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Plastic pollution and climate change effects on nesting beaches of loggerhead turtle *Caretta caretta*

Diana Sousa Guedes

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Diana Sousa Guedes
Thesis carried out as part of the doctoral program in Biology
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Supervisor
Neftalí Sillero, Principal Researcher, CICGE – Faculty of Sciences of the University of Porto

Co-supervisors
Filipa Bessa, Auxiliary Researcher, CFE – University of Coimbra
Adolfo Marco, Researcher, CSIC – Estación Biológica de Doñana

Mãe, Pai, Rita, e Elton

Djam tem andado mundo

Ma n ca ta atxa lugar sab si

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Resumo

Os ecossistemas costeiros destacam-se como um dos ambientes mais produtivos e biologicamente diversos do planeta, mas enfrentam ameaças crescentes devido às alterações climáticas, sobre-exploração de recursos naturais, urbanização e poluição. As praias arenosas, onde nidificam tartarugas marinhas, são dos habitats mais vulneráveis a essas pressões. Estas ameaças contribuem, em conjunto, para a perda de área de praia. O lixo marinho, especialmente os plásticos, tornou-se uma questão ambiental ubíqua, que afeta a fauna marinha e costeira, a saúde humana e a economia. As alterações climáticas, e os seus efeitos no aumento das temperaturas, subida do nível do mar e erosão, agravam ainda mais os desafios enfrentados por estes habitats. Usando Cabo Verde como caso de estudo, esta tese investiga os impactos de duas grandes crises ambientais—poluição por plástico e alterações climáticas—em praias de nidificação da tartaruga-comum (*Caretta caretta*). O arquipélago de Cabo Verde, localizado na costa ocidental de África, alberga uma das maiores populações reprodutoras desta espécie a nível mundial. Neste estudo, aplicámos abordagens experimentais e preditivas a múltiplas escalas ecológicas. O primeiro capítulo introduz a atual crise global causada pelas alterações climáticas e pela poluição por plásticos, focando-se nas suas implicações para os ecossistemas costeiros e para os locais de nidificação de tartarugas marinhas. À escala do ninho (Capítulo 2), avaliámos os efeitos diretos da poluição por plástico nos ninhos de tartaruga-comum através de dois estudos experimentais de campo realizados na ilha da Boa Vista. Os ninhos que foram expostos a maiores níveis de resíduos plásticos apresentaram uma redução significativa no sucesso de eclosão e uma menor sincronização na emergência das crias, aumentando a sua vulnerabilidade à predação. Além disso, foram detetados aditivos químicos nocivos (retardadores de chama) na areia exposta a resíduos plásticos, representando riscos para o desenvolvimento embrionário. À escala da ilha (Capítulo 3), investigámos os padrões de acumulação de lixo marinho em duas ilhas importantes para a nidificação em Cabo Verde. Em Santa Luzia, a única ilha não habitada do arquipélago, identificámos praias viradas a norte e com maiores elevações como pontos críticos de acumulação de lixo marinhos. Na Boa Vista, encontramos evidências de fragmentação *in situ* de plásticos,

com correlações significativas entre densidades de lixo em diferentes escalas espaciais. Em ambas as ilhas, uma grande parte do lixo quantificado é composta por plástico relacionados à atividade pesqueira. À escala do arquipélago (Capítulo 4), avaliámos a vulnerabilidade dos locais de nidificação em Cabo Verde, integrando múltiplos fatores de risco, incluindo lixo marinho, alterações climáticas, poluição luminosa e pressão turística. São Vicente, Santiago e Sal foram identificadas como as ilhas mais vulneráveis, enquanto que Santo Antão e Maio as menos impactadas. Também identificámos uma relação positiva entre a densidade de ninhos e o lixo marinho, sugerindo uma co-ocorrência significativa, enquanto que a poluição luminosa demonstrou uma relação negativa. À escala global (Capítulo 5), examinámos as tendências do número de ninhos de tartaruga-comum em locais importantes para a nidificação da espécie a nível global, com foco na influência do aumento das temperaturas. Avaliámos quatro décadas de tendências de temperatura, comparando com registos de nidificação disponíveis, e detétamos variabilidade regional nos efeitos. Algumas regiões, como as Caraíbas e o Mediterrâneo, registaram um aumento no número de ninhos correlacionado com o aumento das temperaturas, potencialmente devido à feminização, pois as tartarugas marinhas exibem determinação do sexo dependente da temperatura. Os riscos a longo prazo do aumento das temperaturas poderão levar a declínios populacionais. A par da investigação científica, o Capítulo 6 documenta o desenvolvimento e a disseminação de um vídeo documental destinado à sensibilização sobre os impactos da poluição por plásticos e das alterações climáticas nas tartarugas marinhas e em zonas costeiras. O capítulo final (Capítulo 7) sintetiza os principais resultados e lacunas de conhecimento, particularmente as interações entre múltiplas ameaças ambientais, defendendo a necessidade de investigação futura. Ao abordar estas ameaças a níveis local, regional e global, esta tese contribui para a compreensão dos impactos das alterações climáticas e da poluição por plásticos nos habitats de nidificação de tartarugas marinhas.

Palavras-chave: alterações climáticas, Cabo Verde, deteção remota, ilhas Atlânticas, imagens aéreas, lixo marinho, microplásticos, modelos ecológicos, mudanças globais, poluição marinha, praias de nidificação, tartarugas marinhas.

Abstract

Coastal ecosystems are among the most productive and biologically diverse environments, yet they face escalating threats from climate change, resource exploitation, urbanisation, and pollution. Sandy beaches, vital nesting grounds for sea turtles, are among the most vulnerable habitats to these pressures. These threats collectively contribute to losing beach areas, known as coastal squeeze. Marine litter, particularly plastic pollution, has emerged as a ubiquitous environmental issue, affecting marine and coastal wildlife, human health, and coastal economies. Climate change, through warming, rising levels, and increased erosion, further exacerbates the challenges faced by nesting environments. Using Cabo Verde as a case study, this thesis investigates the impacts of two major environmental crises—plastic pollution and climate change—on loggerhead turtle (*Caretta caretta*) nesting sites. The archipelago of Cabo Verde, located off the coast of West Africa, hosts one of the largest loggerhead turtle rookeries worldwide. We employed experimental and predictive approaches across multiple ecological scales. The first chapter introduces the global crises posed by climate change and plastic pollution, focusing on their implications for coastal ecosystems and marine turtle nesting sites. At the nest scale (Chapter 2), we evaluated the direct effects of plastic pollution on loggerhead turtle nests through two experimental field studies conducted on Boa Vista Island. Nests exposed to higher levels of plastic debris exhibited significantly lower hatching success and disrupted synchronised emergence of hatchlings, increasing their vulnerability to predation. Additionally, we detected harmful chemical additives (flame retardants) in the sand contaminated by plastic debris, posing risks to embryonic development. At the island scale (Chapter 3), we investigated marine litter accumulation patterns on two critical nesting islands of Cabo Verde. On Santa Luzia, the only inhabited island of the archipelago, we identified north-facing beaches with higher elevations as hotspots for marine debris accumulation. On Boa Vista, we found evidence of *in situ* fragmentation of larger plastics, with significant correlations between debris densities at different spatial scales. A considerable portion of the debris on both islands was linked to fishing activities. At the archipelago scale (Chapter 4), we assessed the vulnerability of nesting sites across Cabo

Verde by integrating multiple risk factors, including marine litter, climate change, light pollution, and tourism pressure. We identified São Vicente, Santiago, and Sal as the most vulnerable islands, while Santo Antão and Maio were the least impacted. We also found that marine debris correlates positively with nest density, which might suggest a significant co-occurrence, while light pollution has a negative impact. At the global scale (Chapter 5), we examined trends in loggerhead turtle nesting counts across globally significant rookeries, focusing on the influence of rising temperatures. Four decades of temperature data and nesting records revealed regional variability in the effects of temperatures on nesting trends. Some regions, such as the Caribbean and the Mediterranean, have seen increasing nesting numbers, potentially linked to feminisation due to temperature-dependent sex determination. The long-term risks of continued warming could lead to population declines. Beyond scientific research, Chapter 6 documents the development and dissemination of a documentary video aimed at raising awareness about the impacts of plastic pollution and climate change on sea turtles. The final chapter (Chapter 7) synthesises key findings and knowledge gaps, particularly the interactions between multiple environmental threats, and advocates for further research. By addressing these threats at local, regional, and global levels, this thesis contributes to understanding the impacts of climate change and plastic pollution on sea turtle nesting habitats.

Keywords: aerial imagery, Atlantic islands, Cabo Verde, climate change, ecological modelling, global changes, marine litter, microplastics, nesting beaches, remote sensing, sea turtles, trend analysis.

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CHAPTER 1

General introduction

General introduction

Ecosystems on Earth are facing a triple planetary crisis, driven by climate change, habitat loss, and pollution, together contributing to global biodiversity loss (UNEP, 2021). Each issue individually destabilises ecosystems, yet their interactions can amplify impacts on ecological resilience (Brook et al., 2008). Biodiversity, encompassing the variety of life at all levels of biological organisation, from cells, genes and species to entire ecosystems, supports essential ecosystem services such as pollination, water purification, and nutrient cycling. However, it is increasingly threatened by the combined effects of these pressures (Redford and Richter, 1999; Díaz et al., 2019). As species disappear, ecosystems lose not only individual organisms but also the web of interactions and mutual dependencies that maintain their stability. The decline in genetic diversity makes populations more vulnerable to emerging threats, including climate change and diseases (Frankham, 2005). Habitat fragmentation and destruction, mainly human-induced, isolates populations and restricts the movement of individuals and their adaptability, increasing extinction risks (Fahrig, 2003; Mantyka-Pringle et al., 2015). Together, these crises create complex vicious cycles: pollution and habitat degradation may reduce species' resilience to climate change, while biodiversity loss limits the ecosystems' ability to buffer against stressors like pollutants and climate change (Brook et al., 2008; Mantyka-Pringle et al., 2012, 2015; Hooper et al., 2012; Sigmund et al., 2023). While habitat loss is indeed a key driver of biodiversity decline, this study focused on the role of climate change and pollution in driving biodiversity loss and how they intensify the global crisis we face today (Brook et al., 2008; Villarrubia-Gómez et al., 2024).

Climate change

Human activities such as the burning of fossil fuels, deforestation, and industrial processes have contributed to an increase the concentration of greenhouse gases in the atmosphere (IPCC, 2022). Consequently, global temperatures have risen, causing sea level rise, shifts in precipitation

patterns, ocean acidification, melting of glaciers and polar ice caps, and increased extreme weather events (Hoegh-Guldberg et al., 2007; Feely et al., 2009; Nimura, 2013; Ummenhofer and Meehl, 2017; IPCC, 2022; Bosson et al., 2023). While climatic fluctuations have always occurred, the current rate and magnitude of change are unprecedented (Steffen et al., 2018; IPCC, 2022). For vertebrate animals, adapting to the projected changes over the next 100 years would require evolutionary rates far exceeding those observed in the past (Quintero and Wiens, 2023).

Climate change is a major driver of biodiversity loss, altering ecosystems and diminishing ecosystem services (Pereira et al., 2024; Tariq et al., 2024). As global temperatures rise, biomes and ecosystems shift to align with new climate regimes (Sousa-Guedes et al., 2020; Boonman et al., 2022). These warming trends degrade habitats on land, with some areas becoming arid and prone to desertification, while others become vulnerable to flooding (Brook et al., 2008; Mantyka-Pringle et al., 2012). Warmer seas contribute to coral bleaching, habitat degradation, and shifts in ocean dynamics that impact marine ecosystems (Hoegh-Guldberg et al., 2007). Climatic changes can operate at multiple ecological levels, such as individual, species, population, community, or ecosystem, and can drive some populations to extinction (Bellard et al., 2012). But not all species are negatively impacted, with some showing evidence of adaptation and dispersal and may even benefit from changes in landscape and climate (Thomas, 2011; Kerr, 2020). Species may respond to environmental changes through shifts in phenology (timing), geographic range (space) or physiology (biological functions) (Parmesan, 2006; Cleland et al., 2007; Bellard et al., 2012).

Phenology refers to the timing of seasonal life events, such as flowering or migration, which are often triggered by environmental cues like temperature (Schwartz, 2003). Many species are changing their life cycles in response to warming temperatures (Visser and Both, 2005). For instance, plants may flower or fruit earlier, birds may alter their migration schedules, and amphibians and reptiles may shift their breeding and hatching times (Cleland et al., 2007; Körner and Basler, 2010; Mira de Orduña, 2010; Dunn and Møller, 2014; While and Uller, 2014; Bodensteiner et al., 2019; Du et al., 2023). Earlier nesting has been observed in different reptile

species (e.g., terrestrial turtles and tuataras) following warm winters or springs (Schwanz and Janzen, 2008; Nelson et al., 2018). Sea turtles' migratory and feeding patterns may be altered following ocean currents shifts (Poloczanska et al., 2009). Certain butterflies are emerging earlier in spring, which can lead to mismatches with food resources or conditions essential for survival (Stefanescu et al., 2003). These shifts can disrupt food chains, as early flowering plants may not coincide with the availability of pollinators, affecting both plant reproduction and the organisms that rely on these plants (Theurillat and Guisan, 2001).

As temperatures rise, species may shift their geographic ranges in search of cooler conditions (Chen et al., 2011). This includes terrestrial species moving to northern regions or higher elevations (Elsen and Tingley, 2015; Sillero, 2021) and marine species shifting to cooler or deeper waters (Pinsky et al., 2013). Range shifts impact ecosystems, leading to novel species interactions, competition, or genetic isolation (Gilman et al., 2010; Pecl et al., 2017). Range shifts of herbivores may overgraze vegetation as a consequence (Kaji et al., 2000; Kennedy-Slaney et al., 2018; Felton et al., 2024). Species with limited mobility or narrow habitat requirements, such as amphibians in isolated mountain regions, face a heightened risk of local extinctions (Carey and Alexander, 2003; Li et al., 2013; Vale and Brito, 2015).

Species may also adapt to new climate conditions through physiological changes, such as increased tolerance to temperature extremes or desiccation (Bozinovic and Pörtner, 2015). This can include altered metabolic rates, changes in body size, or adjustments in thermal regulation to cope with new environmental conditions (Huey et al., 2012; Bozinovic and Pörtner, 2015). For example, smaller body sizes, as seen in some bird species, facilitate heat dissipation in warmer climates (Sheridan and Bickford, 2011). Likewise, some reptiles have developed physiological mechanisms to regulate water loss, allowing them to persist in habitats where water is scarce and temperatures fluctuate widely (Blaustein et al., 2010; Vale and Brito, 2015).

While some species may cope with changing environments, many will struggle to keep pace as these responses require adaptation time (Quintero and Wiens, 2023). Local extinctions may occur

when species cannot adapt to new climate regimes, triggering cascading effects across food webs. For instance, the loss of pollinators such as bees disrupt plant reproduction, threatening food security by reducing crop yields (Allen-Wardell et al., 1998; Kevan and Viana, 2003). Declines in bat populations can lead to increased agricultural pests and subsequent crop damage due to reduced insect predation (Tuneu-Corral et al., 2023; Frank, 2024). The loss of top predators, such as owls, foxes, or sharks, often results in prey overpopulation, which can degrade vegetation and shift disease dynamics within ecosystems (Gilg et al., 2009). Such climate-driven biodiversity loss has global implications for both ecological balance and human well-being.

Plastic pollution

While often perceived as a localised issue, pollution—including heavy metals, pesticides, nutrient runoff, and plastics—has grown into a pervasive global crisis. Plastics, in particular, have recently raised concerns due to their persistence, versatility and durability, traits that have driven extensive accumulation across almost all ecosystems (Thushari and Senevirathna, 2020). Plastic pollution is a complex environmental challenge, posing serious threats to both wildlife and human health (Wilcox et al., 2015; MacLeod et al., 2021; Thompson et al., 2024).

Concerns over plastic debris in the environment date back to the 1960s, and by the 1970s small plastic fragments and fibres were detected in marine plankton samples (Ryan and Moloney, 1993; Thompson et al., 2024). Plastics break down into progressively smaller fragments, though the rates and timescales of fragmentation and eventual degradation processes remain unknown. Exposure to light, heat, humidity, wind, wave action and oxygen generally accelerates chemical deterioration and material fragmentation, but full degradation may take so long that nearly all conventional plastic ever produced remains on the planet (Thompson et al., 2005; Gedde et al., 2021).

In 2004, the term *microplastics* was introduced, marking a turning point in plastic pollution research (Thompson et al., 2004, 2024). Microplastics are defined as plastic particles smaller than 5 mm (but larger than 0.001 mm) and are categorised as either primary (intentionally produced for cosmetics or industrial uses) or secondary (resulting from the breakdown of larger plastics) (Hartmann et al., 2019). Since then, plastics of various sizes have been documented in diverse environments: shorelines (Browne et al., 2011), deep sea (Woodall et al., 2014), riverbeds, lakes (Eriksen et al., 2013), agricultural soils (Büks and Kaupenjohann, 2020), estuary sediments (Gardoki et al., 2024), sea ice (Obbard et al., 2014), the atmosphere (Wright et al., 2020), and even remote mountains (Napper et al., 2020). Global assessments predict over 52 million metric tonnes of plastic waste emitted into the environment annually, resulting in widespread mismanaged waste across oceans, waterways, and landscapes (Cottom et al., 2024). Current estimates suggest that around 7.6 million metric tons of large plastic waste enter oceans every year (Thompson et al., 2024), with potentially even greater amounts accumulating on land, reaching 10 to 40 million metric tons annually (Earth Action, 2023). This volume has led to the so-called *missing plastic* paradox, where model-based accumulation rates fall short of the observed quantities in the environment (Van Sebille et al., 2015).

Beyond environmental impacts, this pervasive pollution is increasingly raising concerns for human health (Wright and Kelly, 2017). Micro- and nanoplastics (particles < 0.001 mm; Hartmann et al., 2019) have been detected in human tissues and bodily fluids, including blood, lungs, liver, kidneys, reproductive organs, and the placenta (Ragusa et al., 2021; Horvatits et al., 2022; Jenner et al., 2022; Leslie et al., 2022; Liu et al., 2023; Zhao et al., 2023). Common exposure pathways include ingestion (through seafood, drinking water and food packaging; Cox et al., 2019), inhalation (especially from lightweight synthetic textiles and airborne fibres; Chen et al., 2020), and, to a lesser extent, dermal contact (Revel et al., 2018). Although research on long-term effects is ongoing, early evidence suggests potential links to cancer risks, endocrine disruption, and autoimmune diseases (WHO, 2022; Ali et al., 2024). Disposed plastics also contribute to the

spread of vector-borne diseases (such as dengue or malaria), and thus should be considered a public health issue (Krystosik et al., 2020).

This impact extends well beyond humans, as plastic pollution affects the reproduction, growth, and survival of over 1,300 species (Thompson et al., 2024), from aquatic (e.g., fishes, corals, octopus, whales, sea turtles) to terrestrial (e.g., lizards, birds, insects) (Kuhn et al., 2020; Edo et al., 2021; Santos et al., 2021; Rivers-Auty et al., 2023; Thompson et al., 2024). Larger plastic items pose physical threats—such as choking, entanglement, and restricted mobility—that can lead to injury or death, while ingestion of smaller plastics causes cellular and metabolic issues. Species with specific feeding strategies are especially prone to plastic ingestion (Gall and Thompson, 2015; Santos et al., 2021; Savoca et al., 2021a); seabirds, for instance, often mistake floating plastics for food, creating a false sense of fullness which can lead to malnutrition, toxicity, and sometimes starvation (Roman et al., 2020). Filter-feeding marine species, like baleen whales, are also at high risk, as microplastics may reduce feeding efficiency and introduce harmful toxins into their systems (Besseling et al., 2015; Gall and Thompson, 2015). Ingested plastics could serve as long-term bioindicators, providing insights into the trajectory of plastic pollution in marine environments (Savoca et al., 2024).

Indeed, plastic materials may release toxic chemicals into ecosystems and organisms (Mato et al., 2001; Teuten et al., 2009). Plastics are associated with over 16,000 chemicals, including 4,000 known hazardous substances, yet only about 6% are regulated globally (Wagner et al., 2024). These chemicals—either added during production or adsorbed from the environment—can bioaccumulate up the food chain, causing reproductive issues, immune suppression, and hormonal disruption (Andrady and Rajapakse, 2019). Many endocrine-disrupting chemicals (EDCs) and persistent organic pollutants (POPs) adhere to plastic particles, which then act as vectors, carrying pollutants into the food web and exposing organisms to harmful chemicals (Teuten et al., 2009; Rochman, 2015). In addition to carrying chemical pollutants, plastics can also serve as vectors for pathogenic bacteria or viruses (called the *plastisphere:* microbial community specifically

living on plastic debris), introducing additional health issues (Amaral-Zettler et al., 2020; Meng et al., 2021; Marques et al., 2023).

In aquatic systems, entanglement with discarded fishing gear restricts wildlife movement, impairing feeding and reproduction, a phenomenon known as *ghost fishing* (Blettler and Mitchell, 2021). Lobsters and crabs, for example, become trapped in derelict traps, while sea turtles and seals become entangled in nets and lines as they surface to breathe, risking injury, drowning, and death (Page et al., 2004; Nelms et al., 2016). This ongoing threat contributes to population declines, as ghost nets continue to indiscriminately catch marine life long after it has been discarded (Lewison et al., 2014). On land, birds that incorporate plastics into their nests expose their offspring to risks of entanglement and toxic exposure (Votier et al., 2011).

Plastics can also disrupt predator-prey dynamics by altering visibility and camouflage. For example, plastic litter may interfere with visual cues, making it harder for predators to locate prey or for prey to hide effectively. Experimental studies in the laboratory have shown behavioural changes in hermit crabs exposed to microplastics, demonstrating impaired decision-making and spending less time evaluating high-quality shells (Crump et al., 2020, 2023).

The widespread and multifaceted impacts of plastics complicate efforts to establish direct cause-and-effect relationships, especially in wildlife, where interactions with other environmental stressors often occur (Ford et al., 2022). Plastic pollution not only contaminates air, water, and soil but also severely degrades ecosystems, with each stage of the plastic lifecycle—from production to disposal—releasing greenhouse gases that exacerbate climate change (Cabernard et al., 2022; Sharma et al., 2023; Villarrubia-Gómez et al., 2024). Furthermore, it can also alter carbon sinks, increase ocean acidification due to rising CO_2 in the water column, and disrupt biogeochemical flows in both the water column and sediments (Villarrubia-Gómez et al., 2024). Moreover, extreme weather events and floods associated with climate change are expected to intensify the spread of plastic in natural environments (Galgani et al., 2015; Welden and Lusher, 2017; Wang et al., 2019). These two crises—plastic pollution and climate change—frequently

overlap, placing coastal and marine ecosystems among the most vulnerable (Thushari and Senevirathna, 2020; Ford et al., 2022). Shorelines, estuaries, coral reefs, ocean gyres and the deep sea have become long-term reservoirs for plastic accumulation, further damaging ecosystems already under pressure from climate change and other human activities (Woodall et al., 2014; Lavers and Bond, 2017; Horton and Barnes, 2020; Thushari and Senevirathna, 2020; Ford et al., 2022). For example, coral reefs are threatened by disease spread and direct physical damage from plastic pollution, as well as bleaching caused by rising ocean temperatures (Hughes et al., 2018; Lamb et al., 2018). Similarly, marine turtles face entanglement in plastic pollution and disruptions to migration caused by changing ocean currents. Additionally, they are particularly vulnerable because they rely not only on marine ecosystems but also on sandy beaches for nesting—habitats that are highly susceptible to both plastic pollution and climate change.

Vulnerability of sea turtle nesting grounds

With only 16% of global coastal regions remaining ecologically intact (Williams et al., 2022), and 2.4 billion people living within 100 kilometres of the coast as of 2017 (UN, 2017), coastal ecosystems—systems at the land-ocean interface, ranging from wetlands and lagoons to seagrass beds and sandy beaches—are under immense pressure from human activities. These ecosystems provide essential services such as carbon sequestration, nursery grounds for marine life, and storm protection (Barbier et al., 2011; Liquete et al., 2013). Among the most biologically diverse and productive environments

Figure 1. Nesting loggerhead turtle (*Caretta caretta*). Photo: D. Sousa-Guedes

on Earth, they face critical threats due to climate change, urbanisation, resource exploitation, and marine litter pollution (Barbier et al., 2011; Lu et al., 2018; Jorge-Romero et al., 2022; Trégarot et al., 2024). Sandy beaches, making up over a third of global coastlines, are increasingly experiencing *coastal squeeze* (Defeo et al., 2009; Fanini et al., 2020; Defeo and Elliott, 2021): rising sea levels force shorelines to retreat inland, but expanding urbanisation hinders their natural migration, resulting in both the loss of beach area and damage to coastal infrastructure. The low elevation and loose sediment composition of sandy beaches make them highly prone to erosion, further narrowing these coastal areas (Defeo et al., 2009; Nicholls and Cazenave, 2010; Vousdoukas et al., 2020). Climate-driven increases in storm frequency and intensity exacerbate wave action, storm surges, and extreme winds, intensifying erosion and altering beach structure (Lu et al., 2018; He and Silliman, 2019). The stabilising presence of coastal vegetation and dunes, crucial for buffering waves and trapping sand, is also compromised by rising sea levels (Keijsers et al., 2016). These effects together may lead to a reduction in beach areas, particularly in low-lying regions where even minor increases can inundate extensive areas.

For sea turtles, which rely on sandy beaches to nest, these threats are particularly severe (Mazaris et al. 2009; Fuentes et al. 2011; Biddiscombe et al. 2020). While sea turtles have survived environmental shifts over millennia, their long life cycles may limit their capacity to adapt to the current and rapid human-induced changes (Bowen, 1995; Hawkes et al., 2009; Ceballos et al., 2015; Evers and Benson, 2019). As marine ectothermic species depending on two specific habitats, as they spend most of their lives in the ocean and nest on sandy beaches, climate change introduces specific risks (Fuentes et al., 2011; Mancino et al., 2022). Female sea turtles exhibit philopatry, returning to their natal beaches to lay eggs, which incubate for about two months before hatchlings instinctively crawl towards the ocean. Rising sea levels shrink global nesting habitats (Defeo et al., 2009; Lyons et al., 2020), particularly in low-lying areas, while increasingly intense storms cause nest flooding (Limpus et al., 2020; Martins et al., 2022). These impacts are species-specific: species with lower nest-site fidelity, such as leatherback turtles, may be less

vulnerable compared to those with high site fidelity, like loggerheads, which tend to return to the same nesting sites (Pike and Stiner, 2007).

Higher sand temperatures on beaches can skew sex ratios toward females, or even cause embryonic mortality when thresholds are exceeded (Fuentes et al., 2011; Saba et al., 2012; Hays et al., 2017; Laloë et al., 2024; Papazekou et al., 2024). Sea turtles exhibit temperature-dependent sex determination (TSD), where warmer incubation temperatures lead to female-biased hatchlings, while cooler temperatures produce males (Ewert et al., 1994; Howard et al., 2014). Although a female-biased sex ratio can initially boost population growth, extreme feminisation is evident in some populations, with nearly all-female hatchlings in certain regions (Kaska et al., 1998; Marcovaldi et al., 2016; Jensen et al., 2018; Tanner et al., 2019; Laloë et al., 2024). This imbalance reduces genetic diversity, potentially decreasing resilience to environmental changes (Lockley and Eizaguirre, 2021). As global temperatures continue to rise, especially in tropical nesting areas, lethal incubation temperatures may become more common, threatening future generations (Laloë et al., 2017).

The accumulation of marine litter (i.e., anthropogenic materials washed ashore) on nesting beaches, which are often mainly plastic materials, exacerbates these climate-related stresses. Sandy beaches worldwide are increasingly burned by plastic waste driven by ocean currents, tides, and wind (Barnes et al., 2009). Large plastic debris, such as fishing nets and containers, obstructs sea turtles' females' access to nesting sites, while hatchlings face heightened risks if debris blocks their path to the ocean (Triessnig et al., 2012; Aguilera et al., 2018). Microplastics can modify the thermal profile of the sand, potentially affecting sea turtle sex ratios (Lavers et al., 2021; Fuentes et al., 2023). There is even evidence of microplastics and associated chemicals within turtle eggs and embryos, suggesting possible maternal transfer or environmental uptake due to egg permeability (Savoca et al., 2021b; Chemello et al., 2023; Curl et al., 2024). Sea-level rise and increased coastal erosion may unearth old plastic debris buried in dunes, highlighting how the interaction between environmental changes and plastic pollution could intensify these issues

(Andriolo and Gonçalves, 2022). The long-term impact of plastic pollution on nesting beaches is still poorly understood, but plastic pollution will likely continue affecting coastal ecosystems and the species that depend on them. Understanding the combined threats of climate change, pollution, and coastal habitat degradation is essential—not only for the survival of sea turtles but also for preserving the broader marine ecosystems.

Cabo Verde – the largest nesting population of loggerheads in the East Atlantic

Islands, due to their geographic isolation and proximity to ocean currents, often act as sinks for marine debris (Lavers and Bond, 2017). They are also especially vulnerable to climate change, due to their low-lying coastlines, limited land and freshwater resources, and high levels of endemic species that have restricted ranges and small populations (Nimura, 1999; Duvat et al., 2017; Veron et al., 2019). The remoteness and small economies of islands further limit their capacity to effectively mitigate the compounded effects of environmental and climate stressors.

The Cabo Verde archipelago, located in the central Atlantic Ocean approximately 570 kilometres off the west coast of Africa, consists of ten volcanic islands and several smaller islets. These islands are divided into two main groups: the *Barlavento* (windward) islands to the north, including Santo Antão, São Vicente, Santa Luzia, São Nicolau, Sal, and Boa Vista, and the *Sotavento* (leeward) islands to the south, including Brava, Fogo, Santiago, and Maio. The islands are characterised by diverse landscapes ranging from volcanic mountains to vast sandy beaches, particularly in the eastern islands like Boa Vista, Sal, and Maio. The climate is typically arid to semi-arid, with low annual rainfall concentrated in a brief rainy season (August/September), making freshwater resources scarce.

The archipelago is part of the Macaronesia region—a biogeographic area encompassing the Azores, Madeira, Selvagens, Canaries, and Cabo Verde—which was first coined as a term by Philip Barker Webb around 1850 (Fernández-Palacios et al., 2024). More recently, some authors

have argued for the exclusion of Cabo Verde from Macaronesia due to its distinct biodiversity, particularly in the terrestrial flora, insect fauna, skinks, and marine species (Nicolás et al., 1989; Miralles et al., 2011; Tennent and Russel, 2015; Freitas et al., 2019). Instead, some researchers propose classifying Cabo Verde as part of the Sahelian Upwelling marine ecoregion, within the West African Transition province (Spalding et al., 2007; Freitas et al., 2019). While the concept of a Macaronesia bioregion may hold limited relevance beyond vascular plant geobotany, it remains officially recognised as a unified biogeographic region (Fernández-Palacios et al., 2024).

The sandy beaches of the archipelago host one of the largest breeding populations of loggerhead turtles (*Caretta caretta*) in the world, and the only stable reproductive population in the Eastern Atlantic (Marco et al., 2012). Cabo Verde officially ranks third globally in loggerhead nesting density, following the population of Northwest Atlantic (USA, ~80,000 nests annually) and Northwest Indian (Oman, ~70,000 nests annually) (Casale and Marco, 2015). However, recent years have seen a sharp rise in nest numbers in Cabo Verde, with 2021 marking a record of approximately 260,000 nests across the archipelago (Adolfo Marco, personal communication). This population holds significant international conservation importance, representing a genetically distinct lineage from the Mediterranean and American loggerhead populations (Carreras et al., 2011; Baltazar-Soares et al., 2020). Sandy beaches of the islands are crucial habitats for loggerhead turtles but face increasing threats from human activities, such as coastal development, tourism pressure, climate change and marine litter pollution.

Of the seven species of sea turtles on Earth, the loggerhead turtle is among the most widespread, inhabiting temperate and tropical oceans worldwide (Wallace et al., 2010). This migratory species travels long distances between feeding grounds and nesting sites. With a long life span, loggerheads exhibit delayed maturity, with sexual maturity being attained between the second and third decade of their lives depending on the specific population (Casale et al., 2009a, 2009b, 2011; Tucek et al., 2014; Avens et al., 2015; Baldi et al., 2023). Once mature, females display strong natal philopatric behaviour, returning to their natal beaches to lay eggs. Loggerhead nests incubate

for 50-60 days, after which hatchlings emerge at night, instinctively crawling toward the ocean. Early survival rates are low highly due to high predation on both beaches and at sea (Martins et al., 2021). The species exhibits temperature-dependent sex determination (TSD), where nest temperatures influence hatchling sex ratios (Ewert et al., 1994; Howard et al., 2014). Temperatures above the pivotal threshold, which varies by population (around 29°C in Cabo Verde), tend to produce more females—a growing concern as global temperatures rise due to climate change. The IUCN classifies the loggerhead turtle as Vulnerable globally; however, the East Atlantic population, including Cabo Verde, is listed as Endangered, emphasising the need for conservation efforts at both regional and global scales (Casale and Marco, 2015; Casale and Tucker, 2017).

Justification and aims of the thesis

This thesis investigates the effects of plastic pollution and climate change on critical loggerhead turtle (*Caretta caretta*) nesting sites across multiple ecological scales: nest (Chapter 2), island (Chapter 3), archipelago (Chapter 4), and global (Chapter 5). The study, distributed in a total of seven chapters, integrates experimental and predictive analyses to understand the threats to sea turtle nesting sites, using Cabo Verde as a case study.

The first chapter (Chapter 1) is a **general introduction** contextualising two global environmental crises (climate change and plastic pollution), their potential impacts on species, and specifically their effects on sea turtle nesting grounds.

At the **nest level** (Chapter 2), we examined the effects of plastic pollution directly on loggerhead turtle nests, focusing on the physical barrier effect and potential chemical contamination. This chapter comprises two subchapters: 2.1) experimental evidence of plastic debris effects on hatching success and disruption on the synchronised emergence of hatchlings (Manuscript I); and

2.2) chemical contamination from plastic debris into the sand, detecting harmful additives such as flame retardants (PBDEs), posing additional risks to embryonic development (Manuscript II).

At the **island level** (Chapter 3), we quantified marine litter accumulation on two critical nesting islands of Cabo Verde, comprising two subchapters: 3.1) quantification of marine litter accumulation in Santa Luzia, the only inhabited island of the archipelago, and investigation of how beach topography influences accumulation patterns (Manuscript III); and 3.2) quantification of marine litter in Boa Vista, testing the correlation in the density of different debris sizes and between two methods of survey (aerial sampling and sand sampling), serving as a baseline in one of the most important loggerhead nesting sites worldwide (Manuscript IV).

At the **archipelago scale** (Chapter 4), we explored and identified the most vulnerable nesting areas in Cabo Verde (Manuscript V). By integrating multiple risk factors—marine litter, climate change, light pollution, and tourism pressure—the study identifies both high-risk nesting areas and relatively safe beaches that could serve as long-term refuges for sea turtle nesting.

At the **global scale** (Chapter 5), we assessed the trends in loggerhead turtle nesting counts and the influence of rising temperatures on these trends (Manuscript VI). While some regions have experienced temporary increases in nesting numbers, the long-term consequences of continued warming could lead to population declines.

Additionally, a **science outreach** chapter (Chapter 6) is included as part of the original PhD proposal, mainly highlighting the development and media dissemination of a documentary video aimed at raising public awareness.

The last chapter (Chapter 7) is a **general discussion** of the findings of the thesis, contextualizing our results and what it means to the future of sea turtle populations. It highlights the main conclusions, also advocating for further research on the effects of the interplay between climate change and plastic pollution on sea turtle nesting grounds. This thesis addresses local and global environmental challenges in coastal habitats to support sea turtle conservation.

Publications

Manuscripts I, II, III and VI have been accepted or published, while manuscripts IV and V are currently under review. Manuscripts correspond to the chapters or subchapters of the thesis (Chapter 2: Manuscripts I and II; Chapter 3: Manuscripts III and IV; Chapter 4: Manuscript V; Chapter 5: Manuscript VI) and are presented in their original format:

I. Sousa-Guedes. D., Sillero, N., Bessa, F., Marco, A. 2023. Plastic pollution can affect the emergence patterns of loggerhead turtle hatchlings. *Animal Conservation,* 26(4), 492-501. doi.org/10.1111/acv.12837

II. Sousa-Guedes, D., Cunha, S.C., Fernandes, J.O., et al. 2023. Can plastic pollution contaminate loggerhead turtle nests? Evaluation of flame retardants (PBDEs) levels in the sand. *Marine Pollution Bulletin*, 195, 115550. doi.org/10.1016/j.marpolbul.2023.115550

III. Sousa-Guedes, D., Bessa, F., Queiruga, A., et al. 2024. Lost and found: Patterns of marine litter accumulation on the remote Island of Santa Luzia, Cabo Verde. *Environmental Pollution,* 344, 123338. doi.org/10.1016/j.envpol.2024.123338

IV. Sousa-Guedes, D., Sillero, N., Abu-Raya, M., et al. Mapping marine debris hotspots on Boa Vista Island, Cabo Verde. Under review in *Environmental Pollution*.

V. Sousa-Guedes, D., Marco, A., Neves, E., et al. How vulnerable are the nesting sites of loggerhead turtles in Cabo Verde? Under review in *Regional Environmental Change.*

VI. Sousa-Guedes, D., Campos, J.C., Bessa, F., et al. In press. The effects of warming on loggerhead turtle nesting counts. *Journal of Animal Ecology.* doi.org/10.1111/1365-2656.14242

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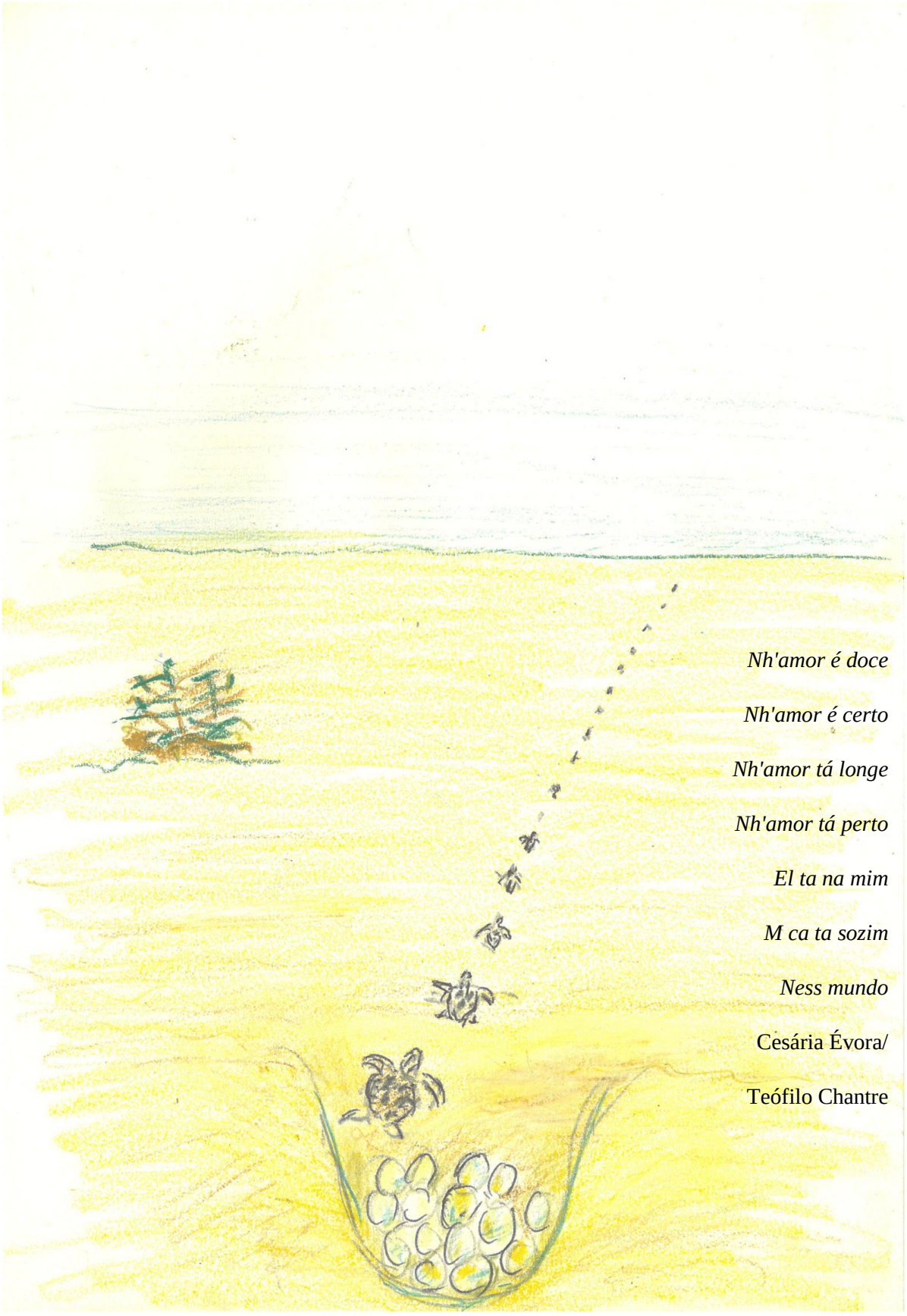

Nh'amor é doce

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Nh'amor tá longe

Nh'amor tá perto

El ta na mim

M ca ta sozim

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Cesária Évora/

Teófilo Chantre

CHAPTER 2

Effects of plastic pollution on sea turtle nests

2.1.

Plastic pollution can affect the emergence patterns of loggerhead turtle hatchlings

Sousa-Guedes, D., Sillero, N., Bessa, F., Marco, A. 2023. *Animal Conservation,* 26(4), 492-501

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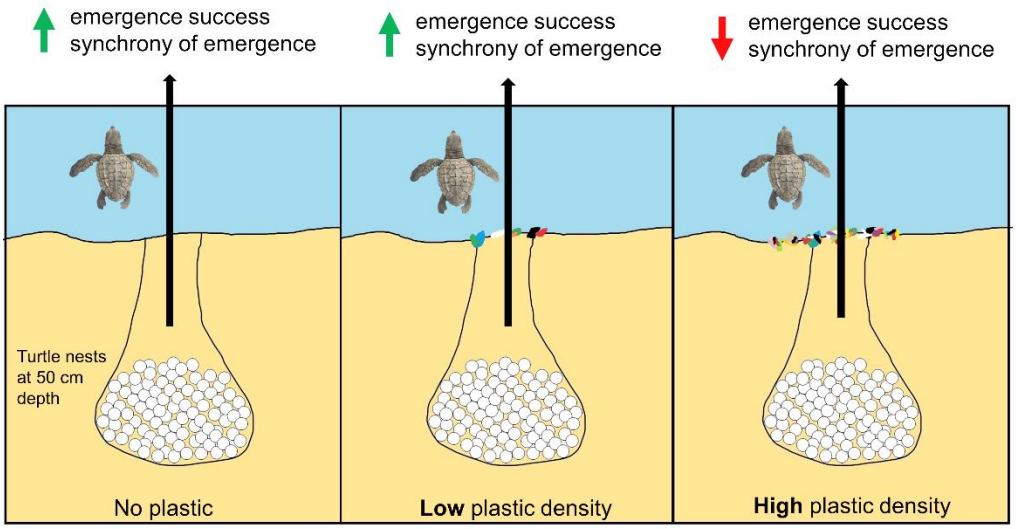

Abstract

Coastal urbanization, plastic pollution and climate change are increasingly affecting marine turtles' nesting habitats. In addition to facing risks of mortality due to saltwater inundation or predation, their eggs and hatchlings' might also be affected by plastic debris accumulation on beaches, but no studies to date have analysed such impact. To analyse whether plastic pollution on nests' surfaces affects the embryos' and hatchlings' survival odds, we designed a field experiment in a turtle hatchery on a nesting beach of the loggerhead turtle (*Caretta caretta*) in Boa Vista Island (Cabo Verde). We applied three treatments with distinct plastic levels (18 nests per treatment): control (no added plastics), low density (64 plastic fragments with 24.5 g of plastic weight per nest) and high density (128 plastic fragments with 49.0 g of plastic weight per nest). Then, we tested 16 variables related to the incubation period, emergence period and hatchlings' fitness. Our results suggest that nests with high plastic density have a significantly lower probability of successful emergence. Moreover, plastics also affected the synchronized emergence of hatchlings, with more scattered and smaller emergent groups, which might increase

the predation risk. Considering that turtle nesting habitats are becoming increasingly threatened, this additional threat might compromise the survival of turtle hatchlings on beaches.

Introduction

Anthropogenic impacts are currently, directly or indirectly, the most important cause of the decline of many species worldwide (Díaz et al., 2019). Multiple species have lost habitat suitability over time (Arenas-Castro and Sillero, 2021). From climatic changes to habitat fragmentation, almost all natural ecosystems are under serious human pressure (Maron et al., 2019). Plastic pollution is receiving increasing attention as an important acting pressure as well, due to its resistance, durability, persistence and easy accumulation in many environments and organisms (Barnes et al., 2009), even in the most remote locations (e.g., in the Antarctic gentoo penguins; Bessa et al., 2019). This type of debris may considerably affect wildlife, by ingestion (Pierce et al., 2004; Schuyler et al., 2015), choking or entanglement (Nelms et al., 2015; Wilcox et al., 2016), or chemical contamination (Rochman et al., 2013; Savoca et al., 2021). Most studies focus on the abundance of plastic debris in freshwater or marine ecosystems (Karbalaei et al., 2018), given that an important portion of the generated plastic waste ends up entering the ocean (Jambeck et al., 2015). Coastal habitats frequently accumulate plastic debris coming from the sea, depending mainly on ocean currents, tides and wind conditions (Barnes et al., 2009).

Coastal environments, namely sandy beaches, are becoming increasingly threatened due to the increasing urbanization of these habitats, increasing use of their natural resources, and decreasing resilience to climate change effects (e.g., sea-level rise) (Defeo and Elliott, 2021; Fanini et al., 2021). The set of these threats is known as the coastal squeeze or triple whammy (Defeo and Elliott, 2021). Moreover, these habitats are also considered marine debris sinks (Olivelli et al., 2020). These complex ecosystems are positioned at the land-sea interface and host important species communities during the total or a portion of their life cycle (Seitz et al., 2014). For

instance, marine turtles, a species group globally threatened (with six out of seven species being classified as vulnerable or worse, and one as data deficient; IUCN, 2021), spend an important part of their life cycle on sandy beaches: females go to land to lay and bury their eggs (usually the same beach they were born), returning to the ocean shortly after (Wyneken et al., 2013). Then, the period of incubation determines the embryos' successful development and survival until emergence. This successful development depends on different factors: sediment properties (sandy substrates rich in clay and silt cause embryos' mortality; Marco et al., 2017), temperature (warmer temperatures cause egg mortality and female-biased offspring; Yntema and Mrosovsky, 1982; Martins et al., 2020), egg predation (e.g., by crabs, domestic dogs, hogs or racoons; Marco et al., 2015; Butler et al., 2020), and nests inundation (saltwater inundation lower the eggs' viability; Patino-Martinez et al., 2014; Pike et al., 2015). After emerging from the nests, the hatchlings face more threats: light pollution causes hatchlings' disorientation and increases the prey-searching behaviour of crabs (Berry et al., 2013; Silva et al., 2017), vegetation increase the crawling time to the sea (Rivas and Marco, 2016) and the possibility of an encounter with a predator is high (Martins et al., 2021a). In addition to these threats, plastic debris accumulation on nesting beaches may also affect the embryos' and hatchlings' survival probability (Aguilera et al., 2018; Beckwith and Fuentes, 2018). For instance, plastic pieces may act as a barrier and trap the hatchlings inside the nest or on their way to the ocean, which may increase the crawling time and effort to reach the ocean, becoming more vulnerable to predators (Nelms et al., 2015; Aguilera et al., 2018). Moreover, although probably through internal transfer from the mother, Savoca et al. (2021) found that turtle eggs (especially eggshell and yolk) can accumulate phthalates, a component frequently used in many plastic types. Furthermore, the accumulation of large debris on beaches may also impact the females' nesting behaviour, with higher nesting activities occurring in cleaner areas (Fujisaki and Lamont, 2016).

To our knowledge, there are no studies on the impact of plastic accumulation on turtle nests, neither on the incubation nor the emergence periods. Data on plastic accumulation on beaches is still scarce (e.g., Monteiro et al., 2018; Gonçalves et al., 2020; Nichols et al., 2021) and it is a

challenge to evaluate this impact. To cover this knowledge gap, we designed a field experiment on an important nesting beach of the loggerhead turtle (*Caretta caretta*) in Boa Vista Island (Cabo Verde). The archipelago of Cabo Verde hosts the third-largest population of loggerhead turtle in the world and the only stable reproductive population of the Eastern Atlantic (classified as Endangered by IUCN; Marco et al., 2011; Casale and Marco, 2015). In this study, we aimed to analyse whether the plastic accumulation on the turtle nests' surface affects the embryos' and hatchlings' probability of survival. For that, we tested 16 variables related to the incubation period, emergence period and hatchlings' fitness. We hypothesized that plastics at the nests' surfaces might: (1) affect the embryo's development at the incubation stage through sand temperature alterations, affecting consecutively the incubation temperature, duration of incubation or hatching success; (2) affect the hatchlings' emergence patterns and hatchlings' fitness through alterations in the incubation stage.

Materials and methods

Study area

The study took place on Boa Vista Island, in the archipelago of Cabo Verde (Africa; Figure 1). Boa Vista is the easternmost island of the archipelago, characterized by a dry and windy climate, with the brief rainy season occurring between August and September. The experiment was performed at the turtle hatchery maintained by the NGO BIOS.CV at the João Barrosa beach, part of the Sea Turtle Natural Reserve. More than 40% of the nesting activity in Cabo Verde occurs in this reserve area of Boa Vista Island (Marco et al., 2012). On the northeast beaches of the island, a high volume of marine debris is accumulated (see Supplementary Materials, Figure S1). Like in other Atlantic islands, this plastic debris seems to come from the ocean, namely through boats, such as fishing vessels or leisure cruise ships (Monteiro et al., 2018), but also from the

African continent (Western Sahara, Mauritania and Senegal) or Cabo Verde itself (Cardoso and Caldeira, 2021).

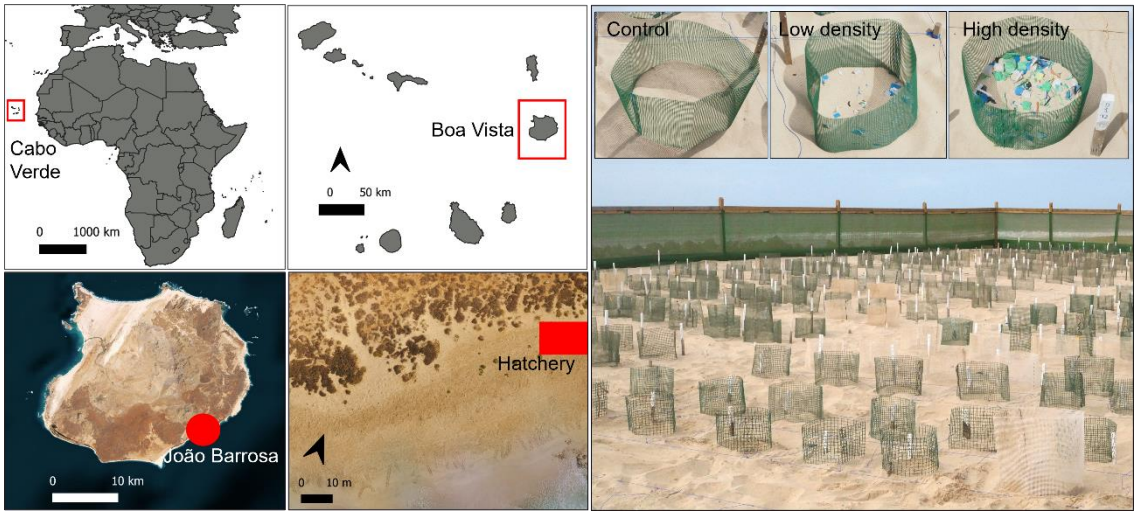

Figure 1. Study area: turtle hatchery of the João Barrosa beach, located on Boa Vista Island in the archipelago of Cabo Verde (Africa). In the upper right, photographs of nests of each treatment of the experimental study: control, low plastic density and high plastic density.

Experimental study

Between 1 August and 3 October 2021, we conducted a field experiment at the turtle hatchery of João Barrosa beach (N 16.016, W 22.741), by placing plastic fragments at the nests' surface. The turtle hatchery (approximately 16×27 m) was built at the beginning of the nesting season in an area easily accessed from the field camp, to allow more effective monitoring (Martins et al., 2021b). The hatchery was constructed in a higher area to prevent flooding and was fenced with nets to avoid the entrance of crabs and nesting females (see Figure 1).

At João Barrosa beach, we searched for nesting females. If the nest was considered at risk (e.g., due to inundation), the eggs were collected, counted and carefully transported to the hatchery, avoiding the rotation and vibration of the eggs. We placed the egg clutches in the nests at the

hatchery for five consecutive nights. At the hatchery, we excavated the nest chamber at 50 cm depth, replicating a natural nest (Abella et al., 2007; Marco et al., 2018). Translocated egg clutches were randomly assigned to each nest chamber; we did not separate the egg clutches into different nest chambers. The total time between nesting and placing at the hatchery never exceeded 6 hours. This translocation technique has been proven to be highly efficient in improving hatching success (Martins et al., 2021b). We placed a data logger (Thermochron iButton, DS1921G-F5, ±0.5°C) in the middle of each nest (after placing the first 40 eggs), which was programmed to measure the temperature every 60 minutes, and we noted the logger code for each nest.

We collected different types of plastic pieces stranded on the beach shore and cut them into smaller pieces (approximately 5×5 cm) to produce two different scenarios: low density (T1, with a mean number of 64 plastic pieces and mean plastic weight of 24.5 g per nest) and high density (T2, with a mean number of 128 plastic pieces and mean plastic weight of 49.0 g per nest). Collected plastics were a mix of different types, mostly thin to allow an easier cut: strings, ribbons, bags, cans, bottles, bottle caps and cups, representing commonly occurring items on these beaches. The density of plastics in each treatment was estimated simulating the density of plastic pollution found on some beaches of the island.

The experiment included 18 nests for each treatment (control, T1 and T2, with a total of 54 nests). We distributed the nests in three experimental blocks (each block with the three nest treatments alternatively placed) located in different zones of the hatchery, thus, each block was at a different distance from the shore, vegetation or dune zone. We marked each nest with an individual code. Plastic fragments were placed at the sand surface and partially buried within the 3 cm top layer of the sand, simulating natural conditions. Plastics were placed the day after the nest was translocated to the hatchery, in the nests with treatments T1 and T2. We did not place any fragments in the control nests. We placed a circular plastic mesh surrounding each nest, trapping the plastic pieces and the emergent hatchlings, to enable them to be counted. Moreover, we measured the temperature of the sand of every nest at two depths (10 cm and 20 cm), using a

probe thermometer (PCE Instruments, PCE-HPT 1, ± 0.1°C), once per week between 2:00 and 3:00 p.m.

After 48 days, during the hatching season, each nest was closely monitored from dusk until dawn. Every time hatchlings emerged, we recorded the number of hatchlings, date and time. We also measured the straight carapace length and straight carapace width (using a Digital Vernier Calliper, 150 mm ± 0.1 mm) and weighted the body mass (using an electronic scale, Mission Quark Pocket Scales – Weigh Darts, ± 0.1 g) of the first 22 hatchlings emerging in each nest. Then, we performed a righting response trial where each hatchling was placed upside down on a smooth sand surface and recorded the time it took to turn by themselves, with a maximum duration of 60 seconds, using a chronometer (Vieira et al., 2014). In addition, we counted the number of supernumerary epidermal scutes and took a dorsal photograph of the body. The collection of the hatchlings from the nests and the individual measurements were performed by different people, to ensure blinding and non-biased recordings. After the measurements, we released all the hatchlings (including the 22 individuals analysed) on the sand close to the ocean. On day 60, we performed exhumation of the nests to count the number of closed eggs, rotten eggs, dead and alive individuals hatching, hatched into the nest chamber, or hatched emerging to the surface.

Nest variables

We tested the influence of the three experimental treatments (response variable) on 16 explanatory variables related to the incubation period, emergence period and hatchlings' fitness (Table 1). The variables duration of emergence, emergence groups, proportion of emergence groups with 1 to 5 individuals, and proportion of individuals on biggest emergence group reflect the synchronization of hatchlings' emergence.

Table 1. Description and units of each selected variable related to loggerhead turtle incubation period, emergence period and hatchlings' fitness.

	Variable	Description	Unit
Incubation	Sand temperature at 10 cm	Mean weekly temperature of the sand at 10 cm of depth.	ºC
	Sand temperature at 20 cm	Mean weekly temperature of the sand at 20 cm of depth.	ºC
	Daily incubation temperature	Mean daily incubation temperature.	ºC
	Duration of incubation	Number of days from the nesting day to the day with the first emergent individual.	-
	Hatching success	Percentage of individuals that hatched. Calculated as the percentage of: (initial number of eggs – number of rotten or closed eggs) / initial number of eggs.	%
Emergence	Emergence success	Percentage of individuals that emerged. Calculated as the percentage of: number of individuals that emerged at nest surface / initial number of eggs.	%
	Duration of emergence	Number of days from the first hatchling emergence to the last.	-
	Emergence groups	Number of hatchling groups that emerged separated in time by at least 10 minutes.	-
	Proportion of emergence groups with 1 to 5 individuals	Percentage of emergence groups with 1 to 5 individuals. Calculated as the percentage of: number of groups with 1 to 5 individuals / number of emergence groups.	%
	Proportion of nocturnal emergence groups	Percentage of emergence groups that emerged during the night period, defined by those groups that emerged between 7:00 p.m. and 6:00 a.m. Calculated as the percentage of: number of nocturnal emergence groups / number of emergence groups.	%
	Proportion of individuals on biggest emergence group	Percentage of individuals on the biggest emergence group. Calculated as the percentage of: number of individuals on biggest emergence / initial number of eggs.	%
Hatchlings	Straight carapace length	Mean individual straight carapace lengths of the first 22 individuals.	cm
	Straight carapace width	Mean individual straight carapace widths of the first 22 individuals.	cm
	Weight	Mean individual weights of the first 22 individuals.	g
	Righting response test	Mean righting response test of the first 22 individuals.	sec
	Supernumerary epidermal scutes	Number of supernumerary epidermal scutes of the first 22 individuals.	-

Data analysis

We tested the normality (Shapiro–Wilk test) and homogeneity (Levene's test) of variances of the residuals and decided to perform the non-parametric Kruskal–Wallis tests to analyse whether each variable was significantly different in each treatment, using the ‘kruskal.test’ function of the ‘stats’ R package. We also performed Dunn's tests for pairwise comparisons between treatments when they were significantly different, implemented in the ‘dunnTest’ function of the ‘FSA’ R package (Ogle et al., 2022). For Dunn's tests, we presented the adjusted results with the Benjamini–Hochberg method. Kruskal–Wallis test and Dunn's test consider significance when

the p-value <0.05. Moreover, we also performed a boxplot for pairwise comparisons between treatments.

We performed a permutational multivariate analysis of variance PERMANOVA implemented in the 'adonis2' function of the 'vegan' R package (Oksanen et al., 2020), to evaluate the significance of differences between the variables within each group of variables. We calculated pairwise dissimilarities using the Gower distance method, which is a generalization of Gower's formula (Gower, 1971), implemented in the 'daisy' function of the 'cluster' R package (Maechler et al., 2022). The experimental design comprised one factor (plastic treatment), and the variables in each group (i.e., five variables in the analysis related to the incubation period, six of the emergence period, and five of the hatchlings' fitness). For each group of variables, we computed a global analysis tested by 999 permutations.

To visualize the interactions between variables and identify patterns, we computed and plotted a principal component analysis (PCA), using the 'prcomp' function of the 'stats' R package and the ggbiplot function implemented in the 'ggplot2' R package (Wickham, 2016). All variables related to the emergence period, incubation period and hatchlings' fitness were included in the PCA. All statistical analyses were carried out with the R software 3.6.3 (R Core Team, 2020).

Ethical statement

Permissions for the translocation of nests to the turtle hatchery and for evaluating the plastic impact on the nesting environment were obtained from the Government of Cabo Verde (licences n° 01/CN/2021 and 023/DNA/2021). All regulations for animal welfare and experimentation were followed. We consider that our field experiment does not threaten or harm the reproductive population of the study area since we used a small number of nests (36 nests with plastic fragments out of 33,500 nests in João Barrosa beach in 2021), all collected from risky areas for incubation (such as areas easily inundated by high tides), which typically have high mortality rates (Martins

et al., 2022). Moreover, the hatching success is typically higher in the hatchery in comparison with nests at the beach (Martins et al., 2021b).

Results

The 54 turtle nests of the field experiment resulted in a total of 2757 emergent hatchlings. The control nests had a total of 1471 eggs ($\bar{X} = 81.7 \pm 12.6$) of which hatched 1085 ($\bar{X} = 60.3 \pm 12.9$) and emerged 951 hatchlings ($\bar{X} = 52.8 \pm 15.6$). The nests of the treatment T1 had 1467 eggs ($\bar{X} = 81.5 \pm 10.7$), hatching 1131 ($\bar{X} = 62.8 \pm 13.0$) and emerging 1016 hatchlings ($\bar{X} = 56.4 \pm 14.8$). The nests of the treatment T2 had 1506 eggs ($\bar{X} = 83.7 \pm 8.5$) of which hatched 976 ($\bar{X} = 54.2 \pm 13.2$) and emerged 790 hatchlings ($\bar{X} = 43.9 \pm 14.9$) (see Supplementary Materials, Table S1). There is no significant difference in the number of total eggs, hatched eggs and emergent hatchlings between the three treatments ($\chi 2$ (2) = 2.776, p-value >0.05).

We found a statistical difference between treatments with the variables emergence success (Kruskal–Wallis chi-squared = 6.541, df = 2, p-value <0.05), proportion of emergence groups with 1 to 5 individuals (Kruskal–Wallis chi-squared = 7.219, df = 2, p-value <0.03), and proportion of individuals on biggest emergence (Kruskal–Wallis chi-squared = 6.267, df = 2, p-value <0.05). Data analyses of the remaining variables did not reveal a statistical significance between treatments (Table 2).

The Dunn test of the emergence success variable did not reveal significant pairwise differences between control and T1 (average difference of −0.418, adjusted p-value >0.05) and between control and T2 (average difference of 1.976, adjusted p-value >0.05), but did reveal a slightly significant difference between T1 and T2 (average difference of 2.394, adjusted p-value <0.05). For the variable proportion of emergence groups with 1 to 5 individuals, the Dunn test did not reveal significant pairwise differences between control and T1 (average difference of −1.780, adjusted p-value >0.05) and between T1 and T2 (average difference of −0.853, adjusted p-value

= 0.394), but did reveal significance between control and T2 (average difference of −2.633, adjusted p-value <0.03). Regarding the proportion of individuals on biggest emergence variable, the Dunn test did not reveal significant pairwise differences between control and T1 (average difference of 0.291, adjusted p-value >0.05), between T1 and T2 (average difference of 2.008, adjusted p-value >0.05) and between control and T2 (average difference of 2.299, adjusted p-value >0.05),

Table 2. Mean values of the collected variables and p-values of the Kruskal–Wallis tests comparing the different treatments (control, low plastic density and high plastic density). Asterisks denote significance.

	Variable	Control	Low density	High density	p-value
Incubation	Sand temperature at 10 cm	32.42 ºC	32.45 ºC	32.45 ºC	0.901
	Sand temperature at 20 cm	31.25 ºC	31.29 ºC	31.31 ºC	0.845
	Daily incubation temperature	31.71 ºC	31.43 ºC	31.83 ºC	0.628
	Duration of incubation	52.56 days	52.44 days	52.44 days	0.876
	Hatching success	75.40%	77.85%	65.43%	0.112
Emergence	Emergence success	65.62%	69.73%	53.56%	**0.038 ***
	Duration of emergence	3.89 days	5.44 days	5.00 days	0.264
	Emergence groups	3.67	5.00	5.06	0.064
	Proportion of emergence groups with 1 to 5 individuals	41.02%	63.02%	67.54%	**0.027 ***
	Proportion of nocturnal emergence groups	92.45%	85.87%	93.07%	0.193
	Proportion of individuals on biggest emergence group	55.00%	51.45%	39.44%	**0.044 ***
Hatchlings	Straight carapace length	42.13 cm	42.01 cm	42.16 cm	0.956
	Straight carapace width	31.61 cm	30.89 cm	31.17 cm	0.365
	Individual weights	16.66 g	16.25 g	16.49 g	0.439
	Righting response trials	12.86 sec	12.32 sec	16.12 sec	0.953
	Supernumerary epidermal scutes	3.39	4.67	4.83	0.522

The boxplots of the variables related to the incubation period and hatchlings' fitness showed no relevant differences between the median of each treatment (Supplementary Materials, Figures S2 and S4). However, boxplots showed a pattern for the variables related to the emergence period

(Figure 2; Supplementary Materials, Figure S3): the emergence success is lower in the treatment T2; the emergence is longer and with more emergence groups on the plastic treatments T1 and T2; the proportion of emergence groups with less than 5 individuals in the treatments T1 and T2 are higher; and the proportion of individuals on biggest emergence is lower in treatment T2.

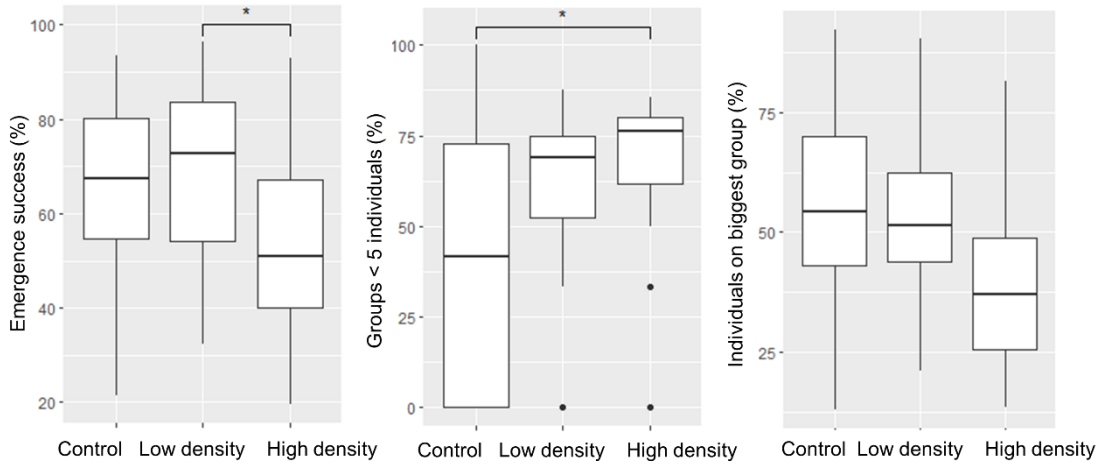

Figure 2. Boxplots for pairwise comparison between treatments (control, low plastic density and high plastic density) of the three significant variables (Kruskal–Wallis tests with p-values <0.05) related to loggerhead turtle emergence pattern: emergence success, proportion of emergence groups with 1 to 5 individuals, and proportion of individuals on biggest group. Boxes show interquartile range, horizontal line shows median value, whiskers show range and dark circles show statistical outlier value. Asterisks denote significance between treatments (adjusted p-values of the Dunn's test <0.05).

PERMANOVA global analysis showed a significant difference between the variables related to the emergence period, with 20% of the variation in distances being explained by these variables (R-squared = 0.20; p-value <0.05), but not between the variables related to the incubation period (R-squared = 0.01; p-value >0.05) and hatchlings' fitness (R-squared = 0.09; p-value >0.05).

The first two components of the PCA explained 40.8% of the data variability, with the first component alone (PC1) explaining 25.1% of the variance (Figure 3). With eight components, we obtained 91% of explained variance (Supplementary Materials, Table S2). The variables emergence success, hatching success and proportion of individuals on biggest emergence contribute to the first component, with overall higher values in the control nests. The variables emergence groups, duration of emergence and proportion of emergence groups with 1 to 5 individuals also have high contribution to the first component, with higher values in the nests with high plastic density.

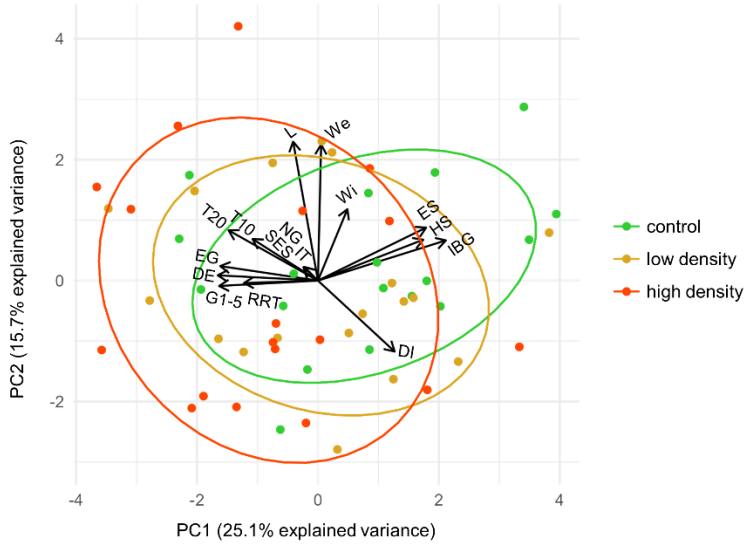

Figure 3. Scores for the first and second principal components (PC1 and PC2) of the three treatments. Black arrows represent the contribution of each one of the 16 variables. The green cluster represents the control nests, the yellow represents the low plastic density nests, and the orange cluster represents the high plastic density nests. T10: sand temperature at 10 cm, T20: sand temperature at 20 cm, IT: daily incubation temperature, DI: duration of incubation, HS: hatching success, ES: emergence success, DE: duration of emergence, EG: emergence groups, G1-5: proportion of emergence groups with one to five individuals, NG: proportion of nocturnal emergence groups, IBG: proportion of individuals on biggest emergence group, L: straight carapace length, Wi: straight carapace width, We: individual weights, RRT: righting response trials, SES: supernumerary epidermal scutes.

Discussion

Turtles' nesting habitats are under serious threat, due to coastal development, plastic pollution and sea-level rise (Defeo et al., 2009; Olivelli et al., 2020). Our preliminary results show that plastic accumulation on nests' surfaces might decrease the emergence success of hatchlings, with nests with a high volume of plastic having a lower probability of hatchlings' successful emergence. Moreover, our results also show that plastics affect the synchronized emergence of hatchlings, with more scattered and smaller groups emerging in nests with higher accumulation. Indeed, synchronized and bigger size emergence groups increase the individual chance of survival, by reducing predation risk (Tucker et al., 2007; Martins et al., 2021a). Particularly in Boa Vista Island, the predation is approximately three times higher in small emergence groups in comparison to larger groups (approximately 75% and 25%, respectively; Martins et al., 2021a). Thus, synchronized and large emergence groups would reduce the individual probability of an encounter with the most frequent hatchlings' predator on the island (the ghost crab *Ocypode cursor*; Marco et al., 2015), increasing the probability of reaching the ocean (Martins et al., 2021a).

The effects of the accumulation of plastic in the environment are vast, but their impact on biodiversity is still a lesser-known topic. Its effect on biodiversity in natural conditions is a key pressure; however, it is still surrounded by uncertainties related to the physical and chemical composition of these materials. In Cabo Verde, waste management is problematic, due to the small size of the territory, worsened by the lack of economic resources and by the exponential increase in touristic activities in the last years (Mohee et al., 2015; Aguilera et al., 2018; Monteiro et al., 2018). Our results suggest that plastics on the sand affect the turtle hatchlings' probability of survival, by decreasing the emergence success and by changing the emergence pattern. Further, higher levels of plastics seem to increase the impact. However, these results need to be interpreted carefully and more studies are necessary to state more conclusions. It is also worth noting that other materials may have similar effects on the emergence and synchronization of turtle

hatchlings. However, we did not evaluate the effects of natural debris or any other materials, as most marine debris reaching those beaches is composed of plastic.

In the absence of explicit scientific conclusions to elucidate the reasons for such impacts, we propose two distinct hypotheses. Plastics might change the substrate humidity and water-holding capacity (Souza Machado et al., 2018; Wan et al., 2019), very important aspects in the successful production of hatchlings (Montero et al., 2018; Gravelle and Wyneken, 2022): high humidity may promote fungal growth (Sarmiento-Ramírez et al., 2010; Gleason et al., 2020), whereas low humidity may lead to egg desiccation (Carson et al., 2011). However, it is unlikely that alterations in the sand water content directly affect the emergence patterns. Nevertheless, we conjecture that nest humidity fluctuations could affect the hatchling physiology at the incubation stage (for instance, muscle formation or physical anomaly), hampering their successful emergence. Although not significant, the mean values for the two incubation variables righting response trials and supernumerary epidermal scutes were higher in the high plastic density treatment, and the hatching success variable was lower, which may reflect some underlying effect on the incubation stage and hatchlings' physiology. Moreover, the interaction between plastics and sand humidity fluctuations might also facilitate chemical contamination or microorganisms' proliferation, which might also have some effect at the incubation stage (Carson et al., 2011; Gleason et al., 2020; Lin et al., 2020; Seeley et al., 2020; Savoca et al., 2021).

The second hypothesis is a merely mechanical effect. The existence of synchronous emergence heavily depends on the physical direct contact between the hatchlings, which move up by stimulus until the final emergence (Patiño-Martínez et al., 2010; Doody et al., 2012). Approximately one week before the emergence, the eggs start to hatch, creating a free space inside the nest. This usually causes the nest to collapse, sinking the sand and everything at the top. Thus, plastic fragments may be buried deeper. Moreover, the movement of the first emergent hatchlings may bury the plastic pieces even further. The plastic fragments may decrease the contact between hatchlings at the middle and final stage of emergence, interfering with the behavioural stimulus

necessary for the hatchlings to emerge altogether. Additionally, plastic is also a smooth and slippery material, hampering the hatchlings to grab and crawl up the nest. This interference of the plastic fragments at the nest might be important in the loss of synchrony and therefore in the survival of the hatchlings on the beach.

Even though we did not find any significant effect of the plastic accumulation on the sand surface temperature (at 10 and 20 cm), previous studies contradict this: Lavers et al. (2021) suggested that plastics (of multiple sizes) cause fluctuations in the circadian temperatures of the sand, increasing the maximum and lowering the minimum temperatures, while Carson et al. (2011) suggested that sand with small plastics (< 10 mm) warm more slowly and reach lower maximum temperatures. Plastic effect on the sand temperature might depend on the plastic thickness, colours, shape or polymer type and also on the per cent coverage of the surface. Thus, our results are limited as we did not analyse thickness, shapes, colours or types of plastics, and we also used plastic pieces that did not cover completely the nest surface. We only measured the sand surface temperature at the warmest hour of the day and did not measure it at nighttime, which may also undergo changes and affect the nest incubation. Moreover, Lavers et al. (2021) state that, at 30 cm depth, significant effects on temperature were not recorded. Our study corroborates this, as our dataloggers recording the incubation temperatures inside the nest (between 40 and 50 cm of depth) did not show significant variations in the temperature between treatments. Thus, we can state that the observed effect on the emergence success and emergence pattern is probably not due to temperature variations.

The rise in sea level due to climate change may as well increase plastic accumulation on higher shores, which will progressively coincide with the nesting areas. Thus, inundation impacts on nests could be exacerbated by the increase in plastic accumulation on beaches. Considering that turtle populations are becoming increasingly female-biased (Abella Perez et al., 2016; Jensen et al., 2018; Tanner et al., 2019), the combination of global warming, sea-level rise and coastal plastic accumulation can bring serious consequences to marine turtle species survival (Tomillio

et al., 2015). It is frequently referred that only 1 in 1000 turtle eggs reach maturity (Frazer, 1986), but these upcoming threats might decrease even more their survival odds (Patrício et al., 2021). With the information gathered in this study, our recommendations for the plastic problem on those beaches rely on better local waste management, empowering local communities through the implementation of educational activities and beach cleaning, which are only temporary solutions but can play a key in the protection of those ecosystems. As most plastics in Cabo Verde seem to come from the ocean, a world systematic change in waste management is essential.

Conclusion

Plastic pollution on beaches may reduce the turtle hatchlings' emergence success and emergence synchrony. This synchrony of emergence is crucial for the survival of the juveniles on the beach, as it significantly reduces the predation risk. The reasons for such impacts prevail were undetermined. Thus, future studies are crucial and should focus on the assessment of the factors that affect the emergence success and emergence patterns in areas with high plastic accumulation and on the understanding of these impacts coupled with climate change.

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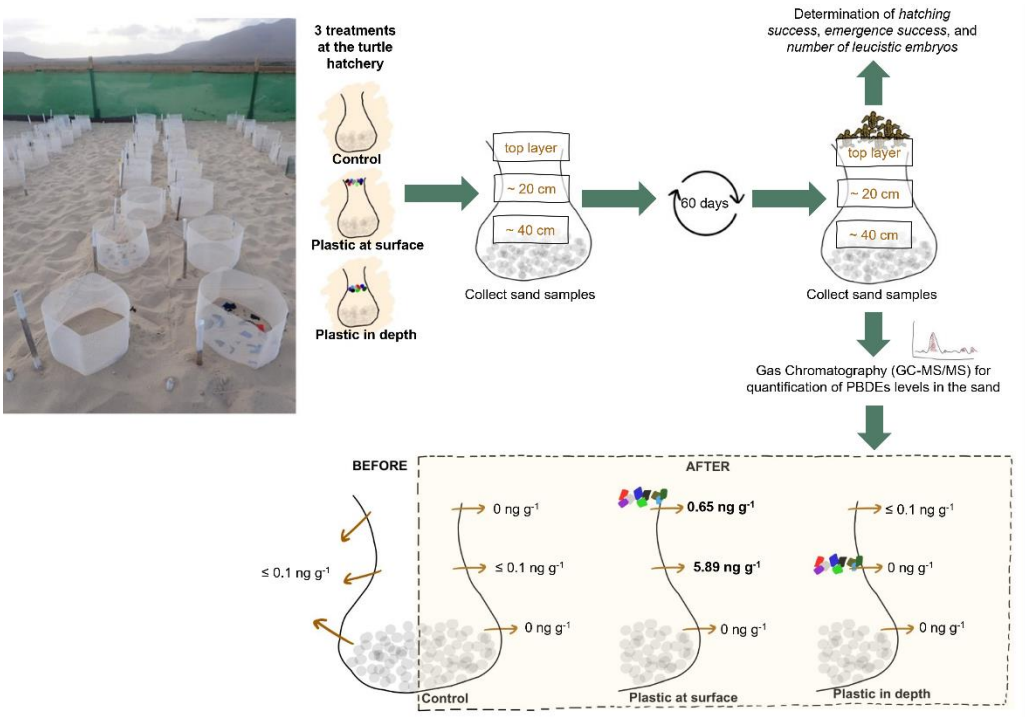
2.2.

Can plastic pollution contaminate loggerhead turtle nests? Evaluation of flame retardants (PBDEs) levels in the sand

Sousa-Guedes, D., Cunha, S.C., Fernandes, J.O., Semedo, D., Sillero, N., Marco, A., Bessa, F. 2023. *Marine Pollution Bulletin*, 195, 115550

Graphical abstract



Abstract

Plastic pollution is a global environmental issue affecting multiple ecosystems, namely sea turtle nesting grounds. We analysed the potential chemical contamination caused by plastic debris in loggerhead turtle (*Caretta caretta*) nests, focusing on polybrominated diphenyl ethers (PBDEs, a class of flame retardants). For that, we conducted a field experiment in a turtle hatchery (Cabo Verde) by placing plastic fragments in the nests at two depths: surface and ~20 cm. We evaluated the nests' success and quantified the levels of PBDEs in the sand using GC–MS/MS. Our results suggest that plastics on the nests' surface can leak contaminants, infiltrating the sand up to 20 cm. Buried plastics showed no relevant leakage of chemicals. While hatching and emergence success was unaffected, we found a relationship between leucistic embryos and contamination levels. Our study highlights the threats of plastic accumulation on beaches, which can potentially leak chemicals and contaminate turtle nests.

Introduction

The negative effects of plastic pollution on wildlife are increasing every day (Lavers et al., 2022). In addition to being ingested by animals (Schuyler et al., 2016), causing choking or entanglements (Wilcox et al., 2016), and promoting pathogenic bacterial colonisation (Marques et al., 2023), these synthetic materials can also release harmful chemicals and contaminate the environment (Gallo et al., 2018; Do et al., 2022). Plastic additives are of particular concern, as they are intentionally incorporated into these materials (Hahladakis et al., 2018; Do et al., 2022). Plastics are associated with more than half of the priority pollutants and substances listed as toxic by the European Union (Rochman et al., 2013), including brominated flame retardants (synthetic chemicals commonly added to many consumer products, such as foams, plastics, electronics, and textiles; de Wit, 2002; Li et al., 2010; Sharkey et al., 2020). These chemicals release bromine atoms that interfere with the chemical reactions involved in combustion, reducing the rate of ignition, and preventing fire eruptions (Birnbaum and Staskal, 2004). Even after recycling the materials, these chemicals can persist in the objects, e.g., recycled children's toys (Ionas et al., 2014). Despite being useful for preventing fires, the improper disposal of those products may lead to the release of many chemicals into the environment (UNEP, 2004). In particular, polybrominated diphenyl ethers (PBDEs), a major class of flame retardants, are persistent in the environment and can accumulate in many species, including humans (Shaw and Kannan, 2009; Hirai et al., 2011; Rotander et al., 2012; Cruz et al., 2018; Menezes-Sousa et al., 2021; Bartalini et al., 2022; Madgett et al., 2022). Due to their persistence and toxicity, these chemicals are classified as persistent organic pollutants (POPs) by the Stockholm Convention (the tetra-, penta-, hexa- and hepta-congeners in 2009; the BDE-209 in 2017; UNEP, 2009; Li et al., 2016; Pei et al., 2018; Sharkey et al., 2020). Their properties permit a stable presence over long periods and consequently become widely distributed, entering the food chain and bioaccumulating in animal and human tissues (Stockholm Convention, 2019). Moreover, PBDEs have been linked to neurological and endocrine disruption in humans and wildlife (Vos et al., 2003; Richardson et al.,

2008; Ross et al., 2009; EFSA, 2011; Annamalai and Namasivayam, 2015), occurring through hormonal shifts that cause issues with fertility, birth defects, sexual expression, and even cancers (Muirhead et al., 2006; UNEP/WHO, 2013). Even though PBDEs production was banned in many areas of the world, their production is still ongoing in others, with several lacking regulations for production and use (Sharkey et al., 2020). For instance, although barely producing these materials, West African countries have already accumulated POPs in the air, sediments and water (Adebusuyi et al., 2022).

In marine and coastal ecosystems, PBDEs can leak from the degradation of plastic debris, posing significant environmental and ecological threats (Andrady, 2011; Hahladakis et al., 2018). As hydrophobic compounds, they have a low solubility in water (de Wit et al., 2002) and a stronger affinity for organic matter such as sediments, which can act as sinks for these compounds (Wang et al., 2016). Sandy sediments, on the one hand, contain less organic matter than other sediment types, reducing their adherence (Olshansky et al., 2011; Tanaka et al., 2023). But on the other hand, they have a greater amount of pore space, which may allow contaminants to penetrate deeper layers in comparison to other more compact sediments, particularly when rainfall occurs. Although these compounds do not mix with water, they can still penetrate the sand during heavy rainfall due to runoff or erosion, causing the movement of the chemicals on the sand itself (Pei et al., 2018). Indeed, studies have detected PBDEs at urban and remote beaches worldwide (Hirai et al., 2011; Ungherese et al., 2012; Ohgaki et al., 2021; Tanaka et al., 2023).

Sandy beaches constitute an important habitat for many species, including marine turtles, that use these ecosystems as nesting grounds (Wyneken et al., 2013). After laying and burying their eggs in the sand, females return to the ocean and the eggs start the incubation period. For roughly 50 days, turtle embryos go through different development stages and hopefully emerge successfully, with multiple threats along the process (e.g., water inundation, or crab predation; Patino-Martinez et al., 2014; Marco et al., 2015). In addition, plastic debris accumulation on nesting beaches also affects the embryos and hatchlings' survival probability, increasing the sand temperature thus potentially affecting sex ratios (Fuentes et al., 2023), and acting as a barrier by trapping the

hatchlings inside the nest (Beckwith and Fuentes, 2018; Sousa-Guedes et al., 2023), or on their way to the ocean (Aguilera et al., 2018). Another threat might be the chemical contamination of the nests through the degradation of plastic debris on the beach (Gallo et al., 2018), with possible negative effects at the incubation stage; however, no studies to date analysed this effect. Exposure to potential endocrine disruptors can be particularly problematic for turtles during their embryonic development (Russart and Rhen, 2016), as turtle eggs are permeable and absorb contaminants present in the environment, resulting in birth defects or mortality (Sahoo et al., 1996; Al-Rawahy et al., 2007; de Solla and Martin, 2011).

The archipelago of Cabo Verde (West Africa), and specially Boa Vista Island, hosts the third-largest population of loggerhead turtle (*Caretta caretta*) in the world (classified as Endangered by IUCN; Marco et al., 2011; Casale and Marco, 2015). In this study, we performed a field experiment in a turtle hatchery at Boa Vista Island, by placing plastic fragments in loggerhead turtle nests at two depths: surface and ~ 20 cm. As the correlation between plastic pollution and the leakage of chemicals is not always linear (as it depends on multiple factors, such as plastic polymer, age of the material and environmental conditions; Masry et al., 2021), we aimed to understand whether the plastic accumulation on the beaches may contaminate the sand where turtle nests are located. Our main questions are: a) does beach plastic pollution chemically contaminate the sand (i.e., release PBDEs) and consequently the turtle nests?, b) does this contamination increase with higher depths? and c) does plastic pollution affect the incubation and emergence periods and consequently the embryos' and hatchlings' survival?

Materials and methods

Study area

The study was conducted on Boa Vista Island, part of the Cabo Verde archipelago and located in the west of Africa (Figure 1). Cabo Verde is a developing country, with tourism as the fastest-

growing sector and a poorly developed industry (Government of Cabo Verde, 2017). Boa Vista is known for its dry and windy climate.

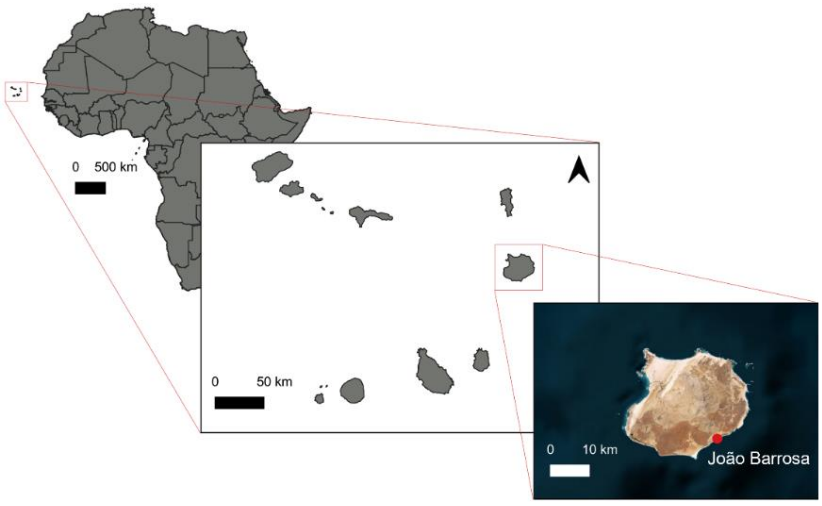


Figure 1. Location of João Barrosa Beach, in Boa Vista Island (Cabo Verde, Africa).

The field experiment was carried out at a turtle hatchery located on João Barrosa Beach (southeast of the island, N 16.016, W 22.741), which is maintained by the NGO BIOS.CV. This beach is part of the Sea Turtle Natural Reserve, which has a very high turtle nesting activity between June and October (Marco et al., 2012). João Barrosa is a remote beach, with difficult access and very few recreational activities. While João Barrosa Beach does not accumulate much marine debris, the northeast beaches of the island do accumulate high volumes (see Supplementary Materials of Sousa-Guedes et al., 2023), presumably coming from the ocean (Cardoso and Caldeira, 2021).

Experimental study

We conducted the field experiment between August and October 2022. The hatchery (~16×27 m) was built in a higher area to prevent inundation and fenced to protect the nests from predators (Martins et al., 2021). In the study area, heavy rainfall occurred during the initial days of August

(at the beginning of the experiment) and intermittently for a few days between the end of August and the beginning of September (midway through the experiment).

At a northern beach of the island, we collected large plastic pieces stranded on the beach and cut them into smaller pieces (~5×5 cm), to produce two different scenarios in the turtle nests: plastic at the surface and plastic in depth (~20 cm). The depth of 20 cm was defined to avoid direct contact between plastics and the eggs (otherwise, they could perforate or mechanically affect the eggs and lead to their immediate death). By cutting the pieces into smaller fragments of the same size, all nests from both treatments had approximately the same plastic density: 20 plastic pieces and a mean plastic weight of 51.1 g per nest. Plastics were placed in an approximate area of 0.2 m^2 in each nest. The selection of the number of fragments was based on studies of plastic density in Atlantic islands (e.g., Tenerife had a maximum of 2510 items per m^2 or São Vicente with maximum of 84 items per m^2; Reinold et al., 2020; Weidlich and Lenz, 2022; our density fall within this range: approximately 100 items per m^2) and we also considered the results of a previous experiment in the study area (Sousa-Guedes et al., 2023). Collected plastics were a mix of different types (fragments and films), colours (black, grey, blue, green, red, and purple), and apparent material deterioration (older and newer), representing items commonly occurring on these beaches. All nests had the same combination of items of different types, cut from the same bigger plastic pieces: thus, the exposure to the potential chemicals in each nest is the same. At João Barrosa Beach, the team of volunteers searched for nesting females. If the nest was considered at risk (e.g., due to inundation), the eggs were collected, counted, and transported to the hatchery. We placed the egg clutches at the hatchery for five consecutive nights. At the hatchery, we excavated the nest chamber at 50 cm depth, replicating a natural nest (Abella et al., 2007; Marco et al., 2018). Translocated egg clutches were randomly assigned to each chamber, we did not separate the egg clutches, and the process never exceeded 6 h. This translocation technique improves hatching success (Martins et al., 2021).

The experiment included 15 nests for each treatment: control – no plastics, plastics at the surface, and plastics in depth (total of 45 nests). At the hatchery, we distributed the nests in three

experimental blocks, each block with the three nest treatments alternatively placed. We marked each nest with an individual code and placed the plastics at the same time the nest was translocated to the hatchery, at the sand surface or ~20 cm of depth from the surface (no plastics in the control nests). To count the emergent hatchlings and retain the plastic pieces, we placed a circular mesh surrounding each nest.

At the same time, from nine selected nests (three of each treatment), and before placing any plastic fragments in the nests, we collected sand samples (approximately 50 g) at three depths: sand at the top layer (CTP for control nests, STP for nests with plastics at surface, and DTP for nests with plastics in depth), sand at ~20 cm (C20, S20, and D20), and sand at ~40 cm (C40, S40, and D40). Sample weight was defined to accommodate chemical analysis, moisture content analysis, and any additional contingency.

After 48 days, during the hatching season, we monitored each nest from sunset until sunrise. At each emergence, we recorded the number of hatchlings, date, and time. On day 60, we exhumated the nests to count the number of closed eggs, rotten eggs, and dead and alive individuals hatched. Closed eggs were opened, and their development stage was determined, as well as noted anomalies such as leucism (i.e., partial absent pigmentation of the skin, causing white colouration; discernible from albinism as leucism does not affect the eyes; Bechtel, 1995). During exhumation, we collected sand samples at the same nests and depths previously collected. Thus, for each one of the nine selected nests, we collected six sand samples, three before and three after the experiment (a total of 54). Samples were collected progressively at different timings: the ‘before’ samples were taken after placing the eggs and while covering the nests with the sand, whereas the ‘after’ samples were collected during the exhumation as the excavation advanced. Thus, the sand of the ‘before’ and ‘after’ samples were from the same portion. Logistical constraints prevented us from collecting more samples. Sand samples were stored in aluminium recipients. After that, we collected and removed the plastic fragments from the hatchery. The experimental design is illustrated in Figure 2.

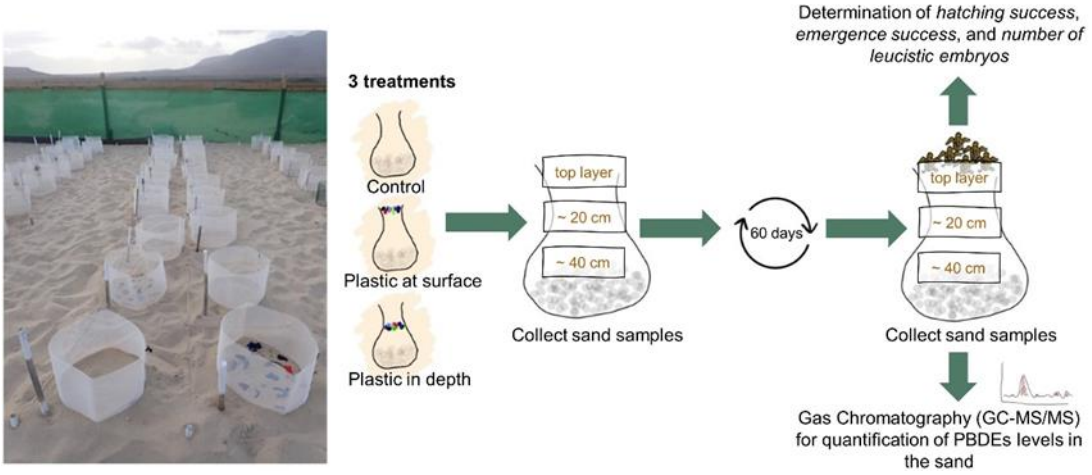


Figure 2. Experimental design at the turtle hatchery: placing plastic fragments at varying depths to assess nests' success (45 nests) and quantify PBDE levels in the sand (9 nests).

Chemical analysis

Standards and chemicals

PBDEs (congeners 28, 47, 99, 153, 154, 183, and internal standards 37, 77) standards were obtained from Wellington Laboratories, all with purity ≥98%. We acquired the internal standard 5′ Fluoro 3,3′,4,4′,5 pentabromodiphenyl ether (FBDE-126) from AccuStandard. We prepared the standard mixtures in n-hexane using individual standards and stored them in amber glass vials at 5 °C. Toluene and acetonitrile were obtained from Honeywell and trichloroethylene from Merck. All organic solvents were at least 99% pure. Deionized water of 0.055 μS cm^{-1} was obtained with a Seralpur Pro 90CN from Merck-Belgolabo. Sodium chloride was obtained from PanReac Quimica and magnesium sulphate from Sigma-Aldrich. Both salts were 99.5% pure and previously baked at 500 °C for 5 h in a muffle furnace. Carrier gas helium for GC analyses was 99.9995% pure.

Sample preparation for PBDE analysis

We performed sample preparation using ~1 g of sand (dry weight basis) weighted into 15 mL amber glass vials, following a previously validated method (Cruz et al., 2019; Menezes-Sousa et al., 2021). Samples had a mean humidity of 1.06%, ranging from 0.59 to 2.41%. We spiked each vial with a 15 μL internal standard mixture (BDE-37, BDE-77, and FBDE-126). Acetonitrile:toluene (5 mL, 4:1) was added for overnight extraction, using a platform mixer. In the morning, we added 3 mL of ultra-pure water to each vial. Then, we added 2 g of magnesium sulphate plus 0.5 g of sodium chloride, and the vials were vortexed for 2 min. Samples were centrifugated at room temperature for 4 min at 2300 rpm. The supernatant (3 mL) was extracted and separated into two 2 mL amber vials (thus, no replication was performed but samples were injected in duplicate) and each one evaporated under a nitrogen stream at 30 °C. Then, it was recovered to a total volume of 100 μL of trichloroethylene, transferred to a 100 μL insert and analysed immediately.

Instrumental analysis

We used a gas chromatograph Agilent 7890B (Agilent Technologies, USA) coupled to an Agilent 7000C triple quadrupole mass spectrometer, in electron ionization mode (EI). The GC system was equipped with an electronic pressure control (EPC) and an auto-sampler 7683 (Agilent Technologies, USA). For data processing, we used the MassHunter quantitative analysis software. The injector was maintained at 280 °C, injecting 1 μL of sample extract in pulsed splitless mode (pulse pressure of 32 psi of 1 min and purge flow of 50 mL min^{-1}). The capillary column was 30 m × 0.25 mm × 0.25 mm Zebron 5MS (Phenomenex, Torrance, CA, USA). We programmed the oven to start at 150 °C, hold for 1.5 min, ramp at 40 °C min^{-1} to 250 °C, ramp again at 7 °C min^{-1} to 320 °C and hold for 3 min, with a total run time of 18.5 min. The flow rate was 1.3 mL min^{-1} using helium as the carrier gas. The temperatures of the transfer line, ion source, 1st and 2nd quadrupole were 230, 280, 150 and 150 °C, respectively. The collision cell gases were nitrogen

(1.5 mL min^{-1}) and helium (2.25 mL min^{-1}). The triple quadrupole MS was operated in multiple reaction monitoring (MRM) modes, detecting two transitions per analyte (Cruz et al., 2019).

Quality assurance/quality control

To assure no background contamination, all the glassware was previously oven-dried for 1 h at 300 °C and washed with acetone. Plastic ware and tools were reduced to the minimum (only screw caps and pipette tips), using glassware whenever possible. Samples were covered with aluminium foil while not being analysed and their processing was the fastest possible.

We assessed the reliability of the procedures through matrix-matched calibration (sand without compounds) with nine calibration levels with well-distributed concentrations throughout the linear range: 0 ng g^{-1}, 0.05 ng g^{-1}, 0.1 ng g^{-1}, 0.25 ng g^{-1}, 0.5 ng g^{-1}, 2.5 ng g^{-1}, 5.0 ng g^{-1}, 10 ng g^{-1}, 25 ng g^{-1}. We generated the calibration curves by the least squares linear regression model, plotting the peak area ratios of the target compound and their respective internal standard versus the concentration of each target substance, obtaining correlation coefficients (r) > 0.99. Quantification limits for each compound were set as the minimum amount required to achieve a signal-to-noise ratio (S/N) of 10. Additionally, we applied a criterion of a relative standard deviation (RSD) of <20%, based on triplicate measurements (n = 3) in the sand matrix, with recovery rates within the range of 60–110%.

Data analysis

Nests success analysis

Using the data from the 45 nests, we tested three variables related to the nest success: hatching success, emergence success, and the number of leucistic embryos. Hatching success is the percentage of individuals that hatched in each nest, calculated as: (initial number of eggs – number of rotten eggs and closed eggs) ÷ initial number of eggs. Emergence success is the percentage of

individuals that emerged in each nest, calculated as: (number of individuals that reached the nest surface) ÷ initial number of eggs. The number of leucistic embryos is the total number of non-hatched leucistic embryos in late-stage development in each nest.

We performed Shapiro-Wilk tests to assess the normality of the variables' distributions and decided to use non-parametric tests to analyse whether each variable was significantly different across treatments. For the proportional nest success variables (hatching and emergence success) we performed Kruskal-Wallis tests. For the variable number of leucistic embryos, due to the presence of zeros and low sample size, we used chi-squared test, by calculating the frequency of the total number of leucistic embryos per treatment (1×3 contingency table). Kruskal-Wallis and chi-squared tests consider significance when the p-value < 0.05.

Chemical contamination analysis

Chemical contamination variables were calculated as the mean concentration of PBDEs of the two duplicates for each sample, using the data from the nine selected nests (three of each treatment). We did not statistically test the differences between the 'before' and 'after' of each sample, due to low sample size and non-independency of both groups. Moreover, we tested the correlation between the contamination levels and the hatching success, emergence success, and the number of leucistic embryo variables of the nine nests, using Kruskal-Wallis. Due to the small sample sizes, we did not undertake further statistical analyses but discussed the results. All statistical analyses were performed in R software 3.6.3 (R Core Team, 2020).

Ethical considerations

We obtained permits for evaluating the plastic effect on the nesting environment from the Government of Cabo Verde (license n° 45/DNA/2022). We followed all regulations for animal welfare and experimentation. We used a small number of nests, all collected from areas with a

high risk of egg mortality (e.g., easily inundated areas; Martins et al., 2022). Because of the requirement for a special license to collect and transport biological materials of protected species in Cabo Verde, we were unable to conduct a chemical analysis on the eggs and embryos.

Results

Nests success

The 45 turtle nests of the field experiment resulted in a total of 2555 emergent hatchlings. The 'control' nests had a total of 1124 eggs ($\bar{X}$ = 80.3 ± 13.5) of which hatched 916 ($\bar{X}$ = 65.4 ± 9.9) and emerged 862 hatchlings ($\bar{X}$ = 61.6 ± 9.6). The nests of the treatment 'plastics at the surface' had 1229 eggs ($\bar{X}$ = 81.9 ± 10.6), hatching 973 ($\bar{X}$ = 64.9 ± 10.5) and emerging 919 hatchlings ($\bar{X}$ = 61.3 ± 10.0). The nests of the treatment 'plastics in depth' had 1138 eggs ($\bar{X}$ = 75.9 ± 8.3) of which hatched 913 ($\bar{X}$ = 60.9 ± 16.2) and emerged 774 hatchlings ($\bar{X}$ = 51.6 ± 19.8). There was no significant difference in the number of total eggs ($\chi 2$ = 5.586, df = 2, p-value >0.05) and hatched eggs ($\chi 2$ = 2.448, df = 2, p-value >0.05) between the three treatments, but there was a significant difference in the number of emergent hatchlings between the treatments ($\chi 2$ = 12.532, df = 2, p-value = 0.002): 77%, 75% and 68% of the eggs emerged successfully in the 'control', 'plastic at surface', and 'plastic in depth' treatments, respectively. However, regarding the proportional variables, we found no statistical difference with the Kruskal-Wallis test for the variables hatching success and emergence success (p-value > 0.05).

The total number of leucistic embryos in the control nests was zero, while in the nests with plastics at the surface was 11 ($\bar{X}$ = 0.73, ranging from 0 to 8, present in three different nests) and in the nests with plastic in depth was 7 ($\bar{X}$ = 0.47, ranging from 0 to 3, present in three different nests). The chi-squared test revealed a statistical difference between treatments with the variable number of leucistic embryos ($\chi 2$ = 10.333, df = 2, p-value = 0.006).

Chemical contamination

The mean levels of PBDEs in the 54 sand samples of the nine nests analysed are presented in Table 1. We detected PBDEs compounds in the 'after' samples of the treatment 'plastic at surface', collected at 20 cm of depth (S20_Aft): in the three nests, we found some level of chemical presence (total PBDEs concentration per nest: 0.77, < 0.05, 16.80 ng g^{-1}), with a mean of 5.89 ± 4.53 ng g^{-1}. Although at lower levels, we also detected contamination in the sample collected at the top layer of the same treatment (STP_Aft), with a mean of 0.65 ± 0.52 ng g^{-1}. Thus, we only detected contamination in the treatment 'plastic at surface', whereas in the remaining treatments we measured trivial levels of PBDEs (≤ 0.1 ng g^{-1}) or we did not detect the contaminants at all (Figure 3).

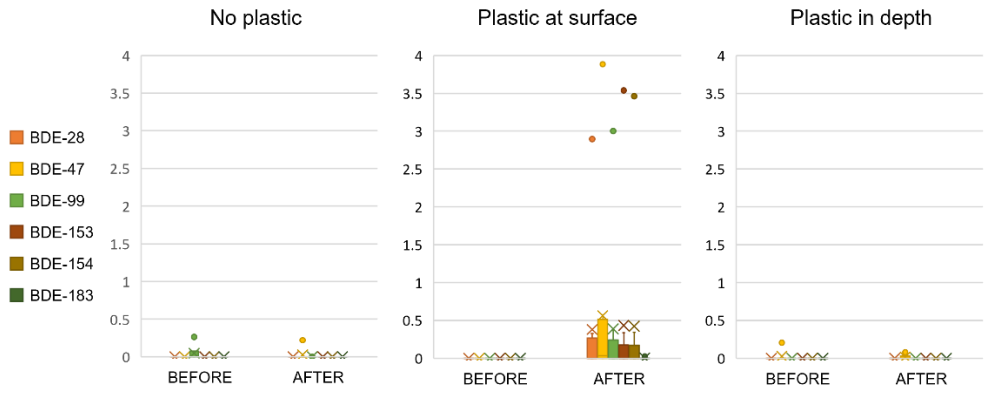


Figure 3. Concentration levels of the six analysed PBDEs (ng g^{-1}) in all sand samples, by treatment (control – no plastic, plastic at surface, and plastic in depth), before and after the 60 days of the experiment. Crosses represent the average of each compound, while points represent the outliers.

Table 1. Concentration levels (mean of the three different nests ± standard deviation) of PBDEs (ng g^{-1}) in the sand samples.

	BDE-28	BDE-47	BDE-99	BDE-153	BDE-154	BDE-183	**ΣPBDE**
NO PLASTIC (CONTROL)							
Sand at top layer							
Before (CTP_Bef)	ND	ND	0.13 ± 0.19	ND	ND	ND	0.13 ± 0.19
After (CTP_Aft)	ND	ND	ND	ND	ND	ND	-
Sand at 20 cm							
Before (C20_Bef)	ND	ND	*	ND	ND	ND	-
After (C20_Aft)	ND	0.07 ± 0.13	*	ND	ND	ND	0.07 ± 0.13
Sand at 40 cm							
Before (C40_Bef)	ND	ND	ND	ND	ND	ND	-
After (C40_Aft)	ND	ND	ND	ND	ND	ND	-
PLASTIC AT SURFACE							
Sand at top layer							
Before (STP_Bef)	ND	ND	ND	ND	ND	ND	-
After (STP_Aft)	0.11 ± 0.19	0.19 ± 0.33	0.13 ± 0.22	0.11 ± 0.20	0.11 ± 0.20	ND	0.65 ± 0.52
Sand at 20 cm							
Before (S20_Bef)	ND	ND	ND	ND	ND	ND	-
After (S20_Aft)	1.05 ± 1.90	1.46 ± 2.11	1.05 ± 2.05	1.18 ± 2.04	1.15 ± 2.00	*	5.89 ± 4.53
Sand at 40 cm							
Before (S40_Bef)	ND	ND	ND	ND	ND	ND	-
After (S40_Aft)	*	*	ND	ND	ND	ND	-
PLASTIC IN DEPTH							
Sand at top layer							
Before (DTP_Bef)	ND	ND	ND	ND	ND	ND	-
After (DTP_Aft)	*	0.05 ± 0.04	*	ND	ND	ND	0.05 ± 0.04
Sand at 20 cm							
Before (D20_Bef)	ND	0.10 ± 0.15	ND	ND	ND	ND	0.10 ± 0.15
After (D20_Aft)	ND	ND	ND	ND	ND	ND	-
Sand at 40 cm							
Before (D40_Bef)	ND	ND	ND	ND	ND	ND	-
After (D40_Aft)	ND	ND	ND	ND	ND	ND	-

ND Not detected, * Below the limit of quantification

Regarding this treatment 'plastic at surface', and their samples collected at ~20 cm, the highest levels were of the BDE-47 congener ($\bar{X}$ = 1.46 ± 2.11 ng g^{-1}), while the lowest were of the BDE-183 congener (< 0.05 ng g^{-1}). In these same samples, we found PBDEs concentrations in the following order: 47 > 153 > 154 > 99 > 28 > 183, with close values except for the last one.

The Kruskal-Wallis test did not reveal a relationship between the contamination levels and the variables hatching success and emergence success (p-value > 0.05), but it did reveal a very slight statistical relationship between the chemical contamination levels of the samples collected at 20

cm and the number of leucistic embryos (Kruskal-Wallis chi-squared = 8.000, df = 3, p-value = 0.046).

Discussion

Our results show that plastic debris accumulated on beaches might release flame retardants such as PBDEs, infiltrating into lower layers of the sand and potentially affecting turtle eggs and other living organisms. Thus, nesting beaches with large accumulations of stranded plastics could pose a new threat to these vulnerable species. Although our study was not able to establish a direct relationship between contamination and its effects on turtle eggs due to the inherent difficulties in the analysis of flame retardants present in plastics, our results suggest an indirect relationship between the contaminant levels and the presence of leucistic embryos. Within only 60 days of exposure to plastic debris, we found mean PBDEs values of 5.89 ng g^{-1} at ~20 cm depth (samples S20_Aft, Table 1). Nevertheless, we did not detect these contaminants in the sand samples collected at ~40 cm (at the egg clutch level, samples S40_Aft <0.05 ng g^{-1}) but did detect them at the top layer at low values (STP_Aft, 0.65 ng g^{-1}). In our experiment, the leaked chemicals may have been driven deeper into the sand by the heavy rainfall that occurred in August and September, explaining why they were detected at a depth of 20 cm but little on the top sand layer. The sample collection and storage were performed in the field camp, implying great logistic restraints: in Boa Vista Island there is no laboratory or any facility where we could perform the chemical analysis, so all samples had to be carefully transported overseas. For this reason, we could not chemically analyse the plastics and determine the PBDEs levels in those fragments (which should ideally be performed in all the plastic fragments used, before and after the experiment). These contamination levels should vary between fragments with different origins, but as we included the same combination of plastic fragments in each nest, we believe that our results are comparable between treatments.

On the contrary, buried plastics did not show any relevant leakage of those chemicals, at any depth (samples DTP_Aft, D20_Aft and D40_Aft ≤0.1 ng g^{-1}). The leaking of plastic contaminants may need elevated exposure to high temperatures and sunlight on the beach surface (Watanabe and Tatsukawa, 1987; Kim et al., 2006). Indeed, in Cabo Verde, the sand temperatures on a sunny day can be very high (for instance, 35 °C at 10 cm deep on a sunny day in August, unpublished data; the mean land surface temperature in that same month in the coast of Boa Vista was approximately 37 °C; Wan et al., 2015). Adding to that, exposure to oxygen can promote the degradation of plastics (Hahladakis et al., 2018). This photo-oxidative degradation of plastics can lead to the leakage and decomposition of chemicals (Shih and Wang, 2009). For instance, PBDE congeners degraded in a few hours (ranging from 31% to 97%) after exposure to UV-LED in freshwater and marine samples (Valentí-Quiroga et al., 2021), albeit the degradation of PBDEs from plastics could occur much slower in compact objects (plastics) in comparison with a pure solvent. Moreover, the leakage and migration of chemicals from plastics also depend on the size of the molecules, with small molecules migrating faster (Hahladakis et al., 2018). Out of the compounds we tested, the heaviest was BDE-183, which were detected in the lowest concentrations (<0.05 ng g^{-1}). BDE-209, a heavier compound that we did not quantify, is typically the most prevalent PBDE detected in sand samples, but studies have also found the congeners 28, 47, 99, 100 and 183 in the sand (Ungherese et al., 2012) and in plastic fragments in beaches (Hirai et al., 2011). Thus, future studies may include the analysis of the BDE-209 compound, as well as other pollutants commonly accumulated and leaked from plastics (e.g., phthalates or polychlorinated biphenyls; Mato et al., 2001; Hahladakis et al., 2018; Do et al., 2022).

Despite detecting contamination up to a depth of 20 cm, we did not find any significant effect of the plastic treatments on the hatching and emergence success of hatchlings. This lack of relationship might indicate that a) the chemicals did not reach the egg clutches, located further down, b) 60 days of plastic exposure is not enough time for the chemicals to leak, infiltrate the nests, and significantly affect the incubation of eggs, c) such a small sample size (nine nests for chemical contamination quantification) is not enough to detect significant relationships, and/or d)

the contamination does not affect the hatching and emergence success. Similarly, Keller (2013) did not find a relationship between contaminated eggs and the hatching and emergence success of hatchlings, corroborating our results. The accumulation of POPs (including PBDEs) in marine turtle eggs typically occurs through internal transfer from the mother (Alava et al., 2011; Stewart et al., 2011; Keller, 2013; Dyc et al., 2015; Savoca et al., 2021), but no study to date clarified whether the contamination in the sand is also a source of contamination of the eggs. Moreover, although not finding significance with the proportional variable emergence success, we detected a significantly lower number of emergent hatchlings in the treatment of 'plastic in depth' (chi-squared test), which suggests a barrier effect. For instance, during exhumation, we found 48, 17 and 14 alive hatchlings in three different nests of the treatment plastic in depth (data not shown), surely trapped by the plastic fragments and the weight of the above sand. This corroborates a previous study in the study area (Sousa-Guedes et al., 2023), in which we found that plastic debris might change the emergence patterns of the hatchlings.

Due to restrictions beyond our control, we could not analyse the PBDE levels in the eggs and dead embryos, which we acknowledge as an important limitation of the study. Nevertheless, we did find an abnormal number of leucistic embryos in the unhatched eggs of the plastic treatment nests (11 in the 'plastic at surface' treatment, and 7 in the 'plastic in depth' treatment, corresponding to 0.90% and 0.62% of the total eggs, respectively), all in the late stage of development (see Figure S1 in Supplementary Materials). For comparison, a study conducted in the hatchery of a Mexican population of the olive ridley turtle (*Lepidochelys olivacea*), in natural conditions, found that 0.27% of the total eggs were leucistic embryos or hatchlings (Sosa-Cornejo et al., 2022), thus, our numbers are not much higher. Nevertheless, we did find a statistical difference in the number of leucistic embryos between plastic treatments, and we did find a slightly significant relationship between leucistic embryos and chemical contamination levels. This weak significant relationship is expectable as we only analysed the chemical contamination of nine nests, thus the sample size is fairly small. Although genetics play an important role in the development of leucistic embryos, studies have suggested that exposure to toxic compounds can

also be linked to leucism and other deformities in marine turtles and other reptiles' embryos, due to the eggs' high permeability (Sahoo et al., 1996; Smith et al., 2007; Martín-del-Campo et al., 2021; Garcês and Pires, 2023). Additionally, when infiltrating deep into the sand, chemicals might contaminate the eggs placed upper in the nest chamber, but not the ones further down. In a normal-sized clutch (60 to 80 eggs), the first laid eggs stay at ~50 cm deep while the last few can stay at 40 or 30 cm. During the exhumation of the nest, it is difficult to determine which eggs were situated at higher or lower positions within the nest chamber, as the hatching turtles move the configuration of the eggs in their movements towards the surface. Thus, while the eggs located at the bottom could have developed normally and hatched successfully, the eggs placed at the top might have been exposed to the chemicals and potentially experienced issues during incubation. Despite not finding significant contamination at ~40 cm of depth, some eggs located upper (for instance, at 30 cm) could have been contaminated. As our sample size is very small, caution must be taken when taking further conclusions. More studies are necessary to understand if the increased contamination in the sand can lead to an increased number of leucistic or malformed embryos, ideally including analyses of sand as well as of eggs and/or embryo contamination levels. In addition, genetic analyses on the nesting female (although more challenging, as those genes could come from either the mother or the father) could help clarify whether the presence of leucistic embryos is inherited from the mother or caused by the contaminated environment.

By the time PBDEs were recognized as environmental contaminants (the European Union banned the use of certain PBDEs in the early 2000s), their consumption peaked in low-industrialised countries (Abbasi et al., 2019). It is expected that global emissions of PBDEs will continue until 2050, with a large delay between their discontinuation and ongoing emissions to the environment (Abbasi et al., 2019). Even though Cabo Verde does not produce these contaminants, improper disposal of waste products represents a significant source of PBDEs contamination, and we believe that marine debris might be an important source of chemical contamination in the most remote areas. While João Barrosa Beach (our study area in Boa Vista Island) does not seem to be much contaminated (controls and samples collected before the experiment had concentrations ≤

0.1 ng g^{-1}), in the northeast beaches of the island (where we collected the plastic pieces) the volume of marine debris is extremely high, thus probably hosting some accumulation of these chemicals. The escalating plastic issue in our oceans combined with the expected rise of temperatures over the next few years may promote a greater leakage and infiltration of these contaminants into the sediments, reaching the nests and potentially affecting marine turtles' populations.

Conclusions

Our results suggest that plastic waste stranded on the beach can contribute to the leakage of PBDEs into the sand, which can potentially reach marine turtles' nests and affect their embryos. These initial results provide a starting point for further research incorporating larger sample sizes, as well as eggs and embryos chemical analysis, and enhance our understanding of the implications of plastic pollution in coastal ecosystems.

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CHAPTER 3

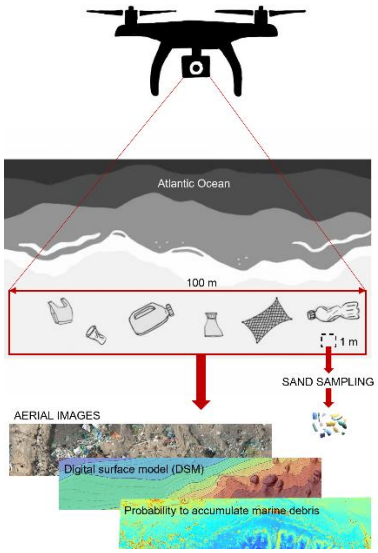
Marine debris pollution on nesting beaches

3.1.

Lost and found: Patterns of marine litter accumulation on the remote island of Santa Luzia, Cabo Verde

Sousa-Guedes, D., Bessa, F., Queiruga, A., Teixeira, L., Reis, V., Gonçalves, J.A., Marco, A., Sillero, N. 2024. *Environmental Pollution*, 344, 123338

Graphical abstract



Abstract

Santa Luzia, an uninhabited island in the archipelago of Cabo Verde, serves as a natural laboratory and important nesting site for loggerhead turtles (*Caretta caretta*). The island constitutes an Integral Natural Reserve and a Marine Protected Area. We assessed marine litter accumulation on sandy beaches of the island and analysed their spatial patterns using two sampling methods: at a fine scale, sand samples from 1×1 m squares were collected, identifying debris larger than 1 mm; at a coarse scale, drone surveys were conducted to identify visible marine debris (> 25 mm) in aerial images. We sampled six points on three beaches of the island: Achados (three points), Francisca (two points) and Palmo Tostão (one point). Then, we modelled the abundance of marine debris using topographical variables as explanatory factors, derived from digital surface models (DSM). Our findings reveal that the island is a significant repository for marine litter (> 84% composed of plastics), with up to 917 plastic items per m^2 in the sand samples and a maximum of 38 macro-debris items per m^2 in the drone surveys. Plastic fragments dominate, followed by plastic pellets (at the fine-scale approach) and fishing materials (at the coarse-scale approach). We observed that north-facing, higher-elevation beaches accumulate more large marine litter, while slope and elevation affect their spatial distribution within the beach. Achados Beach faces severe marine debris pollution challenges, and the upcoming climate changes could exacerbate this problem.

Introduction

The uninhabited island of Santa Luzia (Cabo Verde archipelago) is part of the Macaronesia region, and biogeographically part of the West African Transition Province (Freitas et al., 2019a). The island, together with the Raso and Branco islets, was declared an Integral Natural Reserve in 1990 and a Marine Protected Area in 2003. It is the only uninhabited island of the archipelago and has a long history of failed occupation attempts, due to the harsh conditions, lack of water, scarce precipitation, and strong winds. The short periods of human presence on the island disrupted the ecosystem: the introduction of goats, rodents and cats almost caused the loss of original vegetation and threatened the native wildlife (Vasconcelos et al., 2015; Medina et al., 2021). At least one species was extinct in the island and islets, promoted by the thirst for knowledge of naturalists in the 19th century: the endemic and iconic reptile, the giant skink (Chioninia coctei), was overexploited and transported to European natural museums, and now believed to be extinct (Ceríaco, 2012). Despite that, the island hosts currently important reptile and bird communities (Mateo et al., 1997, 2022; Oliveira et al., 2013; Vasconcelos et al., 2015; Semedo et al., 2020). The natural patrimony of Santa Luzia is not limited to the terrestrial life but hosts a vast array of marine life (Freitas et al., 2019b), important volcanic structures from different time periods (Ancochea et al., 2015), vast dunes and beaches, as well as valuable vegetation communities (Gomes et al., 2023). Moreover, the island is an important nesting ground for loggerhead turtles (*Caretta caretta*; Rocha et al., 2015), with more than 12,000 nests counted in 2021 along its shores (data provided by the NGO Biosfera).

Nowadays the island is well preserved, serving as a living laboratory that mirrors the archipelago's conditions before human colonisation. For instance, there are only about 10% of introduced plant species on the island, in contrast to the very high proportion in the remaining islands (Gomes et al., 2023). However, some beaches on the island suffer from marine litter pollution, which threatens the environmental integrity of many islands around the world (Cooper and Corcoran, 2010; Herrera et al., 2018; Monteiro et al., 2018; Pham et al., 2020; Rodríguez et al., 2020;

Nichols et al., 2021; Portz et al., 2022). On a particular beach, the accumulation of man-made debris is so remarkable that the beach reportedly earned its name from this characteristic – Praia dos Achados, which translates to "beach of the findings". The debris reaching those beaches presumably comes from the ocean, the African continent, or other Cape Verdean islands (Cardoso and Caldeira, 2021).

Oceanic islands, due to their exposure to strong currents, tend to accumulate a greater amount of marine litter along their shores compared to continental areas (Hidalgo-Ruz and Thiel, 2013). Thus, even the most remote beaches can become marine debris sinks (Lavers and Bond, 2017). A large proportion of marine litter reaching the beaches of Cabo Verde is composed of plastics, with other less common debris such as textiles, processed wood, paper, or sanitary waste (Weidlich and Lenz, 2022). Studies quantifying this pollution in the archipelago are still scarce (only available for São Vicente Island; Weidlich and Lenz, 2022). As the most untouched island of the archipelago, hosting important habitats such as nesting grounds for marine turtles, it seems crucial to quantify the accumulation of marine debris along their shores. The effects of plastic pollution on turtle nesting beaches are currently better understood, at multiple stages: on females' nesting (females might avoid nesting in such polluted areas; Fujisaki and Lamont, 2016), eggs' incubation (plastics may leak chemicals and contaminate nests, or cause fluctuations in the sand temperatures and affect sex ratios; Sousa-Guedes et al., 2023a; Fuentes et al., 2023), and hatchlings' emergence (larger pieces might create a loss of synchrony in the emergence of hatchlings, or act as a barrier on their way to the ocean; Aguilera et al., 2018; Sousa-Guedes et al., 2023b). Apart from the impact on the turtle nesting habitats, plastic pollution can affect other living organisms, from terrestrial to aquatic, with larger plastic pieces causing entanglement and choking (Carr, 1987; Gregory, 2009) and smaller pieces (micro- and nanoplastics) entering the food chain and bioaccumulating in the organisms and environment (Courtene-Jones et al., 2022). The effects of this pollution on the fauna groups of the archipelago is an emerging topic, with a few recent studies on Boa Vista Island (Aguilera et al., 2018; Sousa-Guedes et al., 2023a, 2023b; Rodríguez et al., 2023) and Raso islet (Matos et al., 2023).

In this study, we evaluated the accumulation levels of marine litter on three sandy beaches of Santa Luzia Island, as well as their spatial distribution patterns around the island. For that, we employed two complementary sampling approaches: at a fine scale, we collected sand samples in 1×1 m squares and identified all debris larger than 1 mm; and at a coarser scale, we conducted drone surveys and identified all visible debris (> 25 mm) in the aerial images. We aimed to provide a snapshot of the accumulation of different types of marine litter stranded on the beaches of the island, as well as to understand the relationship between marine debris accumulation and beach topographical variables. Specifically, we aimed to a) assess the levels of macro-, meso- and micro-plastics in 1×1 m squares; b) assess the levels of accumulation of marine debris using aerial images; and c) model and determine the spatial patterns of marine debris accumulation on the island.

Materials and methods

Study area

We conducted the study on the uninhabited and remote island of Santa Luzia, located in Cabo Verde (Africa; Figure 1). It is the smallest island of the archipelago, with about 35 km^2 of terrestrial surface. The island is under the influence of the Canary Current and the subtropical North Atlantic Gyre (i.e., one of the five major oceanic gyres in the world, with strong currents rotating clockwise). Like the other islands, Santa Luzia is of volcanic origin. Moreover, it has one of the lowest levels of annual precipitation in the country, with no permanent streams. The island does not have residing human populations, so there are no permanent infrastructures, roads, or any kind of human development. It is however frequently visited by fishermen from the nearby islands.

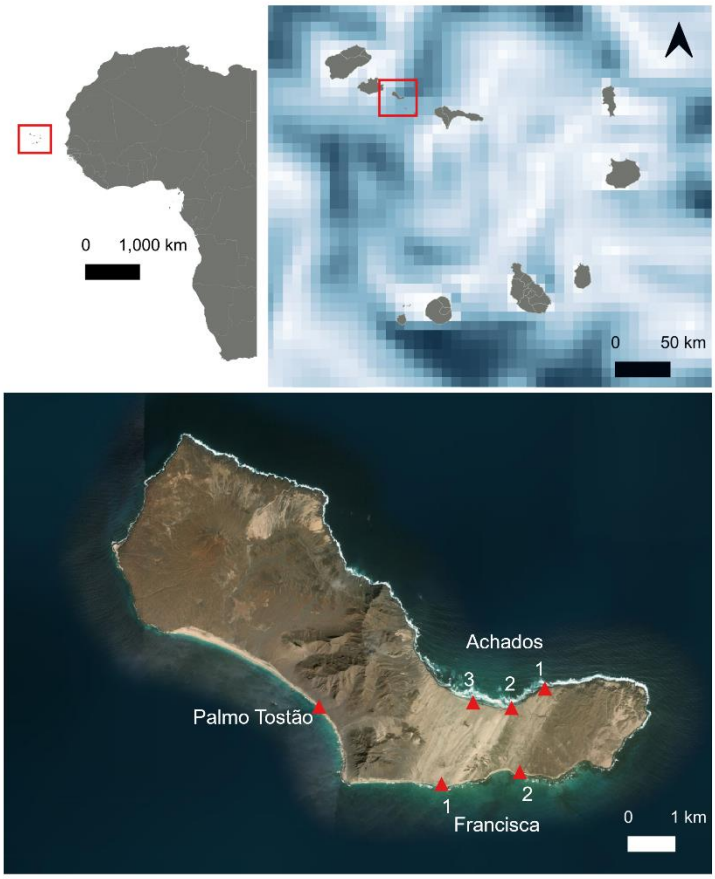


Figure 1. Sampling points in Santa Luzia Island, in the archipelago of Cabo Verde (Africa). The upper right map represents the Eastward Sea water velocity at the surface around the island (Cummings and Smedstad, 2013), with darker blue representing standardized higher values.

In October 2022, we surveyed six sampling points on opposite sides of Santa Luzia (Figure 1): Achados Beach (three points, A1, A2 and A3), Francisca Beach (two points, F1 and F2), and Palmo Tostão Beach (one point, PT). Beaches differed in size and orientation and were within walking distance from the field camp, which is maintained by the NGO Biosfera. The sampling points within the beaches were randomly selected. There are no other sandy beaches larger than 100 m on the island. No beach clean-up events were carried out for four months before the sampling, as required by the OSPAR protocol (OSPAR, 2010). We also fulfilled the remaining criteria: beaches composed of sand and exposed to the open sea, with a minimum length of 100 m, and free of buildings all year, except for not being accessible to surveyors all year.

Sand sampling

At each point, we marked a square of 1×1 m in the strandline and quantified all the anthropogenic debris falling inside the square. The strandline (or high tide line) often contains the most recent deposits of anthropogenic debris (Lefebvre et al., 2021), allowing more standardized comparisons between study sites. For the larger items (>25 mm), we measured each one (the largest cross section), described them in terms of type and colour, and took a photograph. Then, we used a 1 mm mesh sieve (CISA Sieving Technologies, ISO 3310.1, certification number LPEN0752/21) to process the top layer of the sand (∼5 cm) with the help of a shovel, storing the anthropogenic pieces stuck in the sieve for further analysis. Later, in the lab, we separated the items into different size categories, observing the smallest ones under a stereomicroscope LEICA M80 (Leica Microsystems GmbH, Wetzlar, Germany), and photographing them using an IC80 HD Camera with Leica Application Suite software. We classified all items in terms of size, type/shape, and colour. The size was determined by manually measuring the diagonal or lengthiest side of the largest items and the photographs and the ImageJ software for the smallest items. We divided the items into three size categories: large microplastics – 1 to 5 mm, mesoplastics – 5 to 25 mm, and macroplastics – larger than 25 mm (GESAMP, 2016); and in seven types: fragments (pieces that have broken down from larger items), pellets (small raw plastic materials used in plastic manufacturing), filaments (synthetic plastic fibres, usually from fishing ropes), ropes (twisted or braided cords made from synthetic plastic fibres, used often in fishing utensils), foams (lightweight synthetic materials), films (thin and flexible sheets of plastic), and objects (items that are easily identifiable as consumer products, such as caps, bottles or bags). As items detected in aerial imagery could not undergo chemical analysis for polymer classification, we made a parallel decision to also refrain from chemical analysis on the large microplastics (>1 mm) extracted from the sand samples, opting for a needle test and stereomicroscope visualization to discern whether each item was plastic or another material (see Supplementary Materials, Figure S1).

Aerial imagery

We used an unmanned aerial vehicle (UAV, or drone) for the collection of aerial images, which have been successfully used for the detection of large marine debris, in both marine and coastal ecosystems (Gonçalves et al., 2020, 2022; Andriolo et al., 2021; Corbau et al., 2023). We used the drone DJI Mavic Air 2, at a flight height of 15 m, and 80% overlapping between captured images. The flight covered at least 100 m along the coastline and the whole width of the beaches. We obtained images with a spatial resolution of ~5 mm.

The images were later processed and joined in orthophotos with the software Agisoft (AgiSoft Metashape Professional version 2). Then, we clipped the orthophotos to a rectangular shape, excluding blurred areas and the ocean. After that, we performed photo interpretation by manually screening the images to look for anthropogenic debris on the beach. We panned each orthophoto four times, in four different directions at a scale of 1:10. At each debris encounter, we calculated the diagonal or the lengthiest side of the item, colour, and perceived category. We classified the debris into six main categories (adapted from Andriolo et al., 2021): fragments, fishing materials (which included buoys, fishing nets/ropes/strings, foams, and octopus pots), containers and packaging (small and big bottles, drums and buckets, crates, caps, and bags), processed wood (pallets and processed timber), others (shoes, clothing, and tyres), and undefined items. For further analysis, we combined the two last categories (others/undefined) due to their low item counts, which did not warrant separate analysis. We created a 1×1 m grid (aligned with the sand samples square, for further comparisons) and calculated the density of debris in each square (number of items per m^2). Spatial analyses were performed in Quantum GIS software (QGIS version 3.22.15).

Data analysis

Topographical variables

We calculated six topographical variables using the aerial images: elevation, slope, roughness index, topographic position index, northness, and eastness. We calculated elevation in Agisoft by exporting a digital surface model (DSM) at the original resolution of ~5 mm. We calculated the remaining variables in QGIS from the DSM layer. The slope is the ratio of the elevation difference to the horizontal distance between two points on the terrain surface, in percentage. The roughness index is the variations in elevation across the area, indicating how uneven the terrain is, ranging from 0 to 1. We calculated the topographic position index as the difference in elevation between a central pixel and the average elevation of the surrounding pixels, ranging from 0 to 1. We calculated northness as cos(aspect) and eastness as sin(aspect), ranging from 1 (full north/east) to −1 (full south/west) (Guisan et al., 1999; Sillero et al., 2021). Then, we used the variance inflation vector (VIF) to eliminate highly correlated variables (VIF >2), obtaining the final three variables below the correlation threshold: elevation, slope and northness.

Statistical analyses

To understand whether there is a proportional tendency for the accumulation of marine debris of different sizes at the beach, we tested the correlation between the frequency of the different debris categories (three categories of plastic density obtained with the sand sampling, and five categories of debris density obtained with the aerial imagery) with chi-squared tests (for the count data) or Kruskal-Wallis (for the continuous data). Specifically, we analysed the number of items in the categories in the six sampling points (i.e., we counted the number of debris pieces in each category) and the sum of the lengths of each item of the categories (i.e., we summed the lengths of the debris pieces in each category, in metres). Additionally, we tested the correlation between the total number of items in both approaches (with chi-squared test), as well as the sum of lengths in both approaches (with Kruskal-Wallis).

Moreover, to test whether the total accumulation of debris by category in a beach is dependent on the topographical variables, we calculated generalized linear models (GLM) with a Poisson distribution, as the response variable is a count. We used the number of items in each category as response variables in each sampling point (thus, 10 GLMs with different response variables) and the mean values of each topographical variable in each orthophoto (Supplementary Materials, Table S1).

Spatial modelling

We used negative binomial GLM to predict which areas within each beach are more prone to accumulate marine debris. We used the grid of debris abundance as a response variable (thus, data with overdispersion and a high number of zeros), and the three topographical variables and the categorical sampling point variable (with six levels: A1, A2, A3, F1, F2, PT) as explanatory variables. We decreased the topographical raster's resolution through an aggregation GIS function to match the debris density grid (1×1 m), assigning the mean values to the grid. For model evaluation, we divided the dataset into 70% for training and 30% for testing. We evaluated the consistency between predicted and observed abundances of both training and test datasets using accuracy, calibration, and precision metrics (Waldock et al., 2022). For accuracy (i.e., how closely the model predictions align with the true observed values of marine debris abundance), we calculated the mean absolute error (MAE) and mean squared error (MSE; lower values indicate better accuracy, which is relative to the range of the data). We assessed calibration (i.e., how well the model distinguishes low and high values) through both Spearman's and Pearson's correlation (both ranging from −1 to 1, where higher values indicate better-calibrated models and values close to 0.5 indicate moderate calibration), and the slope (ideally close to 1) and intercept (ideally close to 0) of the linear relationship between predicted and observed abundance (Miller et al., 1991; Pearce and Ferrier, 2000). For instance, a model can predict highly accurate abundances but poorly distinguish high and low abundances, e.g., if it excels at estimating the overall average of

the abundance but struggles to capture the data variability, smoothing the differences between high and low abundances (Waldock et al., 2022). For precision assessment (i.e., variability in predicted abundances relative to the observed abundances), we calculated the standard deviation (SD) of the predicted abundances (smaller SD indicates higher precision). Statistical analyses and modelling were conducted using the R software 3.6.3 (R Core Team, 2020).

Results

Plastic accumulation at a fine scale (1 m^2)

The sand samples in the six quadrats resulted in a total of 1478 plastic items >1 mm, with different densities depending on the sampling point (Table 1; Supplementary Materials, Figure S2): 0 items/m^2 (F1 and F2), 1 item/m^2 (PT), 113 items/m^2 (A1), 447 items/m^2 (A2), and 917 items/m^2 (A3). Thus, A3 had the highest density of plastic accumulation, and mesoplastics (5–25 mm) was the most abundant size category (473 items). In the three points with plastics (A1, A2 and A3), we found that the sum of lengths of macroplastics was larger, followed by mesoplastics and large microplastics (Table 1). The most common items found in the three points were fragments (between 64 and 70%), followed by pellets, filaments, ropes, foams, films, and objects. The most common colour found was white or transparent (between 33 and 47%), followed by green, blue, brown, yellow, black, grey, orange, and red (colours and types are indicated in Supplementary Materials, Table S2).

The chi-squared test revealed no correlation between the number of items by category of the sand samples of the three Achados points ($\chi 2 = 7.751$, df = 4, p-value = 0.101). Kruskal-Wallis also did not show a correlation between the total lengths by category (Kruskal-Wallis chi-squared = 2.489, df = 2, p-value = 0.288). Thus, when the number and lengths of one plastic size category increase, the other size categories do not necessarily increase.

Table 1. Number of items and sum of lengths (in metres) per category of plastics in the sand samples (per m^2) and of marine litter in the aerial images (per 100 m^2). In bold, is the sampling point with higher values in each category.

Category		Number of items						Sum of lengths (in metres)					
		A1	A2	A3	F1	F2	PT	A1	A2	A3	F1	F2	PT
Sand samples (per m^2)	Microplastics	49	172	**360**	-	-	-	0.2	0.7	**1.5**	-	-	-
	Mesoplastics	46	232	**473**	-	-	-	0.4	2.6	**5.5**	-	-	-
	Macroplastics	18	43	**84**	-	-	1	4.6	**9.4**	9.3		-	0.8
	All items	113	447	**917**	-	-	1	5.2	12.6	**16.3**	-	-	0.8
Aerial images (per 100 m^2)	Fragments	**55.3**	19.8	48.0	0.2	0.8	1.0	**8.2**	1.6	5.1	-	0.1	0.1
	Containers	**13.0**	1.4	1.7	-	0.1	-	**3.7**	0.4	0.5	-	-	-
	Fishing	**32.3**	6.9	30.3	0.1	-	-	**12.5**	1.1	6.6	-	-	-
	Wood	9.6	1.6	**15.0**	-	-	-	4.8	0.8	**7.1**	-	-	-
	Others	**0.7**	0.2	0.1	-	-	-	**0.5**	0.1	0.1	-	-	-
	All items	**110.9**	29.9	95.2	0.3	0.9	1.1	**29.8**	4.0	19.4	-	0.1	0.1

Marine debris accumulation at a coarse scale (>100 m in length)

We found a total of 10,501 marine debris items in the six orthophotos. We took between 1 h (in PT) to 16 h (in A1) to complete each orthophoto panning, depending on the image size and the quantity of visible debris (7 min per 100 m^2 on average). We obtained different debris densities in each beach (Table 1; Supplementary Materials, Figure S3), with the lowest density at F1 ($\overline{X}$ = 0.3 items/100 m^2; maximum 2 items/m^2), followed by F2 (x = 0.9 items/100 m^2; maximum 3 items/m^2), PT (x = 1.1 items/100 m^2; maximum of 1 item/m^2), A2 (x = 29.9 items/100 m^2; maximum 7 items/m^2), A3 (x = 95.2 items/100 m^2; maximum 23 items/m^2), and A1 (x = 110.9 items/100 m^2; maximum 38 items/m^2). Differing from the sand sample, the beach with the highest marine debris density was the A1. Like the sand sample approach, the most common item found in the six orthophotos were plastic fragments (between 50 and 66% in Achados; 55.3 items/100 m^2 in A1), followed by fishing nets/ropes/strings, processed timber, small bottles, octopus pots, other containers, and other/undefined items. The most common colour found was also white or transparent (between 28 and 48% in Achados), followed by green, blue, brown, yellow, black,

grey, red, and orange (colours and types are indicated in Supplementary Materials, Table S3). Although the fragments category was the most abundant one in all sampling points, the category that occupied more length was the fishing-related items in A1 (12.5 m per 100 m^2; Table 1). Fragments category was the lengthiest in A2 (1.6 m per 100 m^2) and processed wood in A3 (7.1 m per 100 m^2).

We did not find a significant correlation between the number of items by category in the three Achados points (Kruskal-Wallis chi-squared = 1.940, df = 2, p-value = 0.379), nor between the sum of lengths of items by category (Kruskal-Wallis chi-squared = 3.718, df = 2, p-value = 0.156). Thus, like the sand sampling approach, when the number and lengths of one category increase, the other categories do not necessarily increase.

Patterns of marine debris accumulation on the island

Statistical analyses

We found a significant relationship between the total number of items per m^2 of the sand samples and the total number of items per 100 m^2 of the aerial images of the six points ($\chi 2 = 279.9$, df = 2, p-value <0.001), meaning that the total number of items from both approaches are correlated. We did not find a significant correlation between the total lengths of items in both approaches in the three Achados points (Kruskal-Wallis chi-squared = 2.0; df = 2, p-value = 0.368). Therefore, as the total number of items in one of the approaches increases, there is a tendency for the other to increase as well.

Regarding the categories of the sand samples, the GLM models did not reveal significant relationships with the mean value of the topographical variables (p-value >0.05; Table 2). However, we found significant relationships between different debris categories of the aerial images and the two topographical variables elevation and northness (Table 2). Thus, the beach orientation (northness) and elevation seem to be the most important variables explaining why

macro-debris accumulates more in some beaches than others. Both variables showed a positive correlation, suggesting that macro-debris is more likely to accumulate on north-facing beaches and with higher mean elevation.

Table 2. Results of the generalized linear models (GLM) by marine debris size category: estimated coefficients and p-values of each topographical variable. Asterisks denote significance.

Category		**(Intercept)**		**Elevation**		**Slope**		**Northness**	
		Estimate	P	Estimate	p	Estimate	p	Estimate	p
Sand samples (per m^2)	Microplastics	-649.7	0.289	-70.1	0.291	83.6	0.249	148.0	0.236
	Mesoplastics	-871.1	0.293	-100.1	0.274	111.9	0.253	199.5	0.238
	Macroplastics	-136.4	0.289	-14.3	0.302	17.9	0.243	36.5	0.188
	All items	-1657.1	0.291	-184.5	0.282	213.4	0.250	383.9	0.233
Aerial images (per 100 m^2)	Fragments	-14.0	0.467	**10.2**	**0.027***	2.9	0.242	**16.1**	**0.034***
	Containers	19.4	0.290	4.7	0.086	-2.1	0.306	1.0	0.741
	Fishing	-24.1	0.109	**6.1**	**0.023***	3.4	0.075	6.1	0.069
	Wood	-26.5	0.146	0.7	0.638	3.3	0.127	1.6	0.540
	Others	1.3	0.239	0.2	0.105	-0.1	0.258	0.2	0.408
	All items	-44.5	0.225	**21.9**	**0.016***	7.5	0.126	**25.0**	**0.038***

Spatial modelling

The negative binomial GLM showed similar accuracy with both training and test datasets (MAE, training = 0.697, test = 0.687; MSE, training = 3.798, test = 4.408), calibration (Spearman correlation, training = 0.483, test = 0.491; Pearson correlation, training = 0.332, test = 0.245; slope, training = 0.605, test = 0.323; intercept, training = 0.200, test = 0.343), and precision (SD of predicted abundances, training = 1.103, test = 1.452).

The model showed significance for the elevation ($\beta = -0.395$, p-value <0.001) and slope variables ($\beta = 0.063$, p-value <0.001), while the variable northness was not significant (p-value >0.05). Predicted values for each beach are presented in Figure 2. Overall, the model predicted a high probability of accumulation of marine debris on lower elevation and higher slopes parts of the

beach, such as closer to the water line, closer to vegetation, and on beach troughs, which are depressions on the beach that naturally form due to the action of tides and waves, serving as conduits for water to flow back into the ocean as the tide recedes.

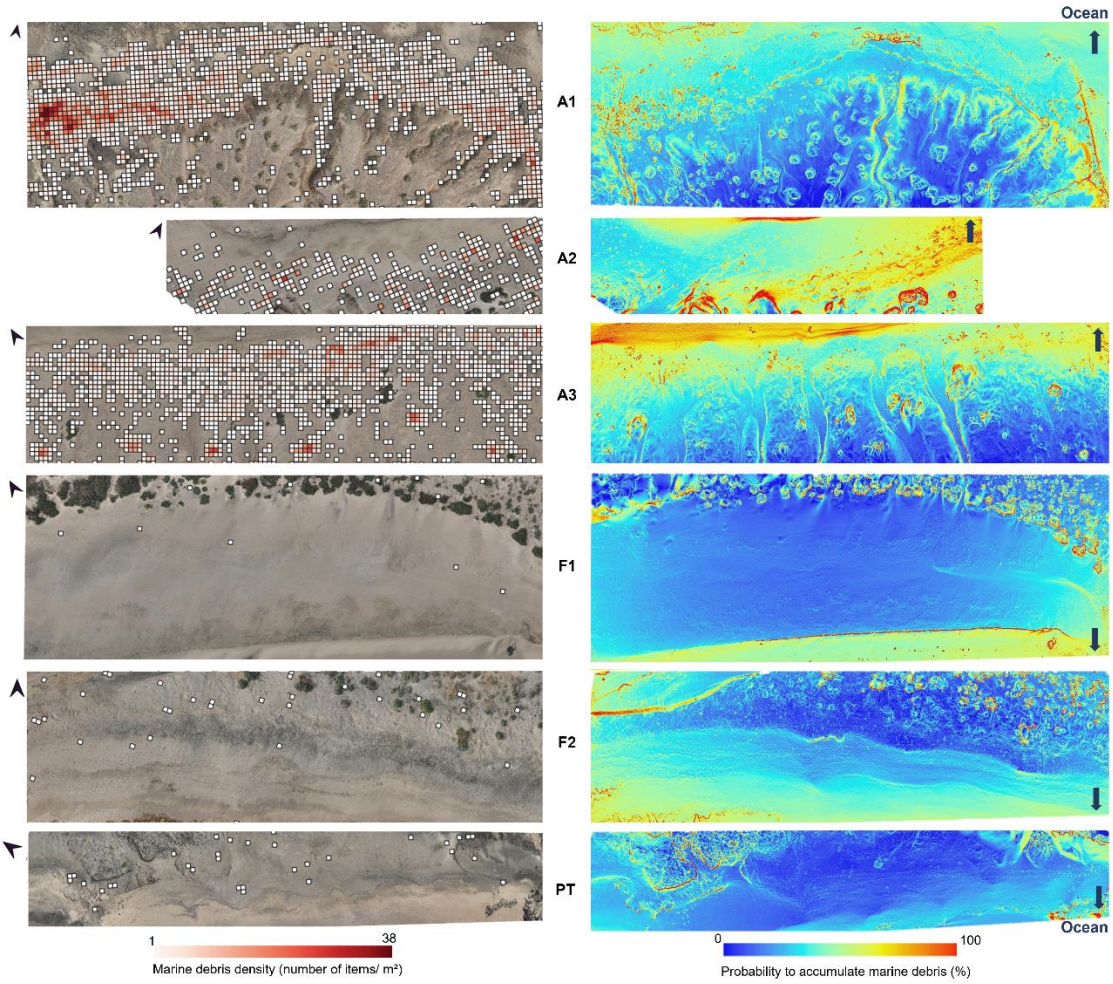


Figure 2. Marine debris density (on the left) and predicted values for the negative binomial GLM model (on the right) of the six sampled points. A1, A2 and A3 points are north-facing, while F1, F2 and PT points are south-facing.

Discussion

Our results highlight that even remote islands such as Santa Luzia are becoming reservoirs for marine litter, with more than 84% being composed of plastics. We found a maximum of 917 plastic items per m^2 in the sand samples (A3 – the western part of the Achados Beach), and a maximum of 38 macro-debris items per m^2 in the aerial images (A1 – the eastern part of the Achados Beach). This emphasises the role of oceanic currents and winds on the path of litter that ends on islands: the exposure to northeast winds and currents leads to an exceptionally high level of marine debris accumulation on the north-facing beaches of Cabo Verde. For instance, a northern beach in São Vicente accumulated 83.1 items per m^2 (Weidlich and Lenz, 2022) and osprey nests of the northern part of Boa Vista Island had more plastics than nests of other parts of the island (Rodríguez et al., 2023). In Santa Luzia, we also found that the three northern points (A1, A2, and A3) had higher volumes of marine litter accumulation in comparison with the three southern points (F1, F2, and PT), with both sampling approaches. We found an additional noteworthy pattern of marine debris accumulation on the northern beaches: in the eastern point of Achados (A1), the accumulation of large debris is extremely high (aerial images with an average of 110.9 items per 100 m^2), while the western point (A3) had lower density (95.2 items per 100 m^2). On the other hand, A3 accumulated a very high number of small plastics (micro- and mesoplastics in the sand samples: 833 items per m^2) and A1 had a much lower number (95 items per m^2). We speculate that the eastern point serves as a source of large debris that may be transported to the western parts, particularly the smaller and lighter items. The strong tidal currents around the island create a wide recirculation zone, retaining marine debris near the shore (Lopes et al., 2015). In Santa Luzia, there is a uniform pattern of oceanic currents, primarily flowing from east to west (Figure 1), with occasional shifts to the northwest (mostly in November and December; Lopes et al., 2015). Thus, the first and larger debris arriving in Santa Luzia would likely be accumulated on the northeastern side of the island, and then be progressively transported to the west along with the currents. This is corroborated by the significant relationship between

the levels of marine debris at the coarse scale (mostly macroplastics) and fine-scale (mostly meso- and microplastics) in this study, suggesting that part of the microplastics accumulating on those beaches may have undergone fragmentation after arriving on the island. This is further supported by the average sizes of each item in each sampled point, with A1 having larger sized items and A3 smaller, both on the sand samples (A1 = 4.6 cm, A3 = 1.8 cm) and on the aerial images (A1 = 26.9 cm, A3 = 20.4 cm).

The two sampling approaches facilitated a complementary understanding of the different types of marine litter arriving on the island. Drone sampling for marine debris quantification comes with inherent limitations, due to constraints in detecting items hidden beneath the sand, size and colour-related challenges, leading to underestimations (38% of macro-debris at the sand surface may remain undetectable; Corbau et al., 2023). Furthermore, a substantial portion of marine debris tends to become buried at <10 cm (approximately 68%; Lavers and Bond, 2017). Considering these percentages of buried and undetected items (Lavers and Bond, 2017; Corbau et al., 2023), we roughly forecast that A1 could have a mean macro-debris density of 5 items per m^2 within the 10 cm sand layer. In our case, with the photointerpretation of the aerial images, we detected on average 22% of the macro-plastics found in the sand samples of Achados; coincidentally, our rough extrapolations would result in the same mean macro-debris density of 5 items per m^2 in A1. While drone-based estimates may not match the precision of in situ sampling, they do offer a broader snapshot of marine litter accumulation in a region. Additionally, aerial imagery enables the derivation of spatialized environmental variables, such as the ones used in this study. Drone surveys have been found to cover the beach area more rapidly than conventional walking approaches (Martin et al., 2018).

The marine debris density in Santa Luzia can be compared with others of similar sampling strategies, such as target item sizes and spatial resolution of the study. For instance, studies comparable with our small-scale approach (i.e., sand sampling targeting plastics >1 mm) in marine beaches around the world, following density values: maximum of 56 items/m^2 in Cocos Islands (Lavers et al., 2019), 84 items/m^2 in São Vicente Island (Cabo Verde; Weidlich and Lenz,

2022), 347 items/m^2 in Zhuhai at the South China Sea (Zhao et al., 2015), 672 items/m^2 in the Henderson Island (Lavers and Bond, 2017), 805 items/m^2 in the Chilean coast (Hidalgo-Ruz and Thiel, 2013), or 2510 items/m^2 in Tenerife Island (Reinold et al., 2020). Except for the last study in Tenerife, the density we found on A3 (917 items/m^2) was higher. Regarding sampling with drones (our coarse-scale approach), we found a higher maximum mean density (110.9 items/100 m^2 in A1) than any other study: 5.7 items/100 m^2 in Italy (Corbau et al., 2023), or 47 items/100 m^2 in Saudi Arabia Red Sea (Martin et al., 2018, 2021); and also higher maximum density (maximum 38 items/m^2 in A1): maximum 13 items/m^2 in Portugal (Andriolo et al., 2020).

Plastic fragments was the most prevalent category in both our fine- (64–70% in Achados) and coarse-scale (50–66% in Achados) sampling approaches, which aligns with the broader trend in marine litter research (Monteiro et al., 2018). The plastic pellets category was the second most abundant in the sand samples, with varying levels depending on the beach (1–19% in Achados; A3 had 167 pellets/m^2). Fishing-associated items (nets/ropes/strings) were the second most common category in the aerial images (23–32% in Achados), supporting prior research (Richardson et al., 2017; Monteiro et al., 2018; Sánchez-García and Sanz-Lázaro, 2023). We also observed a notably high concentration of octopus pots (2.4 items per 100 m^2 in A1) which are large and highly buoyant, frequently lost during adverse sea conditions and transported by ocean currents and wind (Andriolo and Gonçalves, 2023). Moreover, many consumer products stranded on beaches, although not considered fishing utensils, are many times used as that (e.g., using bottles as buoys) or lost during fishing vessel operations, thus, being indirectly related to fishing activities (Richardson et al., 2017). In contrast with larger items, smaller plastics lacked a significant correlation with the three topographical variables (see Table 2), suggesting that they may have a less distinct pattern of accumulation. Thus, while beach orientation towards the north and elevation are important factors influencing the accumulation of larger debris, no correlation was found for large micro- and mesoplastics. Similarly, Sánchez-García and Sanz-Lázaro (2023) found that microplastic distribution remained unaffected by factors such as slope, orientation, distance to villages, currents, or sediment types. Conversely, oceanic currents and wind have been

consistently considered key drivers in the accumulation of larger debris across studies (Eriksson et al., 2013; Andrades et al., 2018; Grillo and Mello, 2021; Sánchez-García and Sanz-Lázaro, 2023). In fact, many Atlantic islands accumulate marine debris almost exclusively on windward beaches (Ivar do Sul et al., 2009; Baztan et al., 2014; Monteiro et al., 2018; Weidlich and Lenz, 2022). Furthermore, Corbau et al. (2023) suggested that marine litter distribution is not correlated to topographical variables, being mostly affected by oceanic conditions (including currents/waves), weather events (such as storms), and the presence of vegetation on the beach. In our study, we did find that north-facing beaches with higher mean elevation have more likelihood of accumulating higher levels of marine debris, but slope did not have any significant effect. On the other hand, slope and elevation seemed to be the most important variables defining the spatial distribution of marine debris within the beach (i.e., after arriving at the beach, marine litter is more prone to accumulate in areas with steeper slopes and lower elevation). Moreover, once reaching a beach, the orientation to the north is no longer decisive in determining where the marine debris will accumulate. Our model predicted that lower elevations near the water's edge and higher elevations closer to vegetation would have a greater likelihood of marine debris accumulation (Figure 2). In some cases, the effects of tides and waves may wash the stranded debris into the ocean or to higher strata of the beach. As our model did not account for currents/wave dynamics, there is a possibility of over-prediction in these areas close to the waterline. In contrast, vegetation does serve as an entrapment mechanism, consistent with prior studies (Corbau et al., 2023). Additionally, beach troughs also have a higher likelihood of accumulation, as they function similarly to vegetation by retaining marine debris. Considering that the number of items across the orthophotos varied between 0 and 38, with positive skewness (i.e., there are more low-count observations than high-count), the overall performance of the model is satisfactory. The similarity in accuracy, calibration, and precision between the training and test datasets suggests that our model generalizes well to unseen data.

Approximately 95% of the loggerhead turtle nesting on the island occurs in Achados and Francisca beaches (Rocha et al., 2015), both with an average nest density of ~1.9 nests per metre

of beach length in 2021 (data provided by the NGO Biosfera). While hosting a significant number of turtle nests, Achados Beach also faces serious challenges from marine debris pollution. This pollution, combined with the upcoming climate change scenarios, poses an even greater threat to the survival of these endangered species. For instance, elevated temperatures may result into higher chemical leakage from plastics and increased sand temperatures, while sea level rise may reduce the available space for nesting. The marine debris density we found on Achados Beach far exceeds the recommended European threshold of 20 macro-litter items per 100 m of beach length (Van Loon et al., 2020): we found a minimum of 528 (in A2) and a maximum of 5038 (in A1) items per 100 m of beach length with the drone surveys. As an archipelago heavily reliant on tourism and marine resources, Cabo Verde faces unique challenges related to waste management, with most being incinerated or ending in landfills (Government of Cabo Verde, 2017; Ferreira et al., 2021). In Santa Luzia, the situation is even more problematic, with anthropogenic materials stranded on the beaches being stored in designated areas built within the dune zone, constructed with pallets found on the beach; a sustainable long-term solution is yet to be found. Beach monitoring and clean-up efforts remain crucial, and our modelling results can help identify the priority areas. However, it is imperative to prioritize preventive measures such as adopting more sustainable materials, e.g., for fishing equipment.

Conclusions

No island, whether remote or inhabited, is immune to the global threat of marine litter pollution. Santa Luzia, while reflecting the pristine conditions of the archipelago, emerges as a reservoir for plastic litter coming from our oceans, stranding mainly on its north-facing beaches, a consequence of its location in the Atlantic Ocean. However, the challenges faced by Santa Luzia are not isolated; they exemplify a pressing need for global waste management measures and policy commitments, and our results represent just the tip of the iceberg of a much larger and global problem.

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3.2.

Mapping marine debris hotspots on Boa Vista Island, Cabo Verde

Sousa-Guedes, D., Sillero, N., Abu-Rhaya, M., Marco, A., Bessa, F. Under review in *Environmental Pollution*.

Abstract

Coastal ecosystems are under increasing threat from pollution, climate change, and other human activities, with marine litter—particularly plastics—posing significant ecological risks. Oceanic islands are especially vulnerable due to ocean currents depositing marine debris on their exposed shores. This study presents the first assessment of marine litter accumulation on sandy beaches of Boa Vista Island, Cabo Verde. Using a combination of drone-based aerial imagery and sand sampling, we quantified micro-, meso-, and macro-debris densities across 29 beaches. North- and east-facing beaches of the island showed the highest accumulation of marine debris (> 85% plastics), driven by ocean currents. The easternmost beach, Ponta de Roque, alone accounted for 31% of the total litter recorded across all locations, with sand samples averaging 1,639 items/m² (1,453 large microplastics), and drone-based surveys averaging 68 macro-debris items/100 m^2. Fishing-related items comprised ~24% of drone-surveyed debris, suggesting input from the Northwest African coast. Plastic fragments predominated, and significant correlations between large plastics and large microplastic densities and colours suggest *in situ* fragmentation. Drone surveys effectively identified marine litter hotspots, aligning with ground-based data. This study provides important baseline data for long-term monitoring in the archipelago and offers a transferable methodology for assessing plastic pollution in other island systems.

Introduction

Coastal ecosystems rank among the most productive and biologically diverse on Earth (Barbier et al., 2011). However, they are increasingly under threat by climate change effects, resource exploitation, growing urbanisation, and pollution (Jorge-Romero et al., 2022; Trégarot et al., 2024). Marine litter, particularly plastic pollution, has emerged as a critical environmental issue, affecting marine and coastal wildlife, human health, and coastal economies (Jambeck et al., 2015). Plastics, known for their durability, lightweight nature and low production cost, are pervasive and persistent; it is estimated that plastic can linger in the environment for centuries (Gedde et al.,

2021). Global assessments predict over 52 million metric tonnes of plastic waste emitted annually, with much of it ending up in marine environments (Cottom et al., 2024). Once disposed into the ocean, plastics can fragment into smaller particles and may eventually reach shorelines. The large items that wash ashore becomes highly visible and may serve as an indicator of overall ocean health (Lavers and Bond, 2017). While large debris can be easily spotted, the smallest pieces (microplastics, i.e., plastic particles under 5 mm) pose an even greater threat due to their ability to infiltrate food webs (de Souza Machado et al., 2018; Thushari and Senevirathna, 2020; MacLeod et al., 2021).

Islands, due to their geographic isolation and proximity to ocean currents, often act as sinks for marine debris (Lavers and Bond, 2017; Sousa-Guedes et al., 2024). The archipelago of Cabo Verde (off the west coast of Africa), together with the Canaries, Madeira, Selvagens, and Azores, is part of the Macaronesia biogeographic region (Fernández-Palácios et al., 2024). Within the archipelago, Boa Vista Island is characterised by its high-energy coastlines, strong wind, vast sandy beaches and rocky shores. The island is exposed to strong ocean currents that transport floating debris to its shores, as it is located at the southern edge of the North Atlantic subtropical gyre (Lebreton et al., 2012). Marine litter found on the island originates from several sources, including passing ships, nearby Africa, and Cabo Verde itself (Cardoso and Caldeira, 2021). In addition to its environmental challenges, Boa Vista is the most important nesting ground for endangered loggerhead turtles (*Caretta caretta*) in the Eastern Atlantic (Marco et al., 2012), an important breeding area for North Atlantic humpback whales (*Megaptera novaeangliae;* Ryan et al., 2014), a nursery ground for various shark species (Rosa et al., 2023), and hosts one of the highest levels of endemicity of *Conus* snails worldwide (15 species endemic to the island; Peters et al., 2016). While there have been recent studies on the effects of plastic pollution on some fauna groups of Boa Vista Island (Aguilera et al., 2018; Rodríguez et al., 2023; Sousa-Guedes et al., 2023a; 2023b), it lacks a baseline study of this pollution on the island, with research being limited to São Vicente and Santa Luzia islands (Weidlich and Lenz, 2022; Sousa-Guedes et al., 2024).

Quantifying marine litter pollution is time-consuming due to its wide range of categories and types, and especially because of the wide variety of size ranges that must be considered, from micro- to macro-sizes. Establishing a relationship on beaches between microplastics and larger debris (which can be surveyed more easily) could streamline monitoring efforts and inform better-targeted clean-up and mitigation strategies (Lee et al., 2013). Therefore, in this study, we analysed the patterns of marine litter accumulation on Boa Vista Island, focusing on the co-occurrence of micro-, meso-, and macro-sized items. By combining sand sampling and aerial imagery from drones, we assessed marine litter pollution across 29 sandy beaches on the island, at two times, focusing on relative patterns rather than precise accumulation rates. We explored the density, composition and environmental drivers of marine litter accumulation across the island. The specific objectives were to: a) establish a baseline for marine litter pollution on sandy beaches of Boa Vista; b) test the correlation between the occurrence of different plastic types, sizes, and colours, and between sampling strategies; and c) analyse the influence of topographic and oceanographic factors in shaping marine debris accumulation across the island.

Methods

Study area

We conducted the study on Boa Vista Island, located in the archipelago of Cabo Verde off the west coast of Africa (Figure 1). Boa Vista has a resident population of ~13,000 inhabitants (INE, 2022). The islands of Cabo Verde are of volcanic origin and experience a short rainy season from August to October, with September being the wettest month (average rainfall in September of 55.8 mm between 1991–2020; World Bank, 2024). On Boa Vista, rainfall is typically low, and the island has no permanent water streams or rivers. The island is under the influence of the Canary Current and the subtropical North Atlantic Gyre (i.e., one of the five major oceanic gyres in the world, with strong oceanic currents rotating clockwise; Lebreton et al., 2012).

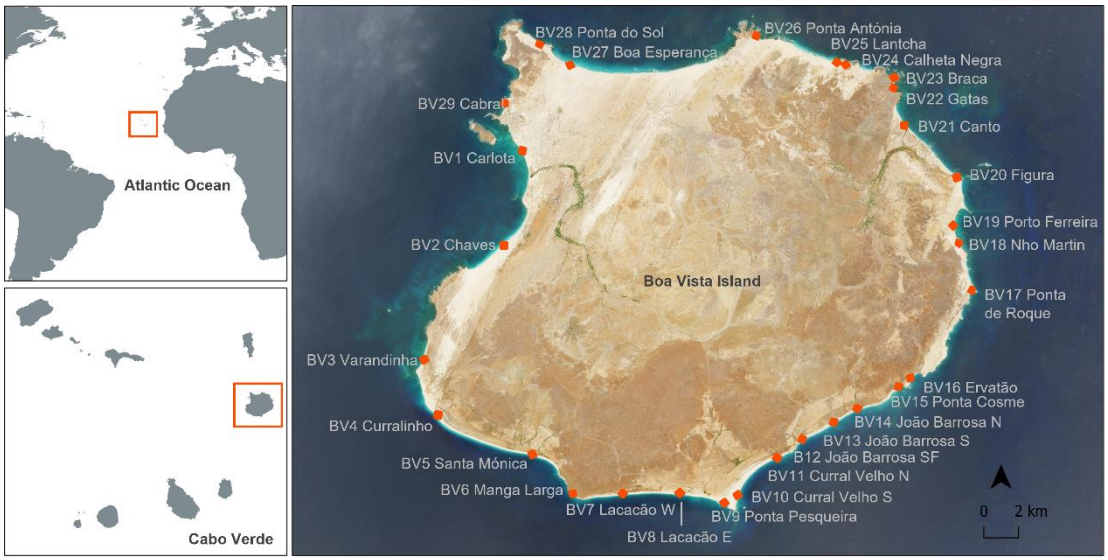

Figure 1. Map of Boa Vista Island, Cabo Verde, and the 29 sampling stations (orange) around the island labelled with corresponding beach names and codes.

Sampling points

In 2021, we surveyed 29 sampling points of Boa Vista (Figure 1) at two different times: early August (before the rainy season), and late September/early October (after the rainy season). These surveys were aligned with a sea turtle conservation program developed by a local NGO (BIOS.CV), and thus our sampling coincided with the turtle nesting season. We selected beaches that were accessible by car or on foot and, once on site, the exact sampling point was chosen unsystematically, but without intentional bias. All selected beaches were sandy, exposed to the open sea, at least 100 m in length, and free of buildings (OSPAR, 2010). Most beaches within protected areas on the north and east coasts are typically cleaned at least once a year before the nesting season (May/June), by various local NGOs. However, specific information regarding beach clean-up timings is unavailable.

Aerial imagery

We used a DJI Mavic Air 2 unmanned aerial vehicle (UAV, or drone) to capture aerial imagery. Drone sampling has been successfully used for the detection of large marine debris in coastal ecosystems (Corbau et al., 2023; Sousa-Guedes et al., 2024). We conducted flights at an altitude of 15 meters and 80% overlap between images (frontal and lateral), covering at least 100 m along the coastline and the entire beach width, following the methodology by Sousa-Guedes et al. (2024). The resulting images had a spatial resolution of ~5 mm.

The images were later processed into orthophotos (Figure 2) using the software Agisoft Metashape Professional v2. We clipped the orthophotos to exclude blurred areas and the ocean. We then performed manual photointerpretation by systematically screening the images two times in two different directions, searching for anthropogenic debris on the beach. At each debris encounter, we recorded the diagonal or the lengthiest side of the item, colour, and perceived category. We classified the macro-debris into six main categories (adapted from Andriolo et al., 2021): fragments, containers and packaging (small and big bottles, drums and buckets, crates, caps, and bags), fishing materials (buoys, fishing nets/ropes/strings, foams, and octopus pots), processed wood (pallets and processed timber), others (shoes, clothing, and tyres), and undefined objects. To minimise operator bias, the photointerpretation of images was conducted by the same person (DSG). In each sampled location, we calculated the macro-debris density for each of the six categories as the number of items per 100 m², the total macro-debris density per 100 m², and the total macro-debris density per 100 m of beach length. We performed the photointerpretation using QGIS (version 3.22.15).

Sand sampling

At each sampling location, we marked two squares of 0.25×0.25 m: one at the strandline (or high tide line) and a second at the start of the dunes (Figure 2). The strandline was chosen for its higher likelihood of containing recent marine debris deposits (Lefebvre et al., 2021), while the dune

sampling aimed to capture older accumulated debris. Then, we collected the top ~5 cm of sand within these squares, resulting in 116 sand samples (two per season and location: 29 beaches × 2 samples × 2 surveys). As Boa Vista do not have laboratory facilities, we stored and transported the sand samples to Santiago Island for further processing at the University of Cabo Verde.

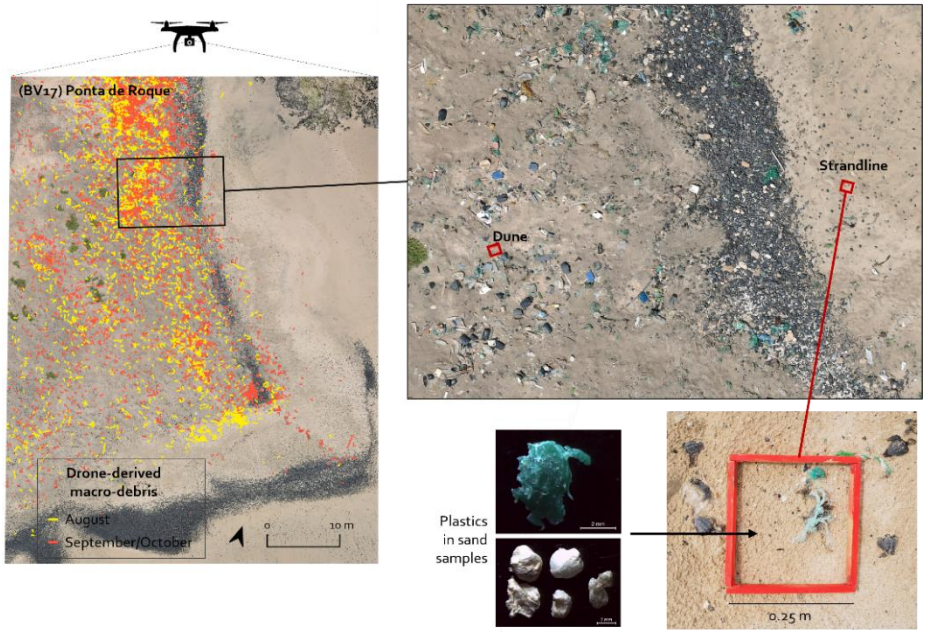

Figure 2. On the left, an example of an orthophoto (BV17) with macro-debris identified through photointerpretation. On the right, a zoom-in approximation of the location of both quadrats (dune and strandline) where sand samples were collected.

In the laboratory, we weighted the dry sand sample (average weight of ~1007.7 g and average volume of 677.2 ml), and sieved the samples using two meshes: 1 mm and 5 mm (CISA Sieving Technologies, ISO 3310.1, LPEN0752/21). We categorised all visible anthropogenic pieces retained in the sieves based on size, type, and colour, and divided the items into three size categories (GESAMP, 2016): large microplastics (1 to 5 mm), mesoplastics (5 to 25 mm), and macroplastics (> 25 mm). The sand left over from the samples (< 1 mm) was stored for future analysis. We further sorted the items by type: fragments (pieces that have broken down from

larger items), filaments (synthetic plastic fibres, usually from fishing ropes), foams (lightweight synthetic materials), films (thin and flexible sheets of plastic), pellets (small raw plastic materials used in plastic manufacturing), ropes (twisted or braided cords made from synthetic plastic fibres, used often in fishing utensils), and objects (items that are easily identifiable as consumer products, such as caps, bottles or bags). We photographed the microplastics under a stereomicroscope LEICA M80 (Leica Microsystems GmbH, Wetzlar, Germany), with an IC80 HD Camera with Leica Application Suite software, and determined the size of each item by measuring the diagonal or largest cross-section. To reduce operator bias, all samples were processed by the same person (DSG). Due to challenges in ensuring contamination control and logistical constraints on the island, we decided to focus exclusively on large microplastics (>1 mm), as particles smaller than 1 mm require validation through spectroscopic techniques (Hidalgo-Ruz et al., 2012; Löder et al., 2015). This approach ensured accurate identification and excluded fibres from our analyses to avoid overestimation due to potential contamination. For items with uncertain composition, we employed a needle test to determine whether they were plastic or another material. Particles of ambiguous composition were excluded, even if tested with the hot needle method (Hidalgo-Ruz et al., 2012). We calculated the average of sand-sampled plastic densities as the number of items per m^2 for each location, size category, and type.

Data analysis

Correlation analysis

We used Spearman correlation to evaluate the consistency of marine litter densities across the two sampling periods (August and September/October) for both drone-derived and sand-sampled data. We evaluated correlations between size categories, comparing the total drone-derived plastic density (macro-debris, excluding wood and others/undefined items), with three sand-sampled densities: large microplastics, meso+macroplastics (sum of mesoplastics and macroplastics, due to low counts), and total items. To further explore these relationships and assess whether one size

category could serve as a proxy for another, we averaged the plastic densities across both seasons and performed linear regressions. Drone-derived plastic density served as the predictor, while the three sand-sampled plastic densities were the response variables, resulting in three linear regression models.

We further analysed Spearman correlations by matching items of the same colour based on their type with shared physical characteristics, including sand-sampled filaments vs. drone-sampled nets/ropes; sand-sampled fragments vs. drone-sampled fragments and plastic objects; and sand-sampled films vs drone-sampled bags. Filaments often originate from the degradation of fishing nets or ropes, while fragments and films represent broken-down pieces of larger plastic objects and bags, respectively. We conducted all statistical analyses in R software 3.6.3 (R Core Team, 2020).

Environmental drivers

To analyse what factors determine the accumulation of marine litter, we calculated six environmental variables: four topographical (beach elevation, slope, northness, and eastness) and two oceanographical (northward and eastward current flow). We selected these variables based on their importance for marine litter accumulation in beaches of Cabo Verde (Sousa-Guedes et al., 2024). We calculated elevation in Agisoft by exporting a digital surface model (DSM) of the orthophotos at the original resolution of ~5 mm. The remaining topographical layers were derived from the DSM layers in QGIS: slope is the ratio of the elevation difference to the horizontal distance between two points, in percentage; northness represents the orientation to the north, calculated as cos(aspect) in radians; and eastness represent the orientation to the east, calculated as sin(aspect) in radians. Northness and eastness ranged from 1 (full north/east) to -1 (full south/west) (Guisan et al., 1999; Sillero et al., 2021). Then, we calculated the median value of each variable for each location and averaged the values of the two seasons. Oceanographic variables were obtained from Bio-ORACLE v3 (Assis et al., 2024) for present-day conditions

(2010-2020), with a spatial resolution of ~5.5 km. We obtained the mean values of seawater direction and calculated northward flow as cos(seawater direction) and southward flow as sin(seawater direction), ranging from 1 (full north/east flow) to -1 (full south/west flow). For each sampling point, we extracted the median values of topographical variables and the closest pixel value of oceanographic variables. Then, to assess multicollinearity among environmental variables, we used the variance inflation factor (VIF) and selected four variables below the correlation threshold (VIF < 2): elevation, slope, northness, and eastward current flow.

We employed negative binomial generalised linear modelling (NB GLM) to test the influence of the four environmental variables, with their median/closest pixel values used as predictors. The response variable was one category (out of eight) of marine debris density: three derived from sand sampling (large micro-, meso+macroplastics, and all plastics) and five from drone sampling (fragments, containers/packaging, fishing-related, processed wood, and all items). This resulted in eight models, each with a different response variable. To assess the goodness of fit of the models, we calculated McFadden's pseudo-R^2, which compares the log-likelihood of the fitted model to the log-likelihood of the null model. All analyses were conducted in R.

Results

Spatial distribution and types

Drone aerial surveys across the 29 sampling stations identified a total of 23,085 macro-debris items during the two sampling seasons, and on average 85.8% were composed of plastics. Mean densities varied between 5 and 2,371 items per 100 m of beach length (and between 0.1 and 68.2 items/100 m^2; Table 1). Overall, fragments were the most common type found (43.2%), followed by fishing materials (23.7%), containers or packaging (18.0%), processed wood (10.2%), undefined objects (3.3%), and others (0.3%). White or transparent items were the most common colour (37%), followed by green (20%), brown (11%), black (11%), blue (6%), orange (4%),

multicolour (3%), grey, yellow and pink/red (each at 2%), beige (1%), and purple (below 1%). Beaches on the northern and eastern sides of Boa Vista Island exhibited higher macro-debris density (Figure 3). Ponta de Roque (BV17) had the highest density (2,254 and 2,487 items per 100 m of beach length in the first and second sampling, respectively; $\bar{x}$ = 2,371 items/100 m), followed by Figura (BV20; 1,176 and 2,726 items/100 m; $\bar{x}$ = 1,951 items/100 m), and Canto (BV21; 601 and 832 items/100 m; $\bar{x}$ = 716 items/100 m).

Table 1. Average density of drone-sampled macro-debris (> 25 mm) by type. Values represent the average number of items across the two sampling seasons, per location. The total average density is shown both per area (100 m²) and per 100 m of beach length. In bold, the beaches with density surpassing the European macro-litter density threshold (Van Loon et al., 2020).

Beach	**Items per type (per 100 m²)**								**Total items/ 100 m²**	**Total items/ 100 m of length**
	Fragments	**Containers**		**Fishing materials**			**Processed wood**	**Others/ undefined**		
		Bottles	**Others**	**Nets/ ropes**	**Octopus pots**	**Others**				
BV1 Carlota	0.04	-	-	-	-	-	0.03	0.01	0.08	8.18
BV2 Chaves	0.48	-	0.01	0.07	-	-	0.10	0.01	0.67	**56.25**
BV3 Varandinha	0.22	0.01	-	0.02	-	-	0.01	-	0.25	**23.50**
BV4 Curralinho	0.09	-	0.01	0.02	-	-	-	-	0.12	15.0
BV5 Santa Mónica	0.05	-	0.01	-	-	-	-	-	0.05	4.67
BV6 Manga Larga	0.54	0.01	0.05	0.15	-	-	0.03	-	0.78	**27.98**
BV7 Lacacão W	0.04	0.03	0.01	0.01	-	-	0.02	-	0.11	9.46
BV8 Lacacão E	0.46	0.03	-	0.02	-	-	0.24	0.02	0.77	**73.42**
BV9 Ponta Pesqueira	0.09	0.02	-	-	-	-	0.01	-	0.11	7.59
BV10 Curral Velho S	0.94	0.08	0.09	0.17	-	0.01	0.23	0.02	1.53	**121.70**
BV11 Curral Velho N	0.12	-	0.01	0.10	-	-	0.03	-	0.26	**20.35**
BV12 João Barrosa SF	0.05	-	0.01	0.02	-	-	0.03	-	0.10	6.30
BV13 João Barrosa S	0.36	-	0.01	0.11	0.02	-	0.12	0.01	0.64	**39.13**
BV14 João Barrosa N	0.08	-	-	0.08	0.01	-	0.01	-	0.17	11.74
BV15 Ponta Cosme	0.29	0.04	0.07	0.27	0.04	0.01	0.03	0.02	0.78	**42.04**
BV16 Ervatão	0.19	0.02	-	0.02	0.02	-	0.05	0.01	0.30	15.20
BV17 Ponta de Roque	27.50	8.26	4.67	10.84	2.51	2.14	10.19	2.05	68.16	**2370.85**
BV18 Nho Martin	7.00	1.15	0.55	1.70	0.08	0.02	1.78	0.18	12.46	**345.61**
BV19 Porto Ferreira	3.71	0.18	0.33	4.04	0.23	-	0.64	0.07	9.21	**474.56**
BV20 Figura	8.10	2.55	2.35	2.32	0.55	0.59	1.87	0.23	18.55	**1951.30**
BV21 Canto	5.40	1.20	1.05	2.03	0.24	0.02	0.61	0.09	10.64	**716.22**
BV22 Gatas	9.88	5.48	0.73	3.14	0.06	0.06	0.26	0.14	19.74	**463.64**
BV23 Braca	5.29	2.40	0.52	2.84	0.17	0.04	0.09	0.05	11.41	**560.09**
BV24 Calheta Negra	6.11	3.43	0.64	2.79	0.54	0.02	0.28	0.03	13.84	**615.20**
BV25 Lantcha	3.54	0.92	0.38	4.52	0.42	0.02	1.33	0.06	11.19	**472.61**
BV26 Ponta Antónia	2.16	1.13	0.26	1.31	0.29	-	0.35	0.01	5.52	**237.85**
BV27 Boa Esperança	1.91	0.37	0.34	3.27	0.23	0.06	1.13	0.06	7.36	**418.52**
BV28 Ponta do Sol	7.79	3.49	0.25	1.13	0.02	0.01	1.58	0.04	14.31	**535.09**
BV29 Cabral	0.04	0.01	-	0.04	-	-	0.10	0.02	0.21	10.95

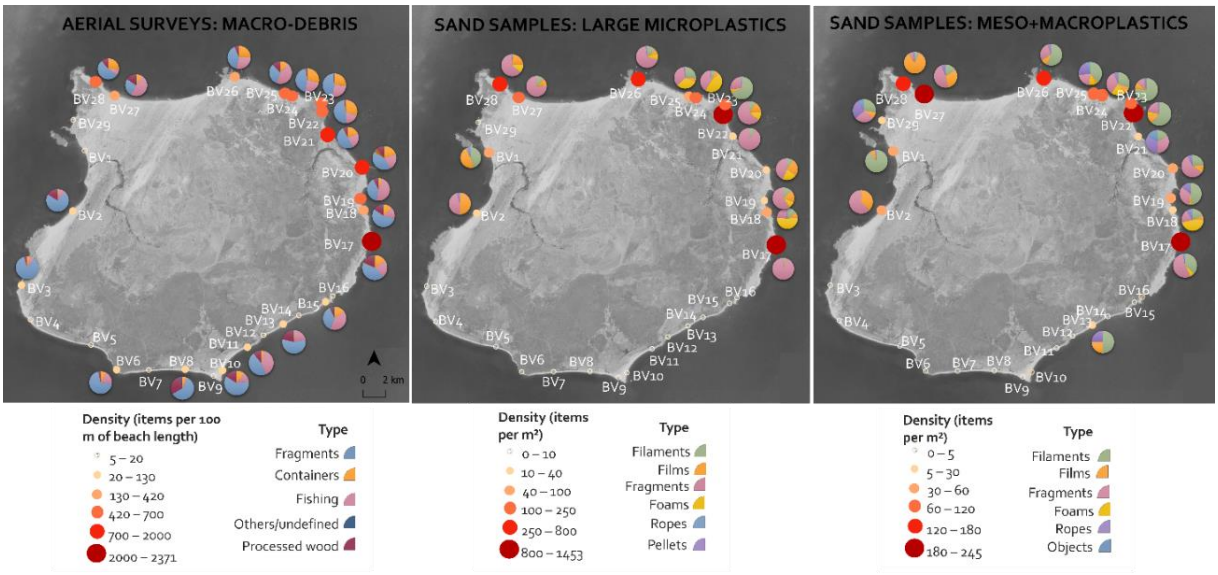

Figure 3. Average density of marine litter debris across the 29 sampled locations (mean of two seasons): drone-sampled macro-debris (on the left), sand-sampled large microplastics (centre), and sand-sampled meso+macroplastics (right). The pie charts represent the proportional distribution of marine litter types for each location. Sand-sampled meso- and macroplastics are combined due to the low item count of macroplastics.

Sand sampling (dunes and strandline) across the 116 quadrats revealed a total of 5,843 items, including macro-, meso-, and large microplastics. Of this total, 4,272 items (73%) were large microplastics (1–5 mm, with mean densities ranging from 0 to 1,453 items/m²), 1,221 were mesoplastics and 350 macroplastics (Table 2). On average, dune samples contained 247.7 items/m² (large micro-, meso-, and macroplastics), while strandline samples had 197.0 items/m². Across all size categories, fragments dominated the samples (67.0%), followed by filaments (15.2%), films (9.8%), foams (7.0%), and others (2.0%; pellets, ropes and objects). White or transparent items were the most common colour (62%), followed by blue (13%), green (10%), pink/red (7%), black, orange, and grey (each 2%), beige (1%), and brown, purple, and yellow (each below 1%). Similar to aerial survey results, the highest accumulation density occurred on northern and eastern beaches, across the three size categories (Figure 3). Ponta de Roque (BV17)

also had the highest density of large microplastics ($\bar{x}$ = 1,453 items/m^2), followed by Gatas (BV22; $\bar{x}$ = 914 items/m^2) and Ponta do Sol (BV28; $\bar{x}$ = 419 items/m^2). The highest density of mesoplastics was found on Gatas (BV22; $\bar{x}$ = 209 items/m^2), followed by Boa Esperança (BV27; $\bar{x}$ = 167 items/m^2) and Ponta de Roque (BV17; $\bar{x}$ = 155 items/m^2). Boa Esperança had the highest density of macroplastics in the sand samples (BV27; $\bar{x}$ = 37 items/m^2), followed by Gatas (BV22; $\bar{x}$ = 37 items/m^2) and Calheta Negra (BV24; $\bar{x}$ = 35 items/m^2).

Table 2. Average density of sand-sampled plastic items, categorised by size (large microplastics, mesoplastics, and macroplastics) and by type (fragments, filaments, foams, films, pellets, ropes, or objects). Plastic types are distributed across the three size categories.

Beach	Items per size (per m^2)			Items per type (per m^2)							Total items (per m^2)
	Micro	Meso	Macro	Fragments	Filaments	Foams	Films	Pellets	Ropes	Objects	
BV1 Carlota	57.0	59.0	10.0	2.0	88.0	3.0	28.0	-	5.0	-	126.0
BV2 Chaves	40.0	60.0	8.0	60.0	-	-	46.0	2.0	-	-	108.0
BV3 Varandinha	4.0	-	1.3	2.7	-	-	2.7	-	-	-	5.3
BV4 Curralinho	-	-	-	-	-	-	-	-	-	-	-
BV5 Santa Mónica	1.3	-	-	-	1.3	-	-	-	-	-	1.3
BV6 Manga Larga	4.0	-	1.0	-	-	-	4.0	-	-	1.0	5.0
BV7 Lacacão W	1.0	-	-	-	-	-	1.0	-	-	-	1.0
BV8 Lacacão E	0.7	-	0.7	0.7	0.7	-	-	-	-	-	1.4
BV9 Ponta Pesqueira	4.0	-	-	4.0	-	-	-	-	-	-	4.0
BV10 Curral Velho S	5.0	2.0	1.0	5.0	2.0	-	-	-	1.0	-	8.0
BV11 Curral Velho N	-	-	2.0	-	-	-	-	-	2.0	-	2.0
BV12 João Barrosa SF	-	-	1.3	-	-	-	-	-	-	1.3	1.3
BV13 João Barrosa S	1.3	4.0	1.3	-	4.0	-	1.3	-	1.3	-	6.6
BV14 João Barrosa N	9.0	1.0	1.0	1.0	6.0	-	2.0	-	2.0	-	11.0
BV15 Ponta Cosme	6.7	-	2.7	2.7	5.3	-	1.3	-	-	-	9.4
BV16 Ervatão	2.7	1.3	1.3	2.7	1.3	-	-	-	0.7	0.7	5.3
BV17 Ponta de Roque	1453.3	154.7	30.7	1492.0	116.0	24.0	1.3	-	2.7	2.7	1638.7
BV18 Nho Martin	62.0	13.0	8.0	18.0	14.0	42.0	6.0	-	2.0	1.0	83.0
BV19 Porto Ferreira	35.4	18.3	12.6	31.4	19.4	4.0	6.9	-	4.0	0.6	66.3
BV20 Figura	34.4	27.2	17.6	41.6	13.6	8.8	12.0	-	2.4	0.8	79.2
BV21 Canto	14.7	2.7	5.3	16.0	2.7	-	-	-	2.7	1.3	22.7
BV22 Gatas	913.7	208.6	36.6	633.1	231.4	123.4	162.9	1.7	5.1	1.1	1158.9
BV23 Braca	154.7	86.7	18.7	52.0	185.3	2.7	14.7	-	4.0	1.3	260.1
BV24 Calheta Negra	142.7	63.3	34.7	90.0	38.7	86.7	17.3	2.0	5.3	0.7	240.7
BV25 Lantcha	87.0	35.0	27.0	44.0	47.0	33.0	6.0	2.0	13.0	4.0	149.0
BV26 Ponta Antónia	296.0	118.4	32.0	246.4	127.2	29.6	28.8	3.2	11.2	-	446.4
BV27 Boa Esperança	248.0	166.7	37.3	281.3	64.0	6.7	85.3	1.3	12.0	1.3	452.0
BV28 Ponta do Sol	418.7	118.7	17.3	272.0	14.7	56.0	205.3	1.3	5.3	-	554.7
BV29 Cabral	6.0	5.0	6.0	5.0	6.0	-	2.0	-	3.0	1.0	17.0

Correlations between sampling seasons

We observed significant correlations in densities between the two sampling seasons for both drone and sand sampling methods. The drone-derived marine debris densities exhibited a strong positive Spearman correlation across the two seasons (rho = 0.967, $p < 0.001$). Similarly, sand-sampled microplastic debris densities exhibited moderate correlations between seasons (rho = 0.691, $p < 0.001$), while meso+macroplastic debris from sand samples were also significantly correlated (rho = 0.586, p = 0.002). Overall, the combined marine debris densities from sand samples showed moderate seasonal consistency (rho = 0.576, p = 0.002).

Relationship between size categories and colours

Meso+macroplastic densities from sand samples were strongly correlated with large microplastic densities (Spearman rho = 0.912, $p < 0.001$). Drone-derived plastic densities were strongly correlated with both large microplastic (rho = 0.737, $p < 0.001$) and meso+macroplastic (rho = 0.701, $p < 0.001$) from sand samples. The plastic debris density from drone data was significantly correlated with sand-sampled debris (rho = 0.733, $p < 0.001$).

Green microplastic filaments of sand samples were strongly correlated with meso+macroplastic filaments of the same colour (rho = 0.83, $p < 0.001$) and with drone-sampled green fishing nets/ ropes (rho = 0.85, $p < 0.001$). Transparent/white microplastic filaments of sand samples were also correlated with drone-derived transparent/white fishing nets/ropes (rho = 0.53, p = 0.003). White, blue, and black microplastic fragments in sand samples showed strong correlations with meso+macroplastics fragments (white rho = 0.89, blue rho = 0.69, black rho = 0.60, all with $p < 0.001$) and with drone-derived plastics of the same colours (white rho = 0.77, blue rho = 0.73, black rho = 0.65, all with $p < 0.001$). Transparent microplastic films of sand samples were significantly correlated with meso+macroplastics transparent films (rho = 0.66, $p < 0.001$) and with drone-derived transparent bags (rho = 0.47, p = 0.010). The remaining combinations of types and colours were non-significant.

The linear regression analysis indicated a significant positive relationship between drone-derived plastic densities (per 100 m^2) and the three sand sample categories: large microplastics (β = 26.818, SE = 2.702, $p < 0.001$; adjusted R^2 of 0.78), meso+macroplastics (β = 4.395, SE = 1.003, $p < 0.001$; adjusted R^2 of 0.39), and total plastic density (β = 31.213, SE = 3.396, $p < 0.001$; adjusted R^2 of 0.75).

Environmental drivers of debris accumulation

The NB GLM models revealed significant negative relationships with the eastward current flow (p-value < 0.05; Table 3) across all marine debris categories. Beach orientation to the north showed a positive significant relationship with five categories (large microplastics, meso+macroplastics, all sand sample items, fishing-related materials, and all drone-sampled items). Beach slope showed a positive significant relationship with both large microplastics and the total sand-sampled items. Beach elevation did not show a significant correlation with any marine debris category. Thus, the seawater current direction and beach orientation seem to be the most important variables explaining marine litter accumulation. Models showed low pseudo-R^2 values, suggesting that other factors may not have been accounted for.

Table 3. Results of the negative binomial generalised linear models (NB GLMs) by marine debris category: estimated coefficients and p-values of each topographical and oceanic variable, and pseudo-R^2 of each model. Asterisks denote significance.

Category		Intercept		Elevation		Slope		Northness		Eastward current		Pseudo-R^2
		Estimate	p	Estimate	p	Estimate	p	Estimate	p	Estimate	p	
Sand samples (per m^2)	Micro	-2.538	0.021*	-0.071	0.206	0.673	**<0.001*****	2.077	**0.002****	-6.400	**<0.001*****	0.064
	Meso+macro	-0.333	0.740	-0.073	0.146	0.301	0.037*	2.543	**<0.001*****	-3.618	**0.011***	0.063
	All items	0.569	<0.001***	-0.081	0.118	0.569	**<0.001*****	2.221	**<0.001*****	-5.661	**<0.001*****	0.061
Aerial images (per 100 m^2)	Fragments	-3.043	<0.001***	0.028	0.594	0.151	0.192	1.178	0.055	-5.017	**<0.001*****	0.147
	Containers	-3.528	0.001**	0.053	0.468	0.074	0.578	1.528	0.051	-4.937	**<0.001*****	0.156
	Fishing	-3.500	<0.001***	0.047	0.432	0.020	0.856	1.885	**0.008****	-5.202	**<0.001*****	0.204
	Wood	-4.767	<0.001***	0.011	0.895	0.125	0.400	1.039	0.281	-5.420	**0.001****	0.187
	All items	-2.901	0.005**	0.045	0.393	0.190	0.127	1.528	**0.012***	-5.730	**<0.001*****	0.128

Discussion

Our study revealed a significant accumulation of marine debris on the windward (north and east-facing) beaches of Boa Vista Island, particularly at Ponta de Roque, Figura, Canto, Gatas, Porto Ferreira, Boa Esperança and Ponta do Sol. These areas act as sinks for marine debris deposition, with over 85% being composed of plastics, primarily driven by ocean currents, as supported by our models (Table 3). The north and east coasts of Cabo Verde, situated in the southern part of the North Atlantic Gyre, are influenced by strong southward and westward-flowing currents (Assis et al., 2024). Boa Vista, being the easternmost island in the archipelago, acts as a natural barrier to these currents. This pattern aligns with findings from other regions where oceanic currents strongly influence litter accumulation, particularly on oceanic islands (Ivar do Sul et al., 2009; Baztan et al., 2014; Monteiro et al., 2018; Rapp et al., 2020; Reinold et al., 2020; Cardoso and Caldeira, 2021; Jones et al., 2021).

Similar trends were observed across other islands in the archipelago, with São Vicente and Santa Luzia showing significant sand-sampled debris densities on north-facing beaches (up to 83 and 917 items/m^2, respectively; Weidlich and Lenz, 2022; Sousa-Guedes et al., 2024). On Boa Vista, a single beach—Ponta de Roque (BV17), the easternmost beach—accounted for ~31% of the total marine litter sampled with both methods across the 29 locations. Sand samples from this site averaged 1,639 plastic items/m^2, including 1,453 large microplastics, although this is likely an underestimation, as we only sampled particles larger than 1 mm. Drone-based surveys further corroborated these findings, with Ponta de Roque averaging 68 macro-debris items per 100 m^2. For comparison, a northern beach on Santa Luzia Island registered 111 items per 100 m^2 (Sousa-Guedes et al., 2024). Santa Luzia is remote and uninhabited, complicating waste management and resulting in greater accumulation of large debris due to less frequent clean-up efforts, whereas Boa Vista experiences more frequent clean-ups (which target larger debris) yet still showed higher maximum levels of large microplastics.

Twenty out of 29 sampled beaches on Boa Vista surpassed the recommended European threshold of 20 macro-litter items per 100 m of beach length (Van Loon et al., 2020; see Table 1). The variation in debris composition across locations suggests differing sources. For instance, beaches near the main city of Sal Rei, such as Carlota and Cabral, had nearly half of their detected macro-litter composed of processed wood, potentially due to proximity to the port, whereas northern and eastern beaches were primarily affected by ocean-based sources, including fishing-related items. Fishing gear accounted for 23.7% of total marine litter on the island, consistent with findings from São Vicente and Santa Luzia (Weidlich and Lenz, 2022; Sousa-Guedes et al., 2024), though this percentage might be underreported, as land-based items like water bottles are often repurposed as fishing buoys. This mirrors global trends, where fishing activities are a major contributor to marine litter on shorelines, especially in remote areas (Barnes et al., 2009; Gall and Thompson, 2015; Monteiro et al., 2018; Sánchez-García and Sanz-Lázaro, 2023). Globally, nearly half of the plastics washing ashore within exclusive economic zones (EEZs) originate locally from the same EEZ (Onink et al., 2021). In islands, however, this local fraction is generally lower, as their open-ocean locations expose them to floating debris from distant EEZs (Onink et al., 2021). Compared to continental regions, islands tend to show more distinct and consistent spatial accumulation patterns. Particularly, islands lacking permanent streams (which significantly contribute to the transport of litter to coastal beaches; Rech et al., 2014) and with low human disturbance, like Boa Vista, primarily accumulate marine litter sourced from the ocean. Moreover, island shorelines often have higher debris densities than mainland coasts. For example, Easter Island's beaches had approximately 30 times more small plastic fragments than those on Chile’s mainland coast (Hidalgo-Ruz and Thiel, 2013). In terms of sources of marine debris pollution, Cabo Verde stands apart from the other Macaronesia archipelagos (Azores, Madeira and Canary Islands; Cardoso and Caldeira, 2021). While the latter are similarly exposed to debris originating from American coasts, most marine litter washing ashore in Cabo Verde comes from the Northwest African coast, which is a major fishing hotspot (Cardoso and Caldeira, 2021), and from other human activities

primarily in Mauritania and Senegal (World Bank, 2023). This difference is driven by the influence of regional oceanic currents and fishing activities, as highlighted in this study.

Plastic fragments were the most common type of debris, making up 43% of drone-sampled debris and 67% of sand-sampled debris. The significant correlation between densities of drone-surveyed plastic and sand-sampled large microplastics on Boa Vista suggests *in situ* fragmentation, which is common on tropical islands (e.g., Pitcairn Island, Ryan and Schofield, 2020; Galapagos Island, Jones et al., 2021). This fragmentation likely results from increased exposure to environmental factors such as sunlight, wind and wave action; prolonged retention of litter on beaches due to the circular movement of currents around islands; and limited waste management infrastructure, often leading to plastic accumulation or improper handling, even within landfills (Barnes et al., 2009; Andrady, 2011; Andrady et al., 2022; Shi et al., 2023). Additionally, high input from ocean-based sources, driven by productive upwelling systems of tropical and subtropical waters and associated fishing activities, contributes to the accumulation on islands (Cardoso and Caldeira, 2021; Watson et al., 2022). The significant correlations between multiple plastic colours across debris sizes reinforce this fragmentation theory, suggesting that objects of specific colours washing ashore are breaking into smaller pieces of the same colour. The EEZ of Cabo Verde averaged 0.023 microplastics/m³ in surface waters during 2014–2015, a medium concentration that is likely to have increased over time (Barrows et al., 2018; NOAA, 2022). Thus, while offshore sources likely account for a portion of microplastic fragments on the beaches of Boa Vista, *in situ* fragmentation appears to be a significant contributor as well.

In our study, drone surveys proved effective, with significant correlations between drone-derived and ground-sampled densities, suggesting they can provide a reliable, rapid assessment of marine debris sink zones. Drones offer several advantages over traditional methods, including faster coverage of large areas (Martin et al., 2018), with the added advantage of generating spatial data on variables such as topography and vegetation (Sousa-Guedes et al., 2024). Recent advancements in automated debris detection algorithms applied to drone imagery are promising steps toward the global standardisation of marine litter monitoring (Gonçalves et al., 2020a,

2020b). Nevertheless, drone sampling has limitations, particularly in detecting small, transparent or hidden beneath the sand items, leading to underestimations (Lavers and Bond, 2017; Corbau et al., 2023). The strong relationship between drone-surveyed plastics and large microplastics suggests that the first may serve as proxies for identifying and monitoring microplastic hotspots, particularly through volunteer efforts. However, these correlations should be interpreted with caution due to the limited temporal replication (only two) and the small scale of sand sampling. Additionally, while sand sampling showed seasonal consistency (with significant correlations between seasons), drone-based density correlations may reflect residual debris from previous sampling, as the beaches were not cleaned. Regardless, drone surveys are valuable for long-term monitoring and identifying accumulation hotspots across the archipelago and potentially in other island systems.

Cabo Verde faces waste management challenges exacerbated by its reliance on tourism and marine resources. Much of the waste is incinerated or ends up in landfills (Government of Cabo Verde, 2017; Ferreira et al., 2021). Identifying the sources of specific debris types, such as fishing gear and packaging, would enable more targeted prevention strategies. Further research should include the analysis of smaller plastic size fractions (< 1 mm), polymer types, and long-term monitoring with increasing sampling replicates to better understand trends over time. Given that the extent of marine litter is largely influenced by oceanic currents, it is challenging to implement initiatives to address the issue on the island. Nevertheless, we recommend some remedial solutions, including clean-up activities and capacity-building efforts. Beach clean-up events have been shown to benefit ecosystems (for instance, sea turtles increased nesting activity after beach cleaning; Fujisaki and Lamont, 2016). Although these actions provide only temporary relief, they remain effective at a local scale. Collaboration among local communities, fisheries, and tourism operators will be essential to reduce debris inputs. As global efforts to tackle plastic pollution continue, high-resolution data on waste emissions, like those provided in our study, are crucial for identifying pollution hotspots and developing mitigation strategies (Cottom et al., 2024). Our study provides key baseline data on marine litter of Boa Vista Island, aiding global efforts.

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Triste, por te deixar, de manhãzinha
Desci ao porto. E logo, asas ao vento,
Fomos singrando, sob um céu cinzento,
Como, num ar de chuva, uma andorinha.

Olhos na Ilha eu vi, amiga minha,
A pouco e pouco, num decrescimento,
Fugir o lar, perder-se num momento
A montanha em que o nosso amor se aninha.

Nada pergunto; nem quero saber
Aonde vou: se voltarei sequer;
Quanto, em ventura ou lágrimas, me espera.

Apenas sei, ó minha Primavera,
Que tu me ficas lagrimosa e triste,
E que sem ti a luz já não existe.

Eugénio Tavares

CHAPTER 4

How vulnerable are the nesting sites of loggerhead turtles in Cabo Verde?

Sousa-Guedes, D., Marco, A., Neves, E., Medina, M., Taxonera, A., Fairweather, K., Queiruga, A., Veiga, J., Patino-Martinez, J., Alírio, J., Bessa, F., Sillero, N. Under review in *Regional Environmental Change*.

Abstract

Marine turtles' nesting grounds face imminent threats from urbanisation, climate change and pollution. In this study, we estimated the vulnerability of loggerhead turtles (*Caretta caretta*) nesting beaches in Cabo Verde, one of the largest rookeries globally. We surveyed 61 sandy beach segments (~100 m) with a drone and modelled nest density by incorporating topographical and oceanographic variables. Then, we digitised all beaches across the islands, divided them it into smaller sections (digitised segments), and projected the model onto this layer. Each digitised beach segment was evaluated considering their exposure to five risk factors: a) marine litter density; b) inundation trends; c) land surface temperature trends; d) light pollution trends; and e) tourism pressure. Our analysis revealed that 48% of digitised segments are exposed to at least one threat. São Vicente, Santiago, and Sal are the most affected islands, mainly from marine debris and light pollution, while Santo Antão and Maio are the least impacted. Sal showed the highest overlap between vulnerable areas and high-density sites, highlighting its priority for conservation, though less affected islands should also be protected. We found that marine debris correlates positively with nest density, while light pollution negatively affects it. Our study emphasises the need for conservation efforts to ensure the sustainability of nesting sites amid escalating global changes.

Introduction

Sandy beaches constitute over one-third of the coastlines on Earth. Situated at the land-ocean interface, these ecosystems are vulnerable due to their low elevation and unconsolidated materials, making them highly susceptible to erosion (Defeo et al., 2009; Nicholls and Cazenave, 2010). By 2050, it is estimated that one-third of all low-elevation coastal zones will face significant erosion (Vousdoukas et al., 2020). This is exacerbated by increasing urbanisation,

natural resource exploitation, and climate change – a phenomenon known as coastal squeeze (Defeo et al., 2009; Defeo and Elliott, 2020; Fanini et al., 2020).

The shrinking of sandy beaches threatens critical habitats for coastal nesters, such as marine turtles (Mazaris et al., 2009; Fuentes et al., 2010; Biddiscombe et al., 2020). Female sea turtles have philopatric behaviour, returning to their natal beaches to lay their eggs. The choice of the nesting site is crucial for the survival of embryos, as the microhabitat conditions determine their successful development (Ackerman, 1997). This site selection can sometimes be unsuccessful due to multiple threat factors, particularly among young females (Pfaller et al., 2009; Martins et al., 2022). For instance, nests can be inundated due to poor site selection, natural events (storms), and sea-level rise, risking nests being washed away or flooded (Pike et al., 2015). Another significant threat is the warming of sand on nesting beaches, often linked to broader climatic trends, as sea turtles have temperature-dependent sex determination (Fuentes et al., 2011; Howard et al., 2014; Laloë et al., 2014). Higher sand temperatures can skew sex ratios toward females (reducing genetic diversity and their resilience to environmental changes in the long term) or cause embryonic mortality (Howard et al., 2014; Lockley and Eizaguirre, 2021; Laloë and Hays, 2023). Moreover, marine litter accumulation on beaches, particularly plastics, poses further threats. It can modify the nesting behaviour of females (Fujisaki and Lamont, 2016); change sediment permeability (Carson et al., 2011); alter sand temperature (Lavers et al., 2021; Fuentes et al., 2023); chemically contaminate the sand (Sousa-Guedes et al., 2023a); and act as physical barriers, disrupting hatchling emergence synchrony or hampering their arrival at the sea (Aguilera et al., 2018; Sousa-Guedes et al., 2023b). Indeed, sandy beaches are increasingly becoming sinks for marine litter (Lavers and Bond, 2017; Sousa-Guedes et al., 2024). Additionally, urbanisation growth has globally increased artificial light pollution, affecting multiple species (Falchi and Bará, 2023). For sea turtles, nocturnal artificial lighting can disorient females and hatchlings, leading them away from the ocean, and reducing their survival chances (Witherington, 1992; Lorne and Salmon, 2007). It can also cause females to avoid bright beaches or delay nesting, resulting in unsuccessful nesting attempts (Silva et al., 2017). Furthermore, recreational and

tourist activities are overwhelmingly concentrated on sandy beaches. Large tourist developments attract a lot of people, leading to increased light pollution, trampling of nests, and accelerated beach erosion due to the destruction of dunes (Costa et al., 2023).

The insular archipelago of Cabo Verde, off the west coast of Africa, hosts one of the largest nesting populations of loggerhead turtles (*Caretta caretta*) worldwide, and the only stable reproductive population of the Eastern Atlantic (Marco et al., 2011, 2012; Casale and Marco, 2015; Patino-Martinez et al., 2022). The discovery of these islands in 1456 was quickly followed by the official record of sea turtles nesting there, described as occurring 'in abundance' (Taxonera et al., 2022). The archipelago hosts a large and growing nesting population, with an increasing annual number of nests (Laloë et al., 2020). This phenomenon is still not fully understood, partially attributed to successful conservation efforts or environmental changes at the sea or on land. Despite this, the loggerhead turtle population in Cabo Verde remains classified as endangered by the IUCN (Casale and Marco, 2015).

Considering all the threats to sea turtle rookeries, our study aims to assess the vulnerability of loggerhead nesting sites across seven islands of Cabo Verde, focusing on the loss of suitable nesting areas by (1) marine litter pollution, which affects incubation, hatchlings' emergence, and females behaviour; (2) increasing nest inundation risk, resulting in egg mortality or displacement; (3) warming sands, leading to female-biased hatchlings or increased mortality; (4) increasing light pollution, which disorients nesting females and hatchlings; and (5) tourism pressure on beaches, increasing direct disturbances. We integrated aerial drone surveys, predictive modelling, satellite remote sensing data, and trend analysis to identify the threats at each site. Additionally, we predicted nests' density across beaches to determine whether they overlap with the most vulnerable areas. By identifying resilient beaches and those losing habitat quality, we seek to inform conservation efforts and provide insights into immediate threats to their nesting beaches (Fuentes et al., 2011; Patrício et al., 2021).

Materials and methods

Study area

The Cabo Verde archipelago is located in the northeast Atlantic Ocean, off the west coast of Africa. All ten islands are of volcanic origin and characterised by a dry, windy, and subtropical climate. Tourism is the fastest-growing economic sector in the country (Akkemik et al., 2024), contributing to over one-third of the country's GDP in 2019 (Sarmento and Monteiro, 2023). Despite that, Cabo Verde faces economic vulnerability and limited natural resources.

Our study focused on seven islands: Santo Antão, São Vicente, Santa Luzia, Sal, Boa Vista, Maio, and Santiago (Figure 1). We excluded the islands of São Nicolau, Fogo, and Brava due to their minimal sandy beaches and low nesting activity (Marco et al., 2011).

To assess loggerhead nest density and marine litter pollution, we conducted aerial surveys on 61 sandy beach segments (~100 m each) across the seven islands. Surveys were conducted in September and October 2021 (Boa Vista), October 2022 (Santo Antão, São Vicente and Santa Luzia), October 2023 (Sal), and December 2023 (Maio and Santiago). We used the DJI Mavic Air 2 unmanned aerial vehicle (UAV or drone), at an altitude of 15 m and 80% image overlap (forward and lateral), following the methodology by Sousa-Guedes et al. (2024). Each surveyed segment represents an independent sampling unit, selected to characterise the diversity of beaches in terms of morphology, environmental conditions, and exposure to risk factors, covering ~100 m along the waterline and the entire beach width. Each segment corresponded to a different beach: there were no continuous segments, with the closest segments being separated by ~600 m. The resulting spatial resolution was ~5 mm. We processed the images into orthophotos using Agisoft Photoscan (Metashape Professional v2).

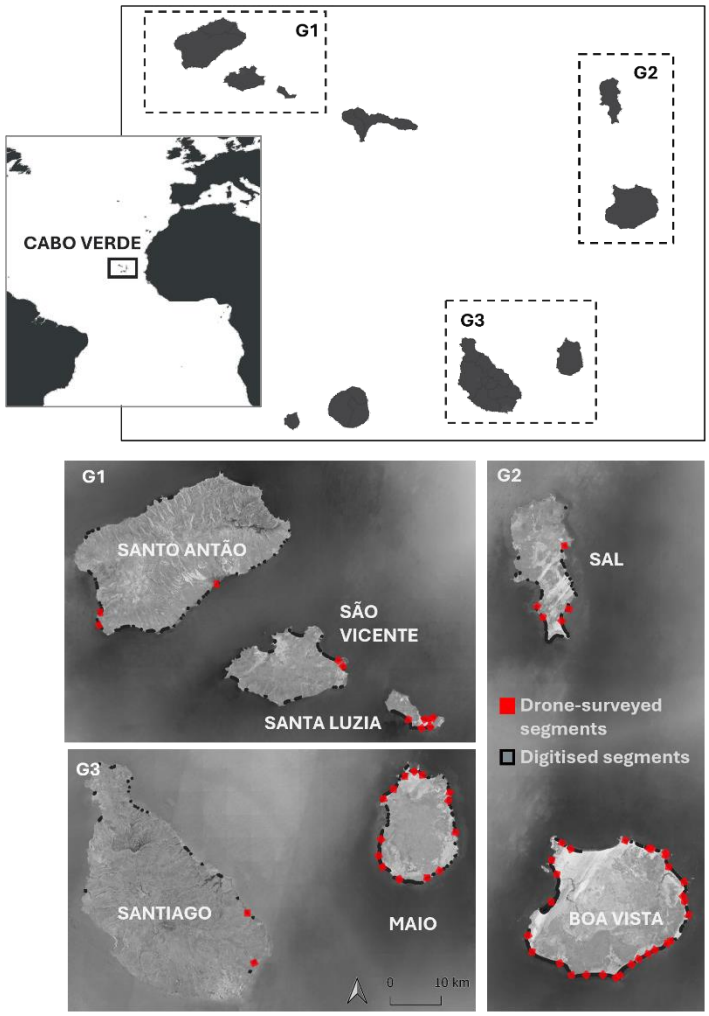

Figure 1. Study area across seven islands in Cabo Verde. *Drone-surveyed* segments are represented in red (61 segments, each ~100 m in length) and *digitised* segments are outlined in black (306 segments manually digitised, 100-1000 m in length). Segments' widths are exaggerated for representation.

To complement the surveyed data, we created a layer of all sandy beaches in the archipelago, delineated using Google satellite imagery within QGIS 3.32.2. For comparability, we divided this digitised layer into segments ranging from 100 to 1000 m in length, depending on the total beach extension. Longer beaches were subdivided into multiple segments (e.g., a 5000 m beach was divided into five 1000 m segments) to capture variability in risk exposure along their extent. Shorter beaches (< 1000 m) were retained as single segments, while very small beaches (< 100

m) were excluded. This segmentation allowed for standardisation across beaches of varying lengths while avoiding the overrepresentation of smaller beaches. By allowing lengths to vary between 100 and 1000 m, we captured variability where needed without unnecessary fragmentation. This facilitated model extrapolation, resulting in a total of 306 segments.

Thus, we obtained two distinct layers of nesting beaches (Figure 1): i) a layer comprising 61 segments (~100 m) independently surveyed using drones, hereafter called *drone-surveyed* layer; and ii) a layer comprising 306 digitised segments of sandy beaches both surveyed and non-surveyed (from 100 to 1000 m), hereafter called *digitised* layer.

Nest density modelling

To predict the density of nests, we counted the number of loggerhead turtle nests within the *drone-surveyed* layer from two sources: i) photointerpretation of orthophotos (nests with freshly visible tracks to ensure they were recently laid; only one day of data from the drone surveys in September/October 2021, 2022, or 2023), and ii) data from local NGOs (ten randomly selected monitoring days between August and September 2020, 2021, and 2022). NGOs that provided data are: *Biosfera*, *Project Biodiversity*, *BIOS.CV*, *Cabo Verde Natura 2000* and *Maio Biodiversity Foundation*. Main nesting beaches are monitored daily during the nesting season by NGOs; however, due to data restrictions, we included data from only ten random days across the seasons in each beach. Moreover, not all beaches are monitored by NGOs.

We calculated a nest density index as the number of nests per 100 m per day, which can be expressed as: $\frac{Total\ number\ of\ nests\ in\ drone-surveyed\ segment}{Segment\ length\ (m) \times Number\ of\ surveyed\ days} \times 100$.

We used predictive modelling to assess the spatial distribution of nest density index across beaches, by assigning to each segment (both *drone-surveyed* and *digitised*) a set of environmental variables: topographical data derived from the digital elevation model (DEM) of the Shuttle Radar Topography Mission (SRTM v3; Farr et al., 2007), with a spatial resolution of ~30 m; and

oceanographic data from Bio-ORACLE v3 (Assis et al., 2024) for present-day conditions (2010-2020), with a resolution of ~5.5 km. We selected the environmental variables based on their importance for nest site selection (Wood and Bjorndal, 2000; Putman et al., 2010; Christiaanse et al., 2024). Topographical variables included slope (the ratio of the elevation difference to the horizontal distance between two points, in percentage); and northness and eastness (respectively calculated as cos(aspect) and sin(aspect), ranging from 1 to -1, from full north/east to full south/west; Guisan et al., 1999; Sillero et al., 2021). Oceanographic variables included minimum, maximum, and median values of ocean temperature (ºC); seawater velocity (ms^{-1}); northward seawater direction (cos(seawater direction), from 1 to -1); and southward seawater direction (sin(seawater direction), from 1 to -1). For each segment of both *drone-surveyed* and *digitised* layers, we extracted the median values of topographical variables and the closest pixel value of oceanographic variables. Additionally, we treated island as a categorical variable (with seven levels corresponding to the seven islands) to account for the philopatric behaviour of sea turtles (~77% of nesting females lay their eggs within 15 km of their previous nests; Patino-Martinez et al., 2022). This resulted in three topographical variables (median slope, northness, and eastness), 12 oceanographic variables (minimum, maximum, and median ocean temperature, seawater velocity, northward seawater, and southward seawater), and one categorical variable (island). We excluded highly correlated variables using the variance inflation factor (VIF > 2) (Sillero et al., 2021).

We modelled the nest density index within the *drone-surveyed* layer using the algorithm Gradient Boosting Machine (GBM), with nest density index as the response variable, and five explanatory variables with correlation below the VIF threshold: median slope, median eastness, minimum northward seawater, maximum seawater velocity and island. We used 10-fold cross-validation to assess model performance and determined the optimal hyperparameters based on the lowest Root Mean Squared Error (RMSE). We fitted the final GBM model using the 'gbm' function in R software 3.6.3 (R Core Team 2020) with Gaussian distribution and projected onto the *digitised*

layer. To evaluate the model's predictive performance, we fitted a linear regression to compare the actual versus predicted values.

Risk factors

The five risk factors were selected based on their impact on sea turtle nesting (Vousdoukas et al., 2020; Simantiris, 2024) and data availability. Risk layers were derived using predictive modelling (marine debris density), trend analyses (inundation, warming, and light pollution), and the identification of tourism pressure. The final output indicates the presence or absence of each risk in every *digitised* segment.

Marine debris density model

We identified large marine debris (> 25 mm; fragments, fishing materials, containers/packaging, processed wood, clothing, and others) through photointerpretation of orthophotos at the *drone-surveyed* layer (Sousa-Guedes et al., 2024). We quantified marine debris density in each segment as the number of items per 100 m of beach length, log-transformed and standardised (between 0 and 1) for analysis.

To predict the spatial distribution of marine debris densities, we used GBM modelling with Gaussian distribution, and four explanatory variables (calculated as in section 2.2): median eastness, median northness, minimum northward seawater, and maximum seawater velocity. We selected the variables based on their role in marine debris accumulation (Cardoso and Caldeira, 2021; Sousa-Guedes et al., 2024). We trained the model on the *drone-surveyed* layer and projected it onto the *digitised* layer using the same procedure as the nest density model in R.

Inundation, warming, and light pollution trends

To assess temporal changes in water inundation, warming, and light pollution, we obtained data from different satellite imagery sources. All satellite imagery processing and trend analyses were conducted in the cloud-based platform Google Earth Engine (GEE; Gorelick et al., 2017).We detected water inundation over time for all islands with the Modified Normalised Difference Water Index (MNDWI; Xu, 2006), using Landsat 8 images (USGS, L2/C2/T1) from 2013 to 2023, during nesting season (June-October) at the original resolution of ~30 m. The MNDWI uses the green and shortwave infrared bands (*Green - SWIR1/ Green + SWIR1*), identifying open water while suppressing noise from built-up, vegetation, and soil. Similar techniques have been used to estimate flooding on beaches (Makris et al., 2023). We removed pixels with clouds and cloud shadows with bitwise operations (QA_PIXEL).

For warming trends, we generated land surface temperature (LST) data from 2000 to 2023, during the nesting season (June-October), from the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor (8-day L3; Wan et al., 2021). LST captures the thermal behaviour of the land surface across large areas and periods (Reiners et al., 2023). We computed the nighttime LST at their original spatial resolution of ~1 km, scaled the values from Kelvin to Celsius, and implemented a cloud masking function (QC_Night). We focused on nighttime LSTs rather than daytime, which have shown stronger trends in recent years (Almeida et al., 2023).

Similarly, to assess light pollution, we calculated the nighttime light using the VIIRS/DNB satellite (monthly Stray Light Corrected Nighttime Day/Night Band Composites v1), at a spatial resolution of ~500 m (Mander et al., 2023; Hu et al., 2018; Attum and Nagy, 2024). We calculated the annual maximum light during the nesting season (June-October) for 2014-2019, excluding post-2020 data due to temporary reductions in tourism and light pollution from COVID-19 lockdowns, which have since returned to pre-pandemic levels (Sarmento and Monteiro, 2023; Attum and Nagy, 2024; Akkemik et al., 2024; Sillero et al., 2024).

Then, we assessed temporal trends in inundation, nighttime LST, and light pollution using the Mann-Kendall test (Kendall, 1990). This non-parametric test identifies monotonic trends in time series data, distinguishing between downward (negative) or upward (positive) slopes over time. We conducted trend analyses at a 95% confidence level and exported the pixels with significant positive trends ($p < 0.05$). By focusing on trends rather than stationary values, we assume that increasing inundation, temperatures, and light pollution will persist due to climate change, urbanisation and population growth (Nicholls and Cazenave, 2010; IPCC, 2021).

We obtained three trend layers (inundation, warming, and light pollution) covering the whole area of the islands. To extract trends within the *digitised* beach segments, we clipped the inundation and LST layers to match the segment boundaries. For inundation trends, we applied an additional filtering step to ensure that segments are not wrongly classified as inundated due to isolated, artificial significant pixels. Thus, segments were only considered inundated if they contained at least three significantly positive pixels (~90 m, equivalent to three times the Landsat pixel size). Light pollution trends were assessed differently, as light sources are located outside the beach. For this, we calculated the visibility from the centroid of each *digitised* segment (306 points) to the nearest light source (i.e., centroids of pixels with significant positive Mann-Kendall slope in light pollution, at the 75th percentile) using the 'intervisibility network' function in QGIS. This function uses the DEM of the islands to determine visibility between an observer and a target point, both set at a ground-level height, within a 5000 m radius.

Tourism pressure

A tourism pressure layer was calculated by identifying the location of major tourist resorts using Google Maps within QGIS.

Vulnerability index

We classified each risk factor as present or absent based on the 75th percentile threshold, identifying 25% of the most vulnerable segments (except for tourism pressure). This conservative threshold prioritises conservation efforts and resources to areas most in-need. We created binary layers, assigning a value of 1 to *digitised* segments exceeding the defined threshold in each risk factor. For tourism pressure, a value of 1 was assigned to *digitised* segments with such infrastructures. We then computed a vulnerability index for each *digitised* segment, ranging from 0 to 5 (considering marine debris density; inundation, warming, and light pollution trends; and tourism pressure), by summing the binary risk factors (presence = 1, absence = 0). We also calculated and normalised the percentage of segments with each risk factor and vulnerability index class by island.

Additionally, to assess whether high nest density index co-occurs with each risk factor, we performed a linear regression using the modelled predicted nest density index as the response variable and the risk factors as explanatory variables, in R.

Results

Nest density modelling

The 61 *drone-surveyed* segments exhibited a nest density index ranging from 0 to 13.3 nests per 100 m of beach length per surveyed day, totalling 5991 nests, with the highest index value observed in eastern Boa Vista (Figure S1, Supplementary Materials).

The performance of the GBM nest density model indicated a good fit ($R^2 = 0.85$). The linear regression presented a strong positive correlation between the predicted and the actual values (estimate = 1.109, SE = 0.059, $p < 0.001$). The most influential variable in the model was seawater velocity (26.3%), followed by island (20.0%), eastness (19.1%), slope (18.6%), and northward seawater (16.0%). When projecting the model to all islands, Boa Vista showed the highest

predicted nest density index (65.5% of all nests; Table 1), with a total of 22 *digitised* segments between 8.1 and 11.5 nests/100m/day (high season), on the eastern side of the island. The second island with the highest proportion of predicted nests is Sal (14.5%), followed by Maio (6.9%), São Vicente (6.2%), Santa Luzia (5.5%), Santo Antão (0.9%), and Santiago (0.4%).

Table 1. Predicted number (n) and percentage (%) of nests per day as estimated with the GBM model, and total length of *digitised* segments per island.

	Santo Antão	**São Vicente**	**Santa Luzia**	**Sal**	**Boa Vista**	**Maio**	**Santiago**	**TOTAL**
Predicted nests/ day (n)	34.7	230.2	203.8	536.0	**2420.8**	256.3	13.5	3695.2
Predicted nests/ day (%)	0.9	6.2	5.5	14.5	**65.5**	6.9	0.4	100
Total length	15.2 km	11.8 km	10.7 km	18.8 km	67.0 km	33.7 km	6.5 km	163.8 km

Risk factors

All *drone-surveyed* segments had at least one item of marine debris, ranging from 1 (in Santo Antão) and 5038 items/100 m (Santa Luzia) (Figure S1 and Table S1, Supplementary Materials). The performance of the GBM model for marine debris density indicated a reasonably good fit (R^2 = 0.56). The linear regression showed a strong positive correlation between the predicted and actual values (estimate = 1.088, SE = 0.125, $p < 0.001$). The most influential variable in the model was northness (40.0%), followed by northward seawater (24.0%), eastness (18.9%) and seawater velocity (17.1%). A total of 78 *digitised* beach segments were above the threshold of predicted values (75th percentile of log-transformed and standardised marine debris density = 0.618), with the most affected island being Santiago (66.7% of its segments) and in absolute numbers Boa Vista (23 segments) (Table 2). Santo Antão had only one *digitised* segment accumulating large volumes of marine litter. Segments oriented to the north and east had a higher probability of accumulating a large number of marine debris across most islands (Figure 2).

We identified significant positive inundation trends (75th percentile of significant positive slopes = 0.007) on 24 *digitised* segments from five islands (Table 2), with the most affected islands being São Vicente (16.7% of its segments) and Boa Vista (10 segments). Santiago and Santa Luzia showed no significant increase in inundation trends. Nighttime LST revealed significant positive trends (75th percentile of significant positive slopes = 0.075 °C/year) on 28 segments from six islands, with Santa Luzia being the most affected (31.3% of its segments) and São Vicente by absolute numbers (seven segments). Santiago exhibited no warming trends. We found increased light pollution levels (75th percentile of significant positive slopes = 0.320 nW/cm²/sr/year) in 54 segments from six islands, with São Vicente being the most affected (58.3%, totalling 14 segments). Santa Luzia showed no increase in light pollution. We observed tourism pressure on 13 segments from four islands, with Sal being the most developed (14.0%, totalling seven segments). Santo Antão, Santa Luzia and Maio showed no evidence of tourism pressure.

Table 2. Number (n) and percentage (%) of *digitised* segments with each risk factor in each island (>75th percentile). In bold, the highest value for each factor.

Risk factor	Santo Antão		São Vicente		Santa Luzia		Sal		Boa Vista		Maio		Santiago		TOTAL SEGMENTS	
	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%
Marine debris	1	2.3	10	41.7	3	18.8	17	34.0	**23**	25.6	10	16.4	14	**66.7**	78	25.5
Inundation	1	2.3	4	**16.7**	0	0	3	6.0	**10**	11.1	6	9.8	0	0	24	7.8
Land surface temperature	1	2.3	**7**	29.2	5	**31.3**	5	10.0	6	6.7	4	6.6	0	0	28	9.2
Light pollution	5	11.4	**14**	**58.3**	0	0	12	24.0	13	14.4	5	8.2	5	23.8	54	17.6
Tourism pressure	0	0	1	4.2	0	0	**7**	**14.0**	4	4.4	0	0	1	4.8	13	4.2
TOTAL SEGMENTS	44		24		16		50		90		61		21		306	

Marine litter is the most widespread risk, affecting 78 segments (25.5%), followed by increasing light pollution (54 segments, 17.6%), increasing nighttime LST (28 segments, 9.2%), increasing inundation (24 segments, 7.8%), and tourism pressure (13 segments, 4.2%; Table 2). São Vicente is at higher risk across all factors, while Santo Antão has the lowest risk (Figure 2b).

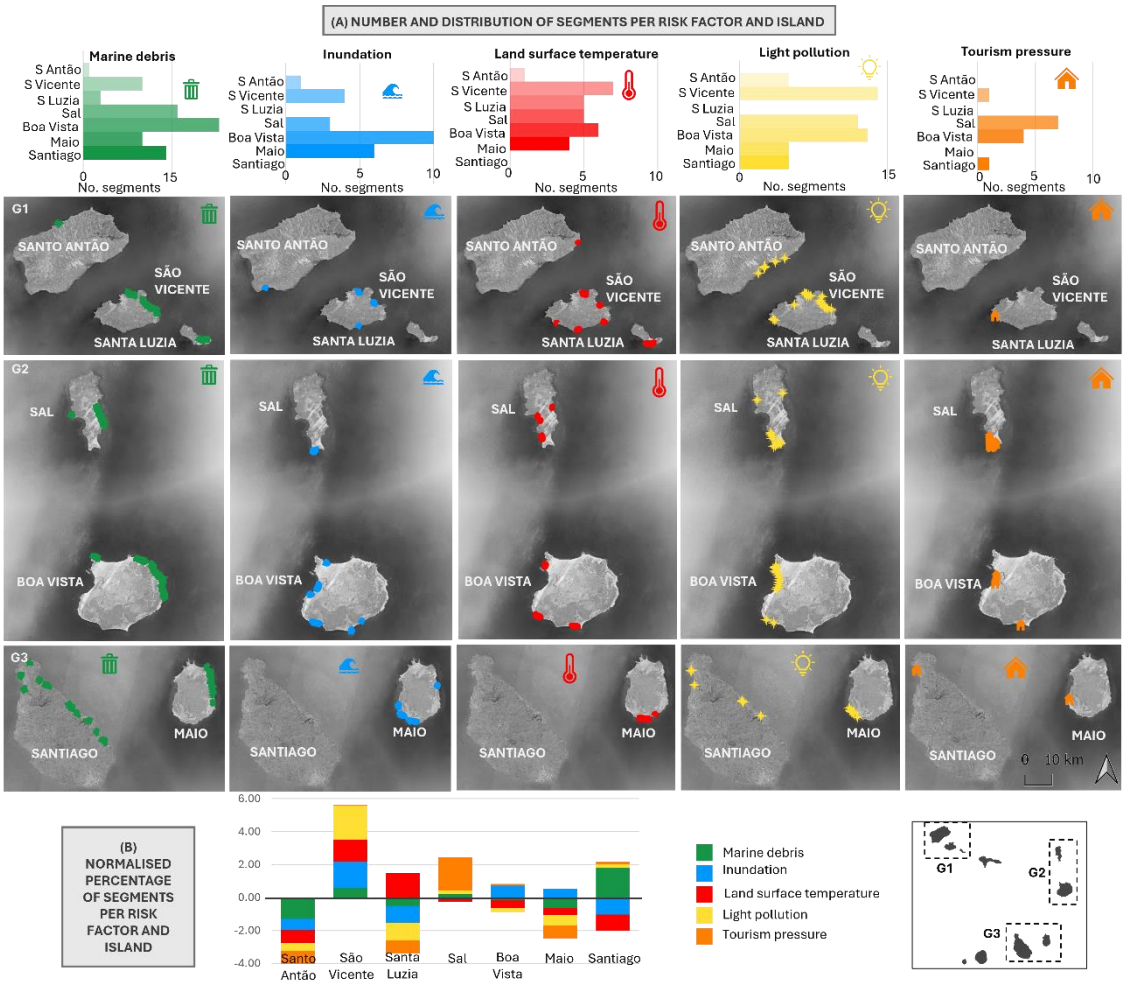

Figure 2. (A) Number and distribution of *digitised* beach segments at risk per risk factor and island; (B) normalised percentage of segments per risk factor and island, where negative and positive values indicate a lower and higher percentage of segments compared to the average, respectively.

Relationship between risk factors and nest density

The linear regression model of the relationship between nest density index and risk factors showed weak performance (adjusted $R^2 = 0.08$). The model indicated that marine debris density and light pollution were significantly related to nest density index, with marine debris having a positive effect (estimate = 1.727, SE = 0.349, $p < 0.001$) and light pollution having a negative effect

(estimate = -1.198, SE = 0.425, p = 0.005). The remaining risk factors were not significantly related to the predicted nest density index.

Vulnerable areas

We identified 158 non-vulnerable *digitised* segments (vulnerability index of 0), with the safest island being Santo Antão (81.8% are safe) and Boa Vista in absolute numbers (45 are safe). São Vicente and Santiago have 83.3% and 66.7% of segments with some risk, respectively (Table 3). Additionally, 112 segments had one risk factor (all islands), 26 had two risk factors (all islands except Santo Antão and Santa Luzia), nine had three risk factors (São Vicente, Sal, and Boa Vista), and only one had four risk factors (São Vicente). No segment had all five risk factors.

Table 3. Number (n) and percentage (%) of *digitised* segments corresponding to each vulnerability index class in each island. In bold, the highest value for each index class.

Vulnerability index	Santo Antão		São Vicente		Santa Luzia		Sal		Boa Vista		Maio		Santiago		TOTAL SEGMENTS	
	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%
0	36	**81.8**	4	16.7	8	50.0	19	38.0	**45**	50.0	39	63.9	7	33.3	158	51.6
1	8	18.2	9	37.5	8	50.0	22	**44.0**	**37**	41.1	19	31.1	9	42.9	112	36.6
2	0	0	**7**	**29.2**	0	0	6	12.0	6	6.7	3	4.9	4	19.0	26	8.5
3	0	0	**3**	**12.5**	0	0	**3**	6.0	2	2.2	0	0	1	4.8	9	2.9
4	0	0	**1**	**4.2**	0	0	0	0	0	0	0	0	0	0	1	0.3
SEGMENTS AT RISK	8	18.2	**20**	**83.3**	8	50.0	31	62.0	45	50.0	22	36.1	14	66.7	148	48.4

There is no substantial spatial overlap between high predicted nest density index and vulnerable areas in Santo Antão, Santa Luzia, Maio and Santiago (Figure 3). In São Vicente, multiple segments with high nest density index face one to three risk factors (Figure 3d). Sal also showed some overlap between high nest density index overlaps and vulnerability, while Boa Vista primarily has segments with either no risks or just one risk factor.

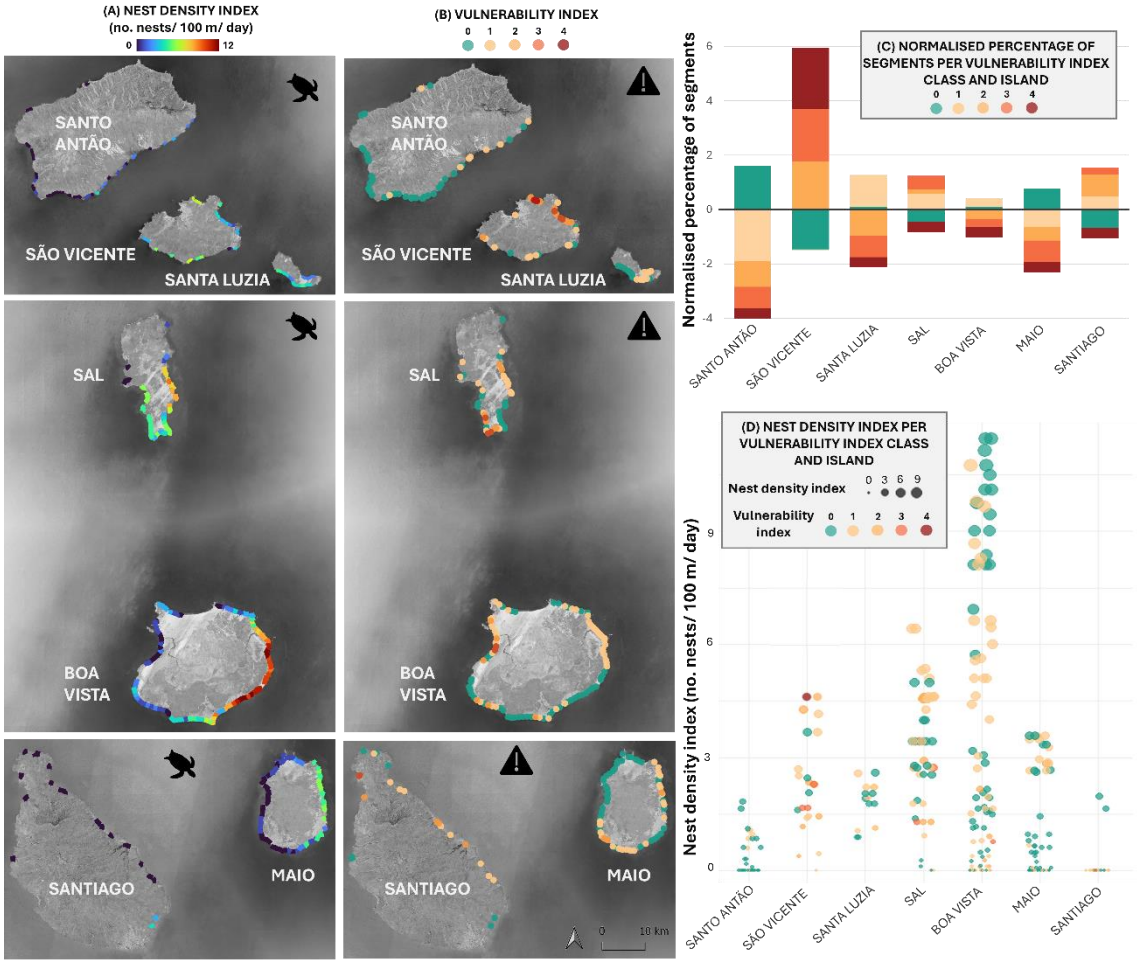

Figure 3. (A) Predicted nest density index across *digitised* beach segments; (B) vulnerability index across segments; (C) normalised percentage of beaches per vulnerability index class and island, where negative and positive values indicate a lower and higher percentage of segments compared to the average, respectively; (D) predicted nest density index per vulnerability index class and island, with circle sizes increasing with nest density index.

Discussion

Our study revealed that 48% of the sandy beaches in Cabo Verde are exposed to some threat, with vulnerability levels varying across islands. Marine debris is the most widespread risk, affecting 26% of the beach segments, including high-density loggerhead nesting areas. Most marine debris is fisheries-related plastics, posing risks of entrapment and toxicity (Aguilera et al., 2018;

Weidlich and Lenz, 2022; Sousa-Guedes et al., 2023a, 2023b, 2024). Of the 61 *drone-surveyed* segments, 47 exceeded the recommended European threshold of 20 macro-litter items/100 m (Van Loon et al., 2020). In fact, five segments exceeded the threshold by over two orders of magnitude: Achados (three segments with up to 5038 items/100 m; Santa Luzia; Sousa-Guedes et al., 2024), Ponta de Roque and Figura (5010 and 2727 items/100 m, respectively; Boa Vista); and 12 segments in Santo Antão, Boa Vista, and Maio surpassed the threshold by over 20 times (Table S1, Supplementary Materials). The absence of data on clean-up frequency (which occurs at least once a year on some of the main nesting beaches) may have skewed results, underestimating pollution levels in some areas. Furthermore, while a single drone survey per beach might overlook seasonal variations (Frias et al., 2018), our marine debris model aligns with previous studies indicating higher accumulation on north and east-facing beaches, driven by ocean currents (Cardoso and Caldeira, 2021; Weidlich and Lenz, 2022; Sousa-Guedes et al., 2024). Northern islands, particularly Santa Luzia and Boa Vista, are more affected because they may act as barriers against the North Atlantic Gyre, with strong clockwise-currents. We also found a significant co-occurrence of marine debris and high nest density index, which could negatively impact incubation and hatchling emergence (Aguilera et al., 2018; Fuentes et al., 2023; Sousa-Guedes et al., 2023a, 2023b). As females seem to avoid nesting in heavily polluted beaches (Fujisaki and Lamont 2016), future studies should explore correlations between marine debris and nesting failure or clustering.

Rising light pollution, affecting 18% of segments, was concentrated near urban centres. A significant negative relationship between light pollution and nest density index suggests potential avoidance of brightly lit beaches by females (Hu et al., 2018). However, this pattern might instead reflect the spatial separation between main urban centres (west coast) and loggerhead nesting preferences (east coast), rather than active avoidance of illuminated beaches. Artificial lighting is known to reduce nesting success and hatchling survival due to disorientation (Lorne and Salmon, 2007; Silva et al., 2017). In Cabo Verde, many isolated areas remain unaffected by artificial light, providing important nesting refuges. Although hatchlings can be influenced by artificial ambient

light from sources several kilometres away, with effects intensifying nearer the source (Kamrowski et al., 2014; Weishampel et al., 2016), this impact is minimal in Cabo Verde, due to the small size and poor illumination of urban settlements. Additionally, artificial lighting on beaches can delay hatchlings' ocean dispersal, keeping them nearshore 23% longer than under ambient light, increasing predation risk (Thums et al., 2016).

Nesting in Cabo Verde currently occurs during the warmest time of the year. Rising temperatures affect 9% of beach segments, with Santa Luzia and São Vicente being the most affected. Wider beaches with less vegetation seem more vulnerable to warming, with an average width of 23 meters versus 15 meters for non-warming segments (Mann-Whitney U test, $p = 0.005$). Other factors, such as exposure to winds, may also contribute. In Sal, nesting occurs mostly on the coolest beaches (Albert Taxonera, personal observation), whereas in Boa Vista, it is mainly concentrated on its warmest beaches (Abella-Perez et al., 2016; Tanner et al., 2019). Despite many beaches in Boa Vista producing nearly all-females hatchlings, the island is considered relatively resilient, with a few cooler beaches producing a significant number of male hatchlings (e.g., Boa Esperança, Lacacão and Varandinha; Tanner et al., 2019). Among these, Lacacão, located in the south, has shown significant warming trends in the present study (Figure 2). Cooler beaches may be more sensitive to rising temperatures, while warmer beaches may have reached a point where further warming is limited. Under a low-emission scenario (1.8°C increase), primary sex ratios in Cabo Verde are projected to exceed 99% female hatchlings by 2100 (Tanner et al., 2019). If temperatures continue to rise, hatching success could be compromised (Abella-Perez et al., 2016; Laloë et al., 2017; Tanner et al., 2019). Conserving cooler beaches should be prioritised to secure the production of male offspring. While ongoing warming can drive temporal or spatial shifts in nesting, these are unlikely to offset the predicted effects of rising temperatures (Laloë and Hays, 2023; Fuentes et al., 2024).

We observed an increasing inundation trend on 8% of beach segments, with higher proportions in São Vicente, Boa Vista, and Maio, particularly on southern shores. Boa Vista and Maio, along with Sal, are the geologically oldest islands and the most eroded ones, which may increase their

flooding risks (Gomes et al., 2019; Samrock et al., 2022). Sea-level rise and more frequent storms are expected to further intensify inundations (Nicholls et al., 2011; Young et al., 2011; Lee et al., 2017), but these impacts will not occur uniformly across the globe (Nichols and Cazenave, 2010; Romine et al., 2013). In Boa Vista, future sea-level rise is predicted to have the greatest impact in Sal Rei (northwest coast; Gomes et al., 2019), which often inundates during winter, potentially due to reduced beach management and deteriorated dunes. Our study, conducted during summer, coincides with winter in the southern hemisphere, a period of frequent storms, potentially exacerbating inundations on southern beaches. Climate change affects erosion-accretion dynamics (Feagin et al., 2005; Romine et al., 2013), amplified by coastal development, that restricts the natural landward migration of beaches, ultimately reducing the area available for nesting (Armstrong and Lazarus, 2019; Patrício et al., 2019). While Boa Vista remains moderately impacted due to its undeveloped coastline and dune systems (Abella-Perez et al., 2016), globally, one-quarter of sea turtle nesting coastlines are bordered by anthropogenic structures (Biddiscombe et al., 2020).

Tourism pressure, affecting only 4% of segments, is heavily concentrated in Sal (14% of its segments) and Boa Vista (4%), the two most important nesting islands. Loggerhead nesting activity has been reduced in areas with tourist developments in Sal (Taylor and Cozens, 2010). Given the growth of the tourism industry, with overnight stays more than doubling since 2010 (~5 million in 2023, more than half occurring in Sal; INE, 2023), the impact on nesting activity is likely even greater today. Large all-inclusive resorts occupy most southern beaches in Sal and some of the northwest coast in Boa Vista, which are also suitable for turtle nesting. Boa Vista has its most important nesting areas protected under the Sea Turtle Natural Reserve. In non-protected areas, a legally established 80-meter coastal buffer zone for infrastructure construction is frequently ignored. Furthermore, tourism activities focused on turtle-watching, especially in Boa Vista and Sal, can have minimal impact on the nesting if conducted responsibly (Marco et al., 2021), but tourism development could exacerbate risks. Current and future planned developments in Sal, Boa Vista, and Maio (outlined in instruments like ZDTIs–Integral Touristic Development

Zone) could further threaten nesting habitats through increased light pollution and beach degradation.

Overall, São Vicente, Santiago and Sal are the most threatened islands (83%, 67%, and 62% of their beach segments at risk, respectively), with marine debris and light pollution affecting the greatest number of segments. These three islands are also the most densely populated (INE, 2023), and their urbanisation results in strong illumination reaching multiple beaches. Conversely, Santo Antão and Maio are the safest islands (18% and 36% at risk, respectively). Their relative isolation, lower urbanisation and limited tourist activity contribute to the reduced risk levels. Furthermore, Santa Luzia and Boa Vista have half of their beach segments at risk, largely due to the accumulation of marine debris. Santa Luzia is a special case as an uninhabited island: even without human settlements, its beaches have some type of risks. Overall, over half of the beach segments in the archipelago remain free from any identified risks, with 158 segments classified as safe.

Our nest density model indicated that seawater velocity significantly influences beach selection. Favourable ocean currents can influence hatchling dispersal by facilitating rapid escape to open waters and providing suitable foraging areas for adult females (Putman et al., 2010). Overall, our model predicted that east-facing beaches have a higher probability of hosting more nests, supported by multiple studies on the islands (Marco et al., 2011, 2012; Laloë et al., 2020; Patino-Martinez et al., 2022, 2023). Our model (Figure 3A) underestimated nest densities on western Sal (Laloë et al., 2020), likely due to better calibration and a larger dataset for Boa Vista. Additionally, the lack of local habitat variables (e.g., sand type), may have caused unsuitable locations to be misclassified as suitable. Among islands with high nest densities (Boa Vista, Sal, and Maio), Sal presents the greatest overlap between vulnerable areas and high-density beaches, making it a conservation priority.

While this study considers cumulative risks, their relative impacts on nesting grounds are not uniform. The interactions between threats can amplify these impacts, as global changes rarely act

in isolation (Harley et al., 2006; Brooks et al., 2009). For example, rising sea-levels could transport marine debris to higher beach strata, increasing the overlap with nests and intensifying density-dependent issues (Tiwari et al., 2006). The development of tourism infrastructure on beaches affects erosion-accretion dynamics and exacerbates beach loss and inundations (Miles et al., 2001). Warmer sands, combined with plastic pollution may increase sand temperatures even further or amplify the leakage of harmful plastic additives (Fuentes et al., 2023; Sousa-Guedes et al., 2023a; Wan et al., 2024).

The resilience of sea turtle populations to environmental changes will depend on the persistence of suitable nesting sites and their adaptive capacity (Patrício et al., 2021). Exposed and highly dynamic sandy beaches, reshaped by wind and waves, support this adaptability. Females may lay multiple clutches over weeks and locations, reducing the risk of losing all nests in an adverse event (Hirth, 1980). In Cabo Verde, around 20% of nests are over 15 km from a female's previous nest, suggesting room for colonization of new areas (Patino-Martinez et al., 2022). Hopefully, sea turtles might adapt to these upcoming climate changes, as they did in the past – which were similar in magnitude but not at the current rate (Fuentes et al., 2011; Quintero and Wiens, 2013; Patrício et al., 2021). Protecting beaches with a high density of nests is a priority, but neglecting other beaches might overlook future suitable sites, and there is no reason to expect that the distribution of nests will remain the same in the future.

Our assessment aims to inform local stakeholders of immediate threats to nesting beaches. A multifaceted approach is needed, including waste management, lighting regulations, and sustainable tourism. Zoning strategies are important for managing spatial gradients of human impact, with site-specific actions based on feasibility, risk, cost, and success probability (Pressey and Bottrill, 2009). For instance, relocating nests to cooler areas may work in some cases but is impractical for remote sites like Santa Luzia. Thus, conservation efforts should be adapted to local risks, and future evaluations should incorporate population sensitivity and adaptive capacity for comprehensive vulnerability analyses of nesting sites (Butt et al., 2022; Lettrich et al., 2020).

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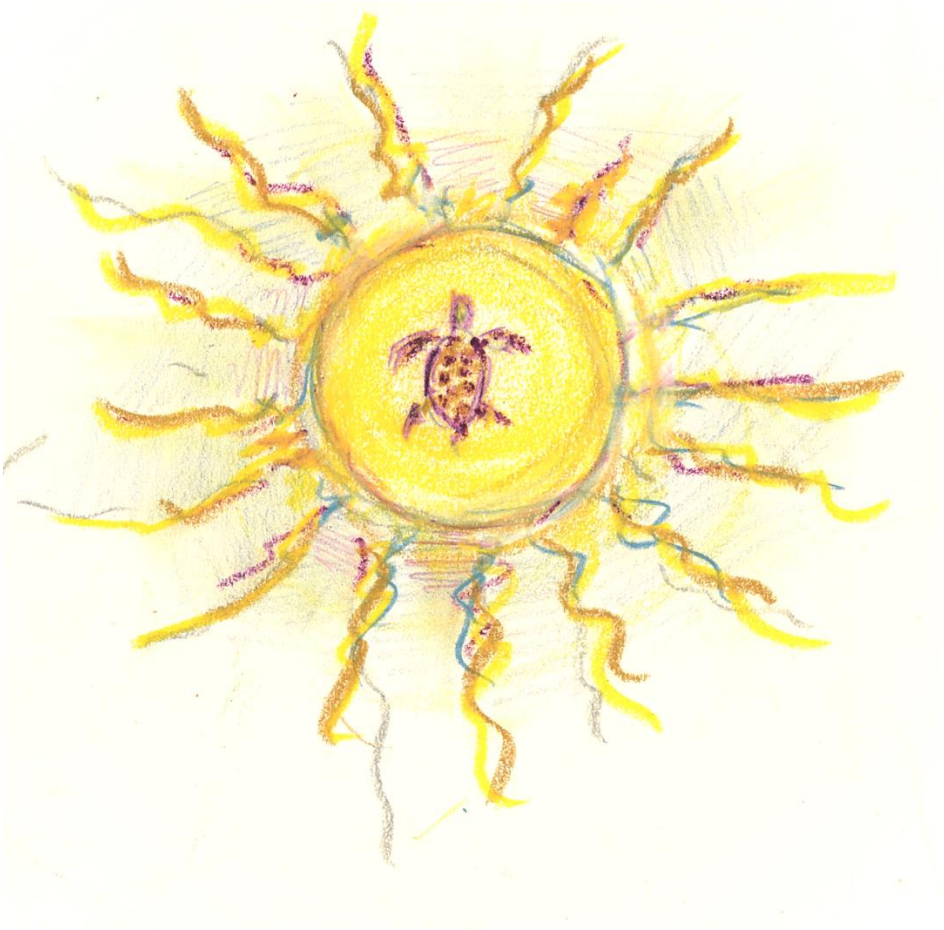


Quem q’ fla ma mund é grand fla m’ fla ma não

Ma náo ma mundo é piquinoti

Grand ness mund é só amor

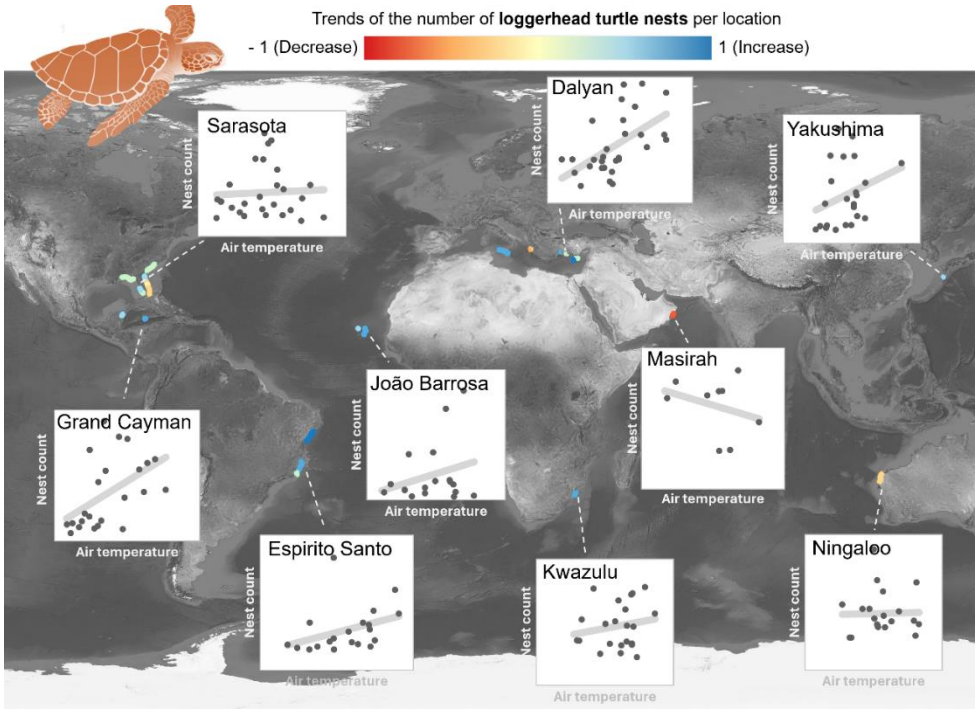
Simentera/ Mário Lucio

CHAPTER 5

The effects of warming on loggerhead turtle nesting counts

Sousa-Guedes, D., Campos, J.C., Bessa, F., Flora Fauna y Cultura de Mexico, Lasala, J.A., Marco, A., Sillero, N. In press. *Journal of Animal Ecology*.

Graphical abstract



Abstract

Global trends in marine turtle nesting numbers vary by region, influenced by environmental or anthropogenic factors. Our study investigates the potential role of past temperature fluctuations on these trends, particularly whether warmer beaches are linked to increased nesting due to higher female production (since sea turtles have temperature-dependent sex determination). We selected the loggerhead turtle (*Caretta caretta*) due to its wide distribution, strong philopatry, and vulnerability to environmental changes. We compiled nest counts per year on 35 globally significant rookeries, analysing trends at regional and individual beach levels. We compiled air (CHELSA) and land surface (MODIS) temperature datasets spanning the last four decades (1979-2023) for each location. To analyse temporal trends in nest counts and temperatures, we used generalised additive models and Mann-Kendall trend tests. Additionally, we correlated nest counts with lagged air temperature variables. We found significant warming at 33 nesting locations, 23 of which also showed significant increases in nest counts. Our results suggest that rising temperatures may be boosting nest numbers in regions of the Caribbean, Atlantic Ocean, and Mediterranean (sites in Cayman, Mexico, Brazil, Cyprus, and Turkey). Furthermore, while

some regions temporarily benefit, continued warming could precipitate long-term population declines. This regional variability helps predict species responses to climate change, with the general global increase in nest counts already indicating short-term warming effects. Nesting count trends might reflect a combination of natural ecological phenomena, conservation efforts, and warming effects. Long-term studies are needed to assess global trends in the sex ratio of hatchlings and the extent to which feminisation is driving nest numbers.

Introduction

Marine turtles are iconic species of planet Earth's oceans, having persisted through millennia of global changes (Bowen, 1995; Evers and Benson, 2019). They have survived multiple landscape and environmental changes throughout time, from fluctuations in sea levels during glacial and interglacial periods to shifts in ocean currents and temperatures, tectonic movements, and volcanic eruptions (Hawkes et al., 2009). However, even resilient species may not be able to cope with the current pace and scale of human-induced environmental changes (Hawkes et al., 2009; Ceballos et al., 2015). Indeed, habitat degradation, pollution, climate change, and wildlife overexploitation are escalating at an unprecedented rate (He and Silliman, 2019; IPCC, 2022).

The rise in temperatures on nesting beaches, where female sea turtles lay their eggs, is of particular concern (Fuentes et al., 2011; Simantiris, 2024). On the one hand, high temperatures during embryonic development cause imbalanced sex ratios of hatchlings, thereby skewing population demographics toward females (Fuentes et al., 2011; Laloë et al., 2014). On the other hand, very high temperatures can result in embryo mortality (Saba et al., 2012; Hays et al., 2017). Like many other reptiles, sex in sea turtles is determined by temperature, a physiological mechanism called temperature-dependent sex determination (TSD): incubation temperature above a pivotal threshold (typically ~29 ºC) results in predominantly female hatchlings (Ewert et al., 1994; Howard et al., 2014). The primary sex ratios of hatchlings often show a female bias, which can be an evolutionary advantage for population growth. A higher proportion of females can lead to

faster recruitment and an increase in the number of eggs produced, provided that there are enough males to fertilize the females (Hays et al., 2010; Santidrián Tomillo, 2022). However, a trend towards extreme feminisation is currently evident in different sea turtle species worldwide, with some populations already producing nearly all-females hatchlings (Hanson et al., 1998; Kaska et al., 1998; Godley et al., 2001; Hays et al., 2014; Wyneken and Lolavar, 2015; Abella-Perez et al., 2016; Marcovaldi et al., 2016; Jensen et al., 2018; Tanner et al., 2019; Fleming et al., 2020; Laloë et al., 2024; Papazekou et al., 2024). Imbalances in sex ratios may reduce genetic diversity and consequently their resilience to climatic changes (Lockley and Eizaguirre, 2021; Heppell et al., 2022). Moreover, as temperatures continue to rise, the risk of incubation mortality also escalates (Howard et al., 2014; Martins et al., 2020; Laloë and Hays, 2023).

Nesting activity trends of marine turtles (that is, the number of nests counted per season in a certain location) currently display considerable variability across regions, with some rookeries exhibiting increases in nesting activity while others experiencing declines (Mazaris et al., 2017; Hays et al., 2024). Coastal development and overexploitation have been suggested as underlying drivers of declines, while positive trends may be influenced by conservation measures; in addition, environmental changes can contribute to increases or declines (Solow et al., 2002; Pike, 2013; Mazaris et al., 2017; Hays et al., 2022a, 2024; Fuentes et al., 2023; Laloë et al., 2024). Furthermore, there is speculation about whether rising temperatures on nesting grounds may lead to an eventual increase in nest counts, as more females are produced (Laloë et al., 2014, 2017; Hays et al., 2022b).

The loggerhead turtle (*Caretta caretta*, [Lineu, 1758]), despite being one of the most widely distributed sea turtle species, nesting on sandy beaches across all continents except Antarctica, is still globally classified as vulnerable by the IUCN (Casale and Tucker, 2017). Warming effects on the sex ratios of hatchlings and embryo mortality are one of their main threats (Simantiris, 2024). For loggerhead turtles, nest temperatures exceeding 35 °C are associated with nearly total embryo mortality, while nest temperatures above 33 °C can cause substantial damage (Yntema and Mrosovsky, 1980; Howard et al., 2014). Although their populations may change nesting

phenology as temperature increases (Hays et al., 2003; Weber et al., 2012; Katselidis et al., 2012; Monsinjon et al., 2019), or colonise new and cooler areas (Mancino et al., 2022; Cardona et al., 2023; Santidrián Tomillo et al., 2023), these adaptive responses may be limited (Stokes et al., 2024) or insufficient to fully mitigate the effects of climate warming (Almpanidou et al., 2018; Laloë and Hays, 2023; Fuentes et al., 2024).

To our knowledge, no study to date explicitly analysed the effect of rising temperatures on nest numbers of loggerhead turtles, or marine turtles for that matter. In this study, we examine the relationship between temperature trends and loggerhead turtle nesting activity over the past four decades. Considering their strong philopatric behaviour, as females return to their natal beaches to lay eggs (often within 5 km of their natal nesting site, with remigration rates up to 70%; Richardson et al., 1978; Schroeder et al., 2003; Lohmann et al., 2013), we hypothesised that an increase in temperature in a specific location would lead to a rise in the number of nests in the same location, due to skewed sex ratios toward females. Therefore, we assume that an increase in female hatchling production would ultimately lead to an increase in nesting adult females, with sexual maturity being attained between the second and third decade of their lives (Casale et al., 2009, 2011; Avens et al., 2015). Herein, we compiled loggerhead nesting counts across globally important rookeries, as well as temperature datasets (air temperatures and land surface temperatures) covering a span of four decades (1979-2023). We performed trend and correlation analyses to evaluate how temperature changes are reflected in the nesting activity trends of loggerhead turtles in selected locations.

Methods

Nesting counts

We used a wide range of literature sources to assemble a database of global trends in loggerhead turtle nesting counts, including 36 references comprising peer-reviewed scientific publications

and grey literature (such as symposium proceedings, regional monitoring reports, newsletters, personal communications, and internet sources). We only selected sources with verified similar monitoring efforts (that is, the same sampling strategies and similar temporal and spatial coverage). The complete list of literature sources is detailed in Table 1. We gathered raw data on the number of nests laid annually when available or by digitising nesting trends presented in graphs when raw numbers were unavailable. We then assigned each temporal series to the appropriate Regional Management Units (RMUs), which are geographically distinct populations integrating biogeographical information (i.e., genetics, distribution, movement, and demography) of sea turtle nesting sites (Wallace et al., 2010, 2023). We retained sites if they recorded at least one year of more than 50 nests. We represented some nesting sites at the regional level, encompassing data from multiple beaches within the same geographical area, and others at the individual beach level, depending on the availability of the literature sources. To verify if patterns are different at the individual beach level and because certain locations were available at both regional and beach levels, we included both with distinct beach codes nested within broader regional classifications, e.g., (2.1) is encompassed within the regional site of (2). We acknowledge that spatial autocorrelation is present (nearby sites may exhibit similar nesting patterns), which might lead to some redundancy in our analysis, but it also highlights the complexity and variability within regions. Additionally, we compiled percentages of estimated loggerhead sex ratios across selected nesting grounds, when available, from peer-reviewed scientific publications, for further comparisons (see Table S2, Supplementary Materials).

Environmental variables

We digitised nesting beaches by delineating polygons using Google satellite imagery within QGIS 3.32.2. Subsequently, we generated two types of freely available temperature time series: a) globally downscaled air temperatures covering the period from 1979 to 2013, sourced from the CHELSA dataset v1.2 (Karger et al., 2017, 2018) and b) satellite-derived land surface temperature

(LST) spanning from 2000 to 2023, obtained from the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor (8-day L3; Wan et al., 2021). The two types of temperature time series offer complementary perspectives: air temperatures (1979-2013) closely correlate to nest temperatures (Lolavar and Wyneken, 2020; Catron et al., 2023) and are available for longer periods, while LSTs (2000-2023) can capture beach-specific variations (e.g., a beach with dark sand can have high LST with lower air temperatures). CHELSA air temperatures are calculated using mechanistic statistical downscaling techniques applied to global circulation models or reanalysed datasets to provide fine-scale temperature estimates. CHELSA is highly correlated to other temperature datasets (Karger et al., 2017). We extracted monthly mean, maximum, and minimum air temperatures and averaged them annually for the peak breeding season, defined as July to October for northern hemisphere sites and November to February for southern hemisphere sites. We selected these months to standardise the breeding season across a wide range of sites, focusing on the period most critical for embryonic development. The temperatures were extracted at the original resolution of 30 arc seconds (~1 km) and then averaged again at each digitised nesting site. Satellite-derived LST is a measure of thermal infrared longwave radiation at the top of the atmosphere that can capture the thermal behaviour of the land surface itself across large areas and periods (Reiners et al., 2023). We computed both daytime and nighttime LSTs at their original spatial resolution of 1 km and averaged them annually at each digitised nesting site, using the cloud-based Google Earth Engine platform (GEE; Gorelick et al., 2017). GEE images were pre-processed for cloud and topographic correction (Hurni et al., 2017). Variables were averaged using R 4.3.0 (R Core Team, 2023).

Temporal trends

For a graphical representation of nest count trends, we used the percentage of nests to avoid publishing restricted raw data. We used the first year with available data as the reference year, and the subsequent years as the percentages relative to this reference year. To represent nesting

trends over time, we fitted a generalised additive model (GAM) with a Poisson distribution, using the percentage of nest counts as the response variable and years as the explanatory variable for each location.

To understand whether air temperatures and LSTs have similar temporal patterns, we assessed the Pearson correlation between LST and air temperature variables for all locations together. For that, we subset the mean, maximum, and minimum air temperatures to match the period of the daytime and nighttime LST: 2000-2013.

To detect spatial-temporal fluctuations of nest counts and temperatures (mean, maximum, and minimum air temperatures, and daytime and nighttime LSTs) across nesting grounds, we applied the Mann-Kendall trend analysis (Kendall, 1990), using the 'MannKendall' function in the 'Kendall' R package. The Mann-Kendall test is a nonparametric test for monotonic trend detection in a time series, analysing differences in signs between two consecutive dates. If a trend is present, the sign values will tend to increase or decrease, and every value is compared to every preceding value in the time series. The minimum sample size required for the Mann-Kendall test is four (Kendall, 1990). However, we opt for a minimum of nine years of data to ensure the capture of meaningful trends while reducing the influence of short-term fluctuations (Mazaris et al., 2017). We calculated the significant slopes per location (trends) at a 95% confidence level.

Relating temperature trends and nest count trends

For each nesting site individually, we built scatter plots to analyse how nest numbers vary in response to each one of the five temperature variables.

To assess the relationship between air temperature trends and overall nest count trajectories, we plotted Mann-Kendall nest count trends against a composite index of air temperature variables. We focused on air temperatures rather than incorporating LST to maintain consistency in the temporal range. We first standardised the annual average mean, maximum, and minimum air

temperature values (TMEAN, TMAX, TMIN) and their respective trends, to ensure that each variable and its corresponding trend contributed equally to the composite index. The index was then calculated as the mean of these standardised layers: *(TMEAN + TMEAN trend + TMAX + TMAX trend + TMIN + TMIN trend) / 6*. We included both the temperature values and their trends in the composite index because temperature increases in already warm areas could have stronger effects compared to areas with low temperatures.

We performed correlation analyses to investigate the relationship between two-time series: annual nest counts and air temperatures. To account for temporal autocorrelation (which can artificially inflate correlation coefficients in time series data), we used the modified Chelton method (Pyper and Peterman, 1998; Hinder et al., 2012). This method adjusts the degrees of freedom to provide a more accurate estimate of the relationship between two variables, by considering the autocorrelation structure of the data. The method results in a correlation coefficient ranging from -1 to 1. We lagged air temperature variables by 16 years (thus, corresponding to 1995-2013) to align with the minimum age at which loggerhead sexual maturity may be attained (Casale et al., 2009). For example, the temperature variables of 1979 were matched to the nest count of 1995. We opted for the 16-year lag as a compromise to minimize data loss, acknowledging the variability in maturity age among populations and ongoing debate among researchers. We performed these analyses only for the CHELSA air temperature variables because their period was long enough (1979-2013); it was not possible to apply the lag to the LST variables. All variables underwent a logarithmic transformation to stabilise variances and normalise the distribution of residuals. We performed separate analyses for each air temperature variable and location. All analyses were calculated in R 4.3.0.

Results

Nesting count trends

We obtained a total of 35 nesting sites across the globe, spanning eight RMUs (Table 1): Caribbean and Gulf of Mexico (RMU 1), Southwest Atlantic (RMU 2), Southeast Atlantic (RMU 3), Mediterranean (RMU 4), Arabian (RMU 5), Western Indian (RMU 6), Eastern Indian (RMU 8), and Western Pacific (RMU 9). The northernmost nesting site was Sicily in the Mediterranean, while the southernmost was Kwazulu, located in the Western Indian unit (Figure 1).

The Mann-Kendall tests showed a significant increase in nest count trends at multiple sites (Table 1, Figure 1). Sharp increases (Mann-Kendall > 0.70) were observed in the Caribbean (Grand Cayman), Southwest Atlantic (Sergipe, Bahia), Southeast Atlantic (Sal, Maio), Mediterranean (West Cyprus, Dalyan, Sicily), and Western Indian (Kwazulu). In comparison, significant positive but less sharp increases (Mann-Kendall < 0.70) were found in the Caribbean and Gulf of Mexico (Quintana Roo, Tankah, South Carolina, Northeast Florida, Sanibel, Sarasota), Southwest Atlantic (Espírito Santo), Southeast Atlantic (Santa Luzia, Boa Vista, João Barrosa), Mediterranean (North Cyprus, Çirali), Western Indian (Malongane), and Western Pacific (Yakushima). Only one site significantly decreased the number of nests over time: Masirah Island in Oman (Arabian Sea), with a significant Mann-Kendall slope of -0.78. The remaining regions had no significant pattern, and thus were considered stable: East Florida, Panhandle and West Florida, Rio de Janeiro, Zakynthos, and Ningaloo.

Table 1. Global nest count trends for loggerhead turtles. The trend (Mann-Kendall) is considered stable (no pattern) when p-value > 0.05; asterisks denote significance. Years is the number of years with available nest count data in each location.

RMU	Location	Country	Level	Trend	Mann-Kendall	Temporal range	Years	Sources
1	(1) Grand Cayman	Cayman	Regional	Increase	**0.80** ***	1999-2021	23	Blumenthal et al., 2021
	(2) Quintana Roo	Mexico	Regional	Increase	**0.57** ***	1987-2020	34	SEMARNAT, 2018; Flora Fauna y Cultura de Mexico, pers. comm.
	(2.1) Tankah	Mexico	Beach	Increase	**0.54** ***	1996-2023	28	
	(3) South Carolina	USA	Regional	Increase	**0.30** **	1984-2022	39	South Carolina state website (dnr.sc.gov)
	(4) Northeast Florida	USA	Regional	Increase	**0.52** ***	1989-2018	30	Ceriani et al., 2019
	(5) Central East Florida	USA	Regional	Stable	-0.11	1989-2018	30	
	(5.1) Brevard	USA	Beach	Stable	0.03	1984-2019	36	Florida Fish and Wildlife website (myfwc.com)
	(6) Southeast Florida	USA	Regional	Stable	-0.01	1989-2018	30	Ceriani et al., 2019
	(6.1) Boca Raton	USA	Beach	Stable	-0.17	1988-2022	35	Boca Raton City Hall website (myboca.us)
	(7) Southwest Florida	USA	Regional	Stable	0.24	1989-2018	30	Ceriani et al., 2019
	(8) Sanibel	USA	Beach	Increase	**0.39** **	1989-2018	30	
	(9) Sarasota	USA	Regional	Increase	**0.59** ***	1982-2021	40	Lasala et al., 2023
	(10) Panhandle	USA	Regional	Stable	0.25	1997-2021	26	Ceriani et al., 2019; Florida Fish and Wildlife website (myfwc.com)
2	(11) Sergipe	Brazil	Regional	Increase	**0.85** ***	2002-2021	12	Marcovaldi and Chaloupka, 2007; TAMAR, 2022
	(12) Bahia	Brazil	Regional	Increase	**0.92** ***	1988-2015	28	
	(12.1) Praia do Forte	Brazil	Beach	Increase	**0.88** ***	1988-2014	27	
	(13) Espírito Santo	Brazil	Regional	Increase	**0.66** ***	1988-2021	21	
	(14) Rio de Janeiro	Brazil	Regional	Stable	0.24	2001-2010	10	Paes e Lima et al., 2012
3	(15) Santa Luzia	Cabo Verde	Regional	Increase	**0.56** **	2011-2023	12	Biosfera website (biosfera1.com)
	(16) Sal	Cabo Verde	Regional	Increase	**0.73** ***	2008-2023	16	Laloë et al., 2020; Hays et al., 2022b; Project Biodiversity website (projectbiodiversity.org)
	(17) Maio	Cabo Verde	Regional	Increase	**0.73** **	2008-2023	10	Patiño-Martinez et al., 2022; Fundação Maio Biodiversidade website (fmb-maio.org)
	(18) Boa Vista	Cabo Verde	Regional	Increase	**0.63** **	2007-2023	14	Marco et al., 2012; Adolfo Marco, pers. comm.
	(18.1) João Barrosa	Cabo Verde	Beach	Increase	**0.49** **	2005-2023	18	BIOS.CV website (bioscaboverde.com)
4	(19) West Cyprus	Cyprus	Regional	Increase	**0.83** ***	1989-2018	30	Demetropoulos et al., 2018
	(20) Chrysochou	Cyprus	Regional	Increase	**0.82** ***	1999-2018	20	Demetropoulos et al., 2018; Casale et al., 2020
	(21) North Cyprus	Cyprus	Regional	Increase	**0.34** *	1995-2019	25	Omeyer et al., 2021
	(22) Zakynthos	Greece	Regional	Stable	-0.07	1984-2021	38	Margaritoulis 2005; Margaritoulis et al., 2011, 2022
	(23) Dalyan	Turkey	Beach	Increase	**0.72** ***	1988-2023	36	Turkozan, and Yilmaz, 2008; DEKAMER website (dekamer.org.tr)
	(24) Çirali	Turkey	Beach	Increase	**0.37** *	2001-2020	20	Sönmez et al., 2021
	(25) Sicily	Italy	Regional	Increase	**0.78** ***	2010-2021	12	Prato et al., 2022
5	(26) Masirah	Oman	Regional	Decrease	**-0.78** **	2008-2016	9	Willson et al., 2020
6	(27) Malongane	Mozambique	Beach	Increase	**0.68** ***	2007-2020	14	Centro Terra Vida website (ctv.org.mz)
	(28) Kwazulu	South Africa	Regional	Increase	**0.72** ***	1984-2022	27	Nel et al., 2013; Ezemvelo KZN Wildlife website (kznwildlife.com)
8	(29) Ningaloo	Australia	Regional	Stable	-0.04	2002-2022	21	DBCA, 2023
9	(30) Yakushima	Japan	Regional	Increase	**0.47** ***	1989-2017	29	Martin et al., 2020

Regional Management Units: Caribbean and Gulf of Mexico (RMU 1), Southwest Atlantic (RMU 2), Southeast Atlantic (RMU 3), Mediterranean (RMU 4), Arabian (RMU 5), Western Indian (RMU 6), Eastern Indian (RMU 8), Western Pacific (RMU 9).

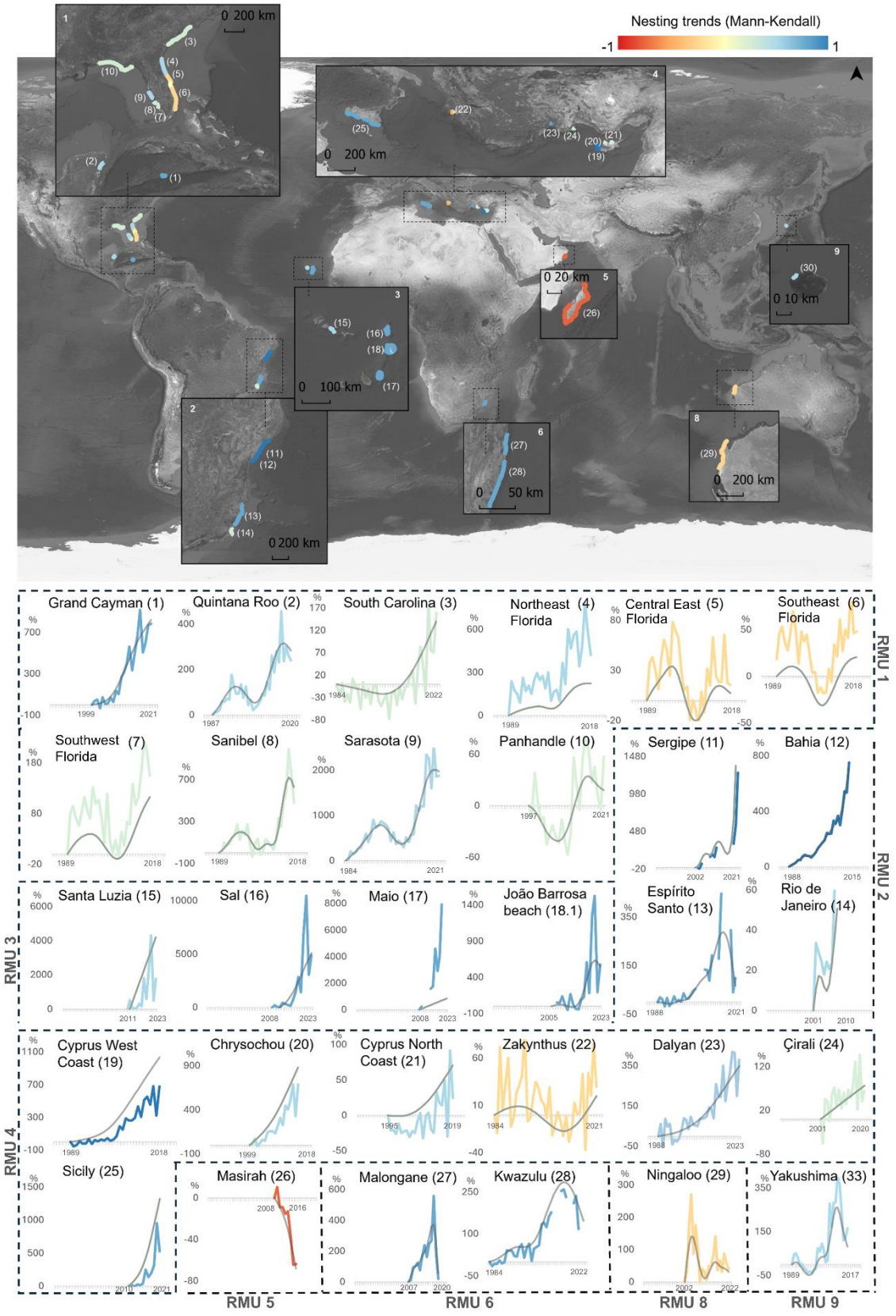


Figure 1. At the top, mapped Mann-Kendall slopes of loggerhead turtle nest count trends across the globe, where negative values represent decreasing trends and positive values increasing trends

(gradient from red to blue). Below are the percentages of change on nesting counts (coloured line, where colour represents the same Mann-Kendall slope) and the GAM model of each nest count trend (grey line) over the years. Locations are grouped by Regional Management Units: Caribbean and Gulf of Mexico (RMU 1), Southwest Atlantic (RMU 2), Southeast Atlantic (RMU 3), Mediterranean (RMU 4), Arabian (RMU 5), West Indian (RMU 6), East Indian (RMU 8), Western Pacific (RMU 9).

Temperature trends

We found the strongest correlations of nighttime LST with mean air temperature (Pearson correlation = 0.88), followed by minimum air temperature (0.84) and maximum air temperature (0.80), for the period between 2000 and 2013. Daytime LST had lower Pearson correlations with mean, minimum, and maximum air temperatures (0.43, 0.48, and 0.33, respectively).

The temperature variable with the highest increasing Mann-Kendall trend over time across nesting sites was the maximum air temperature (significant positive slopes in 28 locations), followed by the mean air temperature (27 locations), minimum air temperature (23 locations), nighttime LST (12 locations), and daytime LST (two locations) (Table S1, Supplementary Materials). No temperature variable showed decreasing trends at any location. Temperatures (at least one of the five variables) significantly increased in almost all sites except Malongane and Kwazulu. Nighttime LST increasing trends were most pronounced (significant Mann-Kendall > 0.5) in the Caribbean and Gulf of Mexico (Grand Cayman, Quintana Roo, Southwest Florida) and Arabian (Masirah). Nesting sites with the highest average temperature values recorded for each location were, in descending order: Grand Cayman, Masirah, and Ningaloo (27.7, 27.6, and 27.5 ºC, respectively) for mean air temperatures; Ningaloo, Masirah, and Sergipe (31.0, 30.0, and 29.7 ºC) for maximum air temperature; Grand Cayman, Masirah, and Sergipe (26.4, 24.8, and 24.3 ºC) for minimum air temperatures; Masirah, João Barrosa, and Maio (34.1, 34.0 and 33.0 ºC) for daytime LST; and Grand Cayman, Quintana Roo and Tankah (23.6, 23.0, and 23.0 ºC) for nighttime LST.

The complete mean values and Mann-Kendall analyses of temperature trends are included in Table S1 (Supplementary Materials).

Are temperature trends and the number of nests related?

For most locations, as temperatures increase, there is a tendency for the number of nests to increase as well (lagged mean air temperatures, nighttime LST, or both; scatter plots in Figures 2 and 3). The exception is Sicily, Kwazulu, and Ningaloo, which showed a decreasing tendency in the number of nests as both temperature variables increased (Figure 3).

Figure 2. Scatter plots of the number of nests versus temperature variables for locations in each Regional Management Unit: Caribbean and Gulf of Mexico (RMU 1, red/orange points),

Southwest Atlantic (RMU 2, green points) and Southeast Atlantic (RMU 3, yellow/grey points). Lagged mean air temperatures (lagged tmean) on the left and nighttime land surface temperatures (LST night) on the right.

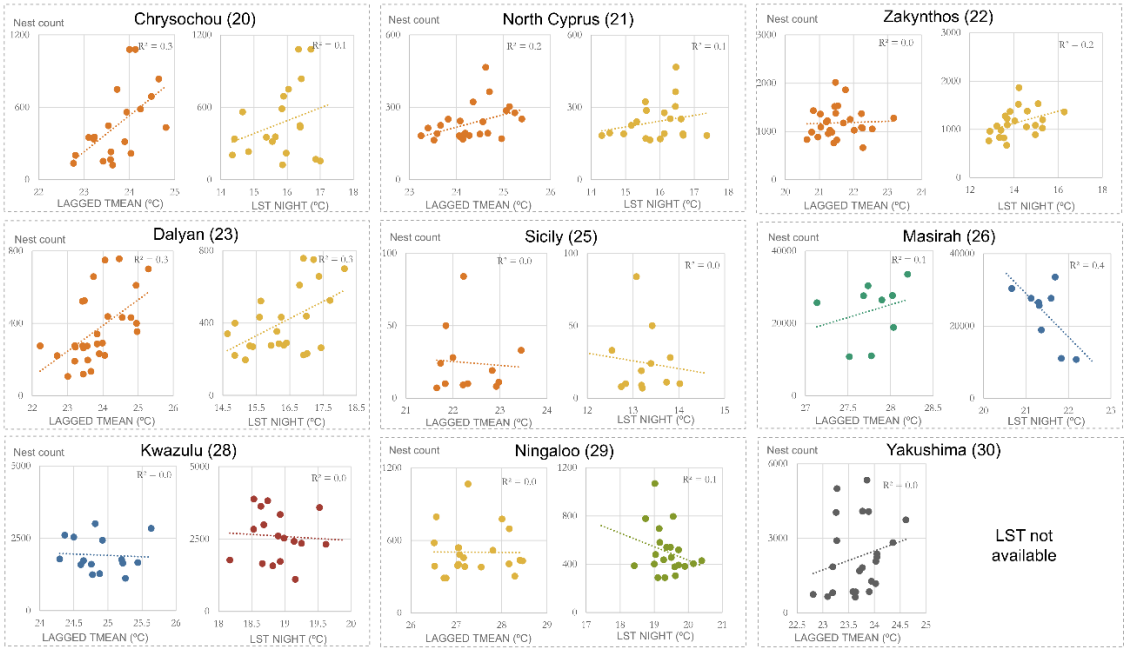


Figure 3. Scatter plots of the number of nests versus temperature variables for locations in each Regional Management Unit: Mediterranean (RMU 4, blue points), Arabian (RMU 5, yellow/orange points), Western Indian (RMU 6, orange/red points), Eastern Indian (RMU 8, blue/green points), and Western Pacific (RMU 9, grey points). Lagged mean air temperatures (lagged tmean) on the left and nighttime land surface temperatures (LST night) on the right.

A slight positive relationship exists between the composite temperature index and nest count trends (Figure 4a), suggesting a weak tendency for higher temperatures to align with increasing nest numbers ($R^2 = 0.025$).

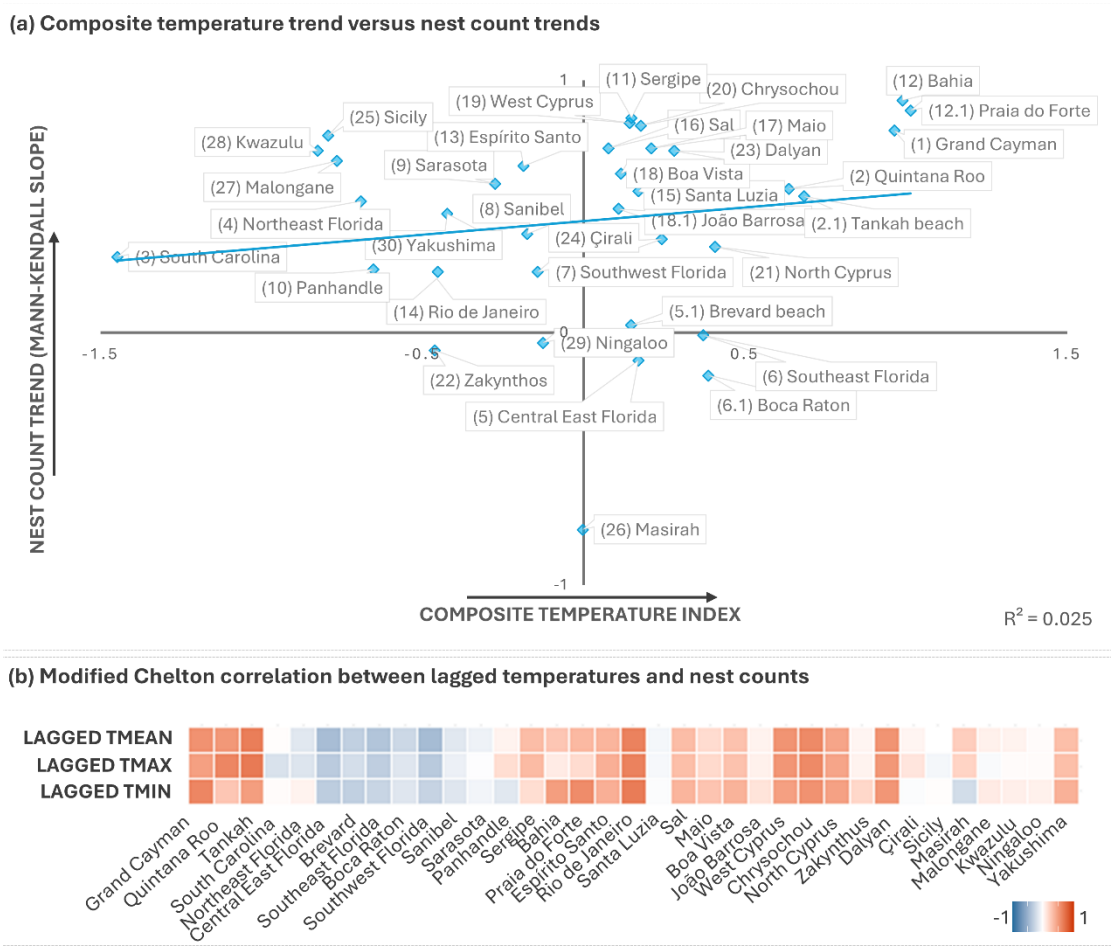


Figure 4. (a) Scatter plot showing the relationship between the composite air temperature indexes (from -1.5 to 1.5) and nest count trends (Mann-Kendall slopes, from -1 to 1) at each site. (b) Heatmap representing the modified Chelton correlation (from -1 to 1) between lagged air mean, maximum and minimum temperatures (TMEAN, TMAX, TMIN) and nest counts.

The modified Chelton method showed a significant positive correlation (p-value < 0.05) between mean, maximum, or minimum air temperatures and the number of nests in ten locations: in the Caribbean (Grand Cayman, Quintana Roo, Tankah), Southwest Atlantic (Bahia, Praia do Forte, Rio de Janeiro), and in the Mediterranean (North and West Cyprus, Chrysochou, Dalyan). In contrast, two locations showed a significant negative correlation: Central East Florida and Southwest Florida. The remaining locations exhibited non-significant effects (Table 2). Overall, temperature appears to be positively correlated (although not significantly) with nest counts

across most RMUs, except for some locations in the Gulf of Mexico (South Carolina and Florida) and the Eastern Indian (Masirah) (Table 2 and Figure 4b).

Table 2. Degrees of freedom (df), correlation coefficient, confidence interval (CI), and significance (p-value) between lagged mean, maximum, and minimum air temperature variables (TMEAN, TMAX, and TMIN) and nest counts, calculated through the modified Chelton method. In bold, the significant positive variables.

		LAGGED TMEAN		LAGGED TMAX		LAGGED TMIN	
	df	**correlation (CI)**	**p-value**	**correlation (CI)**	**p-value**	**correlation (CI)**	**p-value**
(1) Grand Cayman	21	**0.56 (0.20-0.79)**	**0.005 ****	**0.49 (0.10-0.75)**	**0.017 ***	**0.62 (0.28-0.82)**	**0.002 ****
(2) Quintana Roo	24	**0.53 (0.14-0.75)**	**0.005 ****	**0.62 (0.30-0.81)**	**< 0.001 *****	0.29 (-0.11-0.61)	0.156
(2.1) Tankah	26	**0.66 (0.38-0.83)**	**<0.001 *****	**0.68 (0.42-0.84)**	**< 0.001 *****	**0.50 (0.15-0.73)**	**0.007 ****
(3) South Carolina	26	0.01 (-0.36-0.39)	0.941	-0.18 (-0.39-0.36)	0.929	0.02 (-0.36-0.39)	0.924
(4) Northeast Florida	22	-0.14 (-0.51-0.28)	0.525	-0.16 (-0.53-0.26)	0.456	0.06 (-0.36-0.45)	0.798
(5) Central East Florida	22	**-0.41 (-0.70-0.00)**	**0.048 ***	-0.32 (-0.64-0.10)	0.129	-0.31 (-0.63-0.11)	0.139
(5.1) Brevard	23	-0.29 (-0.62-0.11)	0.157	-0.20 (-0.55-0.21)	0.333	-0.29 (-0.62-0.12)	0.156
(6) Southeast Florida	22	-0.36 (-0.67-0.05)	0.082	-0.30 (-0.63-0.12)	0.152	-0.26 (-0.60-0.16)	0.225
(6.1) Boca Raton	26	-0.24 (-0.56-0.15)	0.223	-0.15 (-0.49-0.24)	0.454	-0.15 (-0.50-0.23)	0.438
(7) Southwest Florida	22	**-0.42 (-0.70- -0.02)**	**0.041 ***	-0.33 (-0.64-0.08)	0.112	-0.27 (-0.61-0.15)	0.207
(8) Sanibel	22	-0.14 (-0.52-0.28)	0.502	-0.09 (-0.47-0.33)	0.686	-0.15 (-0.72-0.48)	0.481
(9) Sarasota	25	-0.08 (-0.45-0.31)	0.686	-0.01 (-0.38-0.38)	0.980	-0.06 (-0.42-0.33)	0.780
(10) Panhandle	24	0.06 (-0.33-0.44)	0.766	0.17 (-0.23-0.52)	0.406	-0.14 (-0.50-0.27)	0.507
(11) Sergipe	10	0.34 (-0.29-0.76)	0.286	0.35 (-0.28-0.77)	0.261	0.17 (-0.45-0.68)	0.591
(12) Bahia	19	0.29 (-0.16-0.64)	0.205	0.10 (-0.35-0.51)	0.663	**0.50 (0.09-0.77)**	**0.021 ***
(12.1) Praia do Forte	18	0.36 (-0.10-0.69)	0.120	0.18 (-0.28-0.58)	0.443	**0.59 (0.20-0.82)**	**0.006 ****
(13) Espírito Santo	18	0.38 (-0.08-0.70)	0.099	0.410 (-0.05-0.72)	0.079	0.41 (-0.03-0.72)	0.069
(14) Rio de Janeiro	8	**0.64 (0.01-0.90)**	**0.048 ***	**0.64 (0.02-0.91)**	**0.046 ***	**0.67 (0.06-0.91)**	**0.035 ***
(15) Santa Luzia	11	-0.05 (-0.59-0.51)	0.861	-0.04 (-0.57-0.53)	0.910	-0.02 (-0.56-0.54)	0.954
(16) Sal	14	0.34 (-0.19-0.71)	0.199	0.33 (-0.20-0.71)	0.213	0.38 (-0.15-0.73)	0.152
(17) Maio	8	0.18 (-0.50-0.73)	0.611	0.19 (-0.50-0.73)	0.606	0.30 (-0.41-0.78)	0.403
(18) Boa Vista	12	0.31 (-0.27-0.72)	0.289	0.31 (-0.27-0.72)	0.288	0.39 (-0.17-0.76)	0.164
(18.1) João Barrosa	16	0.06 (-0.42-0.51)	0.813	0.07 (-0.41-0.52)	0.787	0.14 (-0.35-0.57)	0.579
(19) West Cyprus	22	**0.55 (0.19-0.78)**	**0.005 ****	**0.54 (0.18-0.78)**	**0.006 ****	**0.49 (0.11-0.75)**	**0.014 ***
(20) Chrysochou	18	**0.60 (0.21-0.82)**	**0.005 ****	**0.60 (0.22-0.82)**	**0.005 ****	**0.56 (0.15-0.80)**	**0.011 ***
(21) North Cyprus	23	**0.46 (0.07-0.72)**	**0.022 ***	**0.46 (0.08-0.73)**	**0.019 ***	**0.48 (0.11-0.74)**	**0.015 ***
(22) Zakynthos	25	0.05 (-0.33-0.42)	0.793	0.06 (-0.33-0.43)	0.783	0.20 (-0.20-0.54)	0.322
(23) Dalyan	27	**0.55 (0.23-0.76)**	**0.002 ****	**0.53 (0.20-0.75)**	**0.003 ****	**0.54 (0.22-0.76)**	**0.002 ****
(24) Çirali	18	0.05 (-0.40-0.49)	0.820	0.13 (-0.34-0.54)	0.597	-0.02 (-0.46-0.42)	0.927
(25) Sicily	10	0.00 (-0.58-0.57)	0.978	-0.05 (-0.60-0.54)	0.884	0.01 (-0.57-0.58)	0.975
(26) Masirah	7	0.25 (-0.50-0.78)	0.520	0.22 (-0.52-0.77)	0.574	-0.21 (-0.77-0.53)	0.595
(27) Malongane	15	0.07 (-0.43-0.53)	0.802	-0.03 (-0.51-0.45)	0.900	0.10 (-0.40-0.56)	0.695
(28) Kwazulu	20	0.06 (-0.37-0.47)	0.796	0.02 (-0.41-0.44)	0.934	0.08 (-0.36-0.49)	0.734
(29) Ningaloo	19	0.02 (-0.42-0.45)	0.936	0.02 (-0.42-0.45)	0.935	0.07 (-0.38-0.48)	0.773
(30) Yakushima	21	0.33 (-0.10-0.65)	0.127	0.33 (-0.09-0.65)	0.123	0.40 (-0.02-0.70)	0.060

Discussion

Loggerhead turtle nesting count trends are generally increasing across the globe (consistent with Hays et al., 2024), and there are some signs of the influence of rising global temperatures on these numbers. These patterns may extend beyond just warming trends. Our findings show general warming in the nesting sites of loggerhead turtles, with temperatures rising at 33 of 35 locations (that is, a significant increase in at least one temperature variable; Table S1, Supplementary Materials). Among those warmed locations, 23 exhibited a significant increase in nest counts over the years from the Caribbean and Gulf of Mexico (Grand Cayman, Quintana Roo, South Carolina and Florida), Southwest Atlantic (northern Brazil), Southeast Atlantic (Cabo Verde), Mediterranean (Cyprus, Dalyan and Sicily), and Western Pacific (Yakushima) (Table 1). From those, temperature appears to have played a significant role in ten locations in the Caribbean, Southern Atlantic, and in the Mediterranean (Table 2). Conversely, some regions with significant increases in nesting activity did not show rises in temperatures, such as in Western Indian (Malongane and Kwazulu) and others only had one temperature variable rising (South Carolina, southern Brazil). Factors such as successful conservation efforts or other environmental changes may be driving the increases in these areas. Other regions with stable nest counts (East and Northwest Florida, Ningaloo, and Zakynthos) demonstrated significant warming trends over time, suggesting that warming effects are being mitigated in these areas. Masirah Island stands out as the only site with significant declines in nesting counts, simultaneously experiencing warming trends (nighttime LST). Thus, we recognise two groups for conservation priority: i) sites with both temperature and nest count increases, potentially nearing thermal tolerance limits (23 sites); and ii) sites with temperature increases and declining nest counts, which may have already reached those limits (one site). While addressing the latter (Masirah Island) is a priority, preventive measures should also be implemented in locations of the first group, namely those in the Caribbean, Atlantic Ocean, and Mediterranean (different sites in Cayman, Mexico, Brazil, Cabo Verde, Cyprus, and Turkey). Rising nest trends in these areas may obscure the risks of

warming effects, especially in regions that surpass the pivotal nest temperatures for sex determination and near the thermal tolerance limits. Generally, there is a slight tendency for higher and rising temperatures to coincide with locations with increasing nest numbers, although the relationship is very weak (see Figure 4). As the relationship between air and nest temperatures is not linear and can vary significantly between sites (Laloë et al., 2021a), empirical data are needed to determine whether the observed increases or decreases in nesting numbers are related to changes in nest temperatures.

Nesting sites at higher latitudes, such as those found in Cyprus, Turkey, South Carolina, Florida, South Africa, or Australia, despite facing elevated warming trends (up to 2.5 ºC increase in air temperature per century in certain nesting sites; Laloë et al., 2021a, 2024), may better mitigate climate warming through phenological shifts (e.g., shift nesting to a cooler time of the year) when compared to regions closer to the equator like Oman, Brazil, Mexico, or Cabo Verde (Laloë and Hays, 2023). At locations with already high temperatures, a half-degree increase can completely skew sex ratios or compromise nest viability (Howard et al., 2014). Moreover, temperature thresholds may depend on the specific population (e.g., incubation temperatures of nests from Turkey and Cabo Verde are higher than nests in Greece and Australia; Rivas et al., 2024), making some populations more resilient than others. In the case of Brazil, we observed a significant increase in nesting counts in the northern states, despite having high temperatures that continue to rise. In contrast, southern Brazil (Rio de Janeiro) exhibited stable nesting trends and a non-consistent rise in temperatures. Moreover, projections indicate that by the end of the century, warmer beaches in northern Brazil (e.g., Bahia) are expected to experience declines in hatchling production, while southern and cooler beaches (e.g., Rio de Janeiro) may increase hatchling production (Montero et al., 2019). Thus, we suggest that certain locations in northern Brazil may have already exceeded pivotal thresholds for sex determination, as corroborated by estimates of female-biased trends (Hays et al., 2014; Marcovaldi et al., 2016), and could be approaching lethal temperatures. In addition, the mean size of nesting females in Espírito Santo (Brazil) and Sal (Cabo Verde) is decreasing, which may be due to an increase in the number of younger, smaller

females entering the nesting population as recruitment increases (Hays et al., 2022b; Pereira et al., 2024).

Feminised populations around the world may contribute to increased nest counts in many regions, indicating that temperatures have not yet reached lethal levels or that not enough time has passed for population collapse. Indeed, previous literature on sex ratios in Brazil, Cabo Verde, and Greece showed female-biased offspring (Margaritoulis, 2005; Katselidis et al., 2012; Hays et al., 2014; Abella-Perez et al., 2016; Marcovaldi et al., 2016; Tanner et al., 2019; Table S2, Supplementary Materials). However, Laloë et al. (2023) found that hatchlings sex ratios are not consistently linked to warming trends, suggesting that other factors such as nesting behaviour, substrate conditions, shading, wind, humidity, and rainfall may also play significant roles and may regulate temperature levels. Therefore, while female-biased sex ratios can contribute to increased nest counts, it is important to investigate how these factors interact with nest temperatures at each site.

Although some of the warmed locations analysed might have high air temperatures that contribute to female-biased populations, these temperatures are still lower than those on Masirah Island (Table S1, Supplementary Materials, e.g., daytime LSTs: Brazil between 28.1 and 31.4 ºC; Cabo Verde between 30.7 and 34.0 ºC; Cyprus between 29.0 and 30.6 ºC; Masirah with 34.1 ºC). Although there is no knowledge of hatchlings' sex ratios in Masirah, we argue it may be experiencing temperatures close to lethal levels during the nesting season, contributing to the observed decline in nest counts. As temperatures begin to rise, nest counts in some locations could see a short-term increase due to skewed sex ratios and a consequent rise in the number of nesting females (Laloë et al., 2014, 2017). However, in the long term, regions near the upper limit of the lethal temperature range may experience a decline in nest counts, as we may be seeing in Masirah. Factors such as cooler nighttime temperatures and seasonal rainfall can help mitigate these risks (Lolavar and Wyneken, 2020; Laloë et al., 2021b). If temperatures do not exceed the pivotal or lethal threshold for three consecutive days (Howard et al., 2014), populations may experience fewer adverse impacts. For instance, locations with high daytime temperatures but cooler

nighttime temperatures such as João Barrosa in Cabo Verde (average daytime and nighttime LST of 34.0 and 18.4 ºC, respectively), may maintain nest temperatures at non-lethal levels. Additionally, the rainy season in Cabo Verde coincides with the primary incubation months (August and September), further reducing nest temperatures. Estimations suggest that Cabo Verde experienced incubation temperatures near the pivotal threshold (~29 ºC) between 1850 and 2000, which would support balanced or only slightly female-biased sex ratios (Laloë et al., 2014). Incubation temperatures in Cabo Verde are rising, projected to reach ~32º C by 2100, with males making up only 4–17% of individuals on breeding grounds by 2150 (Laloë et al., 2014). Indeed, current estimates suggest a predominance of female-biased offspring in the archipelago (Abella-Perez et al., 2016; Tanner et al., 2019). Despite this, nest counts have increased up to 70-fold between 2008 and 2020, with Sal Island alone rising from 506 to 35,507 nests (Hays et al., 2022b). This suggests that temperature alone is unlikely to drive the trend. Historically, Cabo Verde faced high levels of female and egg harvesting for human consumption, which have declined over time (Taxonera Amoros et al., 2022). This shift, alongside extensive conservation efforts, has likely improved egg, juvenile, and female survival on beaches, contributing to the observed increase in nesting numbers. Thus, the sharp increase in nest counts may be due to a combination of rising temperatures and successful conservation efforts.

It is important to note that correlation does not imply causation. Although fluctuations in nesting trends can be partially linked to temperature changes on land, some sites may experience an increase in nest counts primarily due to colonisation of previously unsuitable nesting grounds (Girard et al., 2021), environmental changes in foraging sites at sea (Monsinjon et al., 2019), or increased monitoring and conservation efforts (Mazaris et al., 2017). This phenomenon is particularly probable in certain Mediterranean locations, such as Sicily, which has only recently seen the establishment of nests (Prato et al., 2022). In Cabo Verde, the huge increase in the annual number of loggerhead turtle nests across different islands has been attributed, in part, to conservation efforts (Laloë et al., 2020; Hays et al., 2022b; Taxonera Amoros et al., 2022), contrasting with declining trends on Masirah partially linked to increased disturbance (Mendonça

et al., 2010; William et al., 2021). Conservation efforts also impact bycatch rates in the ocean, showing reduction in some regions (e.g., Spain, Baez et al., 2019), but not in others (e.g., Cabo Verde; Martins et al., 2022; Roast et al., 2023). Furthermore, the current squeeze of nesting beaches, induced by urbanisation, sea level rise, and overexploitation of natural resources (Defeo and Elliott, 2021), contributes to habitat loss, compelling marine turtles to seek safer areas for nesting, leading to apparent increases in nesting activity in new sites and declines in previously used ones (Fuentes et al., 2010; Chevallier et al., 2023). Additionally, natural ecological factors like food availability or predation dynamics, coupled with events such as El Niño disrupting ocean currents and temperatures, further contribute to fluctuations in nesting activity. We believe that nesting trends reflect a combination of natural ecological phenomena, human activities, and environmental changes. Given the long reproductive cycle of loggerhead turtles (Miller, 2017), we acknowledge that a 40-year timeframe may not fully capture the nuances of temperature fluctuations and their correlation with nest numbers. Nevertheless, the general increase in nest counts might already be a short-term indicator of warming effects. Moreover, physiological adaptation to future climate change might be possible, particularly through natural selection driving changes in the critical thermal limits of incubation (Patrício et al., 2021). This is supported by evidence of gene expression plasticity that mitigates cell damage under heat stress (Tedeschi et al., 2016). However, marine turtles are more likely to respond in the short term through phenological or geographical shifts and adjustments in nesting or foraging behaviour, although these adaptations may be insufficient (Almpanidou et al., 2018; Fuentes et al., 2024).

Our study is limited by the short data coverage for certain locations, the exclusion of potential factors beyond temperature that may influence nesting trends, and possible inconsistencies in historical data accuracy. Long-term studies are needed to analyse the trends in global sex ratios of hatchlings and to understand whether this feminisation effect is a key factor driving nest numbers. As remote sensing tools become more accessible, offering higher spatial and temporal resolution, variables such as land surface temperatures will be a useful tool for determining spatial variability in temperatures across nesting sites (Almeida et al., 2023; Reiners et al., 2023).

Conclusions

The question of whether the warming of nesting grounds over recent decades has led to an increase in female turtle populations and subsequently higher nest counts is nuanced. In certain locations, such as in Cayman, Mexico, Brazil, Turkey, or Cyprus, increased temperatures may have played an important role in driving up loggerhead nesting numbers, potentially due to a feminised population, although other factors may have also contributed. However, in other regions like South Carolina, Florida, South Africa, or Japan, temperatures alone do not account for the observed rising nesting trends. Additionally, Masirah Island in the Arabian Sea, with the highest temperatures among nesting sites and declining nest trends, may be approaching the upper limit of lethal temperatures. If left unchecked, exceeding their tolerance threshold, rising temperatures could precipitate population declines.

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CHAPTER 6

Science outreach

Aim

Engaging with local communities and disseminating research findings to a broader audience is an important part of scientific research. In this chapter, I aimed to raise awareness about global changes, including both plastic pollution and climatic changes. From local implications to global solutions, I engaged with audiences through documentary filmmaking, media, and educational activities.

Documentary work

My main outreach output has been the creation of the documentary film M*arés de Plástico (“Seas of Plastic”*, Figure 1*)*. The documentary explores the growing presence of marine debris, predominantly plastic, on sea turtle nesting beaches in Boa Vista Island. We focused on the ongoing research on the effects on eggs, juveniles, and adult loggerhead turtles in the archipelago. In addition to showcasing the challenges faced by sea turtles, we aimed to raise awareness on the issue of plastic pollution and climate change. Involving researchers, NGOs and local communities, we documented the local efforts and ongoing scientific investigations. Images were captured by Elton Neves, using available filmmaking material, written by myself, and multiple people contributed with ideas, music, and audio. The documentary has received media coverage and has been disseminated through television and journal news.

Link: youtube.com/watch?v=LMzHu271qaE

Figure 1. Cover image of the documentary film *Marés de Plástico*.

Media coverage

November 2023, *The Atlantic*: An interview for an article titled "Plastic has changed sea turtles forever" discussing the long-term impacts of plastic pollution on sea turtles. Link: theatlantic.com/science/archive/2023/11/sea-turtles-plastic-pollution/676009

December 2023, *Público*: An interview for an article titled "Diana usa drones para mapear lixo marinho e proteger tartarugas" covering my use of drones to map marine debris and its impact on sea turtle conservation (Figure 2). Link: publico.pt/2023/12/25/azul/noticia/diana-usa-drones-mapear-lixo-marinho-proteger-tartarugas-2074506

January 2024, *Notícias UP*: An article titled "Estudante da FCUP mapeia Cabo Verde para proteger tartarugas do plástico," highlighted my fieldwork in Cabo Verde. Link: noticias.up.pt/2024/01/05/estudante-da-fcup-mapeia-cabo-verde-para-proteger-tartarugas-do-plastico

January 2024, *Jornal de Domingo, Televisão de Cabo Verde* (TCV): An interview featured on cape-verdean television news, where I discussed the marine litter problem in Cabo Verde and its threat to sea turtles. Link: youtube.com/watch?v=aiRsgmlYkIY

January 2024, *Podcast Comunicar Ciência, Rádio Antena Minho*: A podcast titled "Diana Sousa Guedes: O estudo dos efeitos da poluição marinha e das alterações climáticas nas praias de nidificação de tartaruga-comum," where I discussed my research on marine debris pollution and climate change. Link: open.spotify.com/episode/7qsezWOu17HXSFOaKAxrfd

February 2024, *Primeiro Jornal, SIC*: An interview featured on Portuguese television news highlighting my research on the threat of plastic pollution and its implications for sea turtle survival in Cabo Verde (Figure 3). Estimated audience of 544000. Link: sicnoticias.pt/mundo/2024-02-19-Plastico-em-Cabo-Verde-coloca-em-causa-sobrevivencia-de-tartarugas-0c076f2d

P

CABO VERDE

Diana usa *drones* para mapear lixo marinho e proteger tartarugas

Investigadora da Universidade do Porto cartografa o lixo marinho em sete ilhas de Cabo Verde. O objectivo é proteger a tartaruga-comum dos vários danos causados pela poluição plástica.

Andréia Azevedo Soares
25 de Dezembro de 2023, 11:00

Diana Sousa Guedes, 32 anos, estudante de doutoramento, mapeou o lixo marinho de sete das nove ilhas de Cabo Verde ELTON NEVES/DR

Figure 2. Article page in the journal *Público.*

Figure 3. Television news in the *Primeiro Jornal - SIC*.

Educational activities

22 February 2024, Escola Básica de Azurva – Ciência Viva de Azurva: Conducted an educational activity with children from 1st to 4th grade, to discuss marine plastic pollution on beaches.

14 March 2024, Escola Ciência Viva Vila do Conde: Conducted an activity with preschool children, about the impact of marine litter on sea turtles.

Figure 4. Educational activities in schools.

How distinctly I can call to mind the low cliff of lava beneath which I rested, with the sun glaring hot, a few strange desert plants growing near, and with living corals in the tidal pools at my feet.

Cabo Verde as seen by Charles Darwin in 1832

CHAPTER 7

General discussion

General discussion

What conditions are loggerhead turtles likely to encounter on nesting beaches in the future?

Female sea turtles arriving at nesting beaches in the future are likely to find increasingly warmer, narrower, and more polluted habitats. Climate change is driving global increases in temperatures, sea levels, and the frequency of extreme weather events, and nesting beaches are not exempt from these impacts (Fuentes et al., 2011; IPCC, 2021). The findings of this thesis indicate significant warming trends over the last four decades at multiple loggerhead rookeries worldwide (Chapter 5) and in several important nesting beaches of Cabo Verde (Chapter 4). This warming will be accompanied by rising sea levels and beach erosion, which reduce the available area for nesting. Indeed, many regions around the world are already experiencing beach loss due to the interplay of these factors (Fish et al., 2008; Defeo et al., 2009; Hinkel et al., 2013; Udo and Takeda, 2017). In Cabo Verde, only 8% of beaches are being increasingly inundated during the nesting season (Chapter 4). Indeed, some of the most important nesting beaches in Cabo Verde are relatively buffered against sea-level rise, because of their undeveloped coastline and large dune systems that support inland beach migration (Chapter 4; Abella-Perez et al., 2016). This mitigates habitat loss and additionally reduces light pollution on most beaches. As demonstrated in Chapter 4, only 18% of the analysed beaches in the archipelago have increased light pollution in the last few years, and most of these are in areas that are currently of lower nesting importance.

Nesting beaches are likely to face increased pollution from marine litter in the future, particularly those in remote areas, in part due to the transference of litter from populated areas (Galgani et al., 2021). The north- and east-facing beaches in Cabo Verde accumulate large volumes of marine litter (> 80% being plastics; Chapter 3). Approximately 26% of beaches in the archipelago are significantly affected by marine litter, many of those overlapping with key nesting sites (Chapter 4). This is largely due to the location of the archipelago within the North Atlantic Gyre, which funnels waste to its shores. Fishing-related plastic items are a major litter type found on beaches in Cabo Verde (Chapter 3), aligning with global trends in other regions (Monteiro et al., 2018;

Cardoso and Caldeira, 2021; Sánchez-García and Sanz-Lázaro, 2023). Santa Luzia, despite being an uninhabited island with minimal human activity, has nonetheless become a reservoir for marine litter (Chapter 3.1). Similarly, Boa Vista, one of the most important nesting grounds for loggerheads globally, has 20 of its 29 surveyed beaches exceeding European thresholds for marine litter levels (Chapter 3.2; Van Loon et al., 2020). Plastic accumulation not only creates physical barriers but also introduces chemical contaminants that can disrupt ecosystems and food webs (Chapter 2). Additionally, plastics washed ashore tend to fragment in multiple smaller pieces, producing micro- and nanoplastics harmful to the environment. While this study did not find direct evidence of temperature changes caused by plastics (Chapter 2.1), other research works indicate that they can alter sand thermal dynamics (Lavers et al., 2021; Fuentes et al., 2023).

Despite these challenges, approximately half of the beaches in Cabo Verde remain currently relatively unaffected by significant threats, such as pollution and coastal development (Chapter 4). Nesting beaches in Santo Antão and Maio benefit from their isolation, low urbanisation, and limited tourism activities, whereas those in São Vicente, Santiago, and Sal are more vulnerable, largely due to urbanisation, tourism pressure and associated light pollution.

Given these conditions, what does the future hold for loggerhead turtle populations?

Climate change and plastic pollution on beaches threaten loggerhead turtles throughout their life cycle, from egg incubation to adulthood and breeding (Nelms et al., 2016). These effects begin at the nesting stage, where the accumulation of high volumes of plastic debris can obstruct suitable nesting sites (Fujisaki and Lamont, 2016; Gündoğdu et al., 2019). In such scenarios, litter may prevent females from digging nests to the optimal depth or forcing them to abandon nesting attempts altogether (Gündoğdu et al., 2019). Shallow nests, which can happen because of obstructed digging, are more exposed to predators and elevated temperatures, reducing hatchling survival rates (Marco et al., 2018). Additionally, the presence of plastics in the sand can increase temperatures up to 0.5 ºC, further amplifying temperature-related stressors driven by climate

change (Fuentes et al., 2023). Warmer sands not only skew hatchling sex ratios toward females but also increase embryonic mortality (Howard et al., 2014). In Cabo Verde, incubation temperatures are rising, with projections suggesting they could exceed 32 ºC by 2100, risking population collapse in the absence of cooling factors (Laloë et al., 2014). Moreover, plastics exposed to sunlight can leak harmful pollutants into the surrounding sand, potentially contaminating nests (Chapter 2.2). Given the permeability of turtle eggs, some contaminants could result in a range of adverse effects, including endocrine disruption, carcinogenesis or developmental deformities (WHO, 2022; Ali et al., 2024). In our study (Chapter 2.2), nests with surface plastics exhibited higher levels of PBDEs (flame retardants added to plastics) and a higher prevalence of leucistic embryos. However, the latter was not statistically significant, indicating the need for further research to draw definitive conclusions. During incubation, climate change-related effects such as sea level rise and more frequent extreme storms can inundate or wash away nests due to erosion, further increasing embryonic mortality (Fish et al., 2005; Martins et al., 2022; Simantiris, 2024). These phenomena can also transport debris to higher beach strata, increasing overlap with nests and amplifying the threats posed by plastic pollution (van Emmerik, 2024).

Upon eggs' hatching, loggerhead hatchlings emerging from nests face additional challenges. Plastic debris within nests disrupts synchronised emergence, leaving delayed hatchlings more vulnerable to predators like ghost crabs (Chapter 2.1), as this synchrony is fundamental for predator evasion (Tucker et al., 2007; Marco et al., 2015). Marine litter can also physically trap hatchlings, which can delay or prevent their journey to the sea (Triessnig et al., 2012; Aguilera et al., 2018). Furthermore, plastics can hinder the coordination of hatchling movements by reducing friction and creating slippery surfaces (Patino-Martínez et al., 2010). These delays not only increase predation risk but also result in heightened energy expenditure, reduced fitness, and an elevated likelihood of entanglement, collectively lowering hatchling survival rates. With one-quarter of sea turtle nesting beaches globally already bordered by urbanisation (Biddiscombe et al., 2020), continued coastal development is expected to intensify light pollution, further

disorienting hatchlings and causing many to move away from the sea instead of toward it (Lorne and Salmon, 2007).

As juveniles in the sea, loggerheads increasingly interact with pollutants, including plastics, through both entanglement and ingestion. This developmental stage is especially sensitive, yet poorly studied due to difficulties in obtaining data. Feeding preferences and overlap with areas of high plastic density contribute to this vulnerability (Duncan et al., 2021). These pollutants, in particular the smaller fractions, can bioaccumulate in their tissues, leaking chemicals, and gradually affecting their health and reproductive capacity over time (Nelms et al., 2016). Male fertility may be particularly impacted, as exposure to endocrine-disrupting compounds has been shown to reduce semen quality and overall reproductive success in wildlife (Harrison et al., 1997; Barraza et al., 2021; de Oliveira et al., 2023; Milnes, 2024). A decline in the number of males, coupled with reduced fertility, diminishes population resilience and the effective breeding population (Reed and Frankham, 2003). This imbalance leaves females struggling to find mates, with available males increasingly less fertile due to chemical contamination, morphological abnormalities, or inbreeding issues (Vos et al., 2000; Reed and Frankham, 2003; Marlatt et al., 2022). Additionally, entanglement in plastic fishing gear has been reported across all life stages, but the juvenile stage is particularly concerning (Duncan et al., 2017). The oceanic currents that transport hatchlings to open-water habitats are known to concentrate high levels of marine debris, potentially creating an ecological trap (Duncan et al., 2021).

Upon reaching maturity, females return to their natal beaches to nest, only to find altered environments compared to the ones they left as hatchlings—narrower or eroded shorelines, higher sand temperatures, and increased levels of pollution. The presence of large debris may force females to expend extra energy and make repeated nesting attempts, which heightens their risk of disorientation on the beach (Fujisaki and Lamont, 2016). Additionally, entanglement in fishing gear or debris washed ashore further delays their return to the ocean. Females foraging in polluted environments are also likely to transfer contaminants, including microplastics and associated

chemicals, to their offspring, further affecting embryonic development and sex ratios (Bergeron et al., 1994; Savoca et al., 2021; Barraza et al., 2023; Chemello et al., 2023; Curl et al., 2024).

Over the long term, the combined effects of plastic pollution and climate change could ultimately lead to significant declines in loggerhead populations (Figure 1). Warmer temperatures may initially boost nesting numbers by favouring female hatchling production, but this short-term effect masks long-term declines as populations approach thermal thresholds (Chapter 5). In contrast, areas with mitigating factors such as cooler nighttime temperatures or seasonal rainfall—like Cabo Verde—may temporarily buffer against these impacts. The loss of genetic diversity, driven by feminised populations, weakens resilience to disease outbreaks and environmental changes, further amplifying extinction risks (Simantiris, 2024). Diverse genetic pools are essential for sea turtles to adapt to changing conditions, but reduced male availability and high mortality rates significantly increase their vulnerability (Frankham, 2005; Bowen and Karl, 2007).

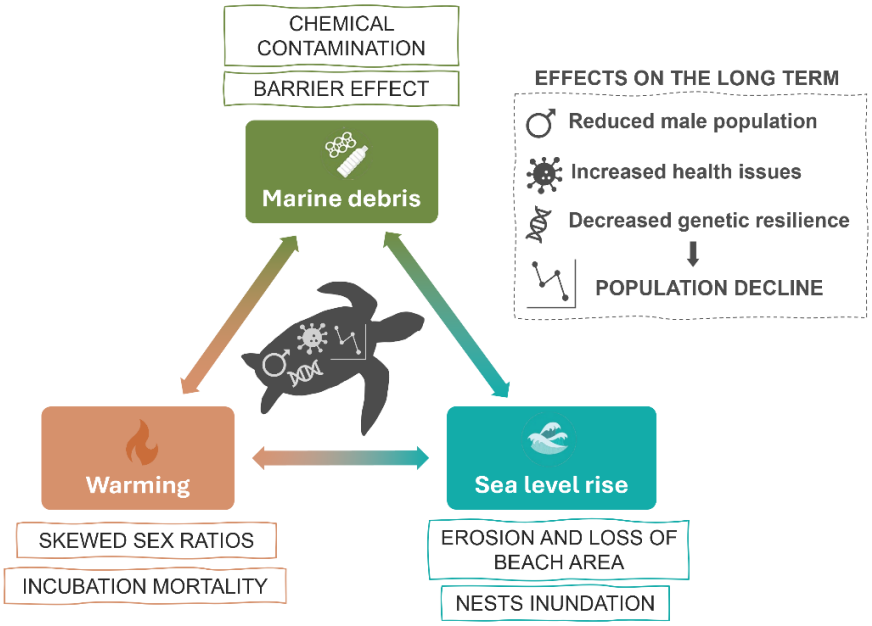

Figure 1. Summarised effects of marine debris pollution and climate change on sea turtle nesting.

Potential for adaptation

Over the next generations, sea turtles nesting earlier or in cooler locations may have higher reproductive success, promoting these traits through natural selection (Weishampel et al., 2004). Similarly, genetic traits for thermal tolerance could become more prevalent as thermally adapted individuals thrive. However, such evolutionary changes require sufficient genetic variation and considerable time (Quintero and Wiens, 2023). In contrast, short-term responses to climate change are more likely to be driven by phenotypic plasticity or environmental cues, which provide immediate but temporary flexibility to cope with such changes (Chevin et al., 2010). Sea turtles might adjust nesting behaviour in response to warming ocean currents or earlier seasonal temperature rises, opting for cooler sites (e.g., higher latitudes), shaded areas, or closer to vegetation or waterlines, protecting embryos from excessive heat (Weishampel et al., 2004; Wood and Bjorndal, 2000).

Reduced natal site fidelity may further enhance adaptability, allowing females to select suitable nesting sites despite rapid environmental changes (Pike and Stiner, 2007). Females have been observed nesting across several kilometres away within a single nesting season, suggesting a capacity for flexible site selection under dynamic conditions (Tucker, 2010; Patino-Martinez et al., 2023). Additionally, phenotypic plasticity may enable populations to develop increased thermal tolerance (Tedeschi et al., 2016), which is particularly crucial in equatorial regions like Cabo Verde, where even modest temperature increases could skew sex ratios, reduce hatchling viability, and amplify incubation mortality (Schwanz and Janzen, 2008).

Adaptations to plastic pollution are less understood. Behavioural responses such as avoiding heavily littered beaches or selecting cleaner microhabitats have been observed (Triessnig et al., 2012; Fujisaki and Lamont, 2016). This avoidance, however, may limit the availability of suitable nesting sites as plastic pollution becomes more widespread. Over time, natural selection might theoretically favour individuals resistant to the toxic effects of plastics and associated chemicals. Yet, the diversity of mechanisms of action in those substances complicates species adaptation

(Loria et al., 2019). Unlike discrete toxins such as pesticides, the multidimensional toxicity of plastic-associated chemicals, often encountered in combination, poses significant adaptive challenges (Whitehead et al., 2017).

Whether sea turtles can adapt quickly enough to keep pace with the rapid environmental changes will largely depend on the level of genetic variation within their populations, which is closely related to population size (Frankham, 1996). Moreover, the adaptation to one stressor may increase vulnerability to others, as it often requires modifications to an optimal phenotype regulated over generations in the ancestral environment (Futuyma, 1998; Coustau et al., 2000).

Mitigation strategies

Addressing climate change and plastic pollution requires both global and local interventions, with collective responsibility. While the complete elimination of these threats is unrealistic in the short term due to the inertia of climate change and population growth, immediate interventions can mitigate their impacts.

Global efforts should focus on reducing greenhouse gas emissions, a priority for limiting long-term ecosystem impacts. The Paris Agreement, adopted in 2015 under the United Nations Framework Convention on Climate Change, aims to limit global warming below 2º C pre-industrial levels (Guiot and Cramer, 2016). Preventing further development in coastal areas prone to be affected by sea level rise is also critical for allowing beach inland migration (Defeo et al., 2009). The relatively undeveloped coastlines in Cabo Verde provide an opportunity for resilience, as these beaches can naturally migrate inland as sea levels rise, reducing habitat loss and additionally light pollution impacts (Abella-Perez et al., 2016). Incorporating sea-level rise projections into land-use planning and protecting natural coastal buffers like dunes is essential. Local approaches can complement global strategies. For instance, mitigating rising sand temperatures on nesting beaches through increased shading or relocating nests to cooler or less inundated areas provides temporary relief (Patino-Martinez et al., 2012; Hill et al., 2015).

As for plastic production and waste management, international agreements are essential. One significant initiative is UNEA Resolution 5/14 (2022) which commits to the treaty targeting plastic pollution across its lifecycle, from production and consumption to disposal. Similarly, the OSPAR Convention (www.ospar.org/) works to reduce marine litter in the North-East Atlantic, focusing on land-based plastic sources and emphasising regional cooperation. While alternatives like bioplastics and reducing reliance on disposable plastics may also help, they are not universally feasible, particularly in low-income countries. Financial and regulatory mechanisms, including incentives for eco-friendly practices and penalties for excessive plastic production, can drive policy and environmental changes (Jia et al., 2019). Cabo Verde faces unique challenges due to insufficient waste management infrastructure and the burden of managing international waste (Brooks et al., 2018). Additionally, the persistence of plastic-associated chemicals, despite global bans, highlights systemic gaps in waste management, with continued emissions projected until 2050 unless robust interventions are implemented (Abbasi et al., 2019). Local measures, including public awareness campaigns (Chapter 6), improved waste management systems, and organised beach clean-ups, remain effective. For example, removing large debris from nesting sites can significantly increase sea turtle nesting activity (Fujisaki and Lamont, 2016). However, regular beach clean-ups face logistical challenges, particularly in uninhabited or remote areas. Thus, proactive strategies addressing the root causes of marine debris, such as reducing plastic production and improving sustainable disposal, are essential. The case of Santa Luzia illustrates how even remote islands with minimal human activity can be heavily impacted by marine debris carried by oceanic currents (Chapter 3.1), highlighting the global nature of this issue and the need for interventions at its source.

Ensuring long-term success in addressing these challenges requires investments in habitat management, sustainable conservation laws, and funding for long-term adaptation measures. By aligning global agreements with local initiatives, governments and communities can enhance resilience and protect sea turtle nesting habitats against global changes.

Future research

Understanding the long-term ecological impacts of climate change and plastic pollution on the life cycle of sea turtles, particularly on nests and nesting behaviours, is a research priority. As warming sands disproportionately favour female hatchling production, the potential for insufficient males to fertilise eggs could destabilise populations (Laloë et al., 2014). This raises essential questions about how population dynamics may respond to climate-induced shifts in operational sex ratios. Future research should focus on identifying critical thresholds at which male scarcity begins to compromise reproductive success. Long-term studies on clutch fertility across rookeries, coupled with fine-scale monitoring of sex ratios, are also necessary to quantify these risks. Complementary genetic studies will provide insights into the effects of reduced male numbers on genetic diversity and assess how this reduction impacts their adaptation to rapidly changing environments. Additionally, research into potential phenological shifts, such as range expansions or colonisation of new nesting areas, will be key to understanding how turtles may redistribute in response to climatic changes.

Accurate predictive models are also needed to forecast how environmental changes may reshape the morphology and structure of beaches. While our models successfully predicted the current distribution of marine debris within individual beaches (considering beach topography, Chapter 3.1) and across the archipelago (incorporating topography and oceanic dynamics, Chapter 4), they were unable to predict future distributions under changing conditions. Further research is needed to refine these models, incorporating the interplay between erosion, accretion, and other coastal processes. Additionally, understanding how sea turtles might adapt to shifts in site suitability, is critical for guiding conservation strategies.

The role of marine debris in shaping nesting behaviours is also highly unknown. Future research should explore whether females are actively avoiding heavily polluted areas and how such avoidance might influence nest site selection. For example, debris avoidance could lead to nest clustering in polluted areas, affecting nest density and consequent hatchlings' survival. Marine

litter may also interact synergistically with other stressors, such as sand temperatures (Fuentes et al., 2023). While their study found an increase in sand temperatures when in contact with plastic, it was conducted under controlled laboratory conditions. Field studies are therefore needed to evaluate how plastics affect sand temperatures in natural habitats, where other dynamic factors, such as wind or moisture, influence the results. Moreover, it is also important to consider the specific types, sizes and colours of plastics, as these may have varying effects. Dark-coloured materials absorb and retain more heat, potentially warming the surrounding sand, while white plastics may have a lesser thermal effect. Large plastic items on nest surfaces could have the opposite effect by providing shade and cooling the nests, while microplastics can penetrate deeper layers and alter the thermal properties and aeration of nesting sites over time.

Further studies should also examine the impact of plastic-associated chemicals on reproductive health, embryonic development, and hatchling viability to better understand their long-term ecological effects. High-priority research includes assessing whether plastic pollutants disrupt endocrine systems, potentially affecting clutch viability, sex determination, or male fertility. Although this study did not establish a direct link between plastic debris contamination and embryonic effects, the potential for chemicals to leak from debris into the surrounding sand and infiltrate into nests requires attention. Future studies should aim to quantify plastic-associated pollutant levels in the sand, as well as in eggs, embryos, and nesting females, to determine whether contamination is primarily maternal or can result from environmental transfer. Additionally, although ingestion of plastic debris has been reported to cause mortality in neonates or post-hatchlings (Duncan et al., 2021; Rice et al., 2021), these critical life stages remain poorly understood (often referred to as the “lost year” due to the challenges in tracking them; Witham, 1980). Chemical contamination through plastic ingestion during this vulnerable stage could have particularly detrimental development and reproductive effects.

Research must also consider how cumulative stressors—such as temperature extremes, habitat inundation, chemical bioaccumulation, and physical barriers—interact to influence nesting success, juvenile recruitment, and adult survival. Experimental and field-based studies are needed

to evaluate how these stressors interact and whether their combined effects may lead to nonlinear declines in population resilience. Finally, understanding the thresholds and tipping points that lead to population destabilisation may require interdisciplinary approaches integrating ecological modelling, earth observation tools, field studies, and experimental work. Questions about how sea turtle populations adapt to rapidly changing environments, the role of genetic diversity in resilience, and the interplay between environmental and anthropogenic stressors need to be addressed.

Concluding remarks

Loggerhead turtles face an increasingly uncertain future as climate change and plastic pollution intensify their effects on nesting habitats. In the decades to come, females arriving at beaches are likely to encounter warmer, narrower, and more polluted environments, with half of the beaches in Cabo Verde already experiencing some level of threat. While undeveloped coastlines and dune systems offer some resilience to rising sea levels, one-quarter of the shores in the archipelago are heavily affected by marine litter pollution. The position of the archipelago within the North Atlantic Gyre further exacerbates marine debris accumulation, posing both physical barriers to nesting and introducing chemical risks to hatchling survival. Rising temperatures further pressure loggerhead populations, disrupting hatchling sex ratios and increasing embryonic mortality. In the long term, the synergistic effects of climate change and plastic pollution could destabilise loggerhead turtle populations, risking significant declines if current trends persist. Mitigating these threats requires coordinated, urgent action, including effective marine litter management, conservation of natural coastlines, and policies to minimize urbanisation and tourism-related impacts. In addition, effectively communicating these issues to the wider society and actively involving them in adaptation and mitigation efforts are important, as their engagement is essential for successfully addressing these challenges in the future.

Main conclusions of the thesis

(1) High plastic debris density on sea turtle nest surfaces can reduce hatchling emergence success and disrupt synchronised emergence, resulting in smaller, scattered groups of emergent hatchlings, which in turn may increase their risk of predation.

(2) Plastic pollution on beaches can release harmful chemicals, such as flame retardants, which infiltrate the sand and eventually reach turtle eggs. While no significant impacts on hatching or emergence success were observed, the long-term implications need further research.

(3) Marine litter, predominantly plastic fragments and fishing materials, accumulates heavily on the north- and east-facing beaches in Cabo Verde, with several beaches on Santa Luzia and Boa Vista Islands exceeding recommended threshold levels.

(4) While 48% of sandy beaches in Cabo Verde face threats like marine debris and light pollution, over half remain relatively safe. Santo Antão and Maio are the least affected islands, whereas São Vicente, Santiago, and Sal are the most impacted. Marine debris spatially overlaps with key nesting sites across the archipelago.

(5) Loggerhead nest counts are rising globally, likely influenced by the short-term warming of nesting grounds. While regions in the Caribbean, Atlantic, and Mediterranean may temporarily benefit, prolonged warming could precipitate long-term population declines.

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Appendix to Chapter 2.1

Plastic pollution can affect the emergence patterns of loggerhead turtle hatchlings

Table S1. Number of eggs, number of hatched eggs, number of emergent hatchlings in each nest, and number of non-hatched eggs (comprising rotten and closed eggs and dead and alive individuals hatching).

Nest ID	Treatment	Nº of eggs	Nº of hatched eggs	Nº of emergent hatchlings	Nº of non-hatched eggs
D1	T2	72	67	63	5
D2	T1	89	61	50	28
D3	C	82	74	66	8
D4	T2	87	54	44	33
D5	T1	91	85	80	6
D6	C	93	28	18	65
D7	T2	95	50	40	45
D8	T1	54	53	52	1
D9	C	81	36	23	45
D10	T2	70	67	65	3
D11	T1	81	66	59	15
D12	C	74	72	72	2
D13	T1	95	57	49	38
D14	T2	88	35	24	53
D15	C	76	71	71	5
D16	T1	87	78	67	9
D17	T2	90	69	46	21
D18	C	72	57	57	16
D19	T1	72	70	66	2
D20	T2	91	22	22	69
D21	C	96	69	61	27
D22	T1	74	49	24	25
D23	T2	82	34	32	48
D24	C	81	73	72	8
D25	T1	95	49	49	46
D26	T2	99	70	58	29
D27	C	85	68	67	17
D28	C	80	72	56	8
D29	T1	88	48	44	40
D30	T2	80	49	39	31
D31	C	55	52	44	3
D32	T1	70	54	51	16
D33	T2	93	62	59	31
D34	C	72	53	39	19
D35	T1	84	46	45	38
D36	T2	82	47	37	35
D37	T2	87	62	17	25
D38	T1	81	76	70	5
D39	C	79	59	42	20
D40	T2	84	61	61	28
D41	T1	89	85	85	4
D42	C	92	53	52	39
D43	T2	71	58	51	13
D44	T1	88	72	57	16
D45	C	76	67	61	9
D46	T1	86	72	70	14
D47	C	115	65	52	50
D48	T2	83	50	32	33
D49	T1	69	50	42	19
D50	C	88	53	50	35
D51	T2	73	61	42	12
D52	T1	74	60	56	14
D53	C	74	63	48	11
D54	T2	79	58	58	21

Table S2. Scores for the components of the principal component analysis: standard deviation, proportion of variance, and cumulative proportion of variance.

	Standard deviation	Proportion of variance	Cumulative proportion
PC1	1.9395	0.2508	0.2508
PC2	1.5347	0.1570	0.4078
PC3	1.4827	0.1466	0.5544
PC4	1.3131	0.1149	0.6693
PC5	1.0684	0.0761	0.7454
PC6	0.9856	0.0648	0.8101
PC7	0.9185	0.0563	0.8664
PC8	0.8158	0.0444	0.9108
PC9	0.6354	0.0269	0.9377
PC10	0.5779	0.0223	0.9599
PC11	0.4963	0.0164	0.9764
PC12	0.3476	0.0081	0.9844
PC13	0.3257	0.0071	0.9915
PC14	0.2862	0.0055	0.9970
PC15	0.2140	0.0030	1.0000

Figure S1. Photograph of one of the most polluted beaches (Carreto beach), located in the northeast part of Boa Vista Island.

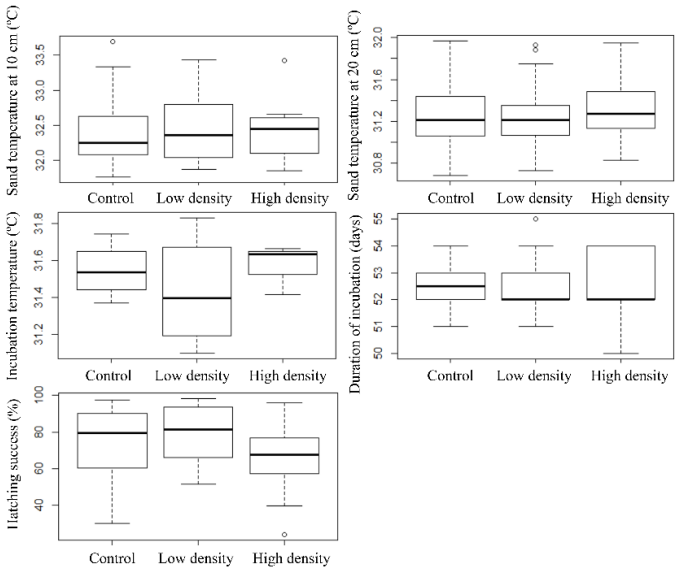

Figure S2. Boxplots for pairwise comparison between treatments (control, low plastic density, and high plastic density) for the five variables related to the incubation period. Boxes show interquartile range, horizontal line shows median value, whiskers show range, and open circles show statistical outlier value. No variables showed significant differences between treatments (Kruskal-Wallis tests with p-values > 0.05).

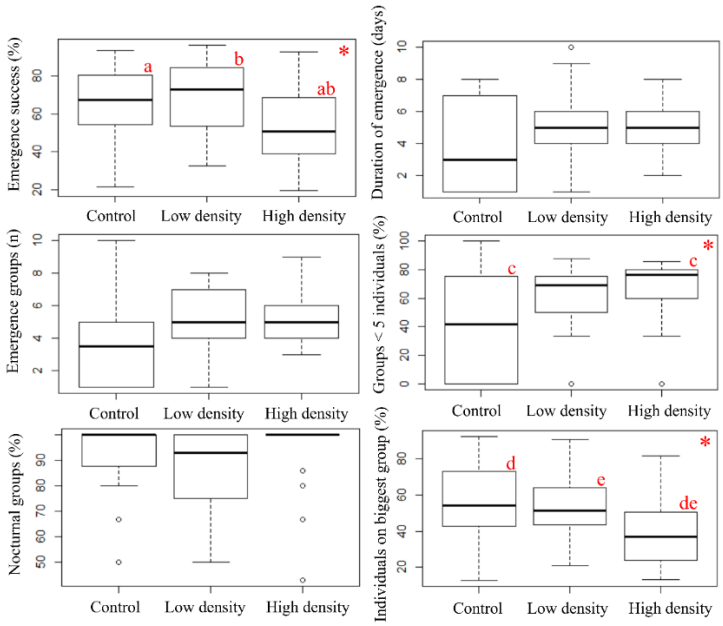

Figure S3. Boxplots for pairwise comparison between treatments (control, low plastic density, and high plastic density) for the six variables related to the emergence period. Boxes show interquartile range, horizontal line shows median value, whiskers show range, and open circles show statistical outlier value. With red asterisks, the variables with significant differences

between treatments (Kruskal-Wallis tests with p-values < 0.05). Red letters denote significance between each treatment (non-adjusted p-value of the Dunn's test < 0.05).

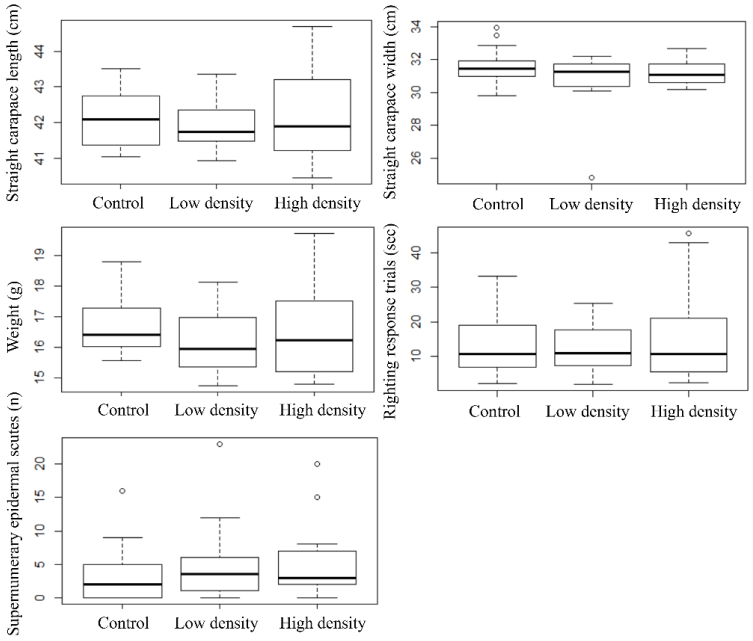

Figure S4. Boxplots for pairwise comparison between treatments (control, low plastic density, and high plastic density) for the five variables related to the hatchlings' fitness. Boxes show interquartile range, horizontal line shows median value, whiskers show range, and open circles show statistical outlier value. No variables showed significant differences between treatments (Kruskal-Wallis tests with p-values > 0.05).

Appendix to Chapter 2.2

Can plastic pollution contaminate loggerhead turtle nests? Evaluation of flame retardants (PBDEs) levels in the sand

Figure S1. Leucistic embryos in the experiment.

Appendix to Chapter 3.1

Lost and found: Patterns of marine litter accumulation on the remote island of Santa Luzia, Cabo Verde

Table S1. Approximate geographic coordinates of each sampling point (in decimal degrees) and mean values of each topographical variable of the aerial images.

Sampling point	Longitude	Latitude	Northness	Slope (%)	Elevation (m)
A1	-24.703508	16.755061	0.53	10.41	2.94
A2	-24.718865	16.752298	0.76	8.29	-0.35
A3	-24.710931	16.750938	0.74	11.43	1.61
F1	-24.708919	16.737159	-0.36	7.80	-0.04
F2	-24.724796	16.735787	-0.60	8.16	-0.28
PT	-24.749361	16.751235	-0.29	8.95	-0.50

Table S2. Total number of items (> 1 mm) by type and colour in each sampled square of 1×1 m: Achados Beach (three points, A1, A2, and A3), Francisca Beach (two points, F1 and F2), and Palmo Tostão Beach (one point, PT).

		A1	A2	A3	F1	F2	PT
Category (per m^2)	**Fragments**	72	313	626	-	-	-
	Pellets	1	84	167	-	-	-
	Filaments	19	17	79	-	-	-
	Ropes	11	31	40	-	-	1
	Foams	7	-	2	-	-	-
	Films	2	-	2	-	-	-
	Objects	1	2	1	-	-	-
Colours (per m^2)	**White/ transparent**	42	205	472	-	-	-
	Green/ blue	39	99	234	-	-	-
	Brown/ yellow	22	74	76	-	-	-
	Black/ grey	7	34	61	-	-	-
	Red/ orange	6	21	43	-	-	-
	Other colours	-	26	31	-	-	-
TOTAL NUMBER		113	447	917	-	-	1
SUM OF LENGTHS (m)		5.2	12.6	16.3	-	-	0.8
AVERAGE SIZE (mm)		45.6	28.2	17.8	-	-	-

Table S3. Total number of debris (> 25 mm) by type and colour in the aerial images: Achados Beach (three points, A1, A2, and A3), Francisca Beach (two points, F1 and F2), and Palmo Tostão Beach (one point, PT), and size of each orthophoto (area and length).

		A1	A2	A3	F1	F2	PT
Fragments (per 100 m^2)		55.3	19.8	48.0	0.2	0.8	1.0
Containers or packaging (per 100 m^2)	**Bottles < 2L**	9.1	0.7	0.9	-	0.1	-
	Bottles > 2L	0.6	0.1	-	-	-	-
	Drums and buckets	0.1	-	-	-	-	-
	Crates	0.5	-	0.1	-	-	-
	Other containers	2.0	0.7	0.7	-	-	-
	Caps	0.6	-	-	-	-	-
	Bags	0.2	0.1	-	-	-	-
Fishing materials (per 100 m^2)	**Buoys**	0.2	0.1	-	-	-	-
	Fishing nets/ropes/strings	29.3	6.5	29.5	0.1	-	-
	Octopus pots	2.4	0.3	0.7	-	-	-
	Other fishing items	-	0.1	-	-	-	-
	Foam	0.4	0.1	0.1	-	-	-
Wood (per 100 m^2)	**Processed timber**	9.6	1.6	15.0	-	-	-
	Pallets	0.1	-	-	-	-	-
Others/ undefined (per 100 m^2)	**Shoes or clothing**	0.3	-	-	-	-	-
	Tyres	-	-	-	-	-	-
	Undefined items	0.1	0.1	0.1	-	-	-
Colours (per 100 m^2)	**White/ transparent**	42.5	14.2	26.2	0.2	0.7	0.7
	Green/ blue	31.3	9.1	32.9	0.1	0.1	-
	Brown/ yellow	17.5	3.7	22.4	-	0.1	0.3
	Black/ grey	10.4	1.9	9.7	-	-	-
	Red/ orange	8.9	0.8	4.4	-	-	-
	Other colours	0.4	0.1	0.2	-	-	-
TOTAL NUMBER		6096	539	3777	15	43	31
SUM OF LENGTHS (m)		1638.6	71.4	768.8	2.4	5.0	3.4
ORTHOPHOTO AREA (m^2)		5496	1804	3969	5822	4640	2910
ORTHOPHOTO BEACH LENGTH (m)		121	102	126	134	128	134
AVERAGE SIZE (mm)		268.8	132.5	203.5	160.0	116.3	109.7

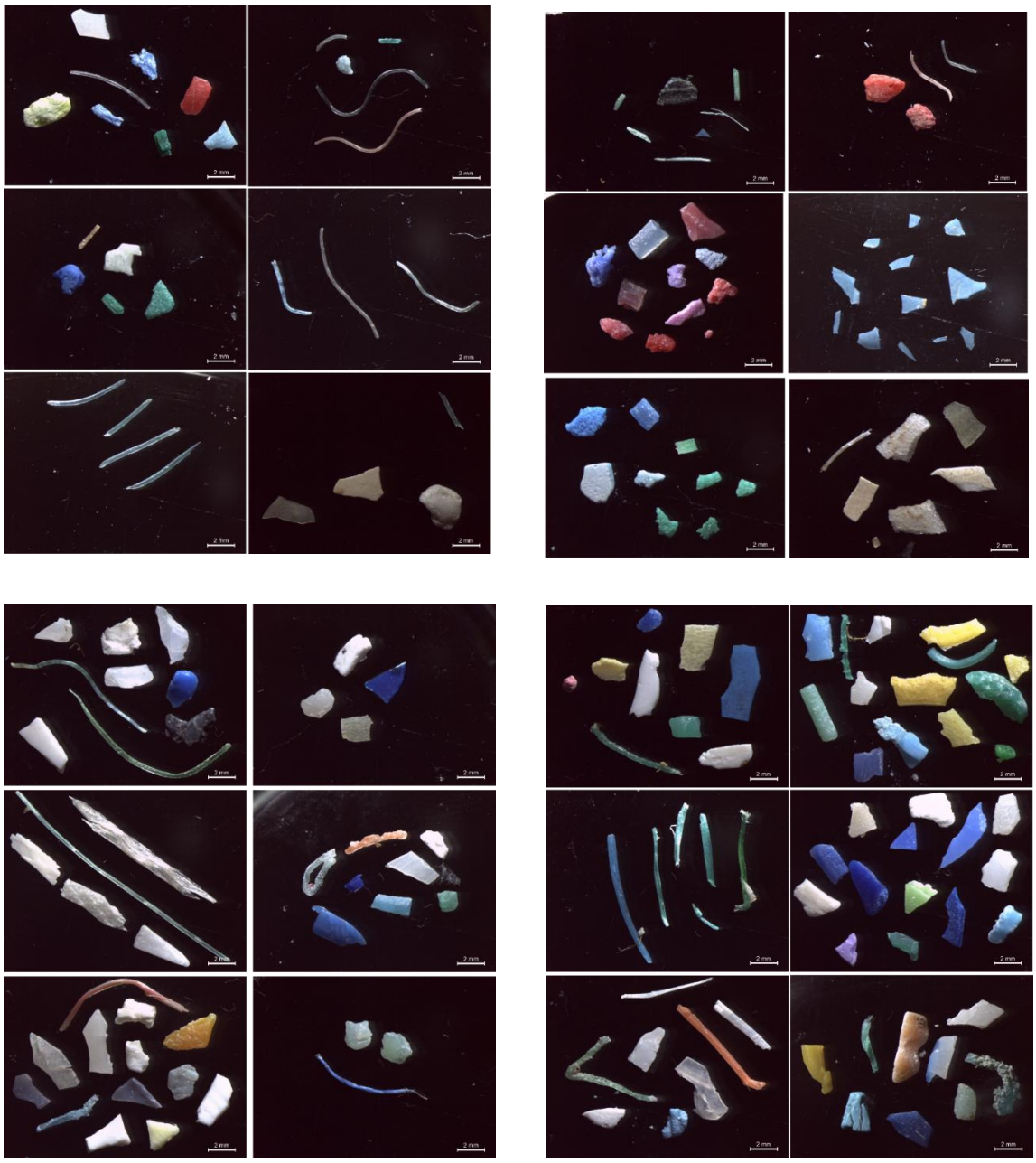

Figure S1a,b,c,d. Photographs of large micro- and mesoplastics (> 1 mm) found on the sand samples.

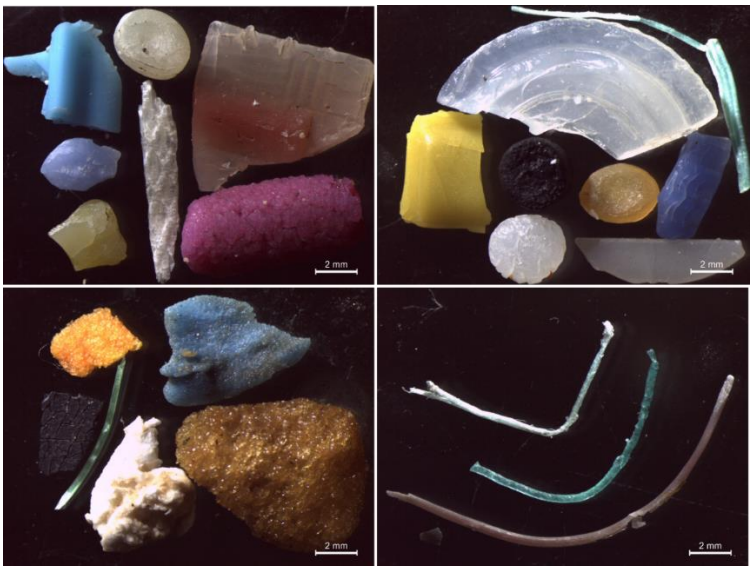

Figure S1e. Photographs of large micro- and mesoplastics (> 1 mm) found on the sand samples.

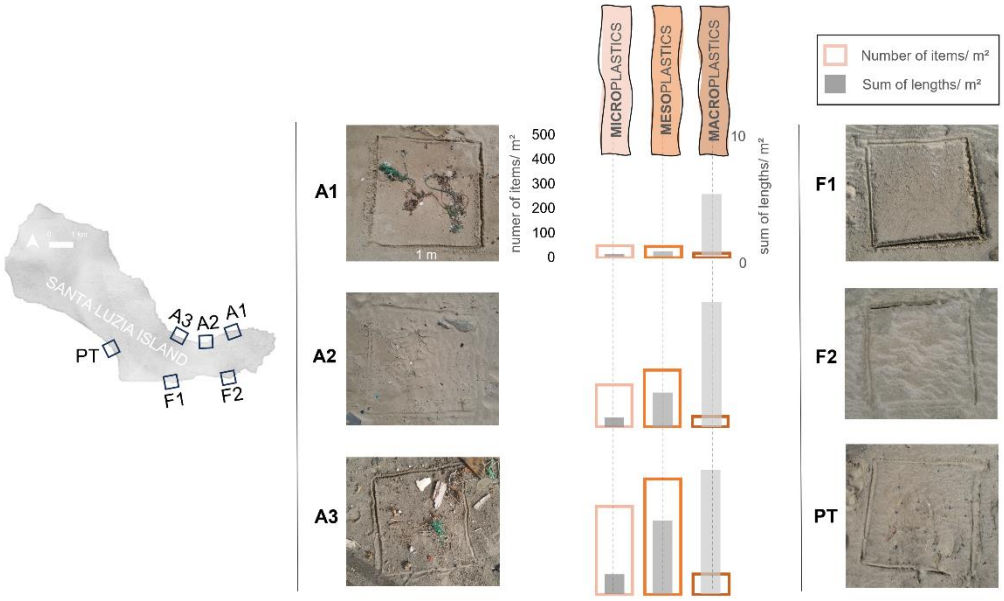

Figure S2. Squares of 1×1 m of the six sampling points. Orange bars of the graphics represent the density of plastics (number of items per m^2) while the grey bars represent the total lengths of the items (in metres, per m^2) in each beach, in the three size categories. The three southern sampling points had very low (1 item in PT) or any plastics (F1 and F2).

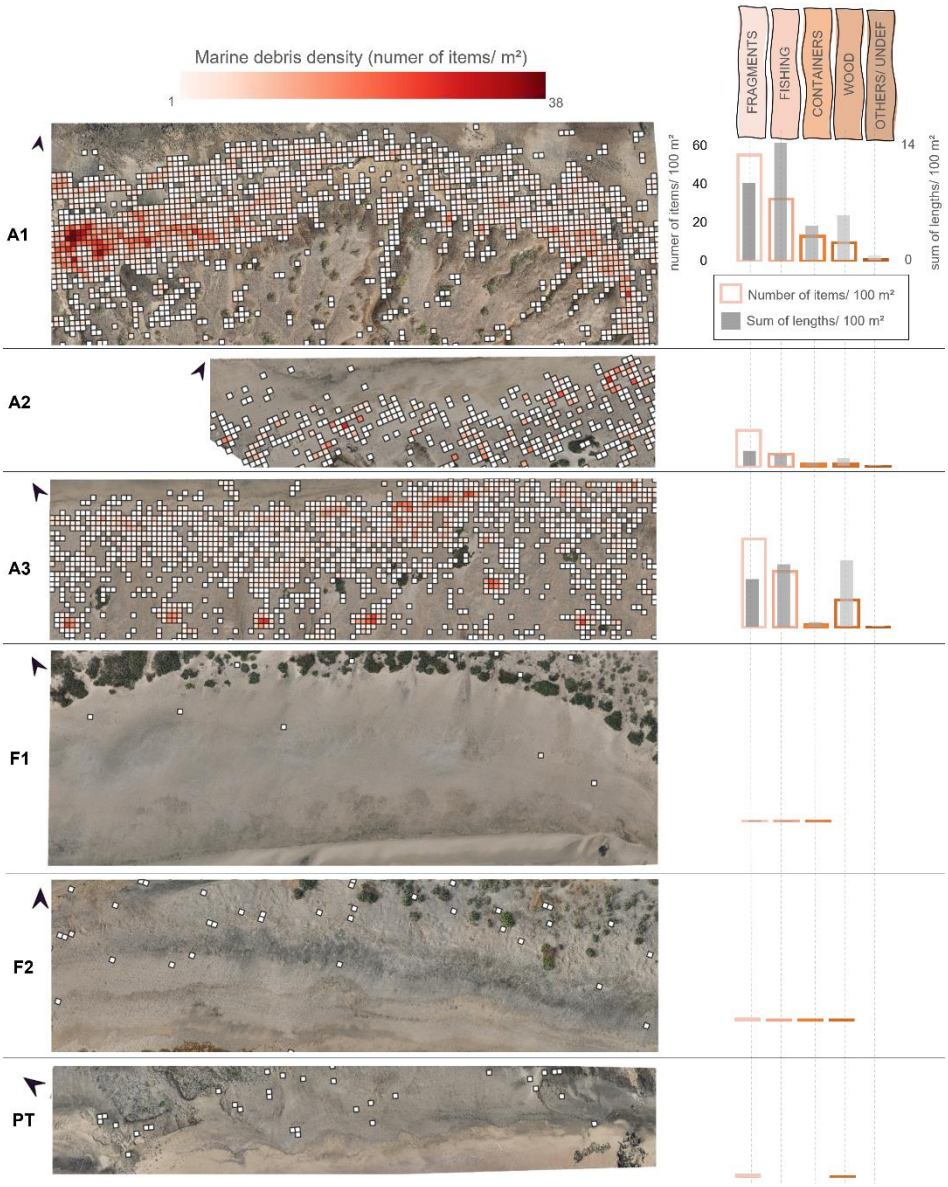

Figure S3. Aerial images and grids (1×1 m) of marine debris density in each beach. On the right, orange bars represent the total density by category (number of items per 100 m^2) and the grey bars represent the lengths of the total items by category (in metres, per 100 m^2).

Appendix to Chapter 4

How vulnerable are the nesting sites of loggerhead turtles in Cabo Verde?

Table S1. Average number of marine debris items per beach area (100 m^2) and per beach length (100 m) of each surveyed beach.

Island	Beach	Longitude	Latitude	Per area (100m^2)	Per length (100 m)	Reference
Santo Antão	Curralinho	-25.315	16.924	2.13	46	This study
Santo Antão	Porto Novo	-25.099	16.999	17.98	516	
Santo Antão	Tarrafal	-25.312	16.948	0.02	1	
São Vicente	Calhau	-24.868	16.849	11.65	391	
São Vicente	Praia Grande	-24.877	16.860	5.5	197	
Santa Luzia	AchadosCentro	-24.711	16.751	29.88	528	Chapter 3.1
Santa Luzia	Achados Este	-24.703	16.755	110.92	5038	
Santa Luzia	Achados Oeste	-24.719	16.752	95.16	2998	
Santa Luzia	Francisca Norte	-24.709	16.738	0.93	34	
Santa Luzia	Francisca Sul	-24.725	16.736	0.26	11	
Santa Luzia	Palmo Tostao	-24.749	16.751	1.07	23	
Sal	Algodoeiro	-22.934	16.630	0.97	21	This study
Sal	Calheta Funda	-22.945	16.651	1.72	61	
Sal	Costa Fragata	-22.900	16.624	1.9	64	
Sal	Pedra Lume	-22.895	16.761	2.69	74	
Sal	Serra Negra	-22.887	16.646	4.94	303	
Boa Vista	Carlota	-22.909	16.161	0.11	12	Chapter 3.2
Boa Vista	Chaves	-22.919	16.110	0.68	58	
Boa Vista	Varandinha	-22.961	16.049	0.35	33	
Boa Vista	Curralinho/ Farrapa	-22.954	16.019	0.22	27	
Boa Vista	Santa Mónica	-22.903	15.998	0.09	7	
Boa Vista	Manga Larga	-22.882	15.977	1.13	40	
Boa Vista	Lacacão Oeste	-22.855	15.977	0.13	10	
Boa Vista	Lacacão Este	-22.824	15.977	1	95	
Boa Vista	Ponta Pesqueira	-22.800	15.972	0.15	10	
Boa Vista	Curral Velho Sul	-22.793	15.976	2.05	162	
Boa Vista	Curral Velho Norte	-22.772	15.996	0.35	27	
Boa Vista	João Barrosa (SF)	-22.759	16.006	0.14	8	
Boa Vista	João Barrosa (S)	-22.742	16.015	0.77	47	
Boa Vista	João Barrosa (N)	-22.729	16.023	0.23	16	
Boa Vista	Ponta Cosme	-22.707	16.034	1.21	65	
Boa Vista	Ervatão	-22.701	16.039	0.39	20	
Boa Vista	Ponta de Roque	-22.668	16.086	71.95	5010	
Boa Vista	Nho Martin	-22.675	16.111	19.25	522	
Boa Vista	Porto Ferreira	-22.678	16.121	12.83	655	
Boa Vista	Figura	-22.676	16.147	27.05	2727	
Boa Vista	Canto	-22.704	16.175	12.64	832	
Boa Vista	Gatas	-22.710	16.195	22.45	517	
Boa Vista	Braca	-22.709	16.200	13.63	665	
Boa Vista	Calheta Negra	-22.735	16.207	15.9	712	
Boa Vista	Lantcha/ Calheta	-22.740	16.208	14.95	630	
Boa Vista	Boa Esperança	-22.883	16.207	9.29	522	
Boa Vista	Ponta do Sol	-22.899	16.218	15.66	580	
Boa Vista	Ponta Antónia	-22.783	16.223	6.46	278	
Boa Vista	Cabral	-22.918	16.186	0.27	14	
Maio	Barreiro	-23.145	15.126	1.07	62	This study
Maio	Calhetinha	-23.225	15.270	1.24	49	
Maio	Galeão	-23.154	15.314	13.09	665	
Maio	Morro	-23.229	15.196	0.38	34	
Maio	Morro Sul	-23.233	15.266	0.07	5	
Maio	Pilao Cão	-23.093	15.209	6.84	229	
Maio	Ponta Preta	-23.196	15.124	0.03	3	
Maio	Porto Cais	-23.168	15.320	40.63	829	
Maio	Praia Gonçalo	-23.106	15.267	1.72	73	
Maio	Praia Real	-23.185	15.312	6.22	140	

Maio	Ribeira São Joao	-23.122	15.139	0.08	4
Maio	Salina	-23.226	15.146	0.05	5
Maio	Santana	-23.206	15.288	1.85	162
Maio	Santo Antonio	-23.103	15.282	2.42	147
Santiago	Praia Baixo	-23.473	15.062	0.74	46
Santiago	São Francisco	-23.461	14.970	0.29	12

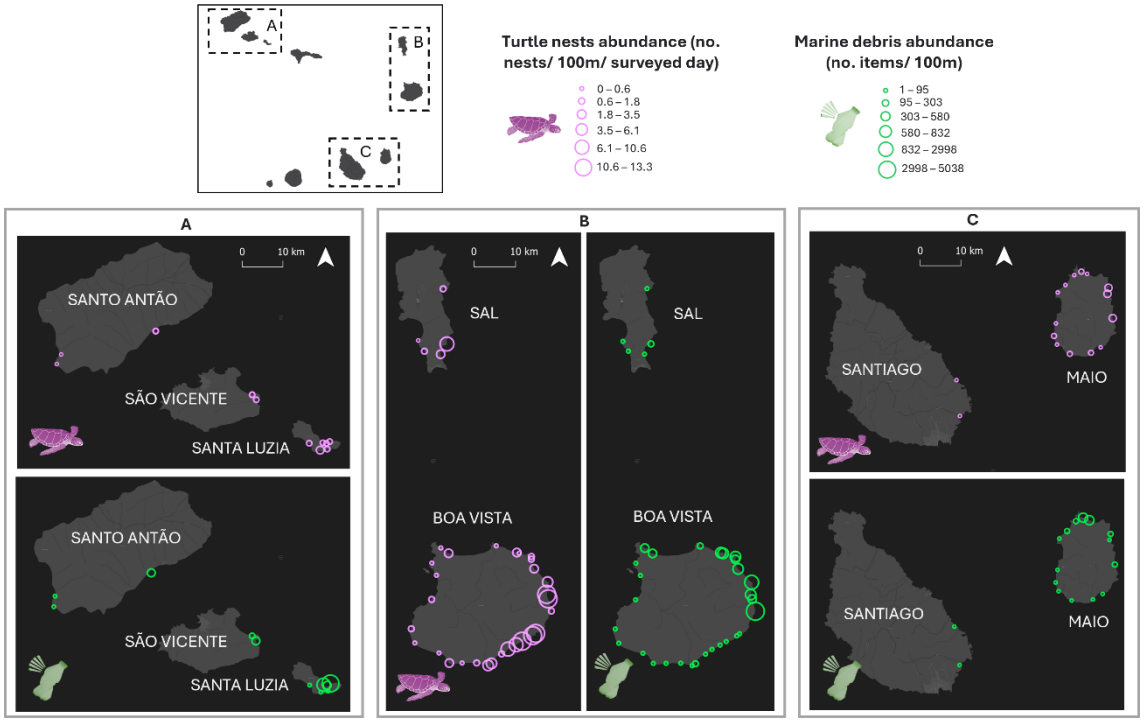

Figure S1. Surveyed points across islands. In purple, the compiled density of loggerhead turtle nests, and in green sampled density of marine debris.

Appendix to Chapter 5

The effects of warming on loggerhead turtle nesting counts

Table S1. Mean values ($\overline{X}$, in ºC), standard deviation (SD), significant Mann-Kendall slopes (MK; p-value < 0.05) of the five variables in each location: maximum air temperature (TMAX), mean air temperature (TMEAN), minimum air temperature (TMIN), diurnal land surface temperature (LST DAY), and nocturnal land surface temperature (LST NIGHT).

Nesting site	TMAX (1979-2013)		TMEAN (1979-2013)		TMIN (1979-2013)		LST DAY (2000-2023)		LST NIGHT (2000-2023)	
	$\overline{X}$ (SD)	MK	$\overline{X}$ (SD)	MK	$\overline{X}$ (SD)	MK	$\overline{X}$ (SD)	MK	$\overline{X}$ (SD)	MK
(1) G Cayman	28.54 (0.27)	0.37 **	**27.78 (0.27)**	0.37 **	**26.36 (0.27)**	0.29 *	28.60 (0.43)	-	**23.61 (0.42)**	0.56 ***
(2) Q Roo	28.80 (0.47)	0.34 **	26.53 (0.36)	0.40 ***	23.46 (0.28)	0.25 *	27.53 (0.62)	-	**23.01 (0.53)**	0.55 ***
(2.1) Tankah	28.81 (0.47)	0.37 **	26.52 (0.37)	0.42 ***	23.42 (0.28)	0.25 *	27.02 (0.81)	-	**22.96 (0.50)**	0.59 ***
(3) S Carolina	25.06 (0.51)	-	22.93 (0.52)	-	17.22 (0.48)	-	20.34 (1.03)	-	16.42 (0.96)	0.46 **
(4) NE Florida	26.47 (0.50)	0.24 *	23.80 (0.50)	0.24 *	18.05 (0.50)	-	23.06 (0.79)	-	18.14 (0.87)	-
(5) CE Florida	27.31 (0.44)	0.35 **	25.10 (0.44)	0.30 *	20.53 (0.48)	0.36 **	25.39 (0.75)	-	20.40 (0.72)	-
(5.1) Brevard	27.32 (0.44)	0.34 **	25.08 (0.44)	0.30 *	20.49 (0.49)	0.35 **	26.20 (0.83)	-	20.53 (0.76)	0.33 *
(6) SE Florida	27.99 (0.40)	0.36 **	25.80 (0.41)	0.31 **	21.61 (0.45)	0.33 **	28.80 (0.98)	-	21.66 (0.67)	0.40 *
(6.1) B Raton	28.08 (0.41)	0.35 **	25.75 (0.42)	0.33 **	21.39 (0.46)	0.35 **	31.28 (1.30)	-	21.46 (0.66)	0.40 *
(7) SW Florida	28.27 (0.42)	0.27 *	25.51 (0.43)	0.25 *	20.49 (0.47)	-	24.08 (0.77)	-	20.41 (0.91)	0.52 **
(8) Sanibel	27.97 (0.40)	0.24 *	25.56 (0.41)	0.25 *	20.82 (0.46)	-	25.95 (0.73)	-	20.38 (0.69)	-
(9) Sarasota	27.53 (0.41)	0.24 *	25.18 (0.43)	0.27 *	20.25 (0.47)	-	25.02 (1.09)	-	19.93 (0.80)	-
(10) Panhandle	26.27 (0.55)	0.28 *	23.73 (0.54)	0.28 *	17.82 (0.47)	-	22.46 (0.74)	-	17.81 (0.78)	-
(11) Sergipe	**29.67 (0.34)**	-	27.31 (0.26)	-	**24.26 (0.23)**	0.28 *	31.40 (0.63)	0.41 *	22.85 (0.34)	0.34 *
(12) Bahia	28.98 (0.44)	0.35 **	26.97 (0.34)	0.43 ***	24.21 (0.28)	0.48 ***	30.06 (0.66)	-	22.75 (0.31)	-
(12.1) P Forte	29.03 (0.47)	0.35 **	26.99 (0.34)	0.44 ***	24.21 (0.28)	0.49 ***	29.03 (0.91)	-	22.67 (0.38)	-
(13) E Santo	28.27 (0.49)	0.24 *	26.27 (0.39)	-	22.84 (0.25)	-	28.10 (0.70)	-	20.45 (0.46)	-
(14) R Janeiro	28.44 (0.57)	-	26.21 (0.46)	-	22.34 (0.27)	-	31.01 (1.23)	-	20.64 (0.49)	0.40 *
(15) S Luzia	24.88 (0.44)	0.42 ***	24.43 (0.43)	0.41 ***	23.05 (0.44)	0.33 **	30.73 (0.65)	-	18.86 (0.69)	-
(16) Sal	25.11 (0.40)	0.39 **	24.64 (0.39)	0.37 **	23.21 (0.41)	0.24 *	31.44 (0.68)	-	18.98 (0.58)	-
(17) Maio	25.69 (0.35)	0.38 **	25.21 (0.35)	0.36 **	23.78 (0.39)	0.24 *	**33.04 (0.71)**	-	19.52 (0.53)	-
(18) Boa Vista	25.34 (0.38)	0.38 **	24.86 (0.37)	0.36 **	23.42 (0.40)	0.24 *	31.46 (0.46)	-	19.07 (0.55)	-
(18.1) J Barrosa	25.42 (0.37)	0.36 **	24.95 (0.37)	0.35 **	23.50 (0.40)	0.24 *	**34.02 (0.80)**	-	18.37 (0.64)	-
(19) W Cyprus	25.21 (0.54)	0.49 ***	23.87 (0.55)	0.49 ***	19.07 (0.47)	0.44 ***	30.09 (0.94)	-	15.64 (0.91)	-
(20)Chrysochou	25.33 (0.54)	0.49 ***	23.86 (0.56)	0.50 ***	18.87 (0.49)	0.47 ***	29.03 (1.22)	-	16.00 (0.82)	-
(21) N Cyprus	26.63 (0.55)	0.51 ***	24.45 (0.58)	0.51 ***	18.64 (0.55)	0.50 ***	30.63 (1.11)	-	15.98 (0.78)	-
(22) Zakynthos	23.69 (0.63)	0.42 ***	21.73 (0.62)	0.45 ***	16.19 (0.46)	0.51 ***	26.03 (1.79)	-	14.20 (0.88)	-
(23) Dalyan	28.20 (0.77)	0.49 ***	23.97 (0.74)	0.49 ***	15.51 (0.62)	0.51 ***	22.55 (1.14)	-	16.30 (0.97)	-
(24) Çirali	27.55 (0.62)	0.47 ***	24.43 (0.64)	0.46 ***	17.15 (0.56)	0.42 ***	26.69 (1.96)	-	16.35 (1.00)	-
(25) Sicily	24.50 (0.57)	0.26 *	22.26 (0.54)	0.25 *	16.55 (0.37)	0.36 **	28.53 (1.10)	-	13.21 (0.64)	-
(26) Masirah	**30.04 (0.27)**	-	**27.59 (0.27)**	-	**24.75 (0.27)**	-	**34.08 (0.79)**	-	21.49 (0.54)	0.59 ***
(27) Malongane	27.02 (0.35)	-	25.21 (0.32)	-	21.22 (0.23)	-	24.51 (0.79)	-	19.77 (0.44)	-
(28) Kwazulu	27.07 (0.39)	-	24.97 (0.35)	-	20.61 (0.24)	-	24.84 (0.98)	-	18.97 (0.42)	-
(29) Ningaloo	**30.96 (0.60)**	-	**27.52 (0.62)**	-	21.40 (0.43)	-	30.84 (0.84)	0.33 *	19.32 (0.61)	0.43 **
(30) Yakushima	24.59 (0.41)	0.30 *	23.76 (0.41)	0.33 **	19.39 (0.38)	0.25 *	No data			

Table S2. Historical sex ratio estimations across nesting sites.

Location	Country	Year	Months	%females	Bias	Estimated	Reference
Central East Florida (Cape Canaveral)	USA	1986	May – Aug	> 93.0	High ♀	Gonads examination, and sand temperatures at 30 and 60 cm with probes	Mrosovsky and Provancha, 1989, 1992
Central East Florida (Cape Canaveral)	USA	1987	May - Aug	98.9 – 100.0	High ♀		
Central East Florida (Cape Canaveral)	USA	1988	May - Aug	46.2 – 100.0	High ♀		
Southeast Florida (Hutchinson Island)	USA	1997	Jun - Jul	97.5	High ♀	Dataloggers in nests	Hanson et al., 1998
Southwest Florida (Ten Thou Islands)	USA	1991-1994	Jul - Aug	~ 50.0	-	Dataloggers in nests	Foley et al., 2000
Sanibel	USA	2013-2015	May - July	~ 72.0	High ♀	Blood samples	Lasala et al., 2018
Southeast Florida (Juno Beach)	USA	2002	May - July	91.0	High ♀	Gonads examination	Wyneken and Lolavar, 2015 Fleming et al., 2020
Southeast Florida (Juno Beach)	USA	2003	May - July	95.0	High ♀	Gonads examination	
Southeast Florida (Juno Beach)	USA	2018	May - July	~100.0	High ♀	Dataloggers in nests	
Boca Raton	USA	2002	May - July	87.0	High ♀	Gonads examination	
Boca Raton	USA	2004	May - July	89.0	High ♀	Gonads examination	
Boca Raton	USA	2007	May - July	100.0	High ♀	Gonads examination	
Boca Raton	USA	2008	May - July	100.0	High ♀	Gonads examination	
Boca Raton	USA	2009	May - July	71.0	High ♀	Gonads examination	
Boca Raton	USA	2010	May - July	100.0	High ♀	Gonads examination	
Boca Raton	USA	2011	May - July	100.0	High ♀	Gonads examination	
Boca Raton	USA	2012	May - July	74.0	High ♀	Gonads examination	
Boca Raton	USA	2013	May - July	65.0	♀	Gonads examination	
Sergipe	Brazil	1989-2014	Nov - Mar	95.6	High ♀	Incubation durations	Marcovaldi et al., 2016
Bahia	Brazil	1989-2014	Nov - Mar	93.4	High ♀		
Bahia (Praia do Forte)	Brazil	1989-2014	Nov - Mar	93.5	High ♀		
Bahia (Busca Vida)	Brazil	1989-2014	Nov - Mar	94.5	High ♀		
Espírito Santo	Brazil	1989-2014	Nov - Mar	58.9	-		
Espirito Santo (Povoação)	Brazil	1989-2014	Nov - Mar	53.8	-		
Espírito Santo (Comboios)	Brazil	1989-2014	Nov - Mar	57.2	-		
Rio de Janeiro	Brazil	2000-2014	Nov - Mar	45.2	♂		
Zakynthos (Gerakas)	Greece	1984-2002	May - Aug	~50.0	-	Incubation durations	Margaritoulis, 2005
Zakynthos (Sekania)	Greece	1984-2002	May - Aug	> 70.0	High ♀		
Zakynthos (Kalamaki)	Greece	1984-2002	May - Aug	> 70.0	High ♀		
Zakynthos (Daphni)	Greece	1984-2002	May - Aug	> 70.0	High ♀		
Zakynthos (East Laganas)	Greece	1984-2002	May - Aug	< 50.0	♂		
Zakynthos (Marathonisi)	Greece	1984-2002	May - Aug	< 40.0	♂		
Zakynthos	Greece	2002	May - Aug	68.0	♀	Incubation durations	Zbinden et al., 2007
Zakynthos	Greece	2003	May - Aug	75.0	High ♀		
Zakynthos (Marathonisi)	Greece	2002	May - Aug	2.0	♂		
Zakynthos (Marathonisi)	Greece	2003	May - Aug	23.0	High ♂		
Zakynthos (East Laganas)	Greece	2002	May - Aug	19.0	High ♂		
Zakynthos (East Laganas)	Greece	2003	May - Aug	24.0	High ♂		
Zakynthos (Sekania)	Greece	2002	May - Aug	87.0	High ♀		
Zakynthos (Sekania)	Greece	2003	May - Aug	84.0	High ♀		
Zakynthos (Daphni)	Greece	2002	May - Aug	~80.0	High ♀		
Zakynthos (Daphni)	Greece	2003	May - Aug	~90.0	High ♀		
Zakynthos (Kalamaki)	Greece	2002	May - Aug	~80.0	High ♀		
Zakynthos (Kalamaki)	Greece	2003	May - Aug	~99.9	High ♀		
Zakynthos (Gerakas)	Greece	2002	May - Aug	~70.0	High ♀		
Zakynthos (Gerakas)	Greece	2003	May - Aug	~85.0	High ♀		
Zakynthos	Greece	2007	May - Aug	77.0	High ♀	Incubation durations, dataloggers in nests and the sand at 40 cm	Katselidis et al., 2012
Zakynthos	Greece	2008	May - Aug	80.6	High ♀		
Zakynthos	Greece	2009	May - Aug	73.2	High ♀		
Zakynthos (Daphni)	Greece	2007-2009	May – Aug	> 90	High ♀		
Zakynthos (Sekania)	Greece	2007-2009	May – Aug	> 90	High ♀		
Zakynthos (Gerakas)	Greece	2007-2009	May - Aug	82.0 – 93.0	High ♀		
Zakynthos (Kalamaki)	Greece	2007-2009	May - Aug	51.0 – 82.0	♀		
Zakynthos (Marathonisi)	Greece	2007-2009	May - Aug	15.0 – 23.0	♂		
Zakynthos	Greece	1994-2010	May - Aug	59.5	-	Air temperatures	
Zakynthos	Greece	1875-2010	Aug	50.9	-		
Zakynthos (Gerakas)	Greece	2019	May - Aug	~ 77.9	High ♀	Dataloggers in nests	Papazekou et al., 2024
Zakynthos (Marathonisi)	Greece	2019	May - Aug	~ 23.8	High ♂		
Dalyan	Turkey	2010	May - Sept	61.0 – 69.3	♀	Dataloggers in nests	Sari and Kaska, 2015
North Cyprus and Dalyan	Cyprus and Turkey	1995	Jun - Aug	91.0	High ♀	Dataloggers in nests	Kaska et al., 1998
North Cyprus (Alagadi)	Cyprus	1993-1998	May - Aug	89.0 – 99.0	High ♀	Incubation durations	Godley et al., 2001
Cabo Verde	Cabo Verde	2012-2014	Jul – Nov	84.0	High ♀	Dataloggers in the sand at 40 cm	Tanner et al., 2019
Boa Vista	Cabo Verde	2012-2014	Jul - Nov	67.5	♀		
Maio	Cabo Verde	2012	Jul – Nov	93.9 – 99.9	High ♀		
Maio	Cabo Verde	2013	Jul - Nov	80.3 – 99.9	High ♀		

Maio	Cabo Verde	2014	Jul - Nov	90.8 – 99.9	High ♀		
Sal	Cabo Verde	2012	Jul - Nov	56.3 – 99.5	High ♀		
Sal	Cabo Verde	2013	Jul - Nov	99.1 – 99.8	High ♀		
Sal	Cabo Verde	2014	Jul - Nov	27.0 – 95.6	♀		
Santiago	Cabo Verde	2012	Jul - Nov	100.0	High ♀		
Santiago	Cabo Verde	2014	Jul - Nov	88.6 – 100.0	High ♀		
Fogo	Cabo Verde	2012	Jul – Nov	100.0	High ♀		
Santa Luzia	Cabo Verde	2014	Jul – Nov	83.8 – 99.4	High ♀		
São Nicolau	Cabo Verde	2012	Jul – Nov	99.8	High ♀		
São Nicolau	Cabo Verde	2014	Jul – Nov	95.7 – 100.0	High ♀		
São Vicente	Cabo Verde	2012	Jul – Nov	96.6 – 100.0	High ♀		
São Vicente	Cabo Verde	2013	Jul – Nov	91.2 – 98.3	High ♀		
São Vicente	Cabo Verde	2014	Jul – Nov	94.7 – 100.0	High ♀		
Boa Vista (Boa Esperança)	Cabo Verde	2012	Jul – Nov	34.4	♂		
Boa Vista (Boa Esperança)	Cabo Verde	2013	Jul – Nov	46.4	♂		
Boa Vista (Boa Esperança)	Cabo Verde	2013	Jul – Nov	2.2	♂		
Boa Vista (Lacacão, Varandinha)	Cabo Verde	2012	Jul – Nov	12.0	♂		
Boa Vista (Lacacão, Varandinha)	Cabo Verde	2013	Jul – Nov	9.3	♂		
Boa Vista (Lacacão, Varandinha)	Cabo Verde	2014	Jul – Nov	4.9 – 30.2	♂		
João Barrosa	Cabo Verde	2012	Jul – Nov	54.3	-		
João Barrosa	Cabo Verde	2013	Jul - Nov	86.6	High ♀		
João Barrosa	Cabo Verde	2014	Jul - Nov	77.2	High ♀		
East Boa Vista	Cabo Verde	2012	Jul - Nov	88.2 – 93.2	High ♀		
East Boa Vista	Cabo Verde	2014	Jul - Nov	35.9 – 80.1	♀		
Boa Vista	Cabo Verde	2005	Jul – Nov	98.3	High ♀		
Boa Vista	Cabo Verde	2006	Jul – Nov	91.8	High ♀		
Boa Vista	Cabo Verde	2007	Jul – Nov	40.2	♂		
Boa Vista	Cabo Verde	2008	Jul - Nov	93.1	High ♀		
North Boa vista	Cabo Verde	2005	Jul - Nov	90.0	High ♀		
North Boa Vista	Cabo Verde	2006	Jul - Nov	84.2	High ♀		
North Boa Vista	Cabo Verde	2007	Jul - Nov	31.4	♂		
North Boa Vista	Cabo Verde	2008	Jul - Nov	81.4	High ♀		
Northeast Boa Vista	Cabo Verde	2005	Jul - Nov	96.8	High ♀		
Northeast Boa Vista	Cabo Verde	2006	Jul - Nov	75.7	High ♀	Dataloggers in nests and air temperatures	Abella-Perez et al., 2016
Northeast Boa Vista	Cabo Verde	2007	Jul - Nov	24.2	♂		
Northeast Boa Vista	Cabo Verde	2008	Jul - Nov	71.0	High ♀		
Southwest Boa Vista	Cabo Verde	2005	Jul - Nov	98.7	High ♀		
Southwest Boa Vista	Cabo Verde	2006	Jul - Nov	93.3	High ♀		
Southwest Boa Vista	Cabo Verde	2007	Jul - Nov	40.9	♂		
Southwest Boa Vista	Cabo Verde	2008	Jul - Nov	96.2	High ♀		
Southeast Boa Vista	Cabo Verde	2005	Jul - Nov	99.5	High ♀		
Southeast Boa Vista	Cabo Verde	2006	Jul - Nov	95.7	High ♀		
Southeast Boa Vista	Cabo Verde	2007	Jul - Nov	44.5	♂		
Southeast Boa Vista	Cabo Verde	2008	Jul - Nov	98.3	High ♀		

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