Using Species Distribution Modeling to Enhance the Detection of an Invasive Soft Coral in Hawai‘i

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Data Availability

The code used in this study is publicly available on GitHub at: https://github.com/krtanaka-NOAA/Unomia_Maxent

All data used in this publication are open-access and were obtained from the Ocean Biodiversity Information System (OBIS), the Global Biodiversity Information Facility (GBIF), and Bio-ORACLE. All information tabulated and graphed in this publication are nonconfidential and are available from the authors upon request.

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Table of Contents

List of Tables

List of Figures

Executive Summary

Introductions of non-native and invasive species are occurring at accelerating rates globally, posing major threats to the maintenance of native ecosystem functioning and services. Despite these impacts, invasive species remain underrepresented in coral reef management, which is especially problematic given that ports represent main vectors of introduction. Therefore, marine tropical regions with high vessel traffic, like the main Hawaiian Islands, face elevated risks of biological introductions.

In the main Hawaiian Islands, specifically on O‘ahu, Pearl Harbor (Pu‘uloa) is an important maritime port due to its strategic geographic location, comprehensive infrastructure, and critical role as a U.S. naval base. The waters of Pu‘uloa are known to harbor several non-native species, from mangroves to corals and fishes. Among these, the pulsing soft coral *Unomia stolonifera* was discovered in 2020 and has rapidly spread within the harbor, threatening native reef communities. This coral is particularly concerning if secondary spread occurs to other parts of O‘ahu and other islands due to Hawai‘i’s ecological vulnerability, geographic isolation, and high rates of endemicity. Therefore, enhancing early detection and rapid response (EDRR) of *U. stolonifera* is critical.

In response to this need, we deployed an ensemble species distribution model (SDM) combined with a Getis-Ord (also known as Gi*) spatial hotspot analysis to map habitat suitability of *U. stolonifera* and identify potential high-risk areas. Our modeling effort revealed the presence of 18 predicted hotspots spread across O‘ahu, Kaua‘i, and Hawai‘i Island. This pattern is indicative of potential secondary dispersal, which is further supported by the role of ports as a significant driver of its habitat suitability.

Out of those 18 hotposts, 12 were located on O‘ahu. To further prioritize areas for management, we ranked the hotspots by the extent of surveyable benthic area, ranging from 0 to 30 meters. While our results indicated the presence of 2 hotspots located in Pu‘uloa (confirming the harbor’s role in the introduction and retention of *U. stolonifera*), 7 more were found outside the harbor toward Barber’s Point (Kalaeloa) and Waikiki-Diamond Head (Lē‘ahi), indicating potential secondary dispersal caused by the prevailing East-West currents.

Additionally, 3 hotspots were predicted in Kāne‘ohe Bay, overlapping with areas containing existing non-native macroalgal incursions, signaling potential additive ecological pressures. By identifying specific hotspots and refining them with their associated surveyable area, our SDM-based framework can help Hawai‘i’s Division of Aquatic Resources to apply EDRR efforts more effectively and guide them toward geographically-focused citizen science and local partnerships while continuing cooperation with the Department of Defense in regard to eradication efforts.

Introduction

Invasive background

Biological invasions are an increasingly major global threat to the functioning of ecosystems today (Levine, 2008; Roy et al., 2024). While most non-native species have neutral or benign impacts, smaller subsets can cause significant ecological and economic harm (Levine, 2008). They are responsible for 60% of documented extinctions in all ecosystems and incurring global economic costs exceeding US$ 423 billion in 2019 (Roy et al., 2024). These harmful species are termed “invasive” and often characterized as fast-growing generalist organisms capable of rapid establishment and spread (Levine, 2008; Walther et al., 2009).

Through mechanisms such as predation, competition, and habitat modification, invasive species can displace native taxa and alter community structure, often leading to ecological homogenization and a subsequent reduction in ecosystem functions and resilience (Levine, 2008; Molnar et al., 2008; Roy et al., 2024). Despite these impacts, invasive species remain underrepresented in management priorities compared to other marine stressors such as pollution and overfishing (Alidoost et al., 2021).

Case study background

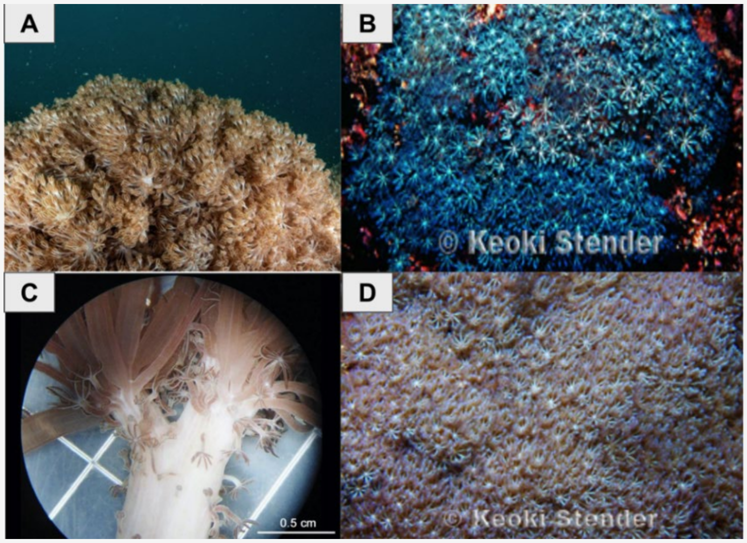

Figure 1. (A) Image of *Unomia stolonifera* in the field, and (C) a close-up on its stalks with the presence of multiple polyps: a unique characteristic of this species (Benayahu et al. 2021). (B & D) Images of *Sarcothelia edmonsoni*, the only native soft coral species in Hawaiʻi, which differs in terms of colors and stalk length. Photos by DLNR (A), Reef Builders (C), and Keoki Stender (B, D).

Unomia stolonifera (Gohar, 1938) is a soft bodied octocoral from the family Xeniidae (Octocorallia, Alcyonacea), formerly known *Cespitularia stolonifera* (Benayahu et al., 2021); it is commonly misidentified as *Xenia* spp. It is distinguished by polyps with eight pulsating tentacles (pink to orange-brown) and additional dispersed polyps along the stalks, unlike other xeniids whose polyps cluster at the stalk tips. (Benayahu et al., 2021; Bolick & Lee 2023). This species inhabits tropical waters at depths varying from 0 meters (m) to 60 m—the deepest depth recorded so far (Ruiz-Allais et al., 2021).

Native to the Western Indo-Pacific, specifically Sulawesi (Indonesia), *U. stolonifera* was introduced to northern Venezuela in 2007 via aquarium release, and spread to other Caribbean nations such as Cuba in 2023 (Bolick & Lee 2023, Ruiz-Allais et al., 2021). In the Pacific, this pulsing coral was introduced to Hawaiʻi in 2020 potentially through the same mechanism. Hawaiʻi only has 1 native soft coral species, *Sarcothelia edmondsoni*, which can be easily distinguished from *U. stolonifera* by differences in stalk morphology and colony color (Figure 1B & 1D), thus reducing the risk of misidentification.

The wide geographic establishment of *U. stolonifera* to new environments is driven by several factors. This species can reproduce both sexually (via propagules) and asexually (via fragmentations), allowing it to rapidly establish new individuals from a single parent. This leads to fast population growth and expansion (Ruiz-Allais et al., 2014). *U. stolonifera* is also capable of settling over diverse substrates, including rock bottoms, sand, and seagrass beds, potentially making it a ubiquitous organism in shallow coastal habitats (Ruiz-Allais et al., 2014).

Likewise, this species can attach to boats and other floating objects (*e.g.*, fishing derelicts) or even highjack organisms such as cone snails (Hayes, 2023), further expanding its spread. Lastly, although corallivores (*e.g.*, butterflyfish and aeolid nudibranchs) have been posited to prey upon *U. stolonifera* and potentially assist in controlling its population, there is no evidence of these natural predators in invaded regions such as Venezuela (Ruiz-Allais et al., 2021). These biological traits contribute to *U. stolonifera's* successful establishment in tropical marine coastal ecosystems in both the Caribbean and central Pacific, posing threats to native benthic communities and ecosystem biodiversity.

Spread in Hawaiʻi

The main Hawaiian Islands host major maritime hubs for the state of Hawaiʻi, U.S. and the broader Pacific region, supporting high volumes of commercial and military shipping traffic (De La Cruz, 2010). Ports and shorelines have long been recognized as introduction points for non-native species (Seebens et al., 2023). Consequently, these islands face elevated risks of marine biological invasions through ballast water discharge and hull fouling (Godwin, 2003).

In O‘ahu, Pearl Harbor (Pu‘uola) is a main military port where several non-native and invasive species have been recorded (Bolick and Lee, 2023). Among these species is *U. stolonifera*, which was first detected in 2020 with a coverage of 20 acres. It is now estimated to cover 80–100 acres (Jacobs, 2025). This 4 to 5-fold expansion in 5 years has prompted containment efforts by the Department of Defense. However, the potential for spread beyond the harbor remains a concern, posing significant ecological risks by rapidly outcompeting native species, altering community composition, and decreasing biodiversity.

Leveraging species distribution models for early detection

The confirmed presence of *U. stolonifera* in Pu‘uloa highlights the need for enhanced monitoring efforts given the species’ recent introduction and potential for rapid spread outside its entry point. Effective and timely invasive species management in the main Hawaiian Islands is particularly critical due to the island’s geographical isolation, high levels of endemic biodiversity, and ecological vulnerability (Manes et al., 2021; Monaco et al., 2012).

This study applies a species distribution modeling (SDM) approach to predict habitat suitability of *U. stolonifera* in Hawai‘i. SDMs are valuable tools for supporting early detection and rapid response (EDRR) frameworks (Reaser et al., 2020; Srivastava et al., 2019) by identifying areas most susceptible to establishment, thereby enhancing spatially targeted conservation and management strategies aimed at limiting further spread (Barbet-Massin, et al., 2018).

Methods

Study area

We specifically focus on shallow coastal waters (extending ~5 km offshore) of the main Hawaiian Islands, which is part of the most geographically isolated archipelago, harboring a very high degree of endemicity and high habitat modification (Friedlander et al., 2005; Monaco et al., 2012).

Species occurrence data

We gathered 31 global georeferenced presence records of *U. stolonifera* from 2 open-source databases: Global Biodiversity Information Facility (GBIF) (gbif.org, 2024) and United States Geological Survey (USGS) (Reaver, 2025). A total of 29 records were from GBIF spanning from 1994 to 2024, while 2 were from USGS recorded in 2023 (Table 1). Local records from Hawai‘i were limited to Pu‘uloa in O‘ahu and, therefore, were insufficient to calibrate a SDM with reliable predictive performance. Due to this, additional global records were utilized to better define the range of environmental conditions where *U. stolonifera* has been observed, providing a stronger empirical foundation for modelling. After combining the 2 datasets, we removed duplicate records and records that lacked coordinates (latitude and longitude).

Table 1. Total number of georeferenced occurrence records of *Unomia stolonifera* with the associated country and year observed. Obtained from 2 open-access databases: GBIF (Global Biodiversity Information Facility) and USGS (United States Geological Survey).

Countries with Records	Years	Occurrence Records	Data Source
Venezuela	2013, 2017, 2021, 2022, 2023	14	GBIF
Philippines	2022	8	GBIF
Indonesia	1994, 2023, 2024	5	GBIF
United States (Pearl Harbor, O‘ahu, Hawai‘i)	2023	2	USGS
Cuba	2023	1	GBIF
Republic of China (Taiwan)	N/A	1	GBIF

Environmental data layers

To model the habitat suitability of *U. stolonifera*, we compiled environmental variables known to influence the physiology, dispersal, and establishment of sessile marine invertebrates. Eighty-five pre-screened parameters were used from Bio-ORACLE, a publicly available database hosting marine environmental dataset and geospatial layers at ~0.05 degrees (~5.6 km at the equator) (Tyberghein et al., 2012).

From these parameters, we narrowed down their numbers and grouped them across 4 thematic categories: (1) ocean conditions (temperature, salinity, seawater speed, mixed layer depth, and seawater direction), (2) nutrient concentrations (nitrate, chlorophyll, phosphate, and pH), (3) atmospheric and light variables (mixed layer depth), and (4) topographic features (slope, aspect, topographic position index, and bathymetry). To account for potential anthropogenic vectors of non-native species spread, we incorporated gridded layers of distance from ports from Global Fishing Watch (Welch et al., 2024). All variables represent long term baseline conditions spanning from 2000–2020.

Lastly, we performed a variance inflation factor (VIF) to test for multicollinearity amongst the selected predictor variables using a variance inflation factor (VIF ≤ 3). This avoids high correlation amongst variables and the inflation of permutation importance. Thus, we could accurately assess the individual influence of each predictor variable on the predicted distribution of *U. Stolonifera*.

Table 2. Environmental and anthropogenic predictor variables used for species distribution modeling and associated ecological relevance.

Variable (units)	**Summary Statistic/Descriptor (VIF)**	**Ecological Relevance**
Bathymetry (m)	Minimum (1.53)	Sessile organisms like corals inhabit shallower depths due to light availability, water temperature, pressure, and the energy of waves and currents (Goodman et al., 2020; Pittman et al., 2009).
Seawater Speed (m.s-1)	Maximum (2.66) Minimum (2.4) Range (1.7)	High speeds of water currents can impact nutrient and larval dispersal or be a source of physical stress and make anchoring onto substrates more difficult (Burrage, 1993; Graus et al., 1977).
Salinity (ppt)	Range (2.1) Maximum (2.05)	Important for water density and osmotic regulation. Large ranges or high levels of salinity can cause stress in corals (Coles & Jokiel, 1992; Moberg et al., 1997).

Variable (units)	**Summary Statistic/Descriptor (VIF)**	**Ecological Relevance**
pH	Average (2.16)	Corals are highly sensitive to pH levels. Acidic conditions can cause stress in organisms (Brownlee, 2009; Chan et al., 2016; Marubini & Atkinson, 1999).
Slope (°)	(1.48)	High slope reduces sediment stress and creates microhabitats sheltered for corals from strong currents (Faure, 1977; Sheppard, 1982).
Aspect (°)	(1.07)	Affects feeding efficiency, exposure to disturbance, and light availability (Faure, 1977; Sheppard, 1982).
Nitrate (ppm)	Range (2.24)	Variability can negatively influence food supply through plankton abundance and potentially affects symbiotic algal-coral dynamics, causing nutrient stress (Fernandes de Barros Marangoni et al., 2020).
Phosphate (mmol. m-3)	Range (1.96)	Large ranges can indicate unstable conditions, impacting tissue growth or lead to eutrophic conditions (Rosset et al., 2017).
Ocean Temperature (°C)	Maximum (1.55) Range (1.83)	Maximum temperatures that exceed a coral's tolerance threshold can lead to bleaching or disease. A wide range in temperature can cause stress to tropical organisms such as corals that thrive in stable conditions (Chavanich et al., 2009; Zeevi-Ben-Yosef & Benayahu, 2008).
Sea Water Direction (°)	Maximum (2.08) Minimum (1.45) Average (2.56)	Impacts direction of nutrient flow and larval dispersal (Maida et al., 1995; Sebens & Johnson, 1991).
Mixed Layer Depth (m)	Minimum (1.33) Range (1.68)	Important for nutrient availability and the distribution of light. A wide range can indicate a variable environment with changing access to resources while a narrow range indicates low access (Jaffrés, 2013; Mackey et al., 1987).
Chlorophyll (mg m-3)	Minimum (1.98)	Minimum chlorophyll values can represent a seasonal low point in primary productivity, indicating the stability of a food web (Fabricius et al., 1998)
Topographic Position Index	(1.25)	Indicator of marine ecosystem complexity, as rocky or coral seabed structures form habitats, and can create shelter from hazards such as

Variable (units)	**Summary Statistic/Descriptor (VIF)**	**Ecological Relevance**
		strong currents and erosion (Sous et al., 2024).
Distance From Port (km)	(1.17)	A close distance to a port can indicate higher levels of vessel traffic and the potential for the introduction of non-native species (Bax et al., 2003).

Ensemble species distribution model parameterization

We implemented the maximum entropy (MaxEnt) algorithm to model the habitat suitability of *U. stolonifera*, as it is well suited for presence-only data and robust to limited occurrence records. MaxEnt estimates a probability distribution of maximum entropy constrained by environmental conditions at known presence locations (Phillips et al., 2006). Its robustness to incomplete or spatially biased sampling enhances its applicability for species with sparse or patchy records, such as *U. stolonifera* (31 records in total) (Elith & Leathwick, 2009; Phillips et al., 2006).

To account for the lack of true absence data, we generated 10,000 background (pseudo-absence) points, following Phillips & Dudík (2008). Background sampling was restricted to tropical marine regions (23.5°N to 23.5°S) to align with the species' known biogeographic range. To further limit ecological bias, we confined background selection to nearshore environments using a buffer defined by multiplying the minimum depth associated with presence records (within a 5 km BIO-ORACLE grid cell) by 1.5, thereby excluding deep or pelagic zones unlikely to represent viable habitat.

To optimize model performance and minimize overfitting, we used the ENMevaluate package in R (Muscarella et al., 2014) to systematically test 30 combinations of feature classes and regularization multipliers (RM = 1–5). Feature classes define the types of mathematical relationships used to model the relationship between species occurrence and environmental predictors. We tested the following feature classes: L (linear), Q (quadratic), H (hinge), P (product), T (threshold) and their combinations (*e.g.*, LQ, LQH, LQHP, LQHPT).

Regularization multipliers serve as a penalty to prevent model overfitting. A higher RM value results in a simpler, more generalized model. By evaluating different combinations, we identified an optimal balance between model complexity and generalizability.

Each model was evaluated using jackknife cross-validation, with k equal to the number of occurrence localities (Shcheglovitova & Anderson, 2013). This method is recommended for sparse datasets as it improves prediction reliability (Shcheglovitova & Anderson, 2013). By testing different combinations of both, we were able to find the optimal balance between model complexity and generalizability.

We implemented an ensemble modeling approach to increase predictive robustness and account for variability across model parameterizations. We averaged predictions from the top 3 performing models, reducing single-model bias (Harris et al., 2024; Jones-Farrand et al., 2011). Predictive performance was assessed using the Area Under the Receiver Operating Characteristic Curve (AUC) (Phillips et al., 2006), which measures the ability to distinguish presence from background points. Model complexity and parsimony were evaluated using the Akaike Information Criterion corrected for small sample sizes (AICc). Model accuracy was further assessed using the 10% training omission rate (OR10), which measures the proportion of known presence points incorrectly predicted as absent using a 10% omission threshold. Predictor variable importance was evaluated using MaxEnt's permutation importance analysis. This approach quantifies each predictor's contribution by permuting its values among presence and background points, then calculating the decrease in model performance (AUC). Higher values indicate stronger influence on the model.

A habitat suitability map was generated by averaging predictions across ensemble models. To quantify uncertainty, we calculated the standard deviation of predicted values across models at each grid cell where a higher standard deviation indicates a greater disagreement among models, thus, higher uncertainty (Araújo & New, 2007; Woodman et al., 2019).

For final analysis, we generated a weighted habitat suitability map by penalizing areas of high uncertainty. For each grid cell, the final suitability score (S') was calculated as the mean predicted suitability (S) minus the standard deviation (σ), such that: $S' = S - \sigma$. This conservative approach emphasizes areas with high predicted suitability and low inter-model variability, improving confidence in spatial prioritization.

Predicted habitat suitability spatial hotspots

To identify statistically significant clusters of high habitat suitability, we applied the Getis-Ord Gi* statistics (Ord & Getis, 1995). This spatial analysis used a *k*-nearest neighbor approach with $k=8$, selected to detect localized clustering patterns within the spatial resolution of the prediction grid. Grid cells with absolute *z*-scores ≥ 2.58 (corresponding to $p \leq 0.01$) were classified as statistically significant hotspots (Jana & Sar, 2016). These cells represent areas where high suitability values are not randomly distributed, but instead form consistent spatial clusters. This threshold ensures a high level of statistical confidence in identifying hotspots of predicted *U. stolonifera* habitat suitability around Hawai‘i.

Prioritizing monitoring of hotspots on O‘ahu

We developed a prioritization of hotspots specifically in O‘ahu because *U. stolonifera* has been confirmed on O‘ahu. We developed a model guided prioritization by ranking habitat suitability hotspots based on a quantifiable metric: total surveyable area. We employed high-resolution bathymetry at a 9 m spatial resolution (Amante et al., 2023), clipped to depths between 0 and 30 m around O‘ahu to reflect standard survey depths conducted by local survey programs (e.g., NOAA Fisheries’ Pacific Islands Fisheries Science Center) (Heenan et al., 2017).

To calculate the total surveyable area within each 5 km × 5 km hotspot grid cell (identified via Gi* analysis), we overlaid these hotspots onto the bathymetry grid and calculated the total number of 9 m x 9 m (81 m^2) cells within the target depth range inside each hotspot. The total surveyable area per hotspot was then derived by summing the area of all qualifying cells. Hotspots with the greatest amount of total surveyable area were ranked highest for management prioritization.

Results

Ensemble maximum entropy output

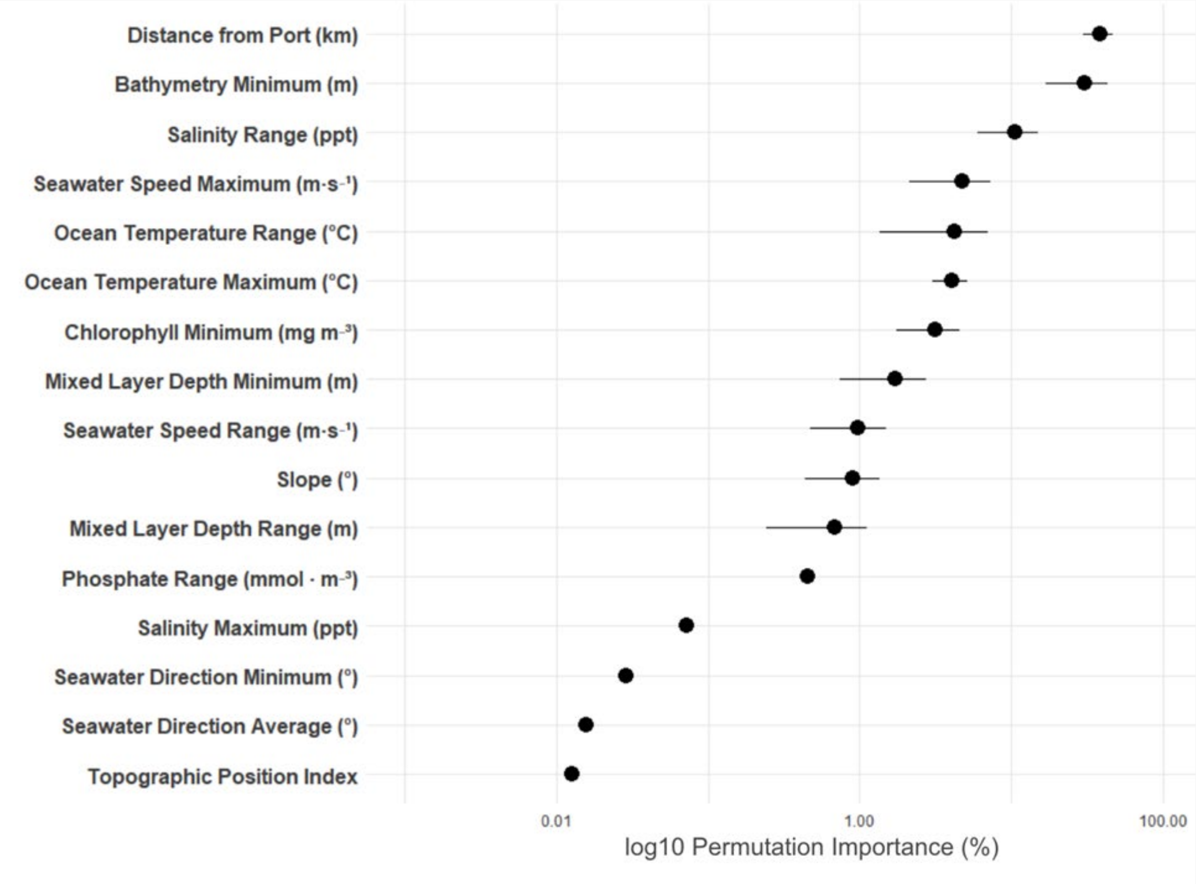

Figure 2. Log_{10} transformed mean permutation importance (%) of the predictor variables contributing to the habitat suitability model for *Unomia stolonifera*. Values represent averages across the top three models in the ensemble; error bars indicate standard error.

The permutation importance analysis identified distance from port (km), bathymetry minimum (m), and salinity range (ppt) as the top 3 predictors contributing most to habitat suitability of *U. stolonifera* in Hawai‘i (Figure 2). Other influential variables included seawater speed maximum ($m \cdot s^{-1}$), ocean temperature range (°C), ocean temperature maximum (°C), and chlorophyll minimum ($mg\ m^{-3}$). Lower-ranked variables such as seawater direction minimum (°), seawater direction average (°), and topographic position index showed minimal influence on model predictions (Figure 2).

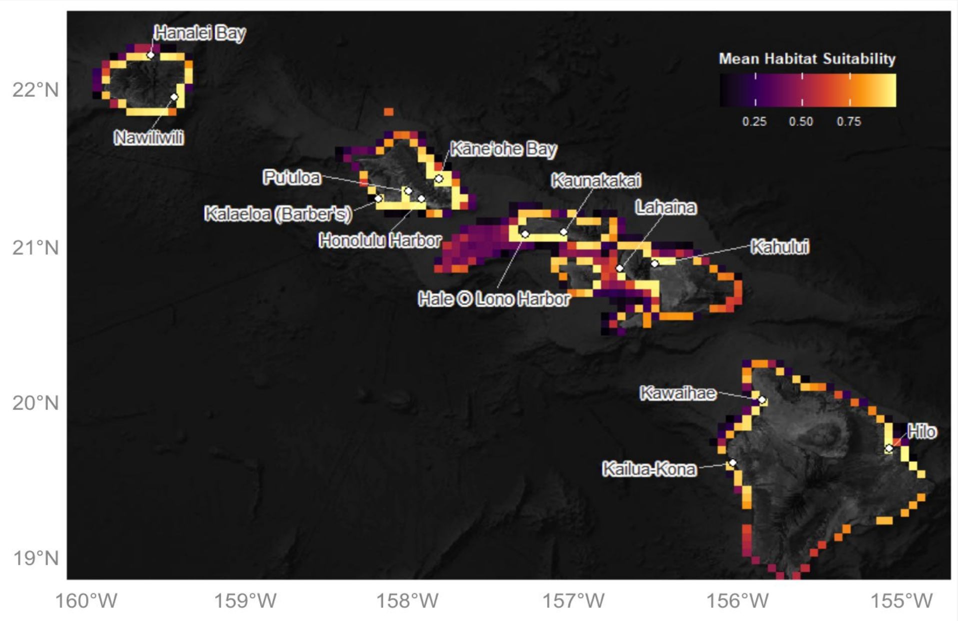

Figure 3. Mean predicted habitat suitability for *Unomia stolonifera* across the main Hawaiian Islands based on the ensemble Maximum entropy model output. Lighter colors in the suitability map indicate areas of higher predicted suitability. Labels indicate major ports.

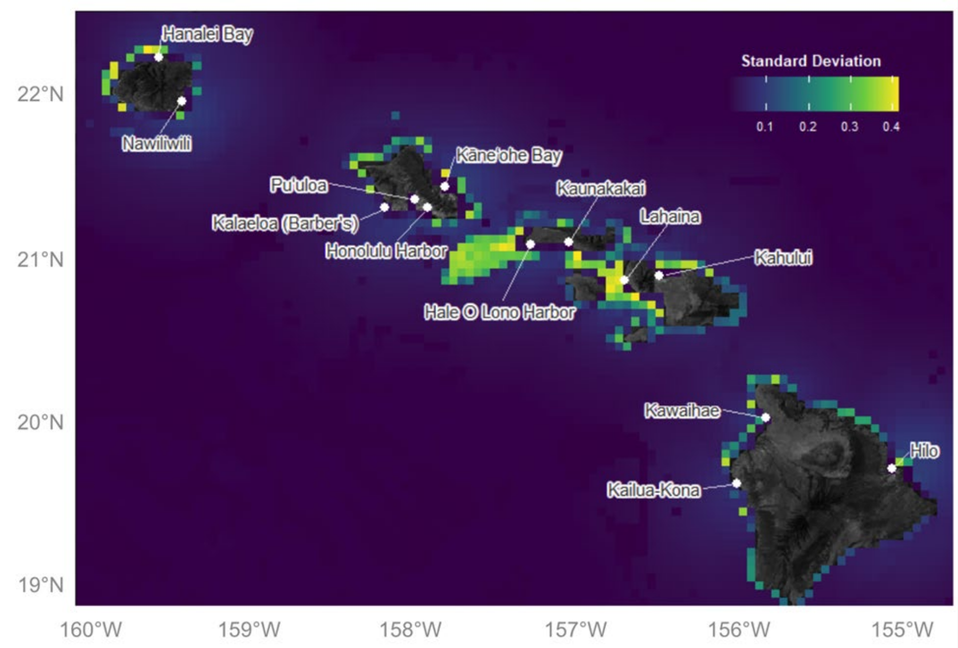

Figure 4. Standard deviation of the mean predicted habitat suitability predictions for *Unomia stolonifera* across the main Hawaiian Islands based on the ensemble maximum entropy model output. Lighter colors represent greater standard deviation or uncertainty across the ensemble. Labels indicate major ports.

Our ensemble MaxEnt models achieved high discriminatory performance with mean AUC of 0.974 ± 0.002, indicating strong discrimination between presence locations and background points. The mean habitat suitability showed distinct spatial gradients across the main Hawaiian Islands (Figure 3). High predicted suitability areas (0.60–1.00) were concentrated along the south, east, and north shores of Kauaʻi, the south and east shores of Oʻahu, all around Molokaʻi and Lānaʻi, along with patches spread in Maui and the Island of Hawaiʻi. Major ports in Hawaiʻi—such as Kauaʻi's Hanalei Bay and Nawiliwili, Oʻahu's Honolulu Harbor, Kalaeloa (Barber's Point), Puʻuloa, and Kāneʻohe Bay, Molokaʻi's Hale O Lono Harbor and Kaunakakai, Maui's Kahului and Lahaina, and Hawaiʻi Island's Hilo, Kawaihae, and Kailua-Kona—are in or near areas of high habitat suitability.

The standard deviation map highlights model uncertainty across grid cells. Areas with high standard deviation (0.3–0.4) are seen scattered across the islands, with concentrations off the East coasts of Molokaʻi and Maui.

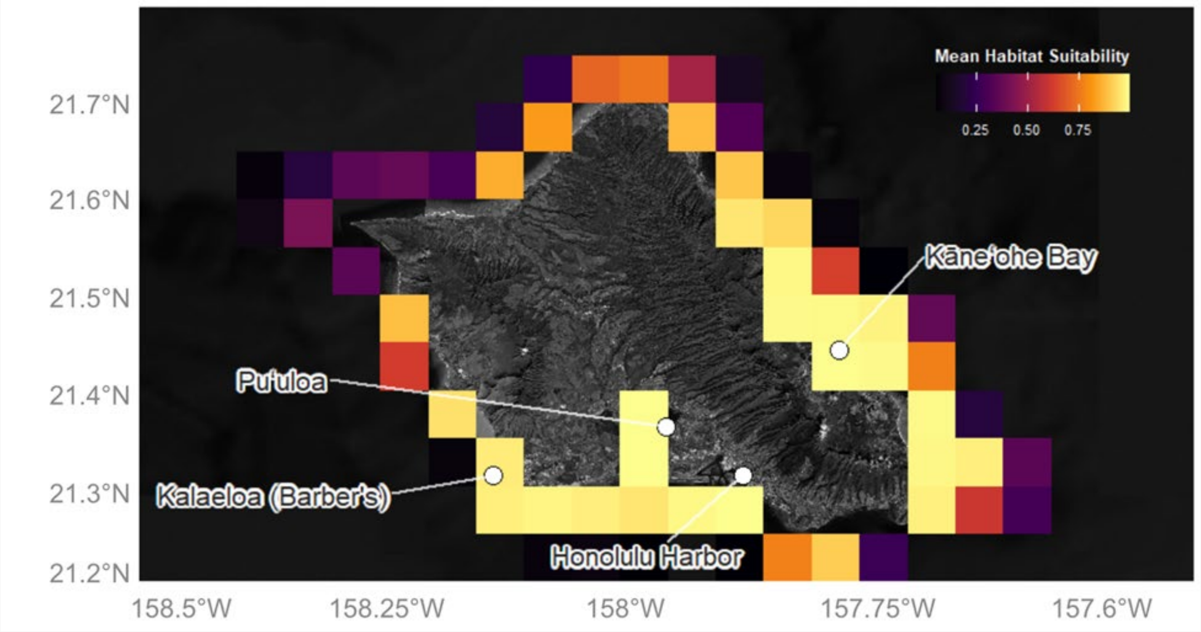

Figure 5. Mean predicted habitat suitability for *Unomia stolonifera* in Oʻahu based on the ensemble maximum entropy model output. Lighter colors in the habitat suitability map indicate higher predicted suitability. Labels indicate major ports.

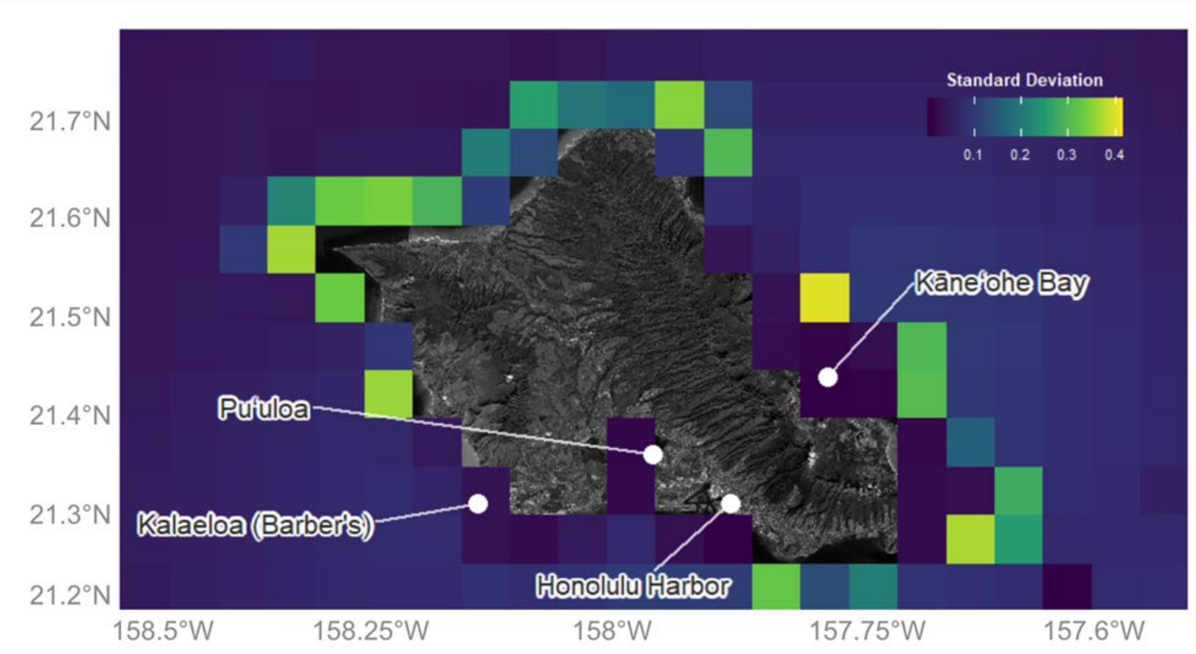

Figure 6. Standard deviation of the mean predicted habitat suitability predictions for *Unomia stolonifera* in Oʻahu based on the ensemble maximum entropy model output. Lighter colors represent greater standard deviation or uncertainty across the ensemble. Labels indicate major ports.

The mean habitat suitability map of Oʻahu showed spatial gradients across the coastline. High predicted suitability areas (0.60–1.00) were concentrated in the south shore and east shore. Oʻahu's major ports (Honolulu Harbor, Kalaeloa (Barber's Point), Puʻuloa, and Kāneʻohe Bay) are all located in high suitability grid cells. Low suitability areas (0.00–0.40) were scattered throughout the coasts, seen in grid cells further off shore and most concentrated across the entirety of North Shore. High standard deviation areas (0.30–0.40) were seen scattered across the island but most concentrated in the North Shore. Low standard error (0.00–0.20) were concentrated across the south and east shores. Low standard deviation scores were overlapped with areas of high habitat suitability and major ports.

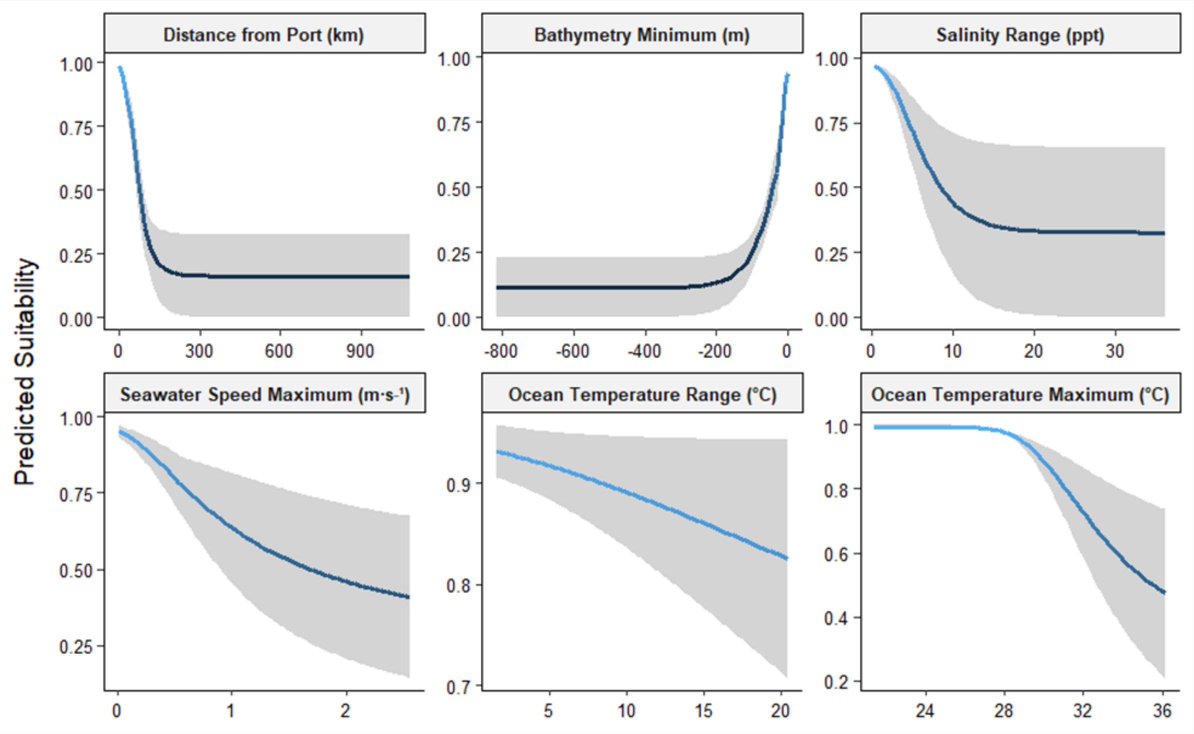

Figure 7. Partial dependence plots from the ensemble maximum entropy model showing the effect of 6 top-ranked predictor variables on the predicted habitat suitability of *Unomia stolonifera*. Curves represent mean response, with predicted suitability on the y-axis and each variable's range on the x-axis. Grey zones around the curves represent the standard deviation between models. Variables include distance from port, bathymetry, salinity, current speed, and ocean temperature.

Partial dependence plots illustrate how the 6 top-ranked environmental predictor variables (Figure 7) influence the modeled habitat suitability of *U. stolonifera* (Figure 3). Suitability declined steeply with increasing distance from port up to about 100 km, then remained low, indicating a higher likelihood of establishment near human activities and lower likelihood in remote areas. *U. stolonifera* showed a strong preference for shallow habitats, increasing sharply with minimum bathymetry from approximately -100 m towards 0 m.

Environmental variability also played a key role as suitability decreased with increasing salinity range, indicating sensitivity to environments with greater physicochemical fluctuation. Similarly, suitability declined with both increasing seawater speed maximum and greater ocean temperature range, suggesting limited tolerance for high hydrodynamic energy and a preference for thermally stable conditions. Suitability remained high across lower ocean temperatures but began to decline notably above approximately 28°C, suggesting a potential thermal maximum tolerance.

Predicted habitat suitability spatial hotspots and surveyable area

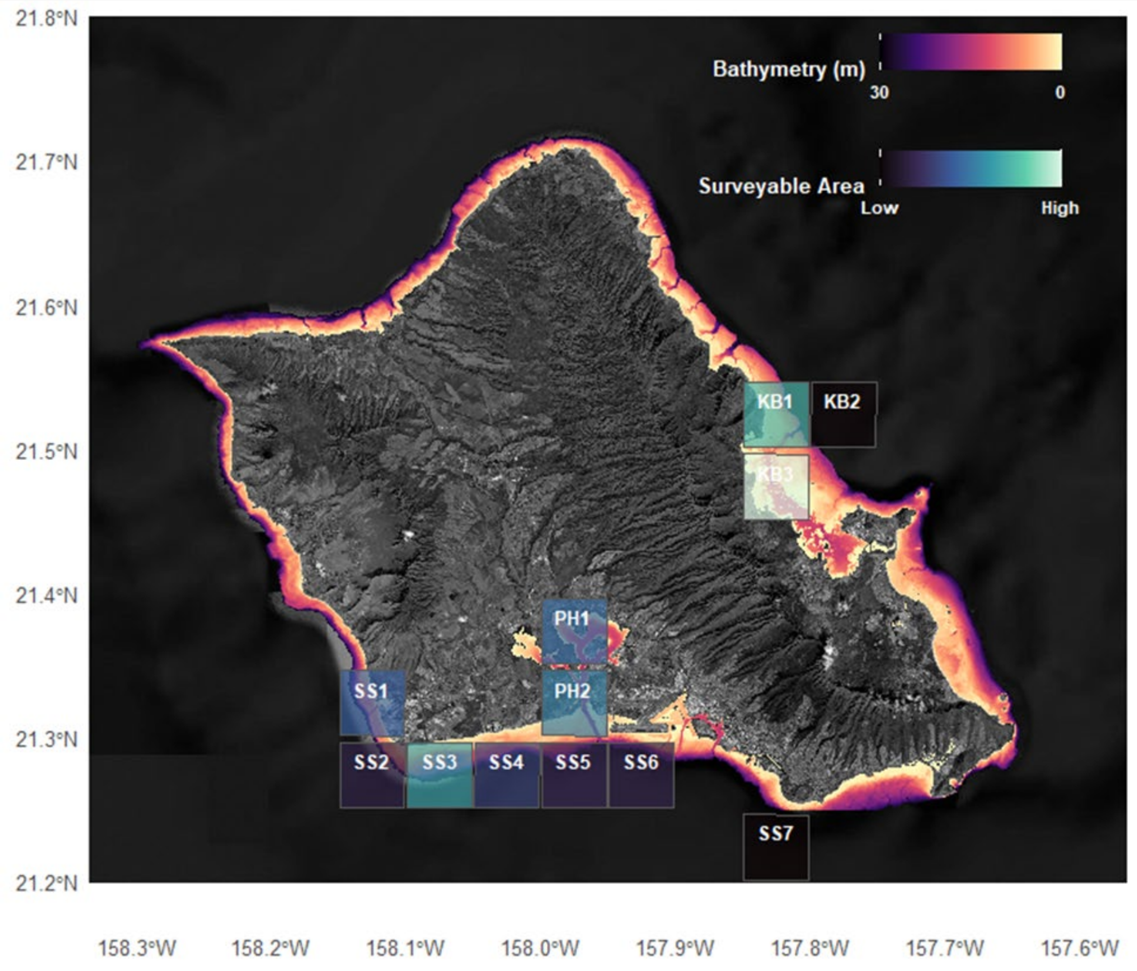

Figure 8. Spatial hotspots of predicted *Unomia stolonifera* habitat suitability on Oʻahu, shown at a 5 km × 5 km grid resolution. Twelve hotspots were identified using the Getis-Ord Gi* statistics (k = 8 nearest neighbors) and are grouped into 3 regions: Puʻuloa (PH1, PH2), south shore (SS1–SS7), and Kāneʻohe Bay (KB1–KB3). Bathymetry is represented by a yellow-to-purple gradient, indicating depths from 0 to 30 m. Grid cells are colored by total surveyable benthic area (0–30 m depth), with lighter blue indicating a greater amount of area suitable for diving-based monitoring.

Eighteen spatial hotspots of high predicted habitat suitability for *U. stolonifera* were identified in the main Hawaiian Islands, with 3 in Kauaʻi, 12 in Oʻahu, and 3 in Hawaiʻi Island. These were identified as having statistically significant high predicted habitat suitability from the Getis-Ord GI* statistics with a z-score threshold of ≥2.58 (Figure 6 & Table 2).

Due to confirmed occurrence records in Oʻahu, further hotspot analysis and ranking was conducted on the island's 12 hotspots. Hotspots were ranked by the total surveyable benthic area, prioritizing regions most accessible for diving-based monitoring. These hotspots were concentrated along the South and East Shores of the island. Seven of the 12 hotspots were found in the south shore (SS1, SS2, SS3, SS4, SS5, SS6, and SS7), 2 were found in Puʻuloa (PH1 and PH2), and a cluster of 3 hotspots were located along the east shore, concentrated in Kāneʻohe Bay (KB1, KB2, and KB3).

Discussion

With non-native species being introduced at accelerating global rates (Seebens et al., 2023), understanding their biogeography is critical for conserving biodiversity, especially in vulnerable systems such as remote oceanic islands (Manes et al., 2021; Monaco et al., 2012). This is particularly critical for Hawai‘i, which harbors a high degree of endemicity yet faces heightened anthropogenic disturbance, making it susceptible to biological introductions (Monaco et al., 2012).

Native species displacement by introduced species can occur rapidly (Fitzpatrick et al., 2010), often outpacing management responses. Moreover, resource and time constraints (Thompson et al., 2025; Hauser & McCarthy, 2009) along with environmental connectivity further complicates monitoring and control, especially in marine ecosystems where survey logistics are challenging (Clements et al., 2021; Giakoumi et al., 2019). In these contexts, SDMs can guide prioritization of early detection and rapid response (EDRR) (Mandrak & Cudmore, 2015; Sepulveda et al., 2023), reducing the likelihood of costly eradication campaigns (Cariton & Geller, 1993; Reaser et al., 2020).

While capable of providing useful habitat suitability maps of non-native species, SDMs are subject to data-driven limitations such as limited data-availability, sampling bias, and false taxonomic identification (Benavides Rios et al., 2024; Lomba et al., 2010; Syfert et al., 2013). These limitations can be challenging for species with few occurrences such as *U. stolonifera* (Brenier et al., 2015; Lomba et al., 2010).

Other challenges that often limit habitat suitability predictions relate to fundamental difficulties in measuring and parameterizing biotic complexities in species dispersal and settling capabilities, species interactions (e.g., predation, competition, mutualism, and commensalism), and phenotypic plasticity or local adaptation Benito Garzón et al., 2019; Camarota et al., 2016; Gaya & Chandler, 2024; Godsoe & Harmon, 2012). Despite these limitations, SDMs remain an effective and practical tool for assessing broad biogeographical trends and guiding invasive species management decisions.

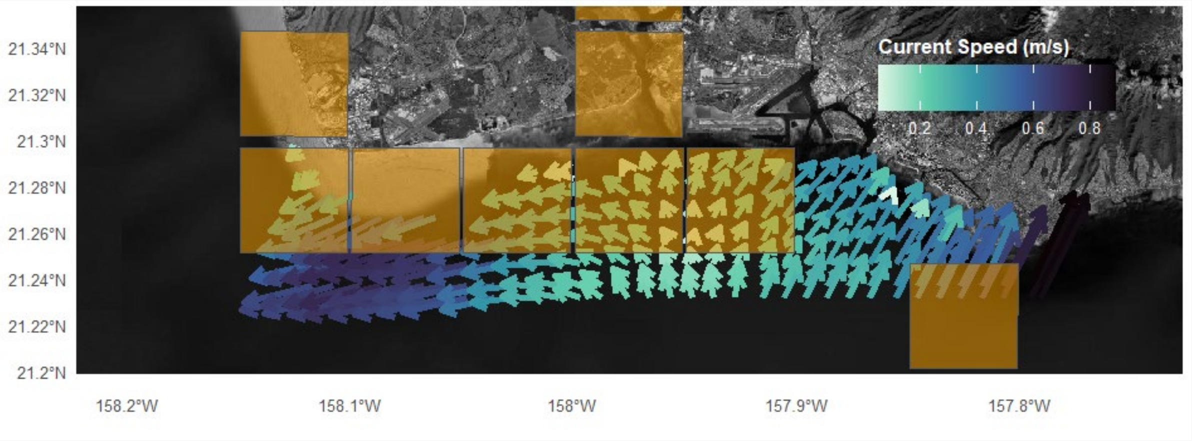

Figure 9. Map of ocean currents on the South Shore of O‘ahu. Arrows indicate the direction and speed of the current, with both arrow length and color corresponding to current speed (m/s); darker blue color represents higher current speeds. Ocean current data were obtained from the PacIOOS South Shore ROMS model, downloaded via the PacIOOS ERDDAP data server, accessed 26/08/2025. Orange squares are predicted habitat suitability hotspots for *Unomia stolonifera* are overlaid on the ocean currents.

Knowing some of the caveats, we modeled the potential distribution of *U. stolonifera* across the main Hawaiian Islands because this xeniid has overgrown native benthic taxa in Venezuelan reefs, reaching 30–80% cover in introduced sites (Ruiz-Allais et al., 2021). Using an ensemble SDM approach and Getis-Ord Gi* spatial statistics, we identified 18 spatial hotspots of predicted habitat suitability across the main Hawaiian Islands.

In O‘ahu, the hotspots were majoritarily concentrated in Pu‘uloa, the south shore (just west-east of Pu‘uloa), and Kāne‘ohe Bay. The presence of 2 hotspots within Pu‘uloa provide further local evidence that this harbor might remain not only as an entry point for *U. stolonifera* but also a potential reservoir for propagules to disperse. Seven additional hotspots were identified just outside the harbor along the south shoreline, potentially indicative of further spread east and west of the south shore via prevailing currents (Figure 7). Lastly, 3 hotspots were detected in Kāne‘ohe Bay on the East Shore, where the invasive macroalgae *Dictyosphaeria cavernosa*, *Eucheuma denticulatum*, *Gracilaria salicornia*, and *Kappaphycus spp.*, have already established and caused negative impacts on native benthic communities (Stimson et al., 2001; Stimson & Larned, 2021; Winston et al., 2023).

These biological pressures suggest that the potential introduction of *U. Stolonifera* may exacerbate the decline of native communities, reducing overall biodiversity. Furthermore, the high prevalence of the invasive macroalgae may be an indicator of a nutrient-rich environment, which xeniids have been seen to be more tolerant of than hard corals (Mezger et al., 2022; Simancas-Giraldo et al., 2021). Lastly, physical conditions such as low wave energy and currents can be ideal for the establishment of *U. Stolonifera* and other sessile species. These factors make Kāneʻohe Bay also a highly suitable habitat for *U. Stolonifera*, necessitating EDRR efforts despite its spatial separation from the confirmed occurrence points in Puʻuloa.

Potential for secondary dispersal

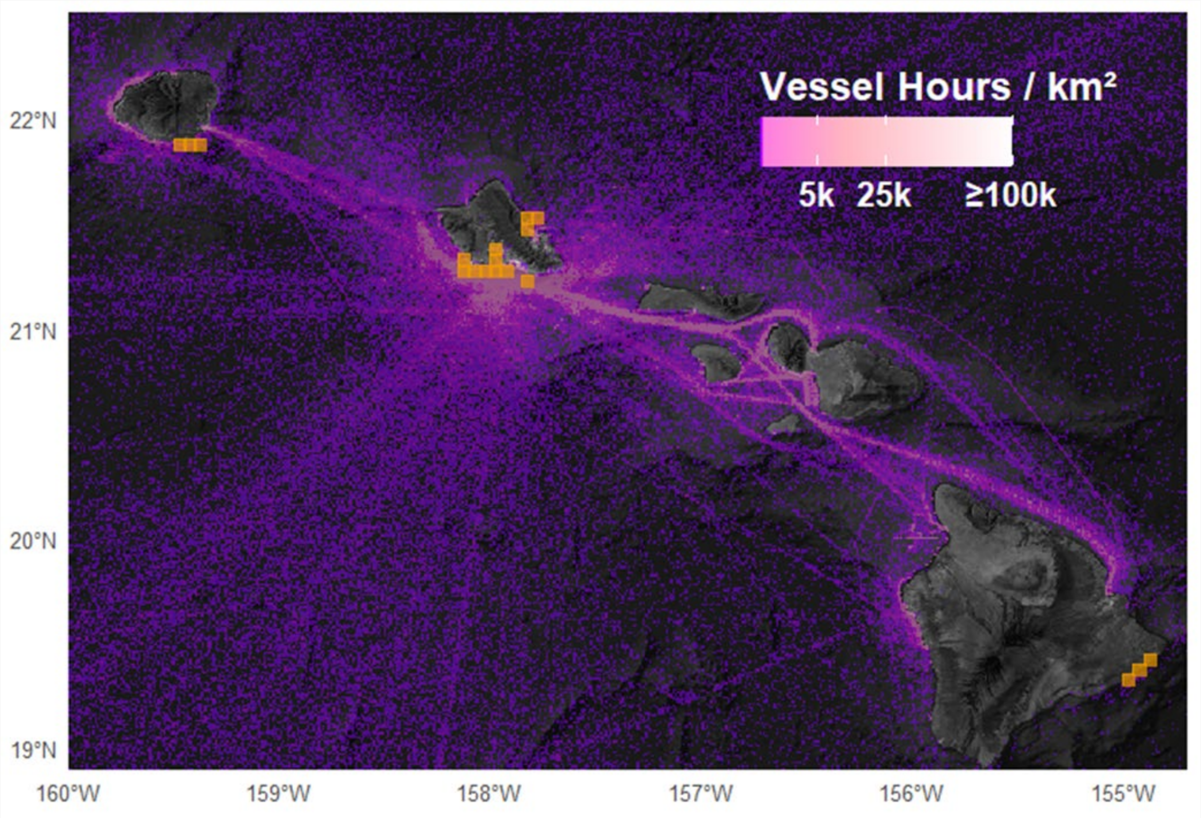

Figure 10. Log$_{10}$ transformed maritime traffic across the main Hawaiian Islands (based on the GFW AIS vessel presence dataset, public-global-presence from January 1, 2024 to January 1, 2025: latest, accessed 26/08/2025). Purple-to-white gradient areas indicate average vessel presence in hours per 31 km². Lighter areas correspond to higher vessel traffic. Orange squares denote predicted habitat suitability hotspots for *Unomia stolonifera*, illustrating overlap between high-traffic zones with several likely invasion areas.

As a major maritime hub in the North Pacific, Hawaiʻi receives substantial maritime traffic, especially in Puʻuloa and Honolulu Harbor in Oʻahu (De La Cruz, 2010). Secondary dispersal is a pattern observed globally, where maritime traffic and ports facilitate the spread of non-native species (Cariton & Geller, 1993; Carlton et al., 1995). With distance from port being a significant predictor variable for the habitat suitability of *U. stolonifera* in Hawaiʻi (Figure 2), secondary dispersal of *U. Stolonifera* between the Hawaiian Islands is a risk. In the main Hawaiian Islands, major ports and areas of high vessel presence are often located in or near suitability hotspots of *U. stolonifera* (Figure 10). Although *U. stolonifera* has only been observed in O‘ahu to date, inter-island shipping routes connecting O‘ahu to ports across the islands is a possible vector for secondary dispersal. Given the decline in native benthic taxa in Venezuela following *U. stolonifera*’s invasion in introduced sites, EDRR efforts in suitability hotspots is of utmost importance to preserve native ecosystem function and resilience (Toledo-Rodriguez et al., 2024).

Management recommendations

The identification of high-ranked suitability hotspots provides a scientific basis that may help inform monitoring and management considerations for *U. stolonifera* on O‘ahu. These locations are characterized by both high predicted suitability and relatively large, accessible benthic areas, suggesting that they represent plausible locations for establishment while also being practical for targeted surveys. Focusing early-detection and rapid-response (EDRR) efforts in these areas could offer a more efficient use of resources than distributing effort uniformly across the island. Current physical-removal measures in Pu‘uloa represent one approach currently being used to limit spread, and continued evaluation of these efforts may help improve understanding of their effectiveness in containing the octocoral (Jaen, 2024).

Community-based observations may offer a cost-effective and efficient response-time approach to increase detection efforts (Scyphers et al., 2015; Thompson et al., 2025) by educating communities on how to identify this soft coral and how to record its presence using photos and geographic coordinates. Educational materials, such as visual identification guides, simple reporting instructions, and general best-practice information, could be shared with schools, dive operations, and surf shops near high-ranked suitability hotspots to support voluntary participation by interested community members (Compagnone et al., 2023; Hart & Larson, 2014). These materials can highlight key morphological features of *U. stolonifera* and outline broadly recommended precautions to reduce unintentional spread (e.g., equipment-cleaning practices; Miralles et al., 2016).

- **Robust morphological Identification**: Visual guides and descriptions can help citizens accurately identify *U. stolonifera*. Providing simple, accessible ways for them to report sightings to managers is equally important.
- **Avoid further spread**: Provide instructions to avoid secondary spread of *U. stolonifera* including but not limited to:
    - Encouraging fishers, beach goers, and scuba divers to wash their equipment (e.g., fishing nets and swim wear that was in contact with algal

material) by soaking them in freshwater for at least 5 minutes to prevent accidental transport of *U. stolonifera* (Miralles et al., 2016).

Market-based approaches used for other non-native species, such as NOAA Fisheries' "Eat Lionfish" campaign (Huth et al., 2018), illustrate potential avenues through which public engagement may contribute to management objectives (Harris et al., 2023). Preliminary efforts to explore potential uses of *U. stolonifera*, including applications of its chemical compounds as waterproofing or dye materials, are ongoing (Montilla, 2024). Continued collaboration among local community groups (e.g., Kuleana Coral Restoration, KUA), state agencies (e.g., Hawaiʻi DAR Aquatic Invasive Species team), and commercial fishers may help improve monitoring capacity and understanding of possible spread pathways, including those associated with marine debris (Soares et al., 2023).

Conclusion

Introduced octocorals are an increasing concern because their resilience to ocean conditions makes them more likely to persist in introduced reef areas as oceanographic conditions continue to change in their favor (Toledo-Rodriguez et al., 2024; Nadir et al., 2023). For example, they have been seen to acclimate to rising sea surface temperatures (Goulet et al., 2017; Steinberg et al., 2022; Thobor et al., 2022) and ocean acidification (Gabay et al., 2014; Inoue et al., 2013; Tilstra et al., 2023).

The expansion of octocorals can drive phase shifts and reduce biodiversity by outcompeting calcifying organisms such as scleractinians, who build structural habitat and support ecological complexity (Johnson et al., 2022; Tilstra et al., 2023). Given this trajectory, proactive management of invasive octocorals is essential. Leveraging SDM provides a framework for targeted monitoring, early detection, and containment, helping to limit spread and mitigate long-term ecological shifts. Incorporating higher-resolution satellite environmental datasets will further improve predictions and provide managers with clearer decision pathways.

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Appendix: Supplemental Material

Table S1. List of coordinates for each spatial hotspot identified using the Getid-Ord GI* statistics. Hotspot IDs are labelled geographically as south shore (SS), Puʻuloa (PH), Kāneʻohe Bay (KB) with corresponding numerical values for identification.

Hotspot ID	**Longitude**	**Latitude**
KB1	-157.825	21.524
KB2	-157.775	21.524
KB3	-157.825	21.474
PH1	-157.975	21.374
PH2	-157.975	21.324
SS1	-158.125	21.324
SS2	-158.125	21.274
SS3	-158.075	21.274
SS4	-158.025	21.274
SS5	-157.975	21.274
SS6	-157.925	21.274
SS7	-157.825	21.225