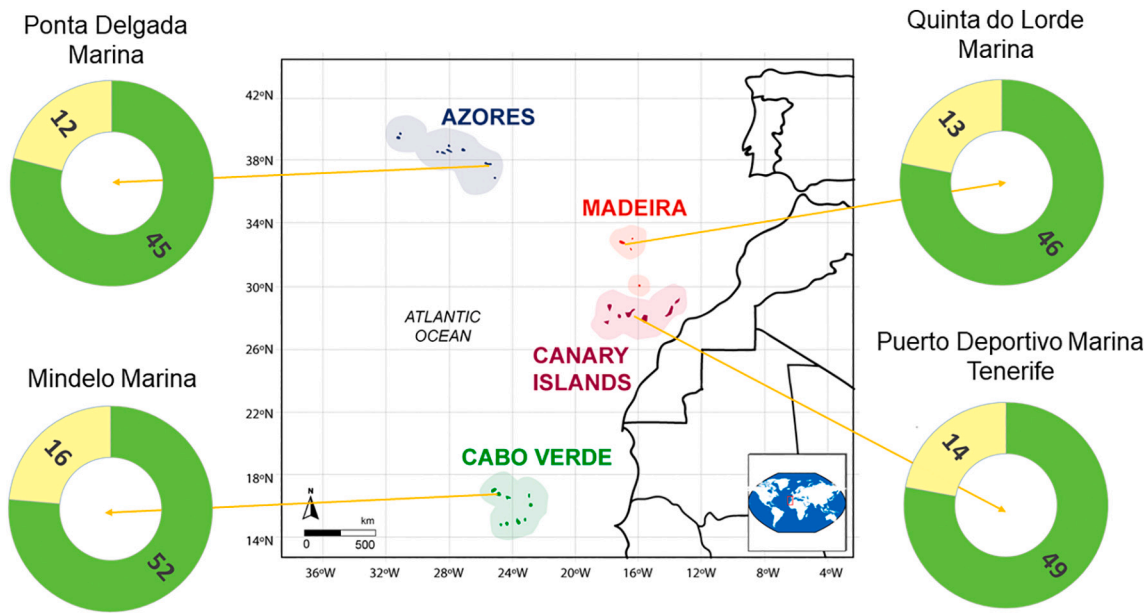


Fig. 1. Location of Macaronesian archipelagos (Azores, Madeira, Canary Islands and Cabo Verde) with the indication of the study sites (Ponta Delgada Marina (Azores), Quinta do Lorde Marina (Madeira), Puerto Deportivo Marina Tenerife (Canary Islands), and Mindelo Marina (Cabo Verde)). The richness ratio of non-indigenous species (yellow) and other species (green - Native, Cryptogenic, and unresolved) is also displayed. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

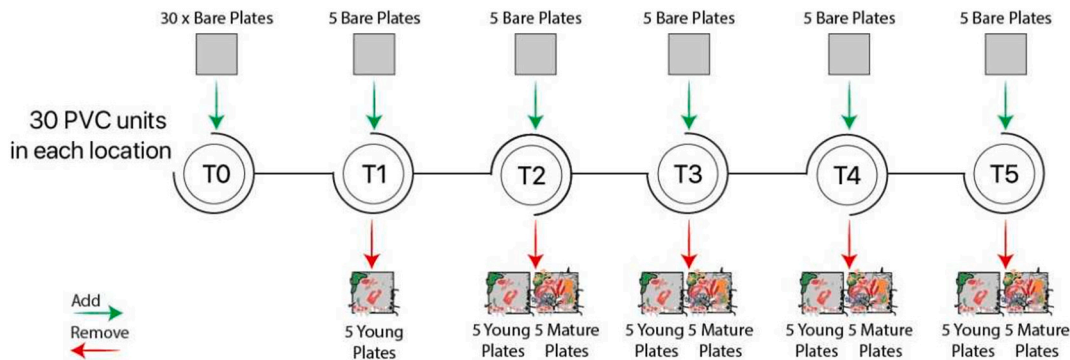


Fig. 2. Diagram of the employed experimental design. For each study location, 30 experimental units of artificial substrate were placed at each selected Marina (Time 0; 30 plates \times 4 locations = 120 plates). Five extra bare plates were placed in each sampling occasion (T1 to T4). Five young plates were subsequently sampled to verify the recruitment cycle, and five mature plates were to monitor the development of assemblages (T0 – January 2018; T1 – May 2018; T2 – October 2018; T3 – March 2019; T4 – August 2019; T5 – January 2020).

replicate independence for a more appropriate analysis of the variability in the assemblages throughout the experiment. Sampling in each location was conducted within one to 10 days. Sampling frequency was established in five months to maximise recruitment across the archipelagos.

2.3. Data collection

Plate underside sampling consists of taxa identification to the lowest taxonomical level through a binocular microscope, and photographs were taken for abundance evaluation. The CPCe software (Coral Point Count with Excel extensions; Kohler and Gill, 2006) was used on each PVC plate photograph to assess taxa relative abundance and estimate the cover percentage by considering 99 stratified random points. This sampling method divided the plate into a 3 \times 3 grid of 9 cells, with 11 random points per cell, resulting in 99 points analysed per image, with points distributed equally to each image region (Kohler and Gill, 2006). This sampling procedure was effectively employed in different experiments (e.g. Cacabelos et al., 2020; Piola et al., 2022; Schwan et al., 2016;

Tamburini et al., 2022). Species biogeographic statuses were assigned (i. e. native, cryptogenic, NIS, or not determined) based on the most recent listings for the area (Castro et al., 2022a; Ramalhosa et al., 2021). Cryptogenic status was considered without clear evidence that a species was native or introduced (Carlton et al., 2011). For example, species with unconfirmed identification, however, where the possible identity does not correspond to the study area (e.g. *Symplegma cf. rubra*), as well as species with different statuses in the various archipelagos (e.g. *Mycale (Carmia) senegalensis*; Castro et al. (2022a)) were classified as Cryptogenic. Finally, unresolved species were assigned to all not identify at the species level taxa.

Following the approach employed by Castro et al. (2022a), the probable native distribution range (origin) for the NIS present in each location was assigned using the 18 large-scale IUCN marine bioregions as defined by Kelleher et al. (1995) and later modified by Hewitt and Campbell (2010) as follows: 1-Antarctica (Ant); 2-Arctic (Arc); 3-Mediterranean including the Black and Azov Sea (Med); 4-North West Atlantic (NWA); 5-North East Atlantic (NEA); 6-Baltic (B); 7-Wider Caribbean Sea (WCS); 8-West Africa (WA); 9-South Atlantic (SA); 10-

Central Indian Ocean (CIO); 11-Arabian Seas (AS); 12-East Africa (EA); 13-East Asian Seas (EAS); 14-South Pacific & Hawaii (SP); 15-North East Pacific (NEP); 16-North West Pacific (NWP); 17-South East Pacific (SEP); 18-Australia and New Zealand (Aus). For assessing species' potential native distribution, several research articles and databases were used (Appendix 1).

Temperature data based on the nearest point to each study location was extracted from NOAA OI SST V2 High-Resolution Dataset for 2018–2020 (Reynolds et al., 2007).

2.4. Data analyses

The locations, Azores, Madeira, Canary Islands and Cabo Verde, were analysed separately in terms of assemblage structure (multivariate analysis on species percentage covers) and NIS composition (univariate analyses of NIS frequency (the number of NIS/the number of total species) and NIS percentage cover). The design employed for these analyses included two orthogonal factors: “Assemblages Age” (2 levels: Young and Mature plates; Fixed) and “Time” (5 levels: T1, T2, T3, T4, and T5 random) ($n = 3$ to 5). For multivariate analysis, a 2-way permutational multivariate analysis of variance (PERMANOVA; Anderson, 2005a) was performed to verify differences between the different factors. PERMANOVA was conducted with unrestricted permutations of the raw data. Samples were square-root transformed before calculating the Bray–Curtis similarities matrix. A Principal Coordinate Analysis (PCO) routine was used to generate an ordination in two dimensions, displaying variations in multivariate patterns among assemblages. For univariate analyses, a 2-way PERMANOVA main test and pair-wise tests were conducted with unrestricted permutations of the raw data. Monte Carlo permutation tests (P(MC)) considering the referred factors were also conducted and chosen when the number of permutations was inferior to 100 (Anderson et al., 2008). Univariate tests were done using Euclidean distance as a resemblance measure (Anderson et al., 2008). PERMDISP was used to check the heterogeneity of data dispersions. A more rigorous $P < 0.01$ was used to reject the null hypothesis when homogeneity was not obtained even after data transformation (Underwood, 1997). When significant differences were detected for the analysed factor, a SIMPER (Similarity Percentages) procedure was

conducted to assess which taxa contributed the most to the similarity or dissimilarity within and between the different levels of that factor, respectively (cut-off level of 90 %, only taxa with a percentage contribution of ≥ 2 % were reported; (Clarke, 1993)). Statistical analyses were executed with PRIMER v7 (Clarke and Gorley, 2015) with the PERMANOVA+ add-on (Anderson et al., 2008). Temperature data extraction and plotting were performed using the R software (R Core Team, 2021) and the package “ggplot2” (Wickham, 2016).

3. Results

The analysis of seawater temperature regimes near the sampling locations verified a decrease in latitude, with archipelagos close to the tropics registering a higher temperature (Fig. 3). Cabo Verde had the highest average seawater temperature (23.7 °C), followed by the Canary Islands (20.7 °C), Madeira (20.3 °C), and the Azores (19.4 °C) (Fig. 3). The lowest seawater temperature was observed in the spring of 2018 in the Azores (15.7 °C), while the highest record was detected in the autumn of 2018 in Cabo Verde (27.4 °C) (Fig. 3). Season fluctuations were detected in all studied locations (Fig. 3).

Overall, 115 taxa were documented in all processed samples (Appendix 2 with Taxonomic authorities). Several new records were detected in the present study: in the Azores, two species, the cryptogenic bryozoan *Cryptosula pallasiana* and tunicate *Trididemnum cf. cereum*; in the Canary Islands, the NIS bryozoan *Celleporaria inaudita*, the cryptogenic bryozoans *Savignyella lafontii* and *Hemicyclopora cf. multispinata*; in Cabo Verde, two NIS bryozoans: *B. neritina* and *C. inaudita*, the invasive sabellid polychaete *Branchiomma bairdi* (Appendix 2), and three species categorised as cryptogenic, the foraminifer *Miniacina miniacina*, the tunicate *Symplegma cf. rubra*, and the bryozoan *Cryptosula pallasiana*. Certain species here categorised as cryptogenic will probably be NIS in future surveys once their identification is fully accomplished (e.g. *Symplegma cf. rubra*, *Celleporaria cf. inaudita*, *Distaplia cf. magnilarva*).

Overall, 25 NIS were detected in Macaronesia, representing 23.1 % of the total documented taxa in the present paper. Four NIS were common to all the studied archipelagos: the tunicate, *Distaplia corolla*; the bryozoans, *Bugula neritina*, *Schizoporella errata*, and *Watersipora subtorquata*. The most frequent taxonomic groups among NIS were

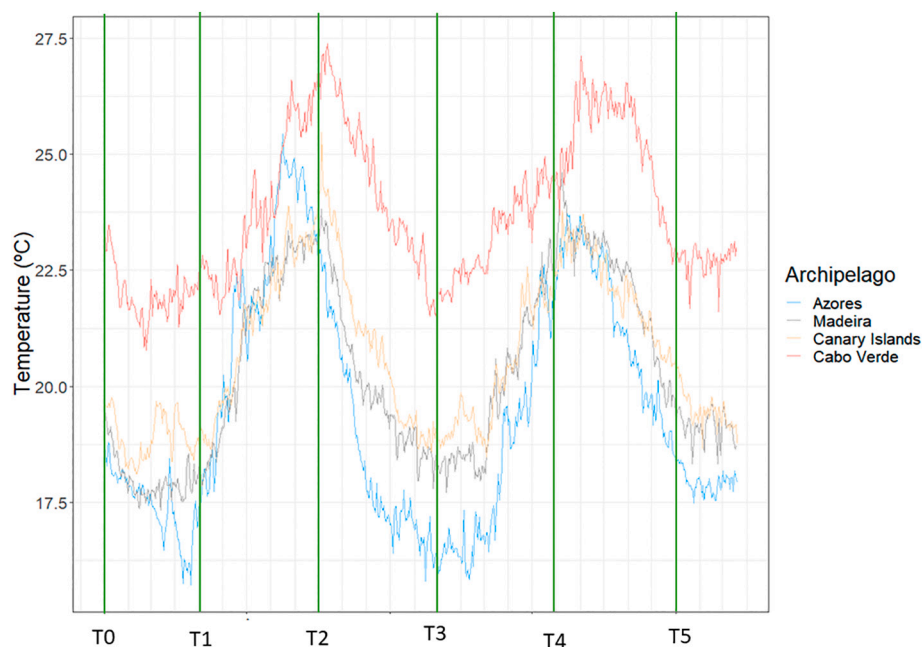


Fig. 3. Temperature ranges in the study locations (Azores, Madeira, Canary Islands, and Cabo Verde), with the indication of the sampling periods (T0 to T5; green vertical line). Temperature analysis was based on daily satellite measurements between 2018 and 2020. Data source: NOAA OI SST V2 High-Resolution Dataset (Reynolds et al., 2007). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

bryozoans (40 %), tunicates (28 %), and arthropods, polychaetes and sea sponges (8 % each). In contrast, other taxonomic groups contributed with a smaller number of NIS, such as cnidarians and algae (both with 4 %) (Appendix 2).

The highest NIS richness was registered in Cabo Verde (16 NIS), followed by the Canary Islands (14 NIS), Madeira (13 NIS) and, finally, the Azores (12 NIS). Bryozoans *S. errata* and *W. subtorquata*, the ascidian *D. corolla*, and the “spaghetti bryozoan” *Amathia verticillata* were the Azores’ most abundant NIS (Appendix 2). Madeira was dominated by the NIS bryozoan *Parasmittina alba*, 2011, the tunicates *D. corolla* and *B. niger*, and the bryozoan *W. subtorquata* (Appendix 2). The most abundant NIS detected in the Canary Islands were the bryozoans, *S. errata* and *C. inaudita*, the tunicate *B. niger*, and the barnacle *Balanus trigonus* (Appendix 2). In Cabo Verde, the bryozoans *S. errata* and *A. verticillata*, and the tunicates *Microcosmus squamiger* and *D. corolla* were the most abundant NIS (Appendix 2).

In general, NIS present in Macaronesia were mainly native to the Mediterranean (18.6 %), the Wider Caribbean Sea and South Atlantic (11.6 % each), North West and North West Atlantic, Arabian Seas, Australia and New Zealand (7.0 % each), among others (Fig. 4). Most NIS detected in the Azores have a native distribution in the Mediterranean (27.8 %), North East Atlantic and Wider Caribbean Sea (11.1 %),

with other bioregions of lesser importance (Fig. 4). Similarly, the origins of NIS detected in Madeira were mostly from the South Atlantic (9.3 %), the Wider Caribbean Sea region and the Mediterranean (7.0 % each) (Appendix 1). The Canary Islands had a higher NIS signature from the Mediterranean (17.4 %), the Wider Caribbean Sea, Australia and New Zealand (13.0 % each), the Arabian Seas, South Atlantic, and North East Atlantic (9.0 % each). Finally, NIS detected in Cabo Verde have their native region in the Wider Caribbean Sea (16.7 %), Australia and New Zealand (12.5 %), and with the same percentage (8.3 %) North West Atlantic, and the Arabian Seas, along with other less essential locations (Appendix 3 - Fig. 1).

The Azores and Madeira PCO analysis revealed groupings for the Assemblage Age factor, with no clear segregation for Time (Fig. 4a and b). In addition, PERMANOVA analysis confirmed, to some extent, the trends visualised, revealing significant effects for all considered factors (Assemblage Age and Time) in the sessile biofouling assemblages colonising the PVC plates, including interaction in the Madeira archipelago (Table 1). For the Canary Islands and Cabo Verde, the PCO diagram was more evident for factor Time (Fig. 4c and d). PERMANOVA revealed that Time was significant in both archipelagos (Table 1).

Pair-wise analysis for Time in the Azores revealed differences between T1 and T4 (P = 0.01) and T3 and T4 (P < 0.05). SIMPER analysis

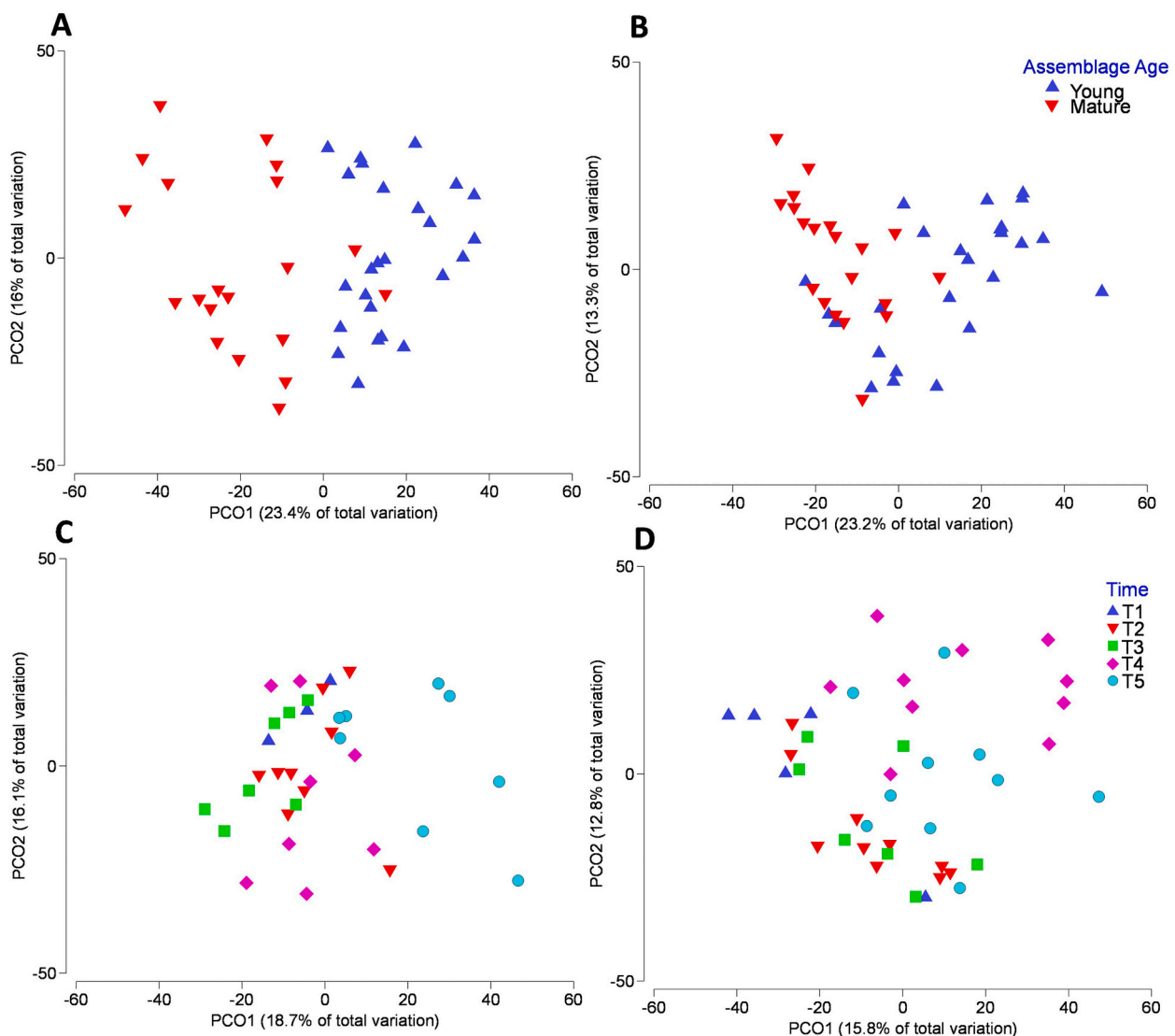


Fig. 4. Principal Coordinate Analysis (PCO) (square root taxon transformation under with Bray–Curtis similarities matrix) processed for the archipelagos Azores (A), Madeira (B), Canary Islands (C), and Cabo Verde (D), with the factors Assemblage Age (Young and Mature plates) and Time (1 to 5).

Table 1

PERMANOVA results of the different archipelagos (Azores, Madeira, Canary Islands and Cabo Verde) on the effects of the different factors in the experimental PVC plates assemblages (% cover), including the PERMDISP results. The studied factors were Assemblage Age (Young and Mature plates) and Time (T1 to T5). Significant differences are indicated in bold ($P < 0.05$).

Source	Df	MS	Pseudo-F	P(perm)	PERMDISP
Azores					
Time	4	2860.8	1.6465	0.012	0.387
Assemblage Age	1	12.878	7.4117	0.001*	0.006
Time × Assemblage Age	3	2537.6	1.4605	0.053	
Res	36	1737.5			
Total	44				
Canary Islands					
Time	4	3163.3	2.3423	0.001*	0.032
Assemblage Age	1	1787.3	1.3234	1.86	
Time × Assemblage Age	3	1635.8	1.2113	0.19	
Res	26	1350.5			
Total	34				
Madeira					
Time	4	4633.8	3.9742	0.001*	0.001
Assemblage Age	1	6650	5.7035	0.001	0.595
Time × Assemblage Age	3	2384	2.0447	0.002	
Res	36	1166			
Total	44				
Cabo Verde					
Time	4	6258.1	2.6224	0.001	0.257
Assemblage Age	1	1512.5	0.63381	0.861	
Time × Assemblage Age	3	3178.7	1.332	0.053	
Res	33	2386.4			
Total	41				

* A more rigorous $P < 0.01$ was used to reject the null hypothesis when homogeneity was not obtained.

revealed that dissimilarities between T1 and T4 (average dissimilarity 70.90 %) were related to a higher abundance and diversity of NIS in T4 (Table 1 in Appendix 3). Between T3 and T4 (average dissimilarity 65.19 %), the differences were related to variability in species abundance rather than NIS presence or dominance (Table 2 in Appendix 3). In terms of assemblage age, SIMPER analysis revealed that dissimilarities between mature and young assemblages in the Azores were due to a higher abundance of, mostly, NIS (in mature assemblages), particularly the bryozoans *S. errata*, *W. subtorquata* and *A. verticillata*, the tunicate *D. corolla*, and variations in abundance of natives and cryptogenic species, like the tunicate *Diplosoma listerianum*, the bristle worms *Spirobranchus triqueter* and *Salmacina dysteri*, and bare space (Table 3 in Appendix 3).

In Madeira, the pair-wise PERMANOVA for the interaction Time vs Assemblage Age (pairs of level Time), showed differences between all sampling periods ($P < 0.05$) in young assemblages. SIMPER analysis demonstrated high variability in species presence and abundance (Average dissimilarities between 43.5 % and 64.3 %). The tunicate *D. listerianum*, the seaworms *S. triqueter* and *Spirorbis* sp., and the NIS bryozoan *P. alba* were the most common in young plates across the sampling periods (Table 4 in Appendix 3). In mature assemblages, differences were only observed between T3 and T4 and T3 and T5 ($P <$

Table 2

Pair-wise test PERMANOVA for Time in the Canary Islands and Cabo Verde archipelagos. The time corresponds to the sampling occasions (T1 to T4). Significant differences in bold ($P < 0.05$).

	Canary Islands				Cabo Verde			
	Time 1	Time 2	Time 3	Time 4	Time 1	Time 2	Time 3	Time 4
Time 2	0.223				0.008			
Time 3	0.109	0.037			0.009	0.954		
Time 4	0.098	0.009	0.413		0.02	0.001	0.002	
Time 5	0.019	0.004	0.001	0.002	0.002	0.001	0.008	0.017

0.05). These differences were related to a higher abundance of the NIS tunicate *D. corolla* in T4 and T5 and a decrease in several other taxa of different biogeographic statuses (Table 5 in Appendix 3).

Regarding the pairs of levels of factor “Assemblage age” differences were detected between new and mature assemblages in T3, T4, and T5 ($P < 0.05$). With SIMPER, it was possible to verify a higher abundance of NIS in mature assemblages, with the presence of the tunicates *D. corolla* and *B. niger*, the bryozoans *P. alba* and *S. errata* (Table 6 in Appendix 3).

In the Canary Islands, pair-wise PERMANOVA revealed differences between sampling periods (Table 2). As for Cabo Verde, those differences were more evident, with most of the sampling periods being different, except for T2 with T3 (Table 2). SIMPER verified that the differences between sampling periods in the Canary Islands (Average dissimilarities between 53.2 % and 62.8 %) and Cabo Verde (Average dissimilarities between 70.3 % and 78.2 %) were related to changes in abundance in several taxa (Tables 7 and 8 in Appendix 3).

Furthermore, the NIS richness PERMANOVA analysis showed significant differences for “Assemblage age” only for the Azores, where NIS numbers were higher in mature assemblages (Table 3 and Fig. 5).

Univariate PERMANOVA (NIS cover) further detected significant differences in Assemblage Age for the Azores and Madeira and for Time

Table 3

Univariate PERMANOVA results on the effects of the different factors on the number of Non-Indigenous Species (NIS), in the different archipelagos (Azores, Madeira, Canary Islands, and Cabo Verde) in the experimental PVC plates, including the PERMDISP results. The studied factors were Assemblage Age (Young and Mature), and Time (T1 to T5). Significant differences are indicated in bold ($P < 0.05$).

Source	Df	MS	Pseudo-F	P(perm)	PERMDISP
Azores					
Time	4	3.515	1.1462	0.37	
Assemblage Age	1	52.9	17.25	0.001	0.845
Time × Assemblage Age	3	1.1667	0.38043	0.751	
Res	36	3.0667			
Total	44				
Canary Islands					
Time	4	3.6383	2.4613	0.079	
Assemblage Age	1	0.5505	0.37244	0.564	
Time × Assemblage Age	3	1.9085	1.2911	0.285	
Res	26	1.2911			
Total	34				
Madeira					
Time	4	1.835	1.1967	0.332	
Assemblage Age	1	0.1	0.065217	0.816	
Time × Assemblage Age	3	0.16667	0.1087	0.955	
Res	36	1.5333			
Total	44				
Cabo Verde					
Time	4	1.4595	0.93886	0.423	
Assemblage Age	1	0.63684	0.40966	0.529	
Time × Assemblage Age	3	1.7507	1.1262	0.35	
Res	33	1.5545			
Total	41				

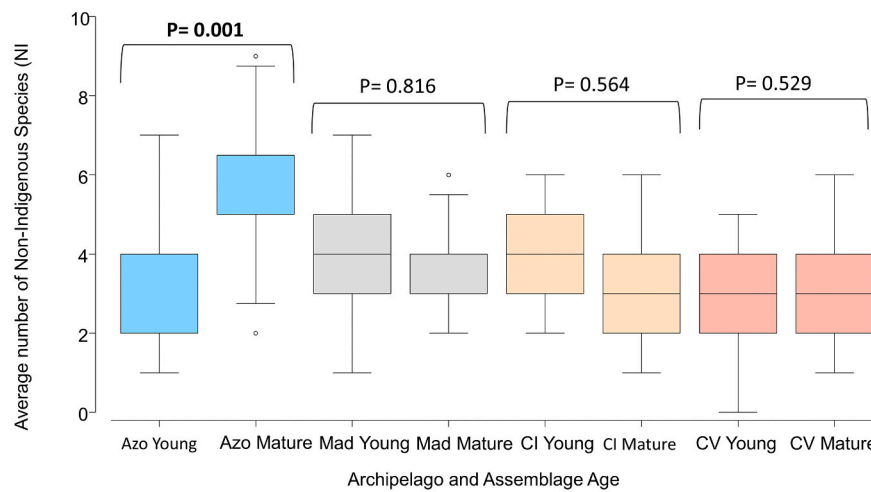


Fig. 5. Average number of Non-Indigenous Species (NIS) detected in the PVC plate of the different archipelagos (Azores (Azo), Madeira (Mad), Canary Islands (CI), and Cabo Verde (CV)) with the factor Assemblage Age (Young and Mature plates). PERMANOVA results showed significant differences between Young and Mature assemblages only for the Azores ($P < 0.05$).

in Cabo Verde (Table 4). In the Azores and Madeira, mature assemblages had more NIS cover. Such differences were not detected in the Canary Islands and Cabo Verde (Table 4 and Fig. 6). Pair-wise PERMANOVA for Time in Cabo Verde detected differences between T2 and T4, T3 and T4, and T4 and T5 (Fig. 7). Time 4 was the sampling period in Cabo Verde with more NIS cover (Fig. 7).

Table 4

Univariate PERMANOVA results on the effects of the different factors on the total Non-Indigenous Species (NIS) cover (%), in the different archipelagos (Azores, Madeira, Canary Islands, and Cabo Verde) in the experimental PVC plates, including the PERMDISP results. The studied factors were Assemblage Age (Young and Mature), and Time (T1, T2, T3, T4 and T5). Significant differences are indicated in bold ($P < 0.05$).

Source	Df	MS	Pseudo-F	P (perm)	PERMDISP
Azores					
Time	4	288.53	0.70285	0.586	
Assemblage Age	1	18,684	45.513	0.001*	0.01
Time × Assemblage Age	3	400.9	0.97658	0.427	
Res	36		410.51		
Total	44				
Canary Islands					
Time	4	439.79	1.2381	0.32	
Assemblage Age	1	80.047	0.22535	0.661	
Time × Assemblage Age	3	48.703	0.13711	0.931	
Res	26	355.22			
Total	34				
Madeira					
Time	4	472.84	1.0989	0.396	
Assemblage Age	1	6874.8	15.977	0.002	0.854
Time × Assemblage Age	3	203.75	0.47352	0.679	
Res	36	430.29			
Total	44				
Cabo Verde					
Time	4	2373.7	3.7812	0.019	0.433
Assemblage Age	1	1607.1	2.5599	0.114	
Time × Assemblage Age	3	308.51	0.49142	0.664	
Res	33	627.78			
Total	41				

4. Discussion

The present study represents a pioneering effort to better understand marine biological invasions in Macaronesia by employing a standardised monitoring approach in the four archipelagos. This method consists of PVC settling plates and is a common approach for non-indigenous management (Marraffini et al., 2017; Muñoz and Bridgwood, 2012; Ramalhosa et al., 2021; Tamburini et al., 2021). As a result, several new NIS were detected in the different archipelagos. In addition, this study further complements recent comprehensive literature research in the region (Castro et al., 2022a). Differences in the sessile macrobenthic assemblages were detected regarding NIS composition, recruitment, and structure. Our study hypothesis was partially verified, where lower latitudes had less NIS recruitment and percentage cover, evidencing a latitudinal propensity. As for NIS richness, no tendency was revealed.

This study unveiled 25 NIS, whereas a recent meta-analysis (Castro et al., 2022a) reported 144 NIS species for the whole Macaronesia region, although in a much longer timeframe (1880 to 2020) and considering all 27 islands that form the region. The overall NIS number reported by Castro et al. (2022a) is not temporally and spatially comparable to the present investigation, where a single location in each archipelago was studied for two years. However, the current experimental approach was designed to avoid bias. For example, Cabo Verde has been subjected to a low sampling effort concerning NIS, and a low number of NIS were detected in the past (Castro et al., 2022a). In the present study, Cabo Verde presented similar NIS richness to the other archipelagos.

The more abundant NIS were the bryozoans, *S. errata*, *W. subtorquata*, *A. verticillata*, *P. alba*, and *C. inaudita*, the tunicates *D. corolla*, *B. niger*, *M. squamiger*, and the triangular barnacle *B. trigonus*. All these species, except for the bryozoans *P. alba* and *C. inaudita*, and the tunicate *D. corolla* have, nowadays, a cosmopolitan distribution (Fofonoff et al., 2018).

According to Souto et al. (2018), *P. alba* was possibly introduced by recreation vessels in Madeira from the Brazilian coast. *Celleporaria inaudita*, initially described as a Pacific Ocean species, was formerly identified in the Red Sea and perhaps introduced in Madeira by marine traffic (Souto et al., 2018). Its new presence in the Canary Islands is no surprise since the archipelagos share closer proximity and a common history of connectivity due to marine traffic (Castro et al., 2022a, 2020). As for *D. corolla*, of Caribbean origin (Canning-Clode et al., 2013), its presence is noted in all the archipelagos of Macaronesia. This tunicate was observed in the Azores during the '70s, probably introduced by

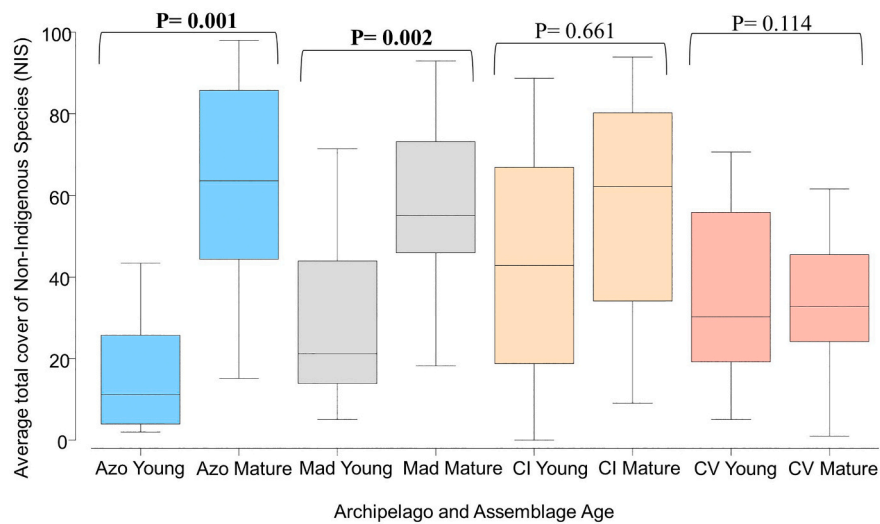


Fig. 6. Average total cover of Non-Indigenous Species (NIS) detected in the PVC plate of the different archipelagos Azores (Azo), Madeira (Mad), Canary Islands (CI), and Cabo Verde (CV) with the factor Assemblage Age (Young and Mature). PERMANOVA results showed significant differences between young and mature assemblages for the Azores and Madeira ($P < 0.05$).

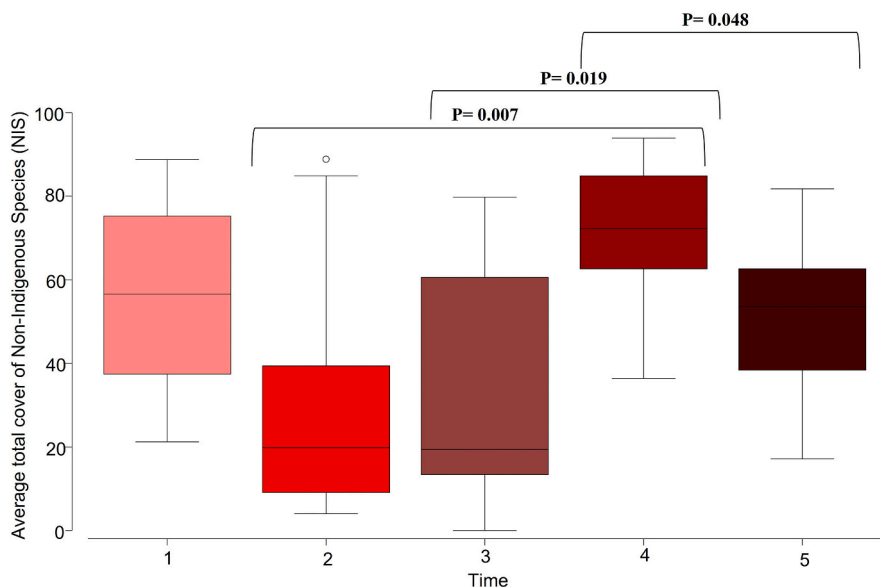


Fig. 7. Average total cover of Non-Indigenous Species (NIS) detected in Cabo Verde PVC plates with factor Time (1, 2, 3, 4, and 5). Pair-Wise PERMANOVA results showed significant differences for Time 2 and 4, Time 3 and 4, and Time 4 and 5 ($P < 0.05$).

sailing yachts from the Caribbean (Monniot and Monniot, 1983). Today the species is recorded in all the Azores islands (Cardigos et al., 2006) and Madeira (Castro et al., 2022a). *Distaplia corolla* was only observed in the Canary Islands in El Hierro (Moro et al., 2018) and now in Tenerife (Present study). In Cabo Verde, it was previously reported in Sal (Monniot and Monniot, 1994; Morri et al., 2000) and now in São Vicente (Present study). All these shreds of evidence imply that most recent introductions in Macaronesia are related to secondary transfers (Castro et al., 2022b; Chainho et al., 2015; Martínez-Laiz et al., 2020). The analysis of the probable native distribution range for the NIS present in each location and Macaronesia supports this argument (Appendix 3 - Fig. 1).

Castro et al. (2022a) verified five shared NIS for all the Macaronesia, the macroalgae *Asparagopsis taxiformis* (Delile) Trevisan, the bryozoans *A. verticillata* and *S. errata*, the barnacle *B. trigonus*, and the tunicate *D. corolla*. In the present study, four common NIS were detected, the tunicate *D. corolla* and the bryozoan *S. errata* observed in both studies.

The list of previously shared species was expanded by finding two common bryozoan species, *B. neritina* and *W. subtorquata*. Linnaeus described *B. neritina*, in 1758, from the Mediterranean Sea. The species is widespread and grows on several substrates, including rocks, seaweed, oysters, ship hulls, maritime structures, power plant intake pipes, and aquaculture equipment (Fofonoff et al., 2018). In the Macaronesia region, *B. neritina* was first detected by Norman (1909) on Madeira Island, near Madeira’s central coaling station. In the 18th and 19th centuries, coaling stations were essential on long-distance voyages and crucial for commercial routes (Crosby, 2004). Almost a century later (2012), *B. neritina* was observed again colonising artificial plates in Madeira and the year after in the Marina of Porto Santo Island (Ramalhosa et al., 2017). In the Azores, there is evidence of *B. neritina*, being introduced in several islands (Micael et al., 2019; Ryland et al., 2011; Tempera et al., 2001). In the present study, *B. neritina* was reported for the first time in Cabo Verde in Mindelo Marina (São Vicente Island), within the largest port of the archipelago (Castro et al., 2022a). The encrusting bryozoan

W. subtorquata is distributed worldwide (Fofonoff et al., 2018). Its presence in the Macaronesia was probably previously detected, with some confusing identifications in the late 19th century in the Azores and Cabo Verde (Jullien and Calvet, 1903; Micael et al., 2019; Viera et al., 2014). This species was observed years later in the Azores on several islands (Micael et al., 2019; Vaz-Pinto et al., 2014). In Cabo Verde, the analysis of voucher specimens collected by Jullien and Calvet (1903) of *W. subtorquata* (and its synonyms) in the late 19th century resulted in being a new species for science, *Watersipora souleorum* Vieira, Spencer Jones & Taylor, 2014 (Viera et al., 2014). The present paper reports *W. subtorquata* in Cabo Verde for the first time detected in Mindelo Marina. As for Madeira and the Canary Islands, the species was first seen in 2006 and 2018, respectively, both records inside recreational marinas (Canning-Clode et al., 2013; Moro et al., 2018). Identification errors with species of the genus *Watersipora* have produced widespread confusion (Reverter-Gil and Souto, 2019). To avoid such bias, we based our identifications on a detailed clarification of the morphological characters to elucidate their taxonomy (e.g. Reverter-Gil and Souto, 2019; Viera et al., 2014).

The overall NIS taxonomic groups detected in the present study are typically found with this methodology. The dominance is among sessile organisms like bryozoans and tunicates (e.g. Canning-Clode et al., 2011; Marraffini et al., 2017; Wahl et al., 2011). Fishes and macroalgae are Macaronesia's most relevant NIS taxa (Castro et al., 2022a). However, this methodology was designed to focus on the underside of the PVC plate only, without direct sunlight exposure, favouring the colonisation of invertebrates. It promotes the growth of typical biofouling assemblages ideal for several types of marine ecology research. For example, sampling early colonisation stages of sessile marine organisms (e.g. Castro et al., 2021; Glasby and Connell, 2001), assess the NIS population dynamics (Canning-Clode et al., 2013; Martin et al., 2011; Sephton et al., 2011), biosecurity programmes and NIS monitoring surveillance (Muñoz and Bridgwood, 2012; Ramalhosa et al., 2021), and manipulative experiments (Castro et al., 2021; Chebaane et al., 2022; Ferrario et al., 2020; Gestoso et al., 2018). This procedure allows comparisons between locations and independence, assuring that each plate replication does not affect the other observations over the studied period. Another advantage is early species detection (e.g. McCann et al., 2019; Ramalhosa et al., 2014) which can be vital in tackling invasive NIS (Amat et al., 2008; Anderson, 2005a). Several new records were detected in the present study, including two cryptogenic species in the Azores, *C. pallasiana* and *T. cf. cereum*. In the Canary Islands, the NIS *C. inaudita*, the cryptogenic bryozoans *S. lafontii*, and *H. cf. multispinata*. In Cabo Verde, six species, two NIS bryozoans: *B. neritina*, *C. inaudita* and the invasive sabellid *B. bairdi*, and three cryptogenic species *M. miniacea*, *S. cf. rubra*, and *C. pallasiana*. These species were previously signalled in the Macaronesia region (Castro et al., 2022a), indicating probably secondary dispersions within the area.

The assemblage structure showed significant variations in all the archipelagos. Assemblage Age (mature vs young) was significant in the Azores and Madeira. Azores and Madeira NIS species were more abundant in mature assemblages leading to a reduction in native and cryptogenic species. Dafforn et al. (2009), also conducting experiments with settlement plates, verified that NIS tend to dominate the substrate over native species. Moreover, some authors demonstrated that with a more extended submersion period, there is a tendency for NIS homogeneity (Tamburini et al., 2021). In the Canary Islands and Cabo Verde, these effects were not observed.

In Madeira, the Canary Islands and Cabo Verde, NIS richness was similar across assemblage ages without significant differences. In a recent paper, Tamburini et al. (2021), monitoring close port facilities within the Gulf of La Spezia (Italy), verified the same NIS richness over time. Only in the Azores, a higher number of NIS was recorded in mature plates. The biotic interaction hypothesis indicates that biotic exchanges are more important in the tropics (Schemske et al., 2009). Lies here a fundamental ecological hypothesis that stronger interactions at lower

latitudes could outline global patterns of community assembly, structure, and ecosystem functioning, translating latitudinal variation in species interactions into a principal theory of contemporary community ecology (Freestone et al., 2021). Ashton et al. (2022), using the same methodology as the present study on a broad spatial scale covering both coasts of the American continent, verified that the predation and impacts on benthic communities were influenced by seawater temperature and latitude, which reached a peak near the equator. Freestone et al. (2021) found an equivalent pattern, adding that predator diversity, size and intensity were higher near the tropics. Such predation also reduced prey biomass and altered prey composition at low latitudes, with no effects at high latitudes. The present results appear to follow a latitudinal and temperature tendency from the Azores up to Cabo Verde, where NIS numbers and cover from the Azores increased with time in mature plates where the biological filters would be weaker (e.g. less predation and less competition). In contrast, decreasing in latitude to Madeira, there was not an increase in new NIS arrivals, but those already established were still able to dominate, as was reflected in the rise of NIS cover on mature plates. With stronger biotic resistance, the Canary Islands and Cabo Verde could explain the maintenance of the same NIS richness and abundance. Cabo Verde is the archipelago with more endemic species of the four (Freitas et al., 2019) and with higher seawater temperatures. Predation was verified in situ in Cabo Verde (Nuno Castro's personal observation), on some occasions, with some fish foraging the experimental units. In this context, a recent predation study conducted in Madeira to detect feeding choices and their impacts on fouling assemblage composition revealed that only one fish species grazed on the floating plates (Chebaane et al., 2022). A latitudinal pattern in the number of coastal fish species can also be detected and used as a proxy for predation from the Azores (165) toward Madeira (208), the Canary Islands (299), and Cabo Verde (303) (Freitas et al., 2019). This pattern was also detected in the PVC plates regarding the number of taxa identified (Fig. 1).

Abiotic features such as temperature can explain the differences found in NIS recruitment and percentage cover decreased following a partial latitude gradient from the Azores to Cabo Verde. The Azores registered the lowest sea water temperature in all the studied locations, with higher seasonal fluctuations. Temperature tolerance significantly influences species survival and establishment (Bereza and Shenkar, 2022; Lord et al., 2015). Moreover, the larvae of a particular species could have a different temperature tolerance than adults (Hewitt et al., 2009), which may restrict some species' survival, for example, in the Azores and Madeira. The Canary Islands and Cabo Verde are examples where continuous reproduction provides less space for recruits. In temperate areas, seasonal growth is more evident due to fluctuations in seawater temperatures (Helio and Yebra, 2009; Lehaitre et al., 2008), reflecting the results obtained in the Azores and Madeira.

Another trait that enhances invasion success is propagule pressure (Duggan et al., 2006; Johnston et al., 2009; Simberloff, 2009), typically defined as the number of arrival events (e.g. increased frequency of ship arrival) or increased intensity of exposure during any given event (Johnston et al., 2009). Propagule sizes, numbers, and temporal and spatial patterns of propagule arrival are essential facets of the invasion process (Simberloff, 2009). For example, Ponta Delgada Marina has a higher propagule pressure (640 berths), which could influence the results like other related characteristics (e.g. marine traffic intensity, soak time, vessel size) (Castro et al., 2020). However, it seems unlikely since Madeira had fewer berths (200) and similar results to the Azores. On the contrary, the Canary Islands and Cabo Verde add very different results with equal berths to Madeira (220 and 140, respectively). Another aspect that could accommodate the present findings is the biogeography and competitive superiority of the arriving propagule, which may reduce the demographic and environmental stochasticity, enhancing the invasion's success (Simberloff, 2009). The species *P. alba* and, notably, *D. corolla* are such examples. In a recent study, Ramalhosa et al. (2021) verified that the Caribbean tunicate *D. corolla* introduced in Porto Santo

in 2004 was present in all the recreational marinas in the Madeira archipelago and also in some adjacent areas (Castro et al., 2021), evidencing such competitive features. Such a latitudinal trend could be promoted by positive interactions between established NIS and new incomers (i.e. The Invasional meltdown hypothesis, Simberloff and Von Holle, 1999), boosting the establishment success of the newcomer NIS (Gestoso et al., 2018; Marraffini and Geller, 2015).

Other significant factors related to the diversity and patterns of marine NIS, especially in oceanic islands (i.e. distance to the mainland, the total number of ports and marinas and area (Castro et al., 2022a)), were not herein considered. Consequently, the present results should be interpreted with caution.

Finally, using a standard and straightforward method of settling plates, the current study further complements the recent findings of Castro et al. (2022a) in a comprehensive analysis. Sessile fouling assemblages of the Macaronesia archipelagos differed in NIS composition, recruitment, and structure. The NIS diversity patterns revealed in the current paper are likely sensitive to further biotic (e.g. predation and competition for space) and abiotic variables (e.g. temperature), which deserve full attention in future research.

CRediT authorship contribution statement

Nuno Castro: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. **Ignacio Gestoso:** Conceptualization, Methodology, Formal analysis, Investigation, Writing – review & editing, Visualization, Supervision, Funding acquisition. **Patrício Ramalhosa:** Investigation, Writing – review & editing. **Evandro Lopes:** Formal analysis, Investigation, Writing – review & editing. **Corrine Almeida:** Investigation, Writing – review & editing. **Ana Costa:** Investigation, Writing – review & editing. **Manuela Parente:** Investigation, Writing – review & editing. **Eva Cacabelos:** Formal analysis, Investigation, Writing – review & editing. **Rogelio Herrera:** Writing – review & editing, Funding acquisition. **José L. Costa:** Writing – review & editing, Supervision. **João Canning-Clode:** Conceptualization, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendices. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marpolbul.2023.115021>.

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