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Original research article

The cone snails of Cape Verde: Marine endemism at a terrestrial scale



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ABSTRACT

Cape Verde in the Eastern Atlantic is typical of many island groups in supporting a wealth of endemic species both terrestrial and marine. Marine gastropod molluscs of the genus *Conus*, commonly known as cone snails, occur in coastal tropical waters throughout the globe, but in Cape Verde their endemism reaches its apogee with 53 out of 56 species occurring nowhere else, the majority of which are restricted to single islands and frequently to single bays. However, Cape Verde is rapidly moving to a tourism-based economy with a projected boom in infrastructure development often coincidental with the shallow-water habitat of many range-restricted *Conus*. The conservation assessment of *Conus* to standards of the International Union for the Conservation of Nature (IUCN) Red List of Endangered Species, found that 45.3% of 53 species assessed from Cape Verde are threatened or near-threatened with extinction compared to 7.4% of 579 species in the rest of the world. The only three *Conus* species globally assessed as Critically Endangered and on the cusp of extinction are all endemic to Cape Verde. Our analysis of *Conus* species distribution, together with spatial data of coastal protected areas and tourism development zones, identify important areas for future research and new marine protection. Our findings show that endemism with its associated risks for *Conus* in Cape Verde has worldwide parallels with many non-marine taxa, while our proposed strategy for *Conus* conservation extends beyond the confines of the country and this taxonomic group.

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1. Introduction

Small islands and archipelagos, isolated by distance and ocean currents, support centres of endemism in both terrestrial and marine taxa (Roberts et al., 2002). However, these endemism 'hotspots' are often subject to threats from natural and anthropogenic forces that can have a disproportionate impact on the biodiversity they support (Fordham and Brook, 2010). Cape Verde in the tropical Eastern Atlantic is such a 'hotspot' and although it is poorly represented by mammals, it is rich in endemic invertebrates including 473 species of arthropod and 140 species of beetle (Triantis et al., 2010), and widely recognised for its endemic plants (Duarte et al., 2008; Romeiras et al., 2016) and reptiles (Vasconcelos et al., 2013). In the surrounding seas endemic zoanthsids occur (Reimer et al., 2010), and it is also here that marine endemism reaches its apogee in the venomous marine gastropod genus *Conus* (Peters et al., 2013).

Cape Verde is an archipelago of ten volcanic islands and several islets (Fig. 1) 570 km west of Senegal and is the most southerly of the Macaronesian islands. There is also a shallow seamount known as the João Valente Shoals between the islands of Boa Vista and Maio, with a platform at 14 m that is probably a guyot (Ramalho, 2011). The Canary Current

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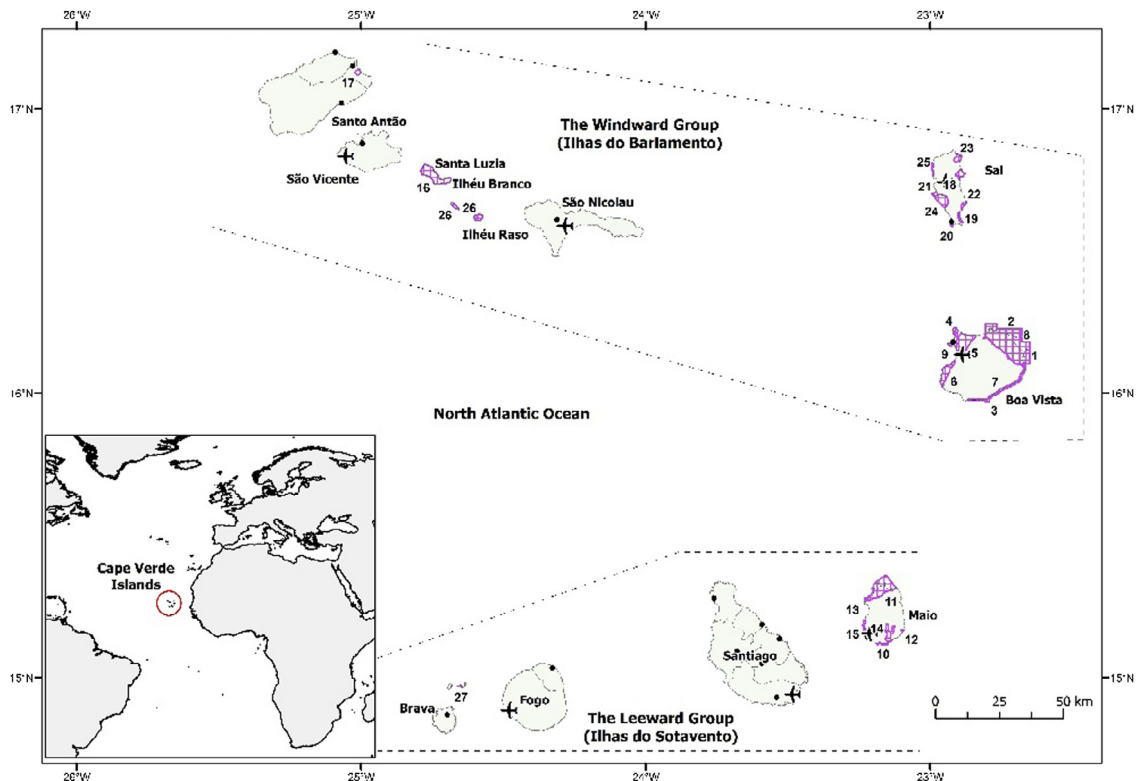


Fig. 1. Map of Cape Verde with protected areas with a marine or coastal element shown in green, major towns as black circles and airports with a plane symbol. Protected Area names and sizes may be cross-referenced to the key in this map from Table S1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

flowing south-west from Morocco brings nutrient-rich waters to the region attracting both artisanal and international fishing fleets (Mundt, 2012). With the exception of Santa Luzia, all the islands are inhabited. Service industries account for 73% of the country's economy, with agriculture and fisheries together constituting only 9% (Nshimyumuremyi and Simpasa, 2015). Cape Verde has few natural resources apart from marine products and services and the land is generally unsuited to agriculture, such that around 80% of food is imported (de Carvalho, 2013).

Tourism is now considered Cape Verde's primary economic force and including directly associated sectors, is responsible for 40% of gross domestic product (2014), forecast to increase to 49% by 2025 with visitor numbers expected to reach nearly 701 000 by 2025 (World Travel & Tourism Council, 2015). In addition to attracting foreign investment tourism also drives the construction sector (AfDB et al., 2013) including new harbour facilities at Porto Grande, São Vicente, and international airports on Boa Vista and São Vicente to augment those already on Sal and Santiago. Plans have also been agreed for the development of a large international casino on the islet of Santa Maria off the southern coast of Praia, Santiago (Semedo and Gomes, 2015).

To support and develop tourism while protecting the natural environment, Integrated Tourism Development Zones (ZDTI) have been delineated (Cabo Verde, 1994) and selected for geographical location and landscape suitability (Fig. 2). Tourism Reserve and Protection Zones serving as buffers to ZDTIs offer some natural protection from development, although incursion from ZDTIs into these zones has made their value questionable (GEF/UNDP, 2013). Prior to development for each ZDTI a management plan is required which must then undergo a full environmental impact assessment. No form of extraction is allowed within a ZDTI (Decree-Law 29/2006). ZDTIs are managed by Cabo Verde Investimentos (CVI) and the Sociedade de Desenvolvimento Turístico das Ilhas de Boa Vista e Maio (SDTIBM) on behalf of the government. Currently, there are 25 ZDTIs designated principally around Santiago, Maio, Boa Vista, Sal and São Vicente, in which large-scale investment in infrastructure is anticipated (Fig. 2) (SDTIBM, 2010).

In 2003, Decree-Law No. 3/2003 (44/2006 amended) nominated 47 protected areas (PA) for Cape Verde (Tables S1 & S2); however, not all have been gazetted and most are not staffed owing to a complexity of land ownership and lack of funding (Laurie and Benchimol, 2013). All have suffered from a general lack of management capability (Laurie and Benchimol, 2013; UNDP, 2009). A large-scale initiative to consolidate all PAs under a single structural plan was launched in 2009 through a joint enterprise between the United Nations Development Programme (UNDP), the Global Environment Facility (GEF), and the Government of Cape Verde (UNDP, 2009). The project's long-term goal was "to conserve globally significant terrestrial and marine biodiversity in priority ecosystems of Cape Verde through a protected area system's approach". Central to the

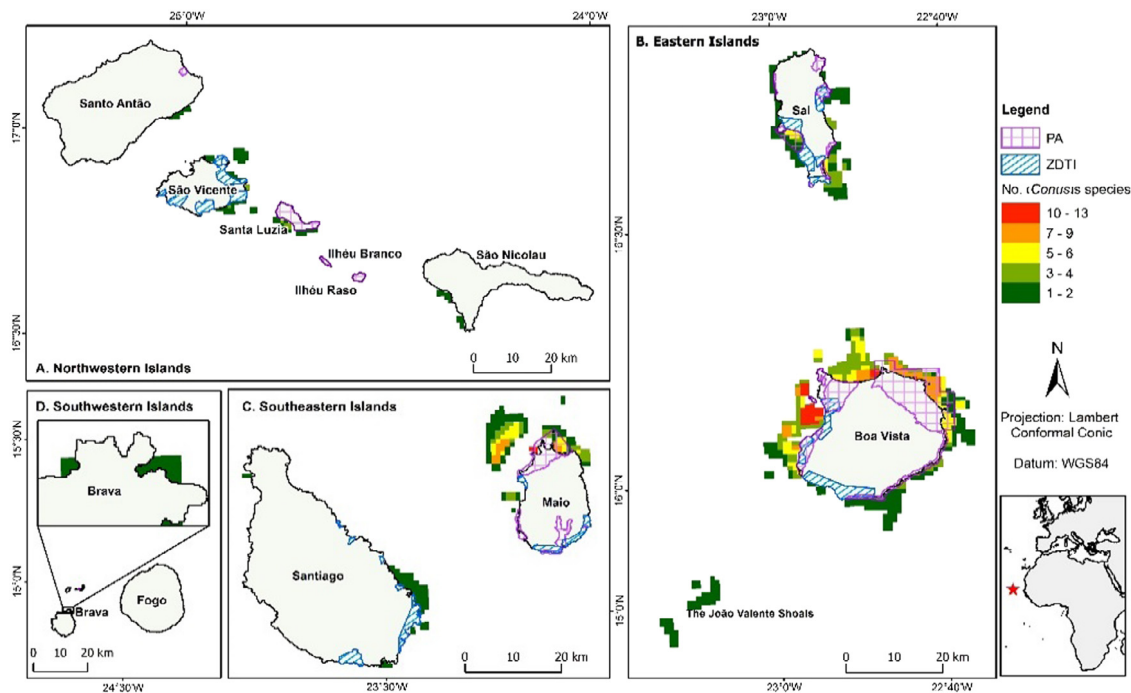


Fig. 2. *Conus* Species richness around Cape Verde with Tourism Development Zones (ZDTIs, Boa Vista, Maio, Sal, São Vicente and Santiago only) and Protected Areas (PAs) with a marine or coastal element.

approach was to be the establishment of a Protected Area Autonomous Authority (PAAA). The project was scheduled for completion by December 2014, however, the latest report indicates that lack of financing for the PAAA together with failure of enforcement of environmental legislation threatens its sustainability (Laurie and Benchimol, 2013).

Currently, 27 PAs have been scheduled that encompass coastal elements of which one, Baía da Murdeira, is exclusively marine (Fig. 2, Table S1). Protection of the shoreline, although typically planned as a constraint on development in order to preserve the landscape, should coincidentally reduce disturbance to taxa that dwell in the shallows. Unfortunately however, the PA network was not created in a scientifically structured way with many areas selected on the basis of features such as their landscape merit, bird nesting sites or recreational appeal without consideration to an overall conservation objective (Vasconcelos et al., 2012). Additionally, they are subject to little in the way of planned wildlife inventories or biodiversity monitoring programmes (Vasconcelos et al., 2012).

The Second National Environmental Action Plan, PANA II (2004), a governmental umbrella programme for environmental management for the years 2004–2014 currently has no successor publication. However, echoing concerns expressed through PANA II, the UNDP on Protected Areas (PAs) in Cape Verde identified key threats to the marine environment quoting: increasing pollution from the dumping of waste, effluent and oil; a lack of waste collection; no effective regulation to compel boats to segregate oil from other effluents; increasing discharge of urban wastewater into the seas; and lack of pollution contingency planning (UNDP, 2009). Development in the interior of the islands has led to deposition of sediment in coastal areas and widespread excavation of marine sand for construction (de Carvalho and Araújo, 2006; Höflinger, 2014; UNDP, 2009). From further afield, oil spills from offshore drilling in Mauritania could be transported by the Canary Current and carried ashore in Cape Verde, as proven by Mauritanian fish traps finding their way onto Cape Verde beaches (FAO/UNEP, 2007).

Cone snails of the genus *Conus* occur within tropical and subtropical coastal waters throughout the world where they have evolved into more than 630 species (Kohn, 1990). Cone snails are carnivorous gastropods that with few exceptions feed exclusively on either fish, molluscs or worms (Duda et al., 2001). They in turn are preyed upon by other carnivorous taxa most notably crabs (Dietl and Hendricks, 2006) and are therefore important components in the marine food web. To immobilise their prey, all cone snails utilise venom known as ‘conotoxins’ that comprise a complex cocktail of peptides delivered via radulae that have been adapted through evolution into harpoons (Olivera, 1997). Biomedical research of conotoxins (Bingham et al., 2010) has gained traction during the past 25 years, but today less than two percent of toxins has so far been characterised (Kaas et al., 2010). Nevertheless, with each species of cone snail developing up to 100 discrete toxins targeted at a broad range of highly-specific cellular receptor sites, and with little replication between species, a considerable reservoir of potential pharmacological agents remains to be explored for use in a wide range of medical therapies (Terlau and Olivera, 2004). Furthermore, outside their ecological and pharmacological utility, cone snails help support a global industry in the trade for specimen shells and shellcraft (Dance, 1966; Floren, 2003; Rice, 2007).

An analysis of the findings by Peters et al. (2013) from their global assessment of 632 species of *Conus* for the International Union for Conservation of Nature (IUCN) Red List of Threatened Species revealed that those endemic to the Eastern Atlantic and to Cape Verde in particular represent a disproportionate number of globally threatened species (Fig. S1) (IUCN, 2013; Peters et al., 2013; Tenorio, 2012). Fifty-three of the 56 *Conus* assessed for the Red List for Cape Verde are endemic (Monteiro et al., 2004; Peters et al., 2013). This includes 24 species, representing over one-third (36%) of the 67 *Conus* species assessed as 'threatened' or 'near threatened' globally, and 45% of the 53 Cape Verde endemic species, compared to 18% of 231 remaining endemic species across the rest of the world. Such a high concentration of endemic marine species of the same genus is exceptional and may be unsurpassed (Duda and Rolán, 2005). Across Macaronesia, other areas are largely devoid of *Conus* (Monteiro et al., 2004).

Unlike many cone snails, all endemic Cape Verde *Conus* larvae are lecithotrophic, and obtain nourishment through an egg sac during their pre-metamorphic dispersal phase (Kohn and Perron, 1994; Perron, 1981). This has resulted in low larval production with limited dispersal ability but accelerated speciation and probably accounts for an unusual diversity of species with the majority restricted to single islands or even single bays (Cunha et al., 2005). Main cladogenetic events of *Conus* in the archipelago are associated with episodes of low sea level that caused an increase in available shallow-water habitat. The increase in the habitat area combined with the reduced dispersal abilities of *Conus* larvae and the irregular shape of the Cape Verde coastline, created conditions for genetic differentiation to occur (Cunha et al., 2005, 2008). A recent study also showed that sea surface temperature is an equally important predictor of *Conus* diversity in Cape Verde, as demonstrated by ecological models (Cunha et al., 2014). This high degree of endemism among Cape Verde *Conus* with a hereditary loss of functionality to freely disperse, low larval production, sensitivity to sea-surface temperatures and highly restricted range, has set the scene for an elevated threat of extinction.

With the exception of *C. atlanticoselvagem*, all Cape Verde endemic *Conus* occur within snorkel depth and only seven descend deeper than 5 m, with none below 15 m (Peters et al., 2013). Although small in size, they generally display an attractive pattern and may easily be gathered by tourists or by international shell traders for direct sale (e.g. www.caboverdeshells.com, www.shellauction.net) where only live animals offer the quality of shell demanded by serious collectors.

To understand why an exceptionally high ratio of threatened cone snail species occurs on Cape Verde compared to other regions with high species richness of *Conus* (Peters et al., 2013, 2015) we analysed the threats to all Cape Verde's 53 endemic species. Building on threat data, species' distribution and bathymetry, we explored the proximity of threatened species across their combined occupancy against areas zoned for tourism development and sites designated for marine and coastal protection, to consider effectiveness of current conservation planning. We identified areas of high value to *Conus* that we consider a priority for future research and conservation, also highlighting where threats to the marine environment generally may be greatest. These areas are likely to require environmental impact assessments in future planning of shoreline development. More broadly our study offers guidance not only for the protection of endemic *Conus* of Cape Verde but helps to inform future strategy on marine management that can be applied equally to other regions of high endemism worldwide, whether marine or terrestrial.

2. Methods

2.1. IUCN Red List assessment

We analysed extinction threats to the 53 *Conus* species endemic to Cape Verde within a global Red List assessment, prepared to IUCN standards (IUCN Standards and Petitions Subcommittee, 2010) as described in Peters et al. (2013). A recent revision of *Conus* systematics resulting in reclassification to 82 genera (Tucker and Tenorio, 2009; Bouchet et al., 2011) is gaining broad acceptance (Petuch pers. comm. 2014). However, with the new taxonomy not yet universally adopted (Kohn, 2014), and to facilitate cross-referencing, all species in our study are referred to by their original Linnaean genus, *Conus*, as presented in the Red List. Furthermore, 19 recently described species endemic to Cape Verde from sites in Boa Vista, Maio and Sal (Afonso and Tenorio, 2014; Cossignani and Fiadeiro, 2014; Cossignani, 2014; Tenorio et al., 2014) have been excluded from this analysis as they have not yet been assessed for the Red List and their range is unknown except for the type locality which provides no measurable distribution.

Three Red List 'threatened' categories define the highest levels of threat to a species, namely: Critically Endangered (CR), Endangered (EN) and Vulnerable (VU), broadly representing 'extremely high', 'very high', and 'high' risk of extinction. Species assessed for likely elevation to a 'threatened' category are categorised as Near Threatened (NT); those with insufficient data for categorisation are classed as Data Deficient (DD) and species not considered to be at current or imminent threat are categorised as Least Concern (LC). Note that although Data Deficient species are not classified as threatened, research suggests that a high proportion of species assessed for this category are also at risk (Howard and Bickford, 2014; Morais et al., 2013). Of 632 *Conus* species assessed world-wide, all 3 CR, 4 of 11 EN, and 5 of 27 VU are endemic to Cape Verde. A further 12 species within Cape Verde from the global total of 26 are categorised as NT, and there is a single DD species from the global total of 87 (Peters et al., 2013).

For our analysis, we extracted data held on the IUCN Red List for each species including associated spatial data. We examined each species' distribution and bathymetric profile with evidence of abundance, sub-populations and habitat preference. For enhanced accuracy in mapping species richness, we used species distribution trimmed to only include the

area within each species' reported bathymetric range using data from General Bathymetric Chart of the Ocean (GEBCO, 2013). ArcGIS version 10.1 with Python version 2.7 (Environmental Systems Research Institute) were used to analyse the data. All data were standardised onto 1 km² grid cells and projected to Lambert Conformal Conic. With the exception of two species (*C. atlanticoselvagem* and *C. luquei*), all endemic *Conus* in Cape Verde are found in the shallow littoral zone in waters up to two metres or less. At these depths precision is found wanting in most published bathymetric chart data, giving rise to small mapping discrepancies in the areas of occurrence of taxa living there. Consequently a few species appear to lie further offshore than would be expected. Nevertheless, their locations still remain relevant to their proximity to neighbouring regions zoned for development, as well as those subject to protection.

2.2. Tourism in Cape Verde

Islands earmarked for major development include Boa Vista, Maio, Sal, São Vicente and Santiago. The scope of the development for Boa Vista and Maio are described in reports by SDTIBM (2013a,b). The most detailed descriptions for Sal and São Vicente ZDTIs descriptions have been published by the Millennium Challenge Account—Cabo Verde II (Millennium Challenge Account, 2012a,b). ZDTIs have also been described for Santiago in Cape Verde government bulletin No. 20 of 23 May 1994.

To explore trends in tourism, we analysed statistical data using descriptive statistics published by Cape Verde National Institute of Statistics (INE, 2015) on annual visitor numbers for each island, including hotel occupancy for the ten years from 2005 to 2014 inclusive (INE, 2015).

2.3. Protected areas

By reference to PANA II (2004) together with UNDP project 4176 (Laurie and Benchimol, 2013; UNDP, 2009) and local development plans, and through exploring the effectiveness of current marine protection strategies, we considered the location of all scheduled marine and coastal protected areas in relation to *Conus* species' distribution. The exposure of *Conus* to possible disturbance from ZDTI development on the islands of Boa Vista, Maio, Sal, São Vicente and Santiago were analysed through a review of existing ZDTI plans and their spatial proximity.

2.4. Proposed priority areas for research and conservation

We adopted four progressively expanding 'scenarios' to provide a context from which the most appropriate priority marine areas for future *Conus* research and conservation could be selected. Each 'scenario' or Proposed Priority Areas for Research and Conservation (PPAC) used the consolidated ranges of all species categorised as: (1) CR; (2) CR and EN; (3) CR, EN and VU; and (4) CR, EN, VU and NT. These PPACs were selected to ensure priority for biogeographical areas containing the most highly threatened species. Incidental species' representation was also considered to identify the added value of each PPAC. We considered the use of a fifth scenario including the distribution of the single DD species, however this was found to be unnecessary as the range of this species was fully represented in scenario 3. We believe this approach is effective in identifying areas with the widest range of threatened *Conus* that may be managed economically.

3. Results

3.1. *Conus* species richness and distribution

Table 1 describes the 53 species of *Conus* assessed, of which 81% (43) are restricted to a single island and mostly within a small area (including *C. atlanticoselvagem* from the João Valente Shoals between Boa Vista and Maio). Distribution is weighted towards the east with the Leeward group in the south having disproportionately fewer species than the Windward group in the north (Figs. 2 and 3). Species richness is greatest on the islands of Sal, Boa Vista and Maio which together account for 41 species (Fig. 3). Together with the distribution of endemic *Conus* species richness, Fig. 2 also describes PAs with a marine element, and ZDTIs.

3.2. Tourism

Statistics from hoteliers for the decade from 2005 to 2014 show registered establishments increased by 73%, hotel arrivals by 131%, and total number of nights spent by 265% (Figs. S2 and S3). Visitors are concentrated on Sal and Boa Vista which together account for nearly 90% of total nights spent in Cape Verde (Fig. S3).

3.3. *Conus* status by Island

Table 1 summarises the assessment category of all endemic species by island (Fig. 1) with the rationale to support this and an outline of the development status of each island. Threatened (CR, EN, VU), Near Threatened (NT) and Data Deficient (DD) species are described in greater detail below:

Table 1

Assessed Cape Verde endemic *Conus* ($N = 53$) by island with rationale on threatened and near threatened species and proximity to areas zoned for tourism development (ZDTIs). Abbreviations for IUCN Red List species status—CR Critically Endangered, EN Endangered, VU Vulnerable, NT Near Threatened, LC Least Concern, DD Data Deficient.

Species names and Red List category of endemic <i>Conus</i>	Species' distribution (except Least Concern)	PAs with marine element & ZDTIs	Threats
Santo Antão (a) <i>C. fernandesi</i> (EN)	Recently described (2008); Porto Novo for 1 km to S of island.	PAs: None ZDTIs: None	Accidental discharge of oil and other pollutants from small but busy ferry port.
São Vicente (a) <i>C. bellulus</i> (DD)* (b) <i>C. decorates</i> (VU)* (c) <i>C. denizi</i> (NT) (d) <i>C. grahami</i> (LC)* (e) <i>C. navarroi</i> (NT)* (f) <i>C. lugubris</i> (CR) (g) <i>C. saragasae</i> (NT)* * also on Santa Luzia	All except (f) restricted to E of island. (a) Not recorded for several years. (b) Calhau S to Saragaça. (c) Praia Grande in NE of island. (e) Calhau (f) Restricted to N where centred at Baía de Salamansa. (g) Calhau to Baía de Saragaça	PAs: None ZDTIs: N: Salamansa SW: São Pedro; Vale de Flamengos SE: Saragaça e Topinho S: Palha Carga; Praia Grande NE: Norte e Sul da Baía das Gatas	(a) Probably always scarce. (b) Population in N lost from development, other scarce and suffering disturbance. (c, e) Pollution, over-gathering & habitat loss. (f) Most of the shallow water, rocky habitats disturbed; probably now extirpated. None collected since 1980s. (g) as (c, e).
Santa Luzia (a) <i>C. curralensis</i> (NT)	(a) Restricted to SW of island. See also São Vicente (*); <i>C. decorates</i> : Curral for approx 3 km in SW of island <i>C. navarroi</i> : Praia Francisca for 2 km. <i>C. saragasae</i> : Água Doce and Curral for 2 km.	PAs: Santa Luzia ZDTIs: None	(a) Pollution, over-gathering & habitat loss. See also São Vicente (*): <i>C. decorates</i> , <i>C. navarroi</i> and <i>C. saragasae</i> are all of highly restricted range on Santa Luzia and at risk from pollution and gathering.
São Nicolau (a) <i>C. kersteni</i> (NT)	Tarrafal in SW and other reported sightings.	PAs: None ZDTIs: None	Highly restricted range with few locations. Pollution.
Sal (a) <i>C. antoniomonteiroi</i> (LC) (b) <i>C. ateralbus</i> (EN) (c) <i>C. cuneolus</i> (EN) (d) <i>C. felitae</i> (VU) (e) <i>C. fontonae</i> (VU) (f) <i>C. longilineus</i> (LC) (g) <i>C. melissae</i> (LC) (h) <i>C. miruchae</i> (LC) (i) <i>C. mordeirae</i> (CR) (j) <i>C. pseudocuneolus</i> (LC) (k) <i>C. regonae</i> (VU) (l) <i>C. serranegrae</i> (LC)	All except (e, k) restricted to W of island. (b) Baía da Murdeira then 2 km to S into Baía do Algodoeiro. (c) As (b), continuing further S to Baía da Santa Maria. (d) N of Baía da Murdeira. (e) Regona in N to Petinha in S, incl. Fontona Bay. (i) Baía da Murdeira. (k) Pedro Lume to Ponta de Rabo de Junco in N of island.	PAs: Salinas Pedra; Lume e Cagaral; Costa da Fragata; Ponta do Sinó; Rabo de Junco; Serra Negra. ZDTIs: W: Murdeira e Algodoeiro S: Santa Maria Este e Oeste SE: Morrinho Branco NE: Pedra de Lume	(b, c, d, i) Tourism development. (e, k) Marine pollution especially accidental discharge of oil from tankers and other vessels using port of Palmeira.

(continued on next page)

3.3.1. Santo Antão

Santo Antão hosts a single species of *Conus*, namely *C. fernandesi* (EN), a recently described and scarce species that occurs along just one kilometre of coast, off Porto Novo and close to the small but busy ferry port, where it is at risk from accidental discharge of oil and other pollutants.

3.3.2. São Vicente and Santa Luzia

Eight species of *Conus* are endemic to these two islands, five of which occur on both. *C. curralensis* (NT) is restricted to Santa Luzia with *C. denizi* (NT) and *C. lugubris* (CR) restricted to São Vicente. With the exception of *C. lugubris* all São Vicente *Conus* occur off the island's east coast. *C. lugubris*, however, is limited to the north shore of the island with its centre of population in the Baía de Salamansa. Most of the shallow water, rocky habitats occupied by this species have been disturbed,

Table 1 (continued)

Species names and Red List category of endemic <i>Conus</i>	Species' distribution (except Least Concern)	PAs with marine element & ZDTIs	Threats
Boa Vista (a) <i>C. atlanticoselvagem</i> (NT) (b) <i>C. boavistensis</i> (LC) (c) <i>C. borgesii</i> (LC) (d) <i>C. crotchii</i> (EN) (e) <i>C. damottai</i> (LC)*** (f) <i>C. delanoyae</i> (LC) (g) <i>C. derrubado</i> (NT) (h) <i>C. diminutus</i> (NT) (i) <i>C. evorai</i> (NT) (j) <i>C. fuscoflavus</i> (LC) (k) <i>C. irregularis</i> (LC)*** (l) <i>C. josephinae</i> (NT)*** (m) <i>C. luquei</i> (NT) (n) <i>C. messiasi</i> (LC) (o) <i>C. pseudonivifer</i> (LC)** (p) <i>C. roeckeli</i> (LC) (q) <i>C. salreiensis</i> (CR) (r) <i>C. teodora</i> (VU) (s) <i>C. trochulus</i> (NT) (t) <i>C. venulatus</i> (LC)* (u) <i>C. vulcanus</i> (LC) * also on Maio, Sal, Santiago. ** also on Sal, Santiago *** also on Maio.	All except (a, g, l, m) restricted to W of island. (a) João Valente Shoals. (d) Morro de Areia S. to Santa Mónica, in centre of Morro de Areia ZDTI and near Chave ZDTI. (g) Derrubado for 5 km in N. (h) Two 2 km sites: Baía de Sal Rei and Morro da Areia. (i) Three sites: Praia Zebraca, Baía das Gatas in NE and the islet off Sal Rei in W of island. (l) Ponto do Rincão in N to Sal-Rei and S to Morro de Areia. Also on Maio. (m) Baía das Gatas in NE for 4 km. (q) Baía Teodora and Sal Rei with islet. (r) As (q), also possibly further to N. (s) Baía Teodora and Baía de Sal-Rei to Curral Velho; adjacent to part of ZDTI.	PAs: I. de Baluarte; I. dos Pássaros; I. de Curral Velho; Ponta do Sol; Boa Esperança; Morro de Areia; Tartaruga; Parque do Norte; I. de Sal-Rei. ZDTIs: NW: Chave W: Morro de Areia SW: Santa Mónica	(a) Only visited by lobster fishers, and does not at present attract divers. Potential for over-gathering and/or habitat degradation. (d) Damage to habitat during resort construction and then tourism. (g, h, i, l, m) All NT with highly restricted ranges at risk from increased tourism although not currently threatened. (q) Impact from harbour construction in early 1990s; now mainly found off the islet where at risk from pollution and human disturbance. Very scarce. (r) As (q) although less scarce. (s) As (g, h, i, l, m)
Maio (a) <i>C. calhetae</i> (LC) (b) <i>C. claudiae</i> (LC) (c) <i>C. crioulus</i> (LC) (d) <i>C. fantasmalis</i> (LC) (e) <i>C. infinitus</i> (LC) (f) <i>C. isabelarum</i> (LC) (g) <i>C. maioensis</i> (LC) (h) <i>C. raulsilvai</i> (LC)	All spp. LC.	PAs: Casas Velhas; Terras Salgadas; Lagoa de Címidor; Praia do Morro; Barreiro Figueira; Salinas de Porto Inglês. ZDTIs: S: Sul da Vila do Maio SE: Ribeira D. João; NW: Pau Seco	None immediate
Santiago (a) <i>C. verdensis</i> (LC)	All spp. LC.	PAs: None ZDTIs: SE: Norte da cidade da Praia; Sudoeste da Praia E: Achada Baleia; Mangue Monte Negro; Porto Coqueiro; Achada Lage;	None immediate
Brava (a) <i>C. furnae</i> (LC)	All spp. LC.	PAs: None ZDTIs: None	None immediate

and most, if not all of their populations are thought to have been extirpated. No specimens of *C. lugubris* have been collected since the 1980s. *C. decorates* (VU), occurs along the southeast coast of São Vicente where it is subject to disturbance from beach tourism, fishers and shell collectors. It is also found along three kilometres in the southwest of Santa Luzia where populations are considered scarce. A further population at Salamansa in the north of São Vicente has been lost. *C. bellulus* (DD) has not been recorded for several years and has probably always been scarce. There are two other NT species, namely *C. navarroi* and *C. saragasae*. As with *C. curralensis* and *C. denizi* both occupy highly restricted ranges in shallow water where they are at risk from pollution, over-gathering and habitat loss, although not yet at a level where they are at immediate risk.

3.3.3. São Nicolau

The island only hosts *C. kersteni*, which is restricted to the southwest. This species has been assessed as NT on a precautionary basis owing to its highly restricted range.

3.3.4. Sal

Twelve species of *Conus* are endemic to Sal. These include one CR, *C. mordeirae*; two EN, *C. ateralbus* and *C. cuneolus*; and three VU, *C. felitae*, *C. fontonae* and *C. regonae*. All six threatened species occur within snorkel reach at depths from

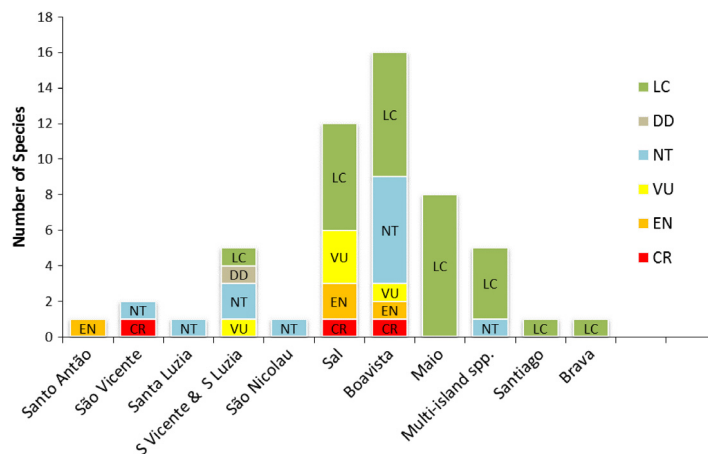


Fig. 3. Number of *Conus* species occurring on each Cape Verde island by category of threat. The four eastern islands of Sal, Boa Vista, Maio and Santiago that together host five species that occur across more than one of the islands are shown consolidated under 'Multi-island spp'. Only one species (*C. atlanticoselvagem*, classified as NT) occurs between two islands (Boa Vista and Maio) and this has been allocated to Boa Vista. Key: CR Critically Endangered, EN Endangered, VU Vulnerable, NT Near Threatened, LC Least Concern, DD Data Deficient.

approximately one to five metres along the western coast of the island, and except *C. fontonae* and *C. regonae* are principally located along Baía da Murdeira. The ranges of *C. ateralbus* and *C. cuneolus* also extend two kilometres to the south into Baía do Algodoeiro, while *C. cuneolus* also occurs along the southern bay of Santa Maria. North of Baía da Murdeira, *C. fontonae* occurs in Baía da Fontona to the south of the port of Palmeira, and *C. regonae* has its habitat extending to the north and south of the port. Both of these range-restricted shallow water species are threatened because of risk to their habitat from marine pollution, in particular the accidental discharge of oil from boat traffic including tankers and other commercial vessels using the port of Palmeira.

C. mordeirae, with its population restricted to the bay that bears its name, has been observed to be in decline, with the highest density of taxa occurring adjacent to resort developments. Similarly, *C. felitae* occurs solely in the north of the bay where plans have been mooted to extend development. Under such eventuality and in the absence of special conservation measures, this species may require re-categorisation from VU to CR.

3.3.5. Boa Vista

Boa Vista has the greatest diversity of *Conus* with 21 species of which 15 are endemic to the island. All three threatened species occur off the west coast of which *C. salreiensis* (CR) is only found in the northwest of Boa Vista in the bay at Sal Rei and its adjacent islet. Harbour construction in the early 1990s impacted abundance and this species is now mainly found off the islet where it is at risk from pollution and human disturbance. *C. crotchii* (EN) occurs from Morro de Areia south to Santa Mónica in the centre of the new tourism zone where paved roads and resort hotels are under construction. This places it at high risk from damage to habitat during the construction phase and of continuing disturbance thereafter from holidaymakers. *C. teodora* (VU) also occurs around Sal Rei continuing north to Baía Teodora for 4.5 km. Around the southern half of its range it is subject to the same pressures as *C. salreiensis*.

There are seven NT species found off Boa Vista of which five are endemic to the island: *C. derrubado* restricted to just five kilometres of coast in the north; *C. diminutus* which is found along two 2 km sites in the west; *C. evorai* and *C. luquei* which occur off Baía das Gatas in the northeast with another population of *C. evorai* at the islet off Sal Rei; and *C. trochulus* which with *C. josephinae* occurs along the western shores of Boa Vista adjacent to part of the development zone and continuing north to Sal Rei. There is a sub-population of *C. josephinae* also on Maio. With the exception of *C. trochulus* and *C. josephinae*, all these NT species have highly restricted ranges, and although not at immediate risk as they are sufficiently remote from main centres of tourism, they may become threatened in the future. *C. atlanticoselvagem* (NT) occurs on the João Valente Shoals which are only visited by lobster fishers, and although within SCUBA depths the shoals do not at present attract divers. However, its solitary site and the potential for over-gathering or habitat degradation have placed this species as a candidate for future review.

3.3.6. Maio, Santiago, Fogo and Brava

There are no threatened or Near Threatened *Conus* species on these islands except where they also occur on other islands (Table 1). However, in the light of recent tourism resort and casino development plans it may be necessary to review their assessments over the short term.

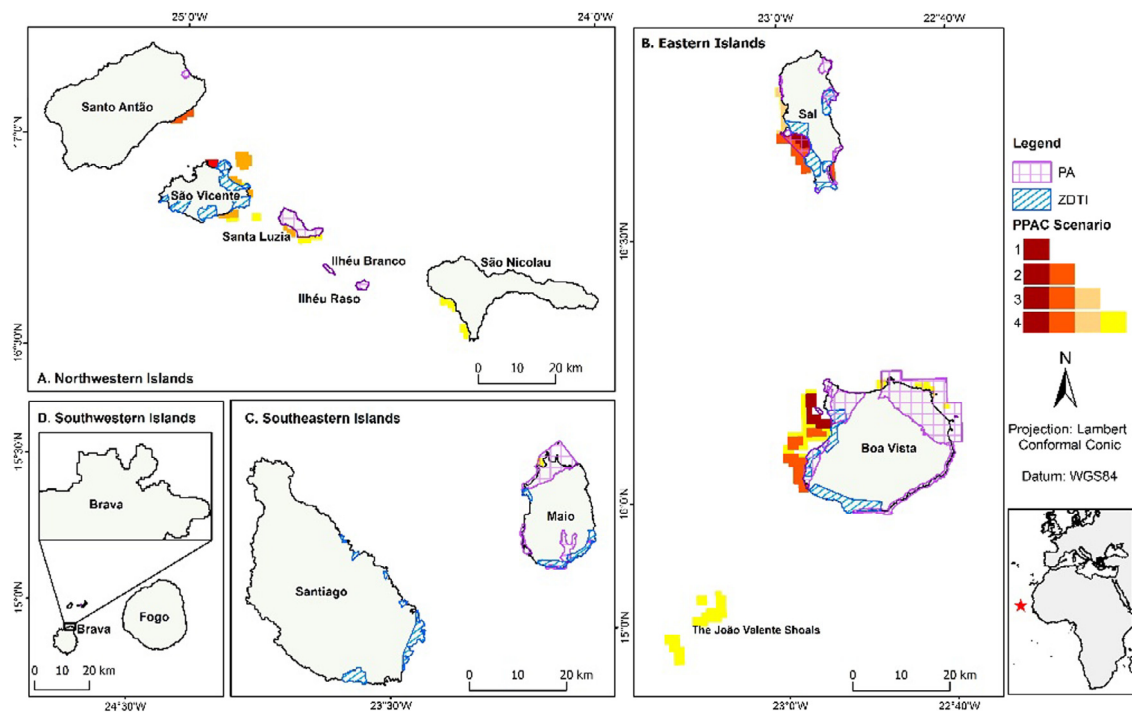


Fig. 4. Proposed Priority Areas for *Conus* research and conservation (PPACs) in Cape Verde according to four progressively expanding scenarios: PPAC 1 represents the range of all Critically Endangered (CR) species ($N = 3$); PPAC 2, all CR and Endangered (EN) species ($N = 7$); PPAC 3, all CR, EN and Vulnerable (VU) species ($N = 12$); and PPAC 4, all CR, EN, VU and Near Threatened (NT) species ($N = 24$). Additional information on each PPAC is provided in Table S4.

3.4. Proposed Priority Areas for Research and Conservation (PPAC)

Proposed priority areas for future research (e.g. ground truthing surveys) and conservation (PPACs) occur mostly around Sal, particularly to the southwest, and in the west of Boa Vista (Fig. 4). Other smaller pockets occur around Santo Antão, São Vicente and Santa Luzia. The combined areas range from 35 km² to 311 km², depending on which level of PPAC is adopted, representing between 4% and 33% of the entire range of *Conus* across Cape Verde (Table S3) and between approximately 0.12% and 1.11% of Cape Verde's territorial waters. Subject to physical survey, between 36% and 93% of species would be represented in any conservation initiative (Table S3). Under the most protective PPAC, i.e. number 4 (CR, EN, VU and NT), only four species, all of Least Concern, would be unrepresented: *C. antoniomonteiroi*, *C. furnae*, *C. melissae* and *C. verdensis*.

3.5. Tourism Development Zones (ZDTIs) with proximity to Proposed Priority Areas for Research and Conservation (PPACs)

Table 1 describes the ZDTIs designated on each island and Fig. 4 shows the position of the ZDTIs in relation to PAs and PPACs. ZDTIs in close proximity to PPACs include:

1. Boa Vista: Chave (PPACs 1–4), Morro de Areia (PPACs 2–4) and Santa Mónica (PPAC 2).
2. Sal: Morrinho Branco (PPACs 2–4) and Murdeira e Algodoeiro (PPACs 1–4).
3. São Vicente: Salamansa (PPAC 2), Sul da Baía, Ponta de Saragaça and Vale Palha Carga, and Calheta (PPACs 3–4).

Areas requiring the most urgent research and potential protection (PPAC 1) are located around the islands of Boa Vista, Sal and São Vicente (Fig. 4 and Table S4). Currently, only Sal has PA conservation support for PPAC 1 (CR) and 2 (CR & EN) areas through the Baía da Murdeira Nature Reserve and the Costa da Fragata Nature Reserve. Only under PPAC 4 do other islands offer any existing protection to PPACs. No PPACs are located around the islands of Brava, Fogo, Santiago, Branco or Raso.

4. Discussion

Cape Verde is a centre of endemism for both terrestrial and marine organisms (Freitas, 2014; Romeiras et al., 2016; Vasconcelos et al., 2012). Twelve Cape Verde *Conus* species are classified as threatened on the Red List of which three attain the highest risk category of Critically Endangered. A further 12 species have been assessed as Near Threatened. All these species have highly restricted ranges, low population sizes and an inability to freely disperse which exposes them to an elevated risk of extinction from a range of pressures. As numbers decline, low-density populations fall subject to the 'Allee

Effect' and become unable to locate a mate (Berec et al., 2007), exacerbated by inadequate genetic diversity to ensure a healthy population (Briggs, 1966).

There are many who consider marine taxa to be less susceptible to extinction risk than terrestrial species (Roberts and Hawkins, 1999; Webb and Mindel, 2015). However, our assessment of Cape Verde *Conus* suggests that threats to its marine endemic species may be comparable to its non-marine endemics. For example, in a Red List assessment of Cape Verde reptiles, only three were non-endemic from the 37 extant species recorded of which approximately 35% are within a threatened category (CR/EN/VU) with none listed as Near Threatened (NT) (Vasconcelos et al., 2013). This compares similarly to three non-endemic *Conus* from 56 species occurring in the archipelago, of which 43% are either threatened or Near Threatened. (Vasconcelos et al., 2013) state natural disasters as representing one of the principle threats to Cape Verde reptiles, but as with *Conus*, threats to reptiles are exacerbated by their highly restricted range further aggravated by specimen collection. A similar picture emerges elsewhere when comparing Cape Verde cone snails with other endemic non-marine taxa at risk: for example, the global threat attributed to island endemic birds (De Lima et al., 2011; Johnson and Stattersfield, 1990; Stattersfield et al., 1998) equates with the 23% of endemic *Conus* in Cape Verde threatened with extinction (CR/EN/VU).

To-date most tourism in Cape Verde has been concentrated on Sal and Boa Vista, but there is intent to expand to other islands, in particular low-tourism areas of Maio (SDTIBM, 2013b), São Vicente (Laurie and Benchimol, 2013), and Santiago (Nshimyumuremyi and Simpasa, 2015). It has been reported that the government would like to see one million visitors by 2020 although many believe this would be unsustainable (Baker, 2009). In common with many developing countries, Cape Verde suffers from inadequate management of its natural resources with damaging practices such as sand extraction. New harbour construction has already resulted in the decline of *C. salreiensis* leading to its Critically Endangered status. Disturbance to habitats from tourism infrastructure projects has had similar impacts on the viability of Cape Verde's two other Critically Endangered species, namely *C. lugubris* and *C. mordeirae*. With multi-million dollar investments also driving an emerging international resort and casino sector, exemplified by large-scale construction that will cover the islet of Santa Maria off Santiago (Semedo and Gomes, 2015), this can be expected to continue.

Our analysis has shown that Cape Verde endemic *Conus* with their narrow bathymetric range biased towards coastal shallows combined with a restricted geographical distribution places all species at risk especially in areas of development for tourism. Although some species are targeted by specimen shell collectors this is not yet believed to have had a major impact on the viability of most (Tenorio pers. comm. 2013). However, rare species already facing pressures from other factors may be pushed further towards extinction by irresponsible gathering for shells.

A recent study revealed there to be scant awareness among citizens of the islands' vulnerability to climate change and its likely impacts (de Carvalho, 2013). It is currently unknown what effect, if any, the hurricane on September 1, 2015 will have had on shallow water marine organisms. This hurricane, the most easterly ever recorded in the tropical Atlantic (NOAA, 2015) is possibly the harbinger of future extreme weather events caused by climate change. Certainly, elevated sea-surface temperatures combined with increasing acidification of the oceans create an uncertain future for all marine calcifying taxa (Doney et al., 2009). This includes cone snails (Peters et al., 2015) and other molluscs whose larvae are at particular risk (Gazeau et al., 2013).

Recognising this lack of environmental awareness, PANA II incorporated programmes of popular education and environmental awareness including marine protection into its strategic plans. Furthermore, the use of ZDTIs to control development with enforceable environmental impact assessments and designation of 47 protected areas, further underscore the government's commitment. This is to be applauded, however, this could be put at risk through a shortage of political will and lack of funding (UNDP, 2009).

Biodiversity hotspots and centres of endemism such as Cape Verde benefit from integrated conservation strategies incorporating both marine and terrestrial ecosystems to the benefit of all taxa within boundaries (Roberts et al., 2002). In its current form, the protected area network in Cape Verde is primarily an ad-hoc collection of zones selected as much for their landscape appeal as for any planned ecological purpose, and generally lack management and scientific monitoring (Vasconcelos et al., 2012). Our proposed priority area approach for *Conus* will enhance Cape Verde's conservation initiative and coincidentally help conserve other shallow water taxa, in particular sessile and semi-sessile marine invertebrates and the habitats in which they occur (Dumas et al., 2013; Edgar and Barrett, 1999; Linares et al., 2011). This can be particularly effective where terrestrial and marine reserves are treated as a combined entity (Roberts et al., 2002). However, to be effective, such areas need to be fully-enforced, permanent no-take zones (Edgar et al., 2014).

To secure the future of Cape Verde *Conus*, further direct and enforceable action is needed before projected increases in tourism are realised. With customs control of threatened species unrealistic, we recommend an export ban on all Cape Verde *Conus* either animals or shells, with exception only through special licence for scientific research. Population assessments with ongoing monitoring of all *Conus* species should be initiated using PPACs as a guide. We have identified 311 km² of *Conus* habitat as PPACs, 11% of which, i.e. those identified under PPAC 1 (Fig. 4) should be considered for immediate protection under the precautionary principle although Sal protected areas in particular already offer protection to some of the PPACs.

In pursuit of effective *Conus* conservation, we recommend further species' habitat and bathymetric assessments via mapping and ground survey techniques, to strengthen knowledge and ensure current and future marine reserves provide adequate protection. With many ZDTIs adjacent to PPACs, further marine protection may be needed. ZDTIs planned for other islands should be considered in line with PPACs. To meet its international commitments under the Convention on Biological Diversity (ratified March 1995), Cape Verde needs to not only legally define protected areas but to also develop effective and transparent management, monitoring and enforcement strategies. To achieve this we strongly support the establishment of

a Protected Area Autonomous Authority (PAAA). We recognise that marine protection can only be effective if it is supported by the populace and in particular by those who are likely to feel disadvantaged by its implementation such as fishers. Consideration therefore needs to be given to the impact on current activity within the proposed areas and how regional authorities, whose responsibility will be to manage and enforce the designated areas, can play a central role supported by international organisations.

Through this study, we have identified shortfalls in current conservation strategy in an attempt to propose solutions against further declines in Cape Verde's *Conus* populations, and to protect the country's shallow water habitat to the benefit of many taxonomic groups, including anthozoa such as sea anemones (Monteiro et al., 1997), corals, crustaceans such as lobsters *Panulirus regius* and *P. charlestoni*, already severely over-fished, as well as many species of fish and other molluscs (Duarte and Romeiras, 2009), and organisms such as amphipods and isopods (Stock and Vonk, 1992).

Worldwide, our methodology is applicable to other regions of high endemism to help inform their marine management strategies. Our findings clearly illustrate that marine organisms can face similar levels of extinction risk to non-marine taxa (McKinney, 1998; Roberts and Hawkins, 1999; Webb and Mindel, 2015) and that many of the management issues raised through our analysis apply to conservation planning in general, thereby supporting the high value of systematic and integrated conservation.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at <http://dx.doi.org/10.1016/j.gecco.2016.06.006>.

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