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RESEARCH ARTICLE

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# Diversity and patterns of marine non-native species in the archipelagos of Macaronesia

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## Abstract

**Aims:** The present study is the first attempt to grasp the scale and richness of marine biological invasions in Macaronesia. We pioneered a comprehensive non-native species (NNS), inventory in the region to determine their diversity patterns and native distribution origins. NNS were defined here as the result of both introductions and range expansions. We also used statistical modelling to examine relationships among NNS richness, anthropogenic activities, demographic and geographical variables across Macaronesia.

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**Location:** Macaronesia.

**Methods:** A comprehensive literature search was conducted for marine NNS records in Macaronesia, registering the first record's location and year from 1884 to 2020. We used univariate and multivariate analyses to evaluate differences and similarities in community composition. By applying a Generalized Linear Model (GLM), we tested hypotheses regarding NNS richness as a function of anthropogenic activities, demographic and geographical variables.

**Results:** A total of 144 marine non-native species (NNS) were recorded for the whole of Macaronesia. The highest NNS richness was registered in the Canary Islands (76 NNS), followed by the Azores (66 NNS), Madeira (59 NNS) and finally Cabo Verde (18 NNS). Some differences amongst archipelagos were observed, such as the high number of non-native macroalgae in the Azores, fishes in the Canary Islands and tunicates in Cabo Verde. Overall, macroalgae, tunicates and bryozoans were the predominant taxonomic groups in the Macaronesian archipelagos. Madeira and Canary Islands were the archipelagos with more similarity in marine NNS, and Cabo Verde the most divergent. Finally, GLM suggested that non-native richness patterns across Macaronesia were dependent on the considered archipelago and strongly affected by (1) minimum distance to the mainland, (2) the total number of ports and marinas and (3) total marinas area ($km^2$).

**Conclusions:** The model results and NNS listing in the present study will likely raise the awareness and response regarding marine NNS in the whole Macaronesia region, serving as a baseline for future research as well as implementing and enforcing regulations related to the introduction of marine NNS in oceanic islands.

**KEYWORDS**
anthropogenic stressors, Azores, Cabo Verde, Canary Islands, Madeira, meta-analysis, modelling, non-indigenous species

## 1 | INTRODUCTION

Anthropogenic pressures cause significant impacts on global biodiversity and ecosystem structure and function (Costello et al., 2010; Mammides, 2020; Thuiller, 2007). Along with habitat degradation, the introduction of non-native species (NNS) is considered one of the greatest environmental and economic threats (Costello et al., 2010; Cuthbert et al., 2021; Diagne et al., 2021). In the last several decades, new estuarine and marine coastal NNS appear to be establishing worldwide at an increasing rate (Tsiamis et al., 2019). For example, NNS numbers increased considerably in European marine waters, reaching up to 824 NNS in 2018, making these waters the highest NNS host worldwide (Katsanevakis et al., 2014; Tsiamis et al., 2019). The vast preponderance of marine NNS established in Europe originates from the Western and Central Indo-Pacific, Temperate Northern Pacific, Tropical Atlantic and Temperate Northwest Atlantic (Tsiamis et al., 2018).

Biological invasions (the arrival, establishment and diffusion of a species) in marine communities occur through two processes, range expansions and introductions. Range expansions consist of dispersal by natural mechanisms into a region where the species did not formerly exist. Introductions consist of transportation by human activity (often across natural barriers) into a region where the species did not exist in historical time (although, in rare instances, the species may have existed in the region in geological time) (Carlton, 1987). Thus, the result of both range expansions and introductions is the arrival and potential establishment of non-native species (Carlton, 1987).

On a global scale, most marine invasions have resulted from the unintentional transfer of large numbers of animal and plant species in ballast water and hull fouling of commercial shipping (Bailey et al., 2020; Chainho et al., 2015; Ruiz et al., 1997). Hull fouling on recreational vessels also accounts for primary and secondary introductions (Ferrario et al., 2017; Marchini et al., 2015; Zabin et al., 2014). In addition, other vectors and pathways have been responsible for NNS introductions, including aquaculture (Grosholz et al., 2015; Toledo-Guedes et al., 2014), live bait trade (Fowler et al., 2015; Sá et al., 2017), aquarium trade (Padilla & Williams, 2004), marine debris/litter (Carlton et al., 2018; Rech et al., 2016; Therriault et al., 2018) and canal excavation (e.g. the Suez Canal and the Panama Canal) (Galil et al., 2018; Ruiz et al., 2006), among others.

In recent decades, there has been an increase in coastal urban development, including the expansion of artificial structures in coastal areas (Elmqvist et al., 2016; Firth et al., 2016). The loss of natural habitats through coastal urbanization affects marine communities' structure and functioning (e.g. Firth et al., 2016; Moschella et al., 2005) and can facilitate the NNS colonization process (Lambert & Lambert, 2003; Tyrrell & Byers, 2007). The late 20th-century proliferation of marinas and ports with numerous artificial structures (e.g. piers, pontoons, seawalls and buoys) further serves as transport hubs or 'stepping stones' for newly established NNS (Bulleri & Chapman, 2010).

Oceanic islands have long served as important models for biogeography, ecology, evolution and conservation biology (Darwin, 1859; Kueffer et al., 2014; MacArthur & Wilson, 1963; Wallace, 1880). Many oceanic islands possess high conservation status due to their endemic species richness (Sax & Gaines, 2008). However, islands have long been used for multiple purposes (i.e. farming, lighthouse stations, prisons, defence emplacements, tourism and more). These activities contribute to the destruction of natural ecosystems and often lead to the introduction of NNS in both terrestrial and aquatic ecosystems (Veitch, 2001). Terrestrial introductions have been well-documented over the last 50 years on many island ecosystems and continue to be the focus of extensive work in invasion biology (e.g. Diamond, 1970; Elton, 1958; Gaston et al., 2008; Lloret et al., 2005; Rojas-Sandoval et al., 2020; Simberloff, 1995; Towns et al., 2012). The study of marine invasions on most of the world's islands only started much later, mainly in the last two decades, in Australia (Hewitt, 2002; Hewitt et al., 2004), New Zealand (reviewed by Inglis et al., 2006), Hawaii (Carlton & Eldredge, 2009, 2015), Guam (Paulay et al., 2002), Palau (Campbell et al., 2016), the Galápagos (Carlton et al., 2019) and in the Macaronesia region, particularly in the Azores and Madeira (Canning-Clode et al., 2013; Cardigos et al., 2006; Chainho et al., 2015; Micael et al., 2014).

Located in the Northeast Atlantic Ocean, the Macaronesia region includes the volcanic archipelagos of the Azores, Madeira, Canary Islands and Cabo Verde. These archipelagos are separated from the nearby mainland and other plausible natural species source regions, such as neighbouring archipelagos or shallow seamounts, by water depths exceeding 1300–1500 m (Freitas et al., 2019). Macaronesia's island systems are interconnected through ocean currents, with surface currents generally moving from the Azores to Madeira and Canary Islands (Morton et al., 1998; Santos et al., 1995). Moreover, Cabo Verde separates two main water masses: the southern boundary of the North Atlantic Subtropical Gyre (NASTG), which is here formed by the North Equatorial Current, and the northern edge of the North Atlantic Tropical Gyre (Pelegrí & Peña-Izquierdo, 2015). In the marine realm, the Azores, Madeira and the Canary Islands are included in the same ecoregion, the Lusitanian province, dominated by rocky reefs. In contrast, Cabo Verde belongs to the West African Transition province (Spalding et al., 2007; Tuya & Haroun, 2009). The latter is under the influence of a more tropical climate, supporting, for example, hermatypic corals. Macaronesia province falls in the West Africa bioregion in IUCN Bioregions (Kelleher et al., 1995).

The Macaronesian Islands all have different degrees of isolation from the nearest continental coast. Such differences have been advocated to explain variations in composition and diversity of marine biota (Hawkins et al., 2000). Previous studies have highlighted a high degree of similarity in the marine flora's composition in each archipelago and the nearest continental (donor) coast. For example, the marine flora of the Azores has elements in common with the North Atlantic, the Western Mediterranean and the coasts of Eastern America (Frud'homme van Reine, 1988), while the Canary Islands shows a greater affinity with the Western Mediterranean and Western Atlantic (van den Hoek, 1987). Recent work proposed newly born biogeographical units excluding the Azores and Cabo Verde from the biogeographical concept of Macaronesia by applying extensive datasets from various marine taxonomic groups (Freitas et al., 2019).

As for marine biological invasions, the Azores was the first Macaronesian archipelago to be the subject of a detailed NNS inventory (Cardigos et al., 2006), followed by Madeira (Canning-Clode et al., 2013), both of which updated in Chainho et al. (2015). For the Canary Islands, a book published in 2003 listed marine species present in the archipelago, with a simple indication of each species indigenous or non-native statuses (Moro et al., 2003). For Cabo Verde, no marine NNS inventory has ever been produced. In recent years, because of ongoing monitoring surveys, several new NNS detections have been documented in the Azores, Madeira, the Canary Islands and a few in Cabo Verde (e.g. Afonso et al., 2013; Canning-Clode et al., 2013; Freitas et al., 2014; Freitas & Wirtz, 2018; García-Jiménez et al., 2008; Micael et al., 2014; Pajuelo et al., 2016; Ramalhosa et al., 2017). However, no previous study has ever attempted to compile the current knowledge on marine NNS in all Macaronesia or relate diversity and distribution of NNS to historical or extent human activities.

In this context, the present study expands the current understanding of marine biological invasions' scale and diversity on insular marine ecosystems, using Macaronesia as a model system. Specifically, we (1) conducted the first comprehensive NNS inventory of Macaronesia; (2) assessed NNS richness patterns across archipelagos and individual islands; (3) identified the possible native distribution of the documented NNS and (4) linked NNS numbers to anthropogenic, demographic and geographical variables.

## 2 | METHODS

### 2.1 | Study region

The Macaronesia region comprises four volcanic archipelagos—the Azores (nine populated islands), Madeira (two populated islands), the Canary Islands (seven populated islands) and Cabo Verde (nine populated islands) (Figure 1). The study region is located in the Atlantic Ocean between 15° and 40°N latitude, with distances from the European or African continents varying from 95 to 1600 km (Aranda et al., 2014). The geological ages of the islands range from

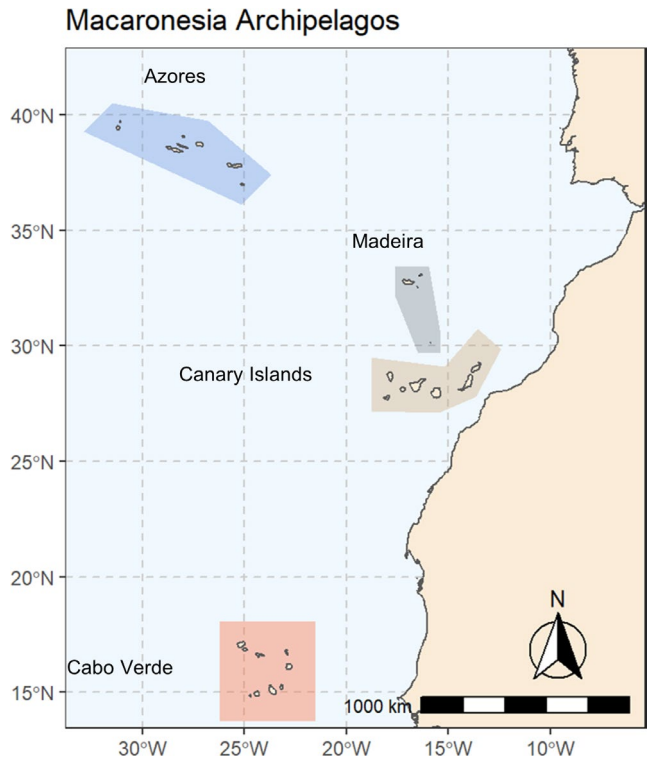


**FIGURE 1** Location of Macaronesia and its archipelagos (Azores, Madeira, Canary Islands and Cabo Verde)

0.18 million years (MY) for Pico (Azores) (Costa et al., 2015) to 27 MY for Selvagem Grande (Madeira) (Aranda et al., 2014). Macaronesia's native flora and fauna reached the islands by long-range dispersal from adjacent continental areas (Whittaker & Fernández-Palacios, 2007) or, in some circumstances, from neighbouring archipelagos/islands (Domingues et al., 2008). Finally, only populated islands in Macaronesia were considered for the present analysis.

## 2.2 | Literature search

In addition to our previous knowledge of published literature, a comprehensive literature search was conducted of scientific papers, books, book chapters, theses and reports. This search included literature published between 1880 and May 2020 in English, Portuguese and Spanish. Web of Science database, Scopus and Google Scholar were examined using the following relevant keywords (and/or): "alien", "invasive", "introduced", "non-indigenous species", "invasion", "non-native", "exotic", "Cabo Verde", "Azores", "Madeira", "Canary Islands" and "Macaronesia". To avoid any bias with medical sciences (i.e. cancer research) due to the use of the terms "invasive" and "invasion", the search was focused on the following research disciplines: ecology, biology, marine biology, fisheries, biodiversity, conservation, environmental sciences, oceanography and zoology. This effort was complemented by local experts, all of which are contributors to the present work. All references were carefully examined for marine NNS records in Macaronesia, and relevant subsequent citations were also analysed. In total, 200 references (Appendix S1) were validated and included in our study. For the present study, marine birds, marine mammals and vascular plants were not included in the search but would bear future work exploration. Finally, brackish and freshwater species were also excluded from the present analysis.

## 2.3 | NNS selection and attributes

For the present work, a species was considered non-native (NNS), and therefore validated (included in the analyses—Appendix S1—"1" included species), when as many as possible of the following criteria were met: (i) reference of its biogeographical status in the literature; (ii) indication that a species found either only or mainly in ports and marinas, as these areas have higher propagule pressure and are considered NNS hotspots (Canning-Clode et al., 2013; Seebens et al., 2013); (iii) expert opinion and/or reference in known marine biological invasions databases (e.g. NEMESIS [Fofonoff et al., 2018], AquaNIS [AquaNIS. Editorial Board, 2015]); (iv) species that underwent tropicalization processes (i.e. shifts in range distribution induced by climate change [Canning-Clode & Carlton, 2017]) and (v) current NNS population status. The use of each criterion is described in Appendix S1—Column 'Criteria' for each species validated.

Relative to criterion (i), we are aware that there is a long history of misconstruing native species as introduced species (i.e. pseudo-indigenous, Carlton, 2009; Carlton & Eldredge, 2009). Thus, we typically relied on the additional evidence outlined above and below for validating NNS. Respectively to criterion (ii), we recognize that native species are also found in port facilities, and intense studies of port systems might reveal native species that are not yet reported elsewhere. However, we use multiple criteria and do not use 'only in ports' as the sole criterion by which to identify a species as NNS. Regarding criterion (v), a species was removed from the analysis when the record in Macaronesia was based on single or few specimens (less than five) collected at one or few locations (less than three). Examples of removed species include the nudibranch *Antiopella cristata* (Delle Chiaje, 1841), the hydroid *Tubularia indivisa* Linnaeus, 1758 and the phoronid *Phoronis hippocrepia* Wright, 1856 (see Appendix S1 for a complete listing). When species with native or non-native status in the literature were doubted (e.g. the bryozoan *Aetea* spp., the tunicate *Botryllus schlosseri* (Pallas, 1766) and the hydroid *Corydendrium parasiticum* (Linnaeus, 1767)) further assessment based on historical, systematic, biogeographic and other criteria were conducted (Chapman & Carlton, 1991, 1994). We followed Carlton (1996) in defining species that were not demonstrably native or non-native as cryptogenic, and therefore those were not included in our analysis.

We are sensitive to the concern that records of apparently new additions to a biota may be previously overlooked species due to a lack of habitat-specific studies (such as in deeper waters) or to the earlier absence of taxonomic specialists. In these cases, we have attempted to rely on evidence of the previous absence of the species in

question as best as possible. Critically, we emphasize that we did not attempt at this time to re-evaluate or to re-categorize many species that are treated as 'native' in the Macaronesia literature that may be non-native or cryptogenic. Many species introduced before modern surveys began and long regarded in the literature as native but now re-interpreted as non-native form a substantial fraction of current inventories of NNS in other archipelagos, such as the Hawaiian Islands (Carlton & Eldredge, 2009, 2015) and the Galapagos Islands (Carlton et al., 2019). Future work in Macaronesia will address such re-evaluations.

The year of the first record for each NNS and cryptogenic species was retrieved from the literature. The species where the first observation date was not mentioned in the bibliography were removed from the analysis but kept in the overall list. When only time ranges were provided (e.g. '1999–2003'), the first year of that time interval was taken as the earliest possible date. Also, species whose records only included reference to the archipelago and not the island (i.e. Azores or Cabo Verde) were excluded from the model but included in the final list. Taxonomic groups were categorized as NNS, and attention has been taken to standardize nomenclature. Taxonomic references were updated according to the Integrated Taxonomic Information System (www.itis.gov), the World Register of Marine Species (Worms Editorial Board, 2020), and in the case of algae, according to AlgaeBase (Guiry & Guiry, 2020).

For each NNS, the likely native distribution range (origin) 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); 14a&b—South Pacific & Hawaii (SP); 15—North East Pacific (NEP); 16—North West Pacific (NWP); 17—Southeast Pacific (SEP); 18—Australia and New Zealand (Aus). For assessing species' potential native distribution, research articles and databases were used (Appendix S2).

## 2.4 | Abiotic data

We characterized islands and archipelagos using categorical variables with 27 and 4 levels respectively (Appendix S4). National official records (www.pordata.pt (Portugal); www.ine.es (Spain); www.ine.cv (Cabo Verde)), provided geographical and demographic variables such as island area ($km^2$), island human population (number of individuals) and human population density (number of individuals/$km^2$). Variables related to marine traffic for each island were used, including the number of ports, number of marinas, the sum of ports and marinas, the number of major marinas (defined as with more than 120 berths), total port area ($km^2$), total port perimeter (km), total marinas area ($km^2$), the sum of berths in all the marinas across islands and the sum of ships departures per month in each island. The number of ports and marinas on each island and the number of departures per month in each port were obtained through MarineTraffic—Global Ship Tracking Intelligence (2021) (www.marinetraffic.com). Areas and perimeters of ports and marinas were determined with Google Earth Pro using the polygon tool. The number of berths was compiled through the official websites of each marina on each island. Distance from several relevant maritime commercial hubs to Macaronesia was also calculated using Google Earth Pro. The most relevant maritime commercial hubs included Lisbon (Portugal), Casablanca (Morocco), Sevilla (Spain), Santos (Brazil), Buenos Aires (Argentina), Bermuda (UK), Saint Martin (French/Dutch), Dakar (Senegal) and Nouadhibou (Mauritania). The selection of these ports was based on expert opinion and official marine traffic records (Port Administration of Madeira—APRAM), Canary Islands (Puertos Canarios) and Cabo Verde (Port Administration of Cabo Verde—ENAPOR). Total mean distance and minimum distance to the mainland were considered as potential proxies for the level of isolation. Finally, a proxy for 'study effort' was used and created based on the number of published papers on invasion ecology per island. For this purpose, our search focused on the main title of the validated references in the present study for similar keywords used in the 'literature search' or related synonyms (Appendix S3).

## 2.5 | Data analysis

Presence/absence NNS matrices were created to quantify biological invasions in the Macaronesia region. A standard exploratory data analysis was conducted, comparing NNS richness and taxonomic group per archipelago. Non-metric multidimensional scaling (MDS) was applied to visualize the similarity between islands, and multivariate analysis of similarity (ANOSIM) was used to test community composition between archipelagos (e.g. Jaspers et al., 2020). The available covariates were used to model the number of NNS per island. Given the nature of the response, the variable is a count (i.e. number of NNS), so we considered a Generalized Linear Model (GLM) (Zuur et al., 2009). We deemed both Poisson and Negative Binomial (NB) responses. After an exploratory examination of the relative merits of both distributions, the NB was chosen. The variance was higher than the mean, and hence not surprisingly, the NB led to far more parsimonious models than the Poisson given Akaike Information Criterion (AIC). We considered a stepwise procedure for model selection based on AIC (e.g. Burnham et al., 2011). Given the small number of observations (i.e. 27 islands), we started from the simplest model and increased its complexity incrementally until adding new covariates no longer increased parsimony. All covariate pairs were checked for correlation, which was generally large across pairs of variables. Hence, we avoided considering highly correlated covariates in the same model, always selecting the one from each pair under consideration to lead to a more parsimonious interpretation. We assessed the fit of the final model used for inference based on visual inspection of residual diagnostic plots. All the analyses were implemented in R (R Core Team, 2019). Multivariate analysis was

implemented via the 'vegan' R package (Oksanen et al., 2012), while the 'mass' package (Ripley et al., 2019) was used for GLM application.

## 3 | RESULTS

In total, 144 NNS were detected and considered for the whole Macaronesia region (Figure 1; Appendix S1). The Canary Islands recorded the highest number (76 NNS), followed by the Azores (66), Madeira (59), and finally Cabo Verde (18), with each archipelago showing a different detection rate, as evidenced in the species accumulation patterns. The earliest NNS species recorded in the Macaronesia region was in the late 1800s (Figure 2). At the beginning of the 20th century, a few records were detected. Still, records soon reached a plateau, only with signs of an increase in the late 1960s and 1970s for all the archipelagos, except for Madeira and Cabo Verde that only increased their NNS numbers during the 1990s.

Our search detected 46 additional species that did not fully meet our criteria and were not included in our analysis (complete detailed list in Appendix S1 including records not considered for analysis purposes (i.e. cryptogenic species and unestablished NNS). In some cases, registered NNS were deemed to be native or cryptogenic in different archipelagos of Macaronesia. In this context, the Canary Islands registered the highest number of cryptogenic species (nine), followed by Cabo Verde (six), Madeira (five) and the Azores, with only one species. Also, Cabo Verde and the Canary Islands were the archipelagos with the highest number of native species, 16 and five respectively. Madeira registered only one native species and none in the Azores (Appendix S1).

Across all four Macaronesia archipelagos, only five shared NNS were detected (Appendix S1): the macroalgae *Asparagopsis taxiformis* (Delile) Trevisan, the bryozoans *Amathia verticillata* (delle Chiaje, 1822) and *Schizoporella errata* (Waters, 1878), the barnacle *Balanus trigonus*, Darwin, 1854 and the tunicate *Distaplia corolla* Monniot F., 1974. The archipelagos with the most shared NNS were Madeira and the Canary Islands (30), followed by the Azores and the Canary Islands (27), and the Azores and Madeira (22). Cabo Verde shared 10 NNS with Madeira, nine with the Canary Islands, and six with the Azores (Appendix S1). Unique NNS, that is, recorded in only one Macaronesian archipelago, was highest in the Canary Islands (20 NNS), followed by the Azores (19 NNS), Madeira (12 NNS) and Cabo Verde (four NNS) (Appendix S1).

For the whole Macaronesia system, macroalgae were the most represented non-native taxonomic group (31), followed by tunicates (28), fishes (Vertebrates) (26) and bryozoans (14) (Figure 3). In contrast, Ctenophora was the least reported taxonomic group with only one NNS record. The Azores had a similar trend to the overall Macaronesia pattern, with macroalgae (22), tunicates (11), bryozoans and arthropods (nine each) as the most observed taxonomic groups. Fishes were the exception of the overall Macaronesia pattern, with only one species registered in the Azores. The Madeira archipelago had a higher number of tunicates (13), followed by bryozoans (12), fishes (nine) and macroalgae (eight) (Figure 3). For the Canary Islands, macroalgae and fishes were the most significant taxonomic groups with 20 and 18 NNS, followed by cnidarians (10) and tunicates (eight). Finally, the latter group was the most important taxa in Cabo Verde (11), followed by bryozoans (two), and macroalgae, fishes, sponges, cnidarians and arthropods with one NNS each (Figure 3).

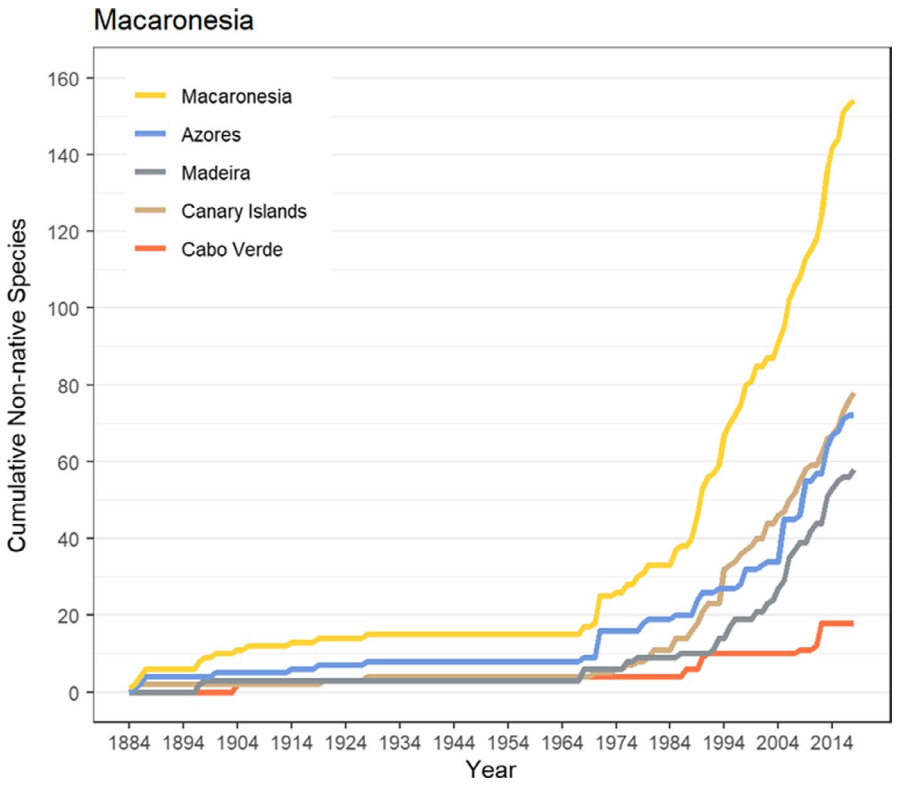


FIGURE 2 The cumulative number of non-native species (NNS) detected in all the archipelagos of Macaronesia (Azores, Madeira, Canary Islands and Cabo Verde) from 1884 to 2020

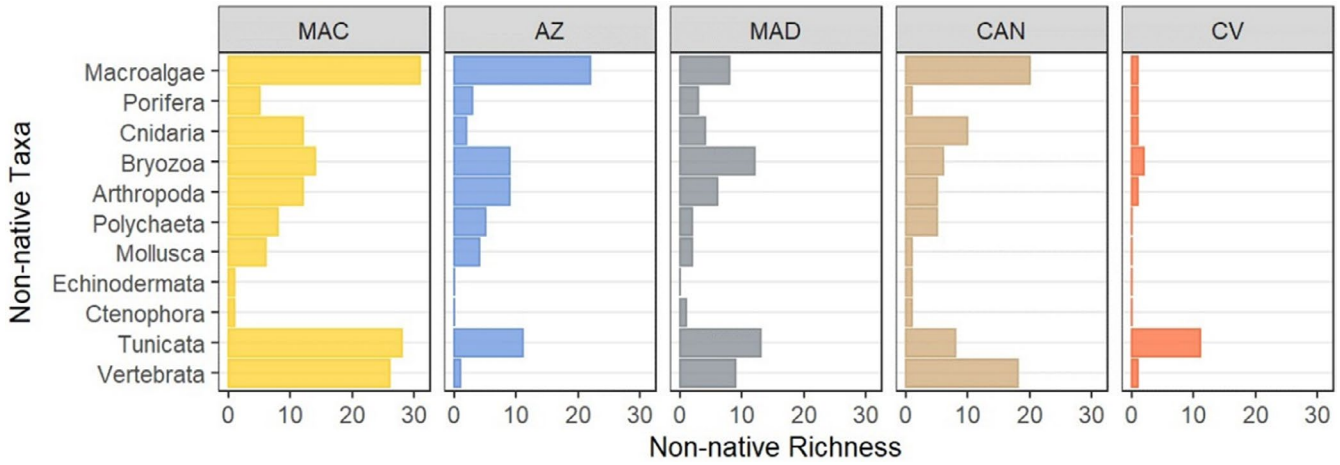


**FIGURE 3** Most representative taxonomic groups for non-native species (NNS) in Macaronesia and each archipelago system (MAC—Macaronesia; AZ—Azores; MAD—Madeira; CAN—Canary Islands; CV—Cabo Verde)

Overall, the NNS present in Macaronesia were mainly native to West Africa (11.3%), Australia and New Zealand (11.0%), the wider Caribbean Sea bioregions (10.6%), North East Pacific (10.3%), North West Atlantic and Mediterranean (8.6% each) and East Asian Seas bioregion (7.9%), among others (Figure 4). Most NNS detected in the Azores have a native distribution in the Australia and New Zealand region (13.3%), followed by North West Pacific (10.9%), East Asian Seas and Mediterranean (7.8% each) and North West Atlantic and Arabian Seas with the same percentage (7.0%) amongst others. The origins of the NNS detected in Madeira were from the Mediterranean (13.3%), Wider Caribbean Sea region (11.5%), West Africa (8.8%), Australia and New Zealand (8.0%), along with other bioregions of less importance. The Canary Islands had a similar overall pattern to Macaronesia, where West Africa (14.4%), the Wider Caribbean Sea (12.3%), Australia and New Zealand (11.0%) and NorthWest Pacific Ocean (9.6%) were the primary source bioregions. Finally, NNS detected in Cabo Verde had their native region in Wider Caribbean Sea (10.9%), Mediterranean, South Atlantic, Pacific North East and North West with the same percentage (8.7%) along with other less essential locations (Figure 4).

There is considerable variation in observed NNS richness among individual islands, with a general tendency for the highest richness on the largest island within each archipelago, probably reflecting increased anthropogenic activity and development in larger islands (Figure 5). In addition, MDS revealed four distinct spatial groups with lower proximity between Cabo Verde and the remaining archipelagos in NNS community composition (Figure 6). Madeira and the Canary Islands were the archipelagos with the highest similarity in their NNS community composition, followed by the Azores and Canary Islands (Figure 6). Those differences in community composition were confirmed by multivariate testing between the four Macaronesia archipelagos (ANOSIM: global $R = 0.9286$, $p = .001$).

For statistical modelling, multicollinearity was quite extreme for some of the available variables used to explain the number of NNS per island, particularly in covariates related to marine traffic (Figure 1 in Appendix S4). Multicollinearity was also high for the different distance variables associated with isolation. For the model implementation, only the minimum distance to the mainland for each island was applied. We considered this to be the best strategy to incorporate the isolation information on the distances while resolving the extreme multicollinearity challenge. The stepwise selection was used to remove marine traffic correlated covariates. The best model based on the stepwise procedure was an NB model where NNS richness is described as a function of (1) minimum distance to the mainland, (2) each archipelago, (3) total marinas area ($km^2$) and (4) the total number of ports and marinas (Table 1 and Table 1 in Appendix S4).

By assessing the visual inspection of the residual diagnostic plots, the model presents a good fit except for the tails, where the islands of Faial (Azores), São Vicente (Cabo Verde) and Santiago (Cabo Verde) are quite influential (Figure 2 in Appendix S4). Overall, the results are satisfactory considering the effects on the islands mentioned before. When averaging the predicted NNS numbers per archipelago, São Jorge (Azores), Terceira (Azores), Madeira, Tenerife (Canary Islands) and La Gomera (Canary Islands) were the more overestimated islands (Figure 7). In contrast, Faial (Azores) and São Vicente (Cabo Verde) were the islands with more underestimated NNS numbers (Figure 7). For more details in predicted values for each island, see Table 2 in Appendix S4.

## 4 | DISCUSSION

This study expands the current understanding of the scale and diversity of marine biological invasions on insular systems, making a pioneer contribution by examining the four archipelagos' marine bioinvasions that constitute the Macaronesian region: Azores, Madeira, Canary Islands and Cabo Verde. By completing this first extensive literature review of marine NNS records in Macaronesia, our study reported a total of 144 NNS for the entire region. The Canary Islands was identified as the Macaronesia archipelago with more NNS (76), followed by Azores (66 NNS), Madeira (59 NNS) and,

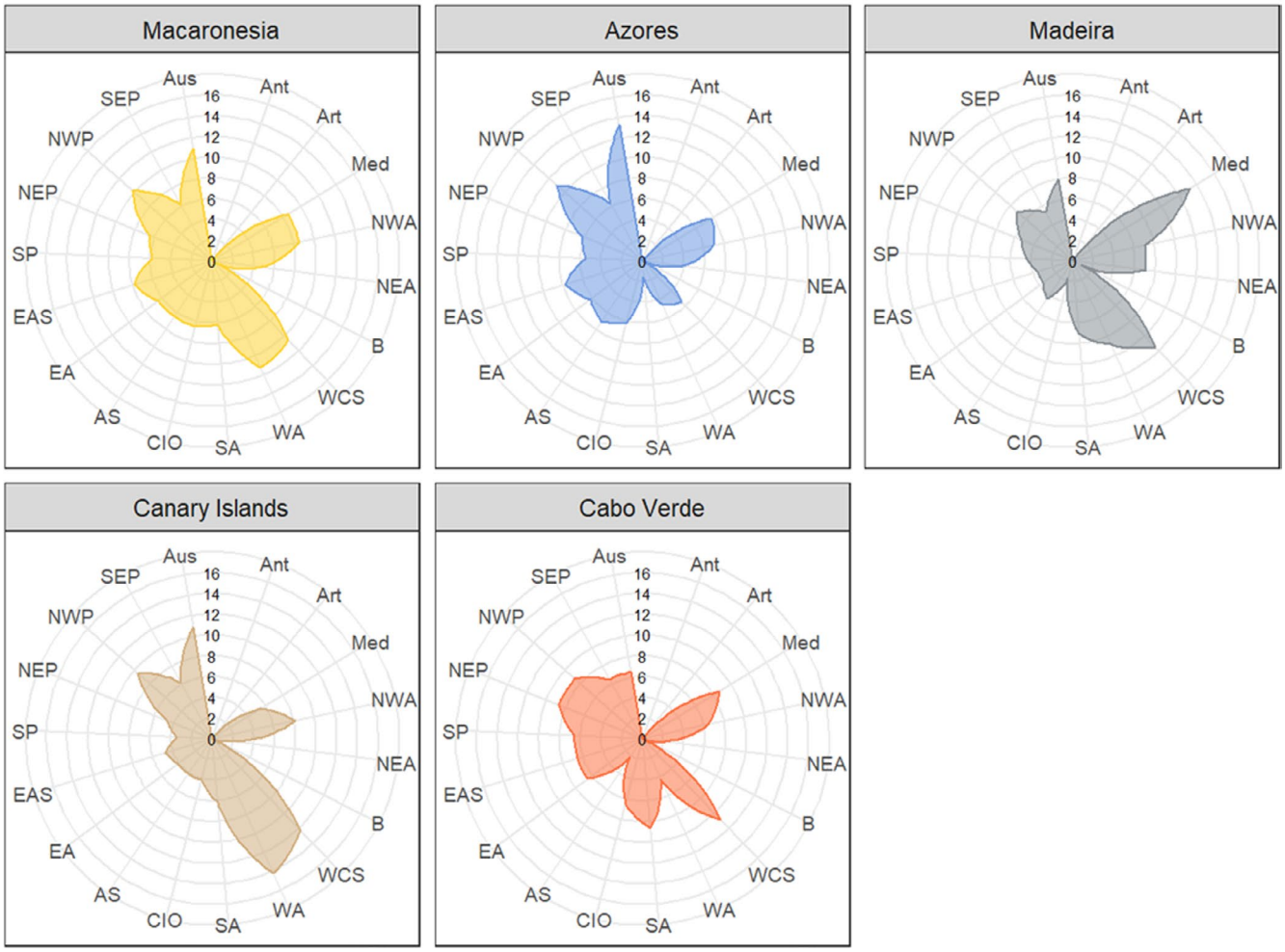


FIGURE 4 Relative frequency (i.e. the sum of each bioregion per archipelago/the sum of all bioregions per archipelago) of the origin of the non-native species (NNS) detected in Macaronesia, Madeira, Azores, Canary Islands and Cabo Verde. Potential native distributions were based on IUCN Bioregions (Kelleher et al., 1995) and later modified by Hewitt and Campbell (2010). Note that some species have more than one native origin. Bioregions codes 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); 14a&b—South Pacific & Hawaii (SP); 15—North East Pacific (NEP); 16—North West Pacific (NWP); 17—Southeast Pacific (SEP); 18 – Australia and New Zealand (Aus) (see Appendix S2 for further details)

finally, Cabo Verde (18 NNS). The four archipelagos displayed specific differences in the composition of taxonomic groups, being the most evident in the highest number of non-native fishes detected in the Canary Islands. In addition, Madeira and Canary Islands were the archipelagos with more similarity, while our analyses identified Cabo Verde as the most different archipelago. Tsiamis et al. (2019) defined NNS baselines inventories in the context of the European Union's Marine Strategy Framework Directive (MSFD). These listings were based on the initial assessment of the MSFD (2012) and the updated data of the European Alien Species Information Network (EASIN) until 2017, collaborating with European NNS experts. In these inventories, Tsiamis et al. (2019) mentioned 91 species for Macaronesia. Differences in the numbers reported by Tsiamis et al. (2019) to the present study are related to several factors, particularly: (1) in Tsiamis et al. (2019) "Macaronesia" only refers to European archipelagos without including Cabo Verde); (2) the NNS list we present here is more detailed, including attributes for NNS selection and validation, namely biogeographical status in the literature, expert opinion, reference in known marine biological invasion databases, range expansion species and species found only in NNS hotspots; (3) our search was conducted in English, Spanish and Portuguese; (4) the timeframe of both lists is different: Tsiamis et al. limit their search until 2017, based only in the European Alien Species Information Network (EASIN) while our search includes records between 1884 and 2020 and other NNS databases (NEMESIS and AquaNIS); (5) the present list also includes information regarding year of the first record, location and source reference; (6) our NNS criteria are conservative by removing some species that represented only sporadic records. However, for management purposes, the list we present here for Macaronesia should be seen as complementary to the one compiled by Tsiamis et al. (2019) and used for MSFD reporting.

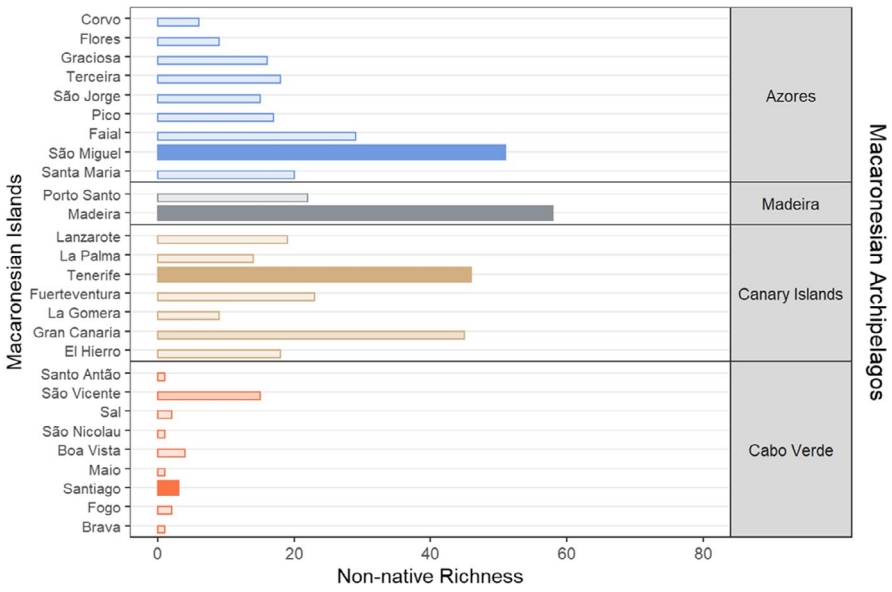


**FIGURE 5** The number of non-native species (NNS) found in the four archipelagos that compose the Macaronesian region with details for each island. Islands are ordered by latitude. Total NIS for Macaronesia is 144. The highlighted bars represent the islands with the highest area

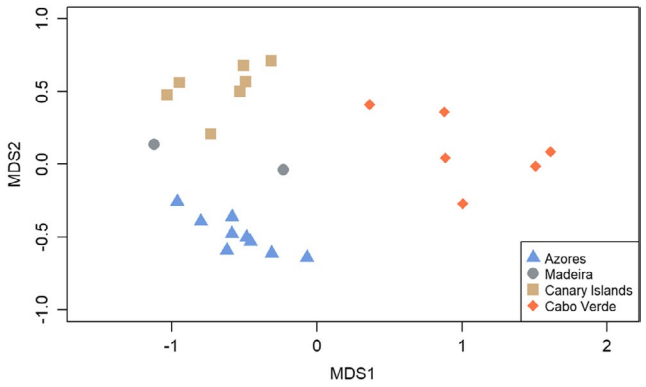


**FIGURE 6** Non-metric multidimensional scaling (MDS) plot showing differences in community composition based on the non-native species (NNS) detected in the different Macaronesian Islands. ANOSIM R = 0.9286, $p = .001$

**TABLE 1** Estimated regression parameters, standard errors, *z*-values and *p*-values for the best Negative Binomial (NB) General Linear Model (GLM) presented regarding non-native species (NNS) richness as a function of anthropogenic, demographic and geographical variables

| | Estimate | Std. error | *z* value | *p*-value |
|---|---|---|---|---|
| Intercept | 5.458 | 0.7387 | 7.390 | <.001 |
| Mindist | −0.002 | 0.001 | −3.849 | <.001 |
| Archipelago_codeCan | −1.562 | 0.382 | −4.077 | <.001 |
| Archipelago_codeCV | −3.121 | 0.437 | −7.142 | <.001 |
| Archipelago_codeMad | −1.112 | 0.365 | −3.063 | <.01 |
| Total_marina_area | 0.001 | 0.001 | −3.589 | <.001 |
| Total_harbors_marinas | 0.020 | 0.003 | 5.788 | <.001 |

*Note:* The estimated value for Theta is 402 ± 3050.

Most NNS present in Macaronesia were native to West Africa, Australia, New Zealand and the wider Caribbean Sea and North West Pacific bioregions, followed by the North West Atlantic, and the Mediterranean. The Azores differs from the most with slighter Australia affinities and the Canary Islands with more West Africa signature. Finally, NB modelling suggested that non-native richness patterns across Macaronesia were strongly affected by (i) minimum distance to the mainland, (ii) each archipelago, (iii) total marinas area ($km^2$) and (iv) the total number of ports and marinas.

By using statistical models, we simplified reality, which assists its interpretation and facilitates exploiting results as a valuable tool to construct and explore different hypothetical scenarios (e.g. Walsh & Brodziak, 2015). In this context, our study predicted the number of NNS present in each Macaronesia Island as a function of geographical variables and coastal development elements. The sample size available was small for modelling routines (27 islands), but we included multiple available covariates. Hence, model fitting and model selection was challenging, and minor changes to the species list tended to lead to different variables being included in the best model, mainly including marine traffic facilities (ports and marinas) and island population (Table 1 in Appendix S4). With such a small sample size, removing observations is far from easy and probably not recommended. The variable total island area was not significant in the present model, but larger islands had a higher NNS number (except Cabo Verde). Usually, larger islands are associated with more human activities and development, resulting in an enhanced anthropogenic disturbance (higher propagule pressure), and consequently, more NNS introduction events (Rojas-Sandoval et al., 2020).

## 4.1 | Overall Macaronesia context

Our analyses detected five shared NNS in the four archipelagos comprising Macaronesia. These include the seaweeds *A. taxiformis*, the bryozoans *A. verticillata*, and *S. errata*, the barnacle *B. trigonus*

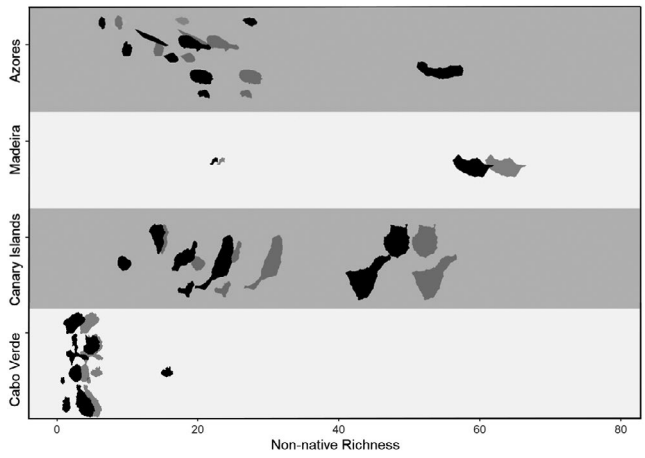


**FIGURE 7** Non-native species (NNS) detected in the present study (black colour) and by the output results predicted by the selected Negative Binomial (NB) model (grey colour) for each island of the four Macaronesian archipelagos. When the models' prediction (grey colour) is not visible, the observed value (black colour) overlaps the predicted value. Predictions close to observed values might, therefore, not be visible

and the tunicate *D. corolla*. The red algae *A. taxiformis* has an Indo-Pacific origin (Micael et al., 2014) with an ostensible cosmopolitan distribution (Andreakis et al., 2007; Chualain et al., 2004). Macaronesia's introduction of this macroalgae species was likely via ship hulls or rafting from other invaded regions (Cardigos et al., 2006). The spaghetti bryozoan *A. verticillata* registered recent introduction events in all Macaronesia archipelagos except in Cabo Verde (Minchin, 2012 and Appendix S1), where it was first collected in 1904 (Waters, 1918). No other records were in hand until 2018 and 2019 when several established colonies were observed in the Marina de Mindelo (São Vicente Island, Cabo Verde) (Nuno Castro, personal observation). Hull fouling is the most likely spreading vector for this species (Marchini et al., 2015). For the bryozoan *S. errata*, we considered earlier reports of *Schizoporella unicornis* (Johnston in Wood, 1844), a colder water European species, from Macaronesia, to very likely represent *S. errata*, with which it was long confused (Tompsett et al., 2009; see also Ryland et al., 2014). The bryozoan *S. errata* is a warmer water European species, which we regard as NNS in Macaronesia, where it has most likely been transported by ship fouling (Carlton & Eldredge, 2015). The barnacle *B. trigonus* of Pacific origin has spread over the Atlantic before the 1900s, most likely on ship hulls (Carlton et al., 2011). This species can be found on both sides of the Atlantic and throughout the Mediterranean (Fofonoff et al., 2018). It is a common element in fouling communities, and likely shipping and aquaculture were the introduction vectors in Macaronesia (Cardigos et al., 2006; Chainho et al., 2015; Fofonoff et al., 2018). The tunicate *D. corolla* of Caribbean origin (Canning-Clode et al., 2013) is abundant in the Azores and Madeira's islands but present in only one island of the Canary Islands and Cabo Verde (Appendix S1). Although only documented for El Hierro island, this tunicate is present in most islands of the Canaries (R. Herrera, personal communication).

Along with many other NNS, each highlights the historical importance of marine traffic to Macaronesia's oceanic islands, often playing a role in the initial introduction and spread across islands. During the Age of Discovery, both Portuguese and Spanish empires have used several Atlantic islands and archipelagos as strategic locations (Garcia, 2017). The Macaronesian archipelagos and other Atlantic islands provided 'port of call' facilities (Garcia, 2017). The triangular commercial sailing route in the late 1800s between Europe, West Africa and the Caribbean (Crosby, 1986) and the British steamer routes and coaling stations (Mack, 2003) could have enhanced the connectivity amongst areas never joined before. Evidence suggests that the first NNS was detected in the late 19th and beginning of the 20th centuries (Castro et al., 2020). Still, it cannot be excluded that some species, considered now as native species, might be earlier introductions from the 15th and 16th centuries. For example, Portuguese navigators probably introduced the Portuguese oyster *Crassostrea angulata* (Lamarck, 1819) to Portugal in the 16th century (Blakeslee, 2015).

The similarity of NNS and the shared NNS among Macaronesian archipelagos could be related to several factors associated with isolation, for example, distance to the mainland and/or amongst islands and/or marine traffic connectivity and intensity. The present study verified the highest similarity in NNS diversity between Madeira and Canary Islands, with 30 shared NNS. These archipelagos are the closest ones in the whole Macaronesia province. They have long been connected as stopovers for yachts crossing the Atlantic from the East (Parrain, 2011) and cruise ship routes (Sousa, 2000). The Azores and the Canary Islands had 27 unique shared NNS. In this latter example, proximity may not be the best explanation for these similarities, which can be better explained by the high number of studies focusing on macroalgae diversity and taxonomy, which have identified 12 macroalgae species that are present in both archipelagos (Appendix S1).

Cabo Verde, the southernmost archipelago of Macaronesia, was particularly differentiated from the remaining archipelagos, both in NNS composition similarity and in shared NNS. Interestingly, Cabo Verde has more shared NNS (10) with Madeira than with the Canary Islands (nine), its closest neighbour, which may be partly explained by the fact that Cabo Verde is a former Portuguese colony that had frequent connections with other Portuguese territories, including Madeira archipelago (Castro et al., 2020).

Each archipelago had some differences related to NNS origin. The Azores are more influenced by Australia and the Pacific, Madeira with a high Mediterranean signature, the Canary Islands with West African heritage, and Cabo Verde with a solid Caribbean input. However, Macaronesia's overall pattern had some Pacific Ocean influence. In this context, Chainho et al. (2015) obtained a relatively similar trend while examining a NNS inventory for Portugal, including the mainland and islands. Moreover, native range patterns are based on the history and traits of each region's dominating primary pathways of introduction (Tsiamis et al., 2018). Secondary spreads could also have played a key role in NNS dispersion in Macaronesia. According to some studies, the most recent introductions often

result from secondary introductions (Chainho et al., 2015; Martínez-Laiz et al., 2020; Souto et al., 2018). Finally, the distance to neighbouring continents and islands that initially affected native species colonization by dispersion (Domingues et al., 2008; Whittaker & Fernández-Palacios, 2007) could also have affected NNS colonization as well.

New species are arriving in many regions due to extreme climatic events induced by climate change. Temperature variations triggered by climate change (increased mean temperatures and/or fluctuations) have already facilitated the establishment of new-arrived species and caused their distribution limits to shift poleward, which may lead to the displacement or substitution of local temperate species by tropical species (Vergés et al., 2014). Occurrences such as 'Caribbean Creep' or 'African Creep' were reported, with several species having their distribution range expanded (Canning-Clode & Carlton, 2017; Canning-Clode et al., 2011). The 'Caribbean Creep' phenomenon relates to invertebrate species invasions from the Caribbean to the US coast in a poleward range expansion (Canning-Clode et al., 2011), whereas the 'African Creep' is a similar occurrence but from Africa to Europe (Canning-Clode & Carlton, 2017). Similar events took place on several Macaronesia archipelagos (Afonso et al., 2013; Brito et al., 2011; Freitas & Castro, 2005; Schäfer et al., 2019).

### 4.2 | NNS patterns in Azores

The Azores registered 66 NNS, being the second archipelago with higher NNS introductions in Macaronesia. In this Portuguese archipelago, macroalgae species (22), tunicates (11), bryozoans and arthropods (9) were the most relevant non-native taxa, similar to the overall pattern of the whole Macaronesia. Studies in marine ecology in the Azores started earlier than in other Macaronesian archipelagos, and there was some interest in marine species introductions as early as in the 1970s (e.g. Monniot, 1971; Morton & Britton, 2000; Tittley & Neto, 1994). In 2006, Cardigos et al. (2006) produced the first NNS inventory for the Azores based on scientific publications, reports and personal data. The work of Cardigos et al. (2006) increased the interest in the study of marine biological invasions in the Azores, and several other papers have been recently published (e.g. Micael et al., 2017; Vaz-Pinto et al., 2014) and have increased the knowledge in marine species introductions in the archipelago. In 2014, a review by Micael et al. (2014) confirmed that the Azores have more macroalgae introductions than other parts of the globe. Marine shipping (mainly through ballast water and hull fouling) is considered the primary introduction vector of NNS into the Azores (Cardigos et al., 2006; Micael et al., 2014). Moreover, the Azores have been selected as a critical destination for transatlantic recreational boating over the years, increasing the likelihood of NNS introductions (Cardigos et al., 2006). Other vectors have also been listed as relevant in facilitating the introduction or spread of NNS in the Azores, including aquarium trade and boating-related scuba diving activities (Cardigos et al., 2006; Parretti et al., 2020). Some NNS detections were a consequence of monitoring programmes that occurred until 2018 (e.g. 2013 (Azores Stopover for Marine Alien Species), 2016 (Waitt Foundation expedition) and 2017 (Program on Marine Invasive Species of the Azores).

### 4.3 | NNS patterns in Madeira

Our search confirmed the Madeira archipelago as the third Macaronesian archipelago in NNS numbers. Madeira has a few research institutions partially working on marine sciences. With a few sporadic records detected during the 1990s (e.g. Wirtz, 1995, 1998), the interest in marine invasions in Madeira is very recent (<10 years) and overlaps with the establishment of a dedicated research group in the archipelago with several ongoing monitoring surveys for NNS detection (e.g. Canning-Clode et al., 2013; Gestoso et al., 2018; Ramalhosa & Canning-Clode, 2015; Ramalhosa et al., 2017). As a result, several new species have been detected and inventoried (e.g. Canning-Clode et al., 2013; Ramalhosa & Canning-Clode, 2015; Ramalhosa, Souto, et al., 2017; Souto et al., 2015). Recently, Castro et al. (2020) verified a connection between NNS present in Madeira with the primary marine traffic into the archipelago, validating this vector as the most relevant for NNS introductions. In addition, a 6-year study conducted in a recreational marina in Madeira confirmed a significant relationship between the number of vessels arriving and the accumulated number of NNS detections over time (Canning-Clode et al., 2013). Moreover, the number of native species in the marina decreased with more colonization by NNS, indicating these species are able to displace local taxa and can be a threat to indigenous communities (Canning-Clode et al., 2013). Some recent introductions in Madeira were also related to tropicalization processes (Ribeiro et al., 2019; Schäfer et al., 2019). Finally, to a lesser extent, other vectors have been suggested to be facilitating NNS introductions in Madeira, including aquaculture (Alves & Alves, 2002) and, more recently, transatlantic rafting (Wirtz & Zilberg, 2019).

### 4.4 | NNS patterns in the Canary Islands

The highest number of NNS was observed in the Canary Islands, and several factors could account for this observation. First, the most frequent taxa detected in the Canary Islands were macroalgae and fish. The biogeographical position of the Canary Islands has been recognized as the major element for the richness of its marine biota (Haroun & Herrera, 2001), with a high interest in phycology, where several publications were produced over the years (e.g. Afonso-Carrillo et al., 2007; Gil-Rodríguez & Afonso-Carrillo, 1980; Haroun & Herrera, 2001; Sangil et al., 2012). Therefore, it is no surprise that macroalgae are amongst the most detected NNS taxa in this archipelago. Recently, the number of non-native fishes detected in the Canary Islands increased considerably (e.g. Falcón et al., 2015; Pajuelo et al., 2016). Our study reports 18 established non-native fish species (see Methods section for more details) in Canarian waters, most of these associated with oil platforms (e.g. Brito et al.,

2011; Espino, 2015; Falcón et al., 2015; Pajuelo et al., 2016; Triay-Portella et al., 2015). The Port of Las Palmas in Gran Canaria and the Port of Santa Cruz de Tenerife are the main hubs for international marine traffic. Their strategic location has consolidated the Port of Las Palmas as a maritime logistic hub that connects with more than 180 ports on the planet, making it one of the most important commercial hubs in Spain. During the last decade, the Port of Las Palmas has established itself as an essential repair and service centre in the Atlantic for oil rigs and drilling ships (Pajuelo et al., 2016; Ports of Las Palmas, 2021). It is plausible to assume that most of these introductions are associated with the current intensity of marine traffic in the Canary Islands, primarily through hull fouling. However, introductions via ballast water may have occurred, especially for fish species and crustaceans (Brito et al., 2011; González et al., 2017). Additionally, other human-induced vectors may be responsible for some of these introductions in the Canary Islands, including aquarium trade (Falcón et al., 2015) and aquaculture (Toledo-Guedes et al., 2014). Besides, range expansions due to anthropogenic-induced climate change could have influenced these numbers (Brito et al., 2005). One other element that may affect NNS distribution per country is the variability in the monitoring and reporting effort (Katsanevakis et al., 2013). In this context, several governmental institutions and Universities in the Canary Islands have been conducting studies related to marine biological invasions. Moreover, the Canary Islands have the highest human population density in Macaronesia, with an estimated 2 million residents and around 10 million tourists every year (Garín-Muñoz, 2006), which exposes these islands to elevated anthropogenic pressure. The Canary Islands hold more ports and marinas and a superior port area among the four Macaronesian archipelagos. This suggests higher propagule pressure (e.g. number of viable NNS individuals, the number of discrete introduction events, their frequency and duration) which is recognized as the primary determinant of NNS invasion success (Ojaveer et al., 2014). Besides, this extended port area, dominated by several artificial structures like piers, pontoons, seawalls and buoys, provides transport hubs or 'stepping stones' for potentially newly established species (Bulleri & Chapman, 2010; Pinochet et al., 2020; Ruiz et al., 2009). Some studies point out that artificial substrates expedite the NNS colonization process compared to natural substrates (Lambert & Lambert, 2003; Pinochet et al., 2020; Tyrrell & Byers, 2007).

### 4.5 | NNS patterns in Cabo Verde

Cabo Verde was the archipelago with the fewest NNS detections in our search. In addition to marine traffic (e.g. Monteiro, 2012), no other NNS introduction vector was ever mentioned in the literature for Cabo Verde (to the best of our knowledge). The archipelago holds the lowest number of research institutions dedicated to marine sciences, all based in São Vicente Island. Most studies conducted in Cabo Verde are not marine invasion related. Consequently, NNS detections in the region remain scarce (see Freitas et al., 2014; Freitas & Soares, 2011; Lopes, 2010; Monniot & Monniot, 1994; Monteiro, 2012). From a political perspective, European Union member states (MS) with the collaboration of experts in each MS have instruments that refine baseline inventories of NNS. The Biodiversity Strategy and the MSFD are examples of such European legislative instruments. Cabo Verde is a non-European archipelago and, therefore, not obliged or supported to follow those instruments. This may reduce certain research efforts exclusively dedicated to marine biological invasions in that archipelago.

However, Cabo Verde has reduced ports and marinas and, consequently, has few artificial structures to shelter NNS, which minimizes 'hotspots' for potential propagule pressure. Also, Cabo Verde holds a high richness of endemic marine fauna, with significant differences to other Macaronesian Islands (Freitas et al., 2019). Ecological theory suggests that communities with high species richness offer more biotic resistance against biological invasions by maintaining high levels of predation pressure or increasing competition for space and resources (Freestone et al., 2013; Gestoso et al., 2017, 2018). However, likely, the number of reported NNS in Cabo Verde is severely influenced by reduced sampling effort in the archipelago.

### 4.6 | Conclusions

Although not detected as a significant component in our model, study effort could also play an essential part in NNS detection. Moreover, NNS findings are usually linked with monitoring and reporting (Chainho et al., 2015; Katsanevakis et al., 2013). In this context, future research in Macaronesia should focus on standardized NNS monitoring surveys using standard protocols.

Coastal development, that is, ports and marina infrastructures, favours species establishment and potential dispersal to adjacent areas (Afonso et al., 2020). Marine traffic played and still plays a vital role in species arrival and dispersal. The 144 NNS listed here will likely increase the awareness regarding marine NNS in the whole Macaronesia region serving as a trigger for future works and implementing and enforcing regulations addressing the introduction of marine NNS in oceanic islands. Given that the majority of marine NNS recently recognized in the Hawaiian Islands (Carlton & Eldredge, 2009, 2015) and Galapagos Islands (Carlton et al., 2019) are those that were previously listed solely as native species and did not appear in any lists of NNS for these archipelagos, we assumed that the number of NNS that we recognized here is likely to be a fraction of the actual NNS diversity in Macaronesia. The overall number of NNS in Macaronesia that we present here will probably never be definitive as new species are constantly arriving and being detected (Álvarez-Canali et al., 2021), or more detailed studies are conducted (Ramalhosa et al., 2021).

In the present paper, NNS reported numbers are dependent on each archipelago, and strongly affected by total marinas area, the total number of ports and marinas, and mean distance to the closest continental landmass. This suggests that more developed islands with higher marine traffic intensity and more prominent port infrastructure host more NNS.

Finally, millions of years of physical isolation have favoured the evolution of unique species and habitats in oceanic islands, which can be quickly exposed to an increasing number of NNS threatening native species and even driving some species to extinction (Micael et al., 2014). Thus, the pressure on the islands' endemic biota is likely greater than the one reflected by the numbers at this moment presented. Nevertheless, using Macaronesia as a study model, the present work represents a pioneer effort to characterize and better understand marine invasions in the northeast Atlantic insular ecosystems. This effort will undoubtedly contribute and serve as a baseline for future ecological, experimental and management studies.

## ACKNOWLEDGEMENTS

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## CONFLICT OF INTEREST

The authors declare there is no conflict of interest.

## PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ddi.13465.

## DATA AVAILABILITY STATEMENT

All newly generated data used in this study are available as supplementary electronic material (Appendices S1–S4).

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## BIOSKETCHES

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Author contributions: NC, JTC, GMR and JCC conceptualized the study. NC, PR, IG, TM, PF, JTC, CLH, GMR and JCC contributed to methodology. NC, CSM and TM performed analyses. NC, TM, CSM and JCC contributed to visualization. NC, JTC, GMR and JCC wrote the original draft preparation. NC, PR, IG, EC, FG, JGM, PC, TM, CSM, JLC, MP, RHA, RHE, EL, PF, JTC, ACC, RSS, CLH, GMR and JCC wrote, reviewed and edited the manuscript. IG, RHE, RSS and JCC provided resources and performed funding acquisition. IG, JLC and JCC supervised the study.

## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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