Check for updates

Received: 12 September 2025 | Accepted: 22 April 2026

DOI: 10.1111/1365-2664.70452

Journal of Applied Ecology

RESEARCH ARTICLE

Persisting, emerging and contracting: The dynamic nature of non-native hotspots and their implications for management

Laura Gajdzik[1,2] | Kisei R. Tanaka[2]

[1]Cooperative Institute for Marine and Atmospheric Research, University of Hawai'i, Honolulu, Hawaii, USA

[2]Pacific Islands Fisheries Science Center, National Marine Fisheries Service, Honolulu, Hawaii, USA

Correspondence
Kisei R. Tanaka
Email: kisei.tanaka@noaa.gov

Funding information
Coral Reef Conservation Program

Handling Editor: Lorenzo Álvarez-Filip

Abstract

1. Non-native species threaten coral reefs by altering ecosystem structure and resilience, particularly on isolated tropical islands experiencing strong local and global stressors. In Hawai'i, native reef communities face cumulative impacts from the incursions of multiple non-native fishes.
2. We combined species distribution models and hotspot analyses to identify potential high-risk areas where environmental conditions favour co-occurrences of non-native species under present and future scenarios.
3. While predicted non-native richness was similar across islands, sub-island patterns were highly heterogeneous, with areas near ports and developed shorelines consistently exhibiting elevated co-occurrence risk. Baseline hotspot analyses indicated that O'ahu and Hawai'i Island host the majority of high-risk areas, followed by Kaua'i and Moloka'i.
4. Crucially, we identified three hotspot trajectories across time and emission scenarios: persisting hotspots remaining high-risk (e.g. Pearl Harbour on O'ahu; western Moloka'i), emerging hotspots developing by mid- to late-century (e.g. Po'ipū on Kaua'i) and contracting hotspots disappearing under future ocean conditions (e.g. Kailua-Kona on Hawai'i Island).
5. These patterns demand differentiated management strategies: (i) early detection and rapid response (also including biosecurity measures) in emerging hotspots, (ii) a combined approach that encompasses removal, monitoring and targeted outreach when non-native threats remain and (iii) habitat restoration or rehabilitation where invasion risk contracts.
6. *Synthesis and applications*. By linking explicit hotspot projections to distinct management phases, this study provides a proactive framework for non-native species control, transitioning from reactive eradication efforts to future-oriented planning that optimizes managers' often limited resources. This predictive framework is readily adaptable to other tropical island ecosystems facing similar biological and environmental pressures.

Laura Gajdzik and Kisei R. Tanaka contributed equally.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2026 The Author(s). *Journal of Applied Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society. This article has been contributed to by U.S. Government employees and their work is in the public domain in the USA.

KEYWORDS
adaptive management, climate change, coral reef, invasive, predictive modelling, risk assessment

1 | INTRODUCTION

The introduction of non-native species is increasingly recognized as a global environmental concern (Simberloff et al., 2013). In marine ecosystems, biological invasions pose direct threats through predation, competitive displacement and increased mortality of native species (Molnar et al., 2008; Salimi et al., 2021). Beyond ecological disruption, non-native species inflict substantial economic costs, now exceeding USD 423 billion in damages annually, a figure that has quadrupled each decade since the 1970s (Roy et al., 2024). The total number of non-native species worldwide is projected to rise by 36% by 2050 (Seebens et al., 2024). Yet, the threat posed by non-native species in marine environments is often overshadowed by other stressors such as overfishing, pollution and rising temperatures, particularly in tropical regions that are vulnerable to the combined pressures of environmental change and biological invasions (Salimi et al., 2021). Therefore, identifying 'hotspots'—areas where environmental conditions favour the co-occurrence of multiple non-native species—is critical for prioritizing targeted conservation and management actions (Li et al., 2016; O'Donnell et al., 2012).

Species distribution models (SDMs), also referred to as habitat suitability or ecological niche models, are widely used to predict species geographical distributions. These models incorporate georeferenced occurrences and abundance data from surveys and open-source databases with environmental variables (e.g. temperature, salinity, productivity) to identify habitats that meet the conditions necessary for species survival (Valavi et al., 2023; Wiens et al., 2009). While SDMs have some limitations, such as not accounting for species dispersal, competition or habitat filtering (Elith & Graham, 2009; Guisan et al., 2017), they have been extensively applied to predict range shifts in reef organisms (Chaudhary et al., 2023; Couce et al., 2012). Yet, relatively few studies have leveraged this tool to identify hotspots in tropical marine regions with multiple non-native species. This represents a key knowledge gap for decision-making, particularly for remote oceanic islands, which are both highly endemic and ecologically vulnerable (Manes et al., 2021).

Hawai'i is a prime example of such vulnerability and significant conservation interest (Friedlander et al., 2020). Its geographical isolation has fostered high levels of endemicity, with 25% of nearshore reef fishes found only there (Randall, 2007), yet it also ranks among the world's most invaded marine regions (Molnar et al., 2008). High volumes of maritime traffic serve as key vectors for non-native species introductions via ballast water and hull fouling (Eldredge & Carlton, 2002). Additional introductions have occurred through both intentional and accidental releases from aquaria and state-led fisheries enhancement programmes (Molnar et al., 2008). For instance, the State of Hawai'i introduced several food and bait fishes in the 1950s, including the Bluestripe snapper or Ta'ape (*Lutjanus kasmira*), Blacktail snapper or To'au (*L. fulvus*), Peacock grouper or Roi (*Cephalopholis argus*) and the Marquesan sardinella (*Sardinella marquesensis*) (Gaither et al., 2013; Maciolek, 1984; Randall, 1987). Others entered Hawaiian waters through the aquarium trade and mainly include ornamental butterflyfish and surgeonfish (Franklin et al., 2019). These species differ widely in their degrees of establishment and ecological impacts. Documented effects include predation on juvenile native fishes, competitive displacement of endemics and transmission of pathogens (Dierking et al., 2009; Giddens et al., 2014; Schumacher & Parrish, 2005; Work et al., 2003). Despite their negative impacts on reef communities, those species are often not the focus of management efforts.

Early Detection and Rapid Response (EDRR) is a key tenet in non-native management by coupling timely monitoring with swift intervention to prevent establishment and further spread (Reaser et al., 2020; Venette et al., 2021). EDRR efforts are most effective when directed towards high-risk areas identified by predictive models, especially when non-native populations are small and localized, which greatly increases the likelihood of successful eradication (Venette et al., 2021). Recommended response measures include direct species removal, deployment of emerging monitoring tools and raising public awareness to expand observation networks (Reaser et al., 2020). Crucially, EDRR programmes require clear decision-making protocols, dedicated funding and interagency coordination to enable managers to act within weeks, not months, of detection to implement control measures (Simberloff et al., 2013).

To support EDRR and other management strategies, we generated SDMs for 27 non-native reef fishes across the main Hawaiian Islands. We quantified the relative importance of static (e.g. distance to shore and ports) and dynamic (e.g. ocean productivity, salinity, temperature) predictors based on the premise that certain environmental and anthropogenic factors influence the distribution of non-native fishes. After that, we conducted hotspot analyses to identify high-risk areas under baseline (2000–2020) conditions and then projected changes under two carbon emissions scenarios (Shared Socioeconomic Pathways: SSP 1–2.6 and 3–7.0) and selected two time-steps (2050 and 2090) to enhance the ecosystem-informed management of non-native species. By producing risk maps based on future predictions, our approach offers a spatially explicit framework to guide early detection, prevention and long-term strategies for managing non-native reef fish.

2 | MATERIALS AND METHODS

2.1 | Species selection and occurrence data

We focused on 27 non-native fish taxa that are recorded in the non-indigenous aquatic species database from the U.S. Geological Survey (2025). Over half are snappers and groupers intentionally

13652664, 2026, 6, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2664.70452, Wiley Online Library on [28/09/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

introduced for fisheries enhancements, with some species well established throughout the Main Hawaiian Islands (MHI; Table S1). These ubiquitous taxa (e.g. *Lutjanus kasmira*, *L. fulvus*, *Cephalopholis argus*) have broad habitat use (including sand habitats, deep waters, artificial structures such as wrecks) and are generalist carnivores (Dierking et al., 2009; Schumacher & Parrish, 2005), which likely facilitated their establishment in Hawaiian waters. Approximately 30% of the other focal taxa are angelfishes and butterflyfishes, released from aquarium trade. Unlike introduced groupers and snappers, these highly prized ornamental fishes have not widely spread across the MHI, potentially due to more restrictive habitat and/or dietary requirements (e.g. reliance on living corals for food or shelter; Semmler et al., 2025), more extreme environmental conditions (including strong swells during winter times along the north shore coastlines), or other ecological and biological attributes (naivete, slow maturation, etc). These mechanisms remain hypothetical because Hawai'i-specific studies are rare; except for *C. argus*, *L. kasmira* and *L. fulvus*, *Upeneus vittatus* (a goatfish).

Occurrence data for the 27 fish species in Hawai'i (Table S1) were compiled from two open-source databases: the Global Biodiversity Information Facility (GBIF) via the *rgbif* R package (Chamberlain et al., 2024; Chamberlain & Boettiger, 2017) and the Ocean Biodiversity Information System (OBIS) via the *robis* R package (Whiting et al., 2016). Data pre-processing followed best practices to ensure spatial accuracy. We excluded vagrant records outside each species' known distribution and retained only records from 2000 onwards to match the BioOracle baseline (2000–2020). We used the *CoordinateCleaner* R package (Zizka et al., 2019) to remove spatial errors and retain only marine records. In GBIF, we retained records labelled 'PRESENT', excluded fossils, and omitted captive or cultivated specimens. We removed records with coordinate uncertainties over 5000 m, problematic values (e.g. 301, 999, 9999, 3036), coordinate precision under 0.01 or zero coordinates. For OBIS, we similarly excluded records with coordinate uncertainties over 5000 m or missing and zero coordinates. After filtering, we merged the GBIF and OBIS datasets for each species.

Because model calibration requires sufficient georeferenced data aligned with the Bio-ORACLE baseline, some non-native or potentially emerging taxa are not represented due to recency, rarity/low density, cryptic occurrence or limited digitization in public repositories. These exclusions reflect current data constraints rather than management importance. Therefore, our hotspot products should be interpreted as risk prioritization for the modelled taxa rather than a complete inventory of all non-native fish risks in Hawai'i.

2.2 | Species distribution modelling procedure and performance evaluation

We modelled the potential distributions of each non-native species using Maxent (v3.4.4), which is well suited for presence-only datasets and performs reliably with limited occurrence data (Pearson et al., 2007; Phillips et al., 2006). To reduce the influence of outliers and potential overprediction, we used the DBSCAN (Density-Based Spatial Clustering of Applications with Noise) algorithm to identify high-density clusters of species occurrence points (Ester et al., 1996). We then defined core habitat areas as the central 50% and, where appropriate, the central 80% of occurrence records within these clusters for model calibration. Trimming occurrence data to these core habitats minimized outlier influence and led to more conservative models. We first calibrated the Maxent models with the central 50% range of occurrence data and, if necessary, expanded to the central 80% range to ensure robust prediction while reducing the overestimation of non-native species potential.

We calibrated the Maxent models using high-resolution, open-source environmental data (~0.05°) (Phillips et al., 2006). Predictor variables, available for both baseline and future projection scenarios, were selected from 85 pre-screened parameters in the Bio-ORACLE database (https://www.bio-oracle.org/; Assis et al., 2018, 2024; Tyberghein et al., 2012). These include maximum, minimum and average ocean conditions (temperature, salinity, water velocity and direction), along with nutrient concentrations, dissolved oxygen, iron, primary productivity, pH, bathymetry and topographic features (slope, aspect, position index and terrain ruggedness). Bio-ORACLE v3 integrates in situ, satellite and reanalysis products with CMIP6 model projections using delta-method bias adjustments to estimate future conditions across environmental parameters.

We also included Euclidean distance to shoreline and distance to the nearest port (Global Fishing Watch layers) as static spatial covariates to capture coarse coastal gradients relevant to non-native occurrences. We interpret these distance layers as composite proxies that can reflect multiple processes operating in invaded coastal systems, including coastal access and habitat modification, propagule pressure associated with maritime infrastructure and residual detectability/sampling gradients. Accordingly, we use them to improve risk-of-occurrence mapping rather than as a direct, single-mechanism measure of 'anthropogenic impact' or fisheries extraction.

We reduced predictor multicollinearity using variance inflation factor (VIF) analysis, removing variables with correlation coefficient ≥0.8 or VIF >5. This narrowed the predictors from 21 key variables to a final 10 variables (Table 1). The selected predictors represent baseline conditions (2000–2020) and two future (2020–2100) scenarios based on Shared Socioeconomic Pathways: SSP1-2.6, which limits warming to 1.8°C by 2100, and SSP3-7.0, which projects a 3.6°C increase. We trained each Maxent SDM on 80% of the occurrence records and evaluated it with the remaining 20% using a bootstrap approach (Förderer et al., 2018). Model accuracy was assessed with AUC (Phillips et al., 2006), ranging from 0.5 (random) to >0.9 (high performance) (Metz, 1978).

2.3 | Environmental predictors and scenario projections

For baseline SDMs, we used Bio-ORACLE v3 variables summarized over 2000–2020 to align with the filtered occurrence record

13652664, 2026, 6, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2664.70452, Wiley Online Library on [28/09/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

TABLE 1 Environmental and anthropogenic variables used for species distribution modelling.

Variables (units)	VIF	Ecological relevance
Maximum ocean temperature (°C)	1.91	Temperature governs metabolic rates, with warmer waters promoting the range expansion of non-native fishes. (Friedlander & Parrish, 1998; Pickens et al., 2021)
Range ocean temperature (°C)	1.48	Fluctuations in temperature can stress species, creating new 'thermal niches' for non-native fishes (Johnson et al., 2017; Pickens et al., 2021)
Mean pH	1.41	pH affects reef fish through impacts on calcification and acid–base regulation, with shifts favouring non-native species better adapted to changing ocean chemistry (Doney et al., 2020; Pickens et al., 2021)
Mean phytoplankton ($mg\,m^{-3}$)	1.41	Phytoplankton concentration (proxy for primary productivity) can attract early life stages of non-native fishes seeking foraging hotspots (Pickens et al., 2021; Pittman & Brown, 2011)
Minimum salinity (PSU)	1.97	Osmotic constraints impact growth and survival, with non-native fishes with broader salinity tolerance may out-compete natives in nearshore brackish conditions (Carlton, 1999; Pickens et al., 2021)
Mean ocean current speed ($m\,s^{-1}$)	1.17	Currents disperse larvae and can facilitate the geographical range expansion of non-native fishes (Pickens et al., 2021; Toonen et al., 2011)
Minimum bathymetry/depth (m)	1.66	Depth dictates light availability and habitat complexity. Deeper areas can act as refugia for certain organisms (Pickens et al., 2021; Pittman & Brown, 2011), such as non-native fishes
Distance from nearest port (km)	1.96	Ports are key entry points for non-native species through maritime traffic with the potential corollary that areas closer to ports may harbour more non-native fishes (Bax et al., 2003; Pickens et al., 2021)
Distance from shoreline (km)	1.69	A coarse proxy for coastal accessibility and nearshore gradients that may influence non-native occurrence through multiple pathways, including habitat modification, propagule pressure near developed coastlines, observation probability (detectability/sampling) and higher likelihood of introductions. This variable is interpreted as a composite risk proxy rather than a direct measure of fishing pressure (Friedlander et al., 2003; Pickens et al., 2021)

Note: Environmental variables (1–7) are derived from Bio-ORACLE v3 (Assis et al., 2024) as long-term climatological surface averages for the baseline period (2000–2020) and were time-varying across future projections. Spatial layers (8–9) were derived from Global Fishing Watch and, together with bathymetry, were treated as static covariates and held constant across baseline and future projections. Variables 1–7 were extracted from surface layers; variables 8–9 were calculated as Euclidean distances. Pairwise Pearson correlation coefficients ranged from −0.0027 (bathymetry [min] ~ average ph) to 0.5242 (distance from shore ~ distance from port). No multicollinearity was detected (all Variance Inflation Factor [VIF] < 2).

period. For future projections, we used Bio-ORACLE v3 CMIP6 delta-method products under SSP1-2.6 and SSP3-7.0 and generated projections for two time slices: mid-century (2050–2060) and late-century (2090–2100). Dynamic predictors consisted of the Bio-ORACLE environmental variables (Table 1) and were allowed to vary across scenarios and time slices. Static predictors, bathymetry and Euclidean distance layers to shoreline and to the nearest port, were held constant across baseline and future projections because these layers are not scenario dependent and because our objective was to isolate the influence of changing oceanographic conditions on predicted suitability while retaining a consistent representation of coastal access and infrastructure. All predictor rasters were harmonized to a common grid prior to modelling. Bio-ORACLE rasters were used at their native resolution (~0.05°) and projected layers were resampled as needed to match the baseline grid. Predictors were masked to the MHI modelling domain (consistent across baseline and projections), and no-data cells were excluded from prediction surfaces. For each species, a single Maxent model was trained using the baseline predictor stack and projected onto each future predictor stack (SSP × time slice) to generate scenario- and period-specific suitability maps. To reduce spurious inference in environmentally novel conditions, we applied Maxent's extrapolation controls consistently across projections (i.e. clamping settings reported in the model configuration) and interpret projections as relative risk surfaces rather than deterministic forecasts.

2.4 | Non-native species richness and hotspot analysis

We estimated grid-cell non-native species richness by summing Maxent-derived species occurrence probabilities across 27 species (Calabrese et al., 2014), yielding continuous richness values from 0 to 27. To detect statistically significant clustering, we applied the Getis–Ord Gi* statistic (Ord & Getis, 1995) to the richness surface using a spatial weight matrix with $k = 8$ nearest neighbours. Grid cells with high positive z-scores ($|Gi^*| \geq 2.58$) were classified as high-risk areas (hotspots) where non-native fish species are likely to co-occur. To ensure our results were not overly influenced by any single species, we

13652664, 2026, 6, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2664.70452, Wiley Online Library on [28/09/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

performed a leave-one-out sensitivity analysis, iteratively removing one species and averaging the resulting hotspot maps.

3 | RESULTS

3.1 | Species-specific model performance

All 27 non-native fish SDMs achieved AUC values >0.9 (Table S2). Predicted habitat suitability varied across species and islands (Figure S1). For instance, *Paracanthurus hepatus* exhibited a broad suitability (0.63–1.00) across nearshore and mid-shelf zones, suggesting a wide environmental tolerance and potential for widespread establishment. *Lutjanus kasmira* showed moderate-to-high average suitability in coastal habitats (0.60), consistent with its observed dominance in nearshore reef systems. In contrast, *Epinephelus irroratus* showed restricted suitability, primarily confined to isolated, low-productivity areas, reflecting a narrower niche. These spatial differences highlight heterogeneity in suitability patterns across non-native reef fishes in Hawai'i.

3.2 | Drivers and spatial patterns of non-native fish richness

We quantified environmental factors shaping non-native reef fish distributions by averaging variable contribution metrics across the 27 Maxent SDMs. Distance from shoreline and ports was the most influential predictors, followed by ocean productivity and minimum salinity, sea surface temperature (range and maximum), pH and current velocity contributing moderately (Figure 1a).

Predicted species richness (sum of occurrence probabilities across grid cells) was relatively consistent across islands (10–11 species per island) but showed pronounced sub-island variability. Higher richness was found in southern Kaua'i (15.13 ± 0.36), south O'ahu (16.93 ± 0.35) and coastal Hawai'i (16.41 ± 0.35; Figure 1a). These localized hotspots, particularly near major ports (Figure S3) and along densely populated coastlines (Figure S5), suggest an association between co-occurrence risk and developed, high-access nearshore settings.

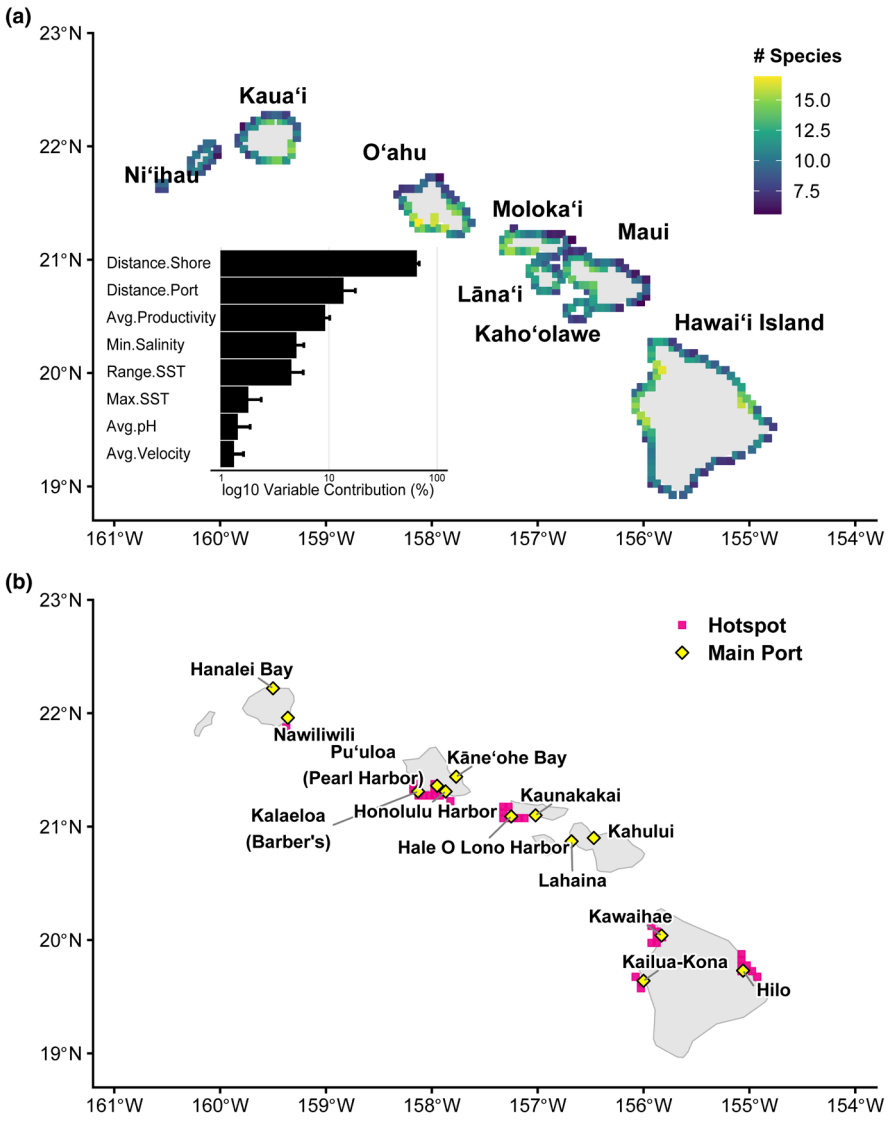


FIGURE 1 Spatial patterns and drivers of non-native reef fish richness across the Main Hawaiian Islands. (a) Map of summed Maxent occurrence probabilities for 27 non-native species, showing predicted richness across grid cells (blue–green gradient). The accompanying bar chart displays the mean permutation importance (%) of the top eight predictors: Distance from shore and port, average (avg.) productivity, minimum (min) salinity, range and maximum (max) sea surface temperature (SST), average pH and velocity (current). (b) Getis–Ord Gi* hotspot analysis of the same richness surface, highlighting statistically significant high-richness clusters (pink squares) that indicate areas of high-risk for non-native fishes. Major port locations (yellow diamond icon) based on the Global Fishing Watch dataset (Global Fishing Watch., 2020. Distance from Port, Version 1.0.) are also shown for reference. For the continuous 'distance from port' map see (Figure S3).

13652664, 2026, 6, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2664.70452, Wiley Online Library on [28/09/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Baseline hotspot analysis (2000–2020) identified 36 high-risk areas across four islands, concentrated on Hawai'i and O'ahu (70%), followed by Moloka'i (22%), and Kaua'i (8%) (Figure 1b). Predicted richness exhibited greater uncertainty near populated coastal zones (Figure S2). Within islands, hotspots clustered near major ports and adjacent developed shorelines, including Pu'uloa (Pearl Harbour) on O'ahu and Waikoloa-Waikui, Kailua Bay and Pier, and Hilo Bay on Hawai'i (Figure 1b). These patterns indicate that nearshore conditions and maritime infrastructure align with non-native co-occurrence risk at multiple spatial scales.

3.3 | Projected shifts in non-native fish hotspots under future projection scenarios

Our projections under two emissions scenarios (SSP1-2.6 and SSP3-7.0) and two time slices (mid-century: 2050–2060, and late-century: 2090–2100) revealed shifts in the distribution of non-native fish hotspots (Figure 2a,b). Temperature exhibits the largest projected change. But declines in pH and salinity, as well as modest increases in total phytoplankton and lower current speeds, also occurred and altered habitat suitability (Figure S4). Under SSP3-7.0, hotspot counts generally increased across most islands, except Hawai'i Island. Several areas consistently emerged as high-risk under both scenarios and time slices, including Pu'uloa-Barbers Point Harbour on O'ahu, Kaluako'i (western end) on Moloka'i and areas near Waikoloa-Waikui and Hilo on Hawai'i Island. Additional emerging hotspots under SSP3.7–0 included Kāne'ohe Bay and Kailua Bay on O'ahu, and Līhu'e and Kōloa in Kaua'i (Figure 2b). Under SSP1-2.6, more high-risk areas were projected on Hawai'i Island than under SSP3-7.0, including the late-century reappearance of hotspots around Waikoloa-Waikui and Kailua-Kona after their absence at mid-century (Figure 2). In contrast, under SSP3.7-0, hotspots around Kailua-Kona Bay and the Honokōhau Harbour were no longer identified. A hotspot off Pākanaka Fishpond on Moloka'i was only detected under baseline conditions (Figure 2b). Together, these projections show that environmental trajectories may shift, expand or contract hotspot locations.

4 | DISCUSSION

4.1 | The power and limitations of modelling non-native incursions

Although long-term environmental changes remain a predominant threat to coral reefs, the introduction of non-native species poses an additional risk, particularly in regions where high endemicity and localized human impacts heighten vulnerability. In this context, species distribution models (SDMs) that identify 'high-risk' hotspot



FIGURE 2 Projected changes in non-native reef fish hotspots under two emissions scenarios and three-time steps. Hotspots were identified using Getis–Ord Gi* on summed occurrence probabilities for 27 species under (a) low (SSP1-2.6) and (b) high (SSP3-7.0) carbon emissions. Each panel shows hotspot cells for baseline (pink; 2000–2020), mid-century (blue; 2050–2060) and late-century (green; 2090–2100) conditions. Overlapping hues denote persistence across two periods (pink + blue = dark blue; blue + yellow = green, pink + yellow = red), and dark grey cells indicate hotspots maintained in all three-time steps. These projections highlight how alternative climate trajectories may shift, expand or contract high-risk areas for non-native fishes.

13652664, 2026, 6, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2664.70452, Wiley Online Library on [28/09/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

areas can support targeted monitoring and management actions. Prioritizing early detection and rapid response (EDDR) in these areas can increase cost-effectiveness and reduce reliance on intensive, and often infeasible, eradication campaigns (Cariton & Geller, 1993; Westbrooks & Eplee, 2011). A proactive approach requires identifying current hotspots and anticipating where new ones may emerge as environmental conditions depart from historical baselines. Extreme events and associated environmental shifts can facilitate the spread and establishment of non-natives into native communities (García Molinos et al., 2016), making scenario-based projections a practical component of long-term management.

While hotspot analyses provide a useful framework for mapping non-native co-occurrence risk, application in local contexts requires careful interpretation. Model performance depends on data availability and quality. Because our framework relies on public georeferenced records aligned with environmental baselines, it will under-represent taxa that are newly introduced, rare, cryptic or inconsistently reported. This constraint is particularly problematic early in an incursion, when low detection probability and delayed digitization can lag on-the-ground management needs. Thus, absence from our models reflects a reporting gap rather than low risk. Improving coverage requires targeted surveys in locations prone to introductions (e.g. major ports, boat ramps and other high-access shorelines) and standardized reporting workflows that include effort information and, where feasible, true absences.

Additionally, Maxent modelling links occurrences to environmental gradients but does not explicitly represent the biological and contextual processes shaping realized spread and persistence (Elith & Graham, 2009; Guisan et al., 2017; Syfert et al., 2013). Such processes likely operate non-uniformly across our pool of 27 species, which span diverse introduction pathways (e.g. aquarium vs fisheries release) and habitat associations (e.g. artificial wrecks vs living corals; Table S1). Dispersal pathways, fine-scale habitat features (e.g. depth, rugosity), biotic interactions (e.g. naivete, competitive advantage) and life-history traits (e.g. maturation rates, thermal tolerance) can constrain expansion even where predicted suitability is high. Unlike native assemblages, which have adapted to Hawaiian conditions over evolutionary timescales, non-native fishes are introduced at specific foci and must establish over shorter, ecological timescales, potentially limiting spread and establishment even under favourable environmental conditions. While these constraints must be considered when interpreting hotspot projections, scenario-based SDM analyses remain the most practical tool for broad-scale risk mapping and surveillance.

4.2 | Ports and coastal proximity remain persistent hotspots, requiring multifaceted management actions

Ports and nearshore-access gradients emerge as dominant predictors in our SDMs (Figures 1 and 2), consistent with global marine invasion patterns (Cariton & Geller, 1993; Carlton, 1985; Coles et al., 2004; Seebens et al., 2013). Distance-to-port and distance-to-shore are coarse, composite covariates that can reflect maritime traffic, structural habitat alteration and detectability/sampling gradients associated with accessibility. Accordingly, these predictors function as spatial indicators of non-native co-occurrence risk rather than direct measures of species-specific habitat preference. This is supported by the fact that several ports (Figure S3), did not correspond to predicted hotspots, indicating that proximity to infrastructure alone does not guarantee establishment.

Hawai'i is a major maritime hub in the North-central Pacific, receiving vessels from North America, Asia and the South Pacific (Carlton, 1987). Maritime traffic concentrates through Pu'uloa (Pearl Harbour), Honolulu Harbour and Kalaeloa Barbers Point on Oa'hu (Coles et al., 2002, 2006), which are focal points for introductions (Figure 2). Secondary dispersal may also occur via inter-island shipping routes to ports such as Kawaihae and Hilo, which were also identified as baseline hotspots (Figure 2). Our results indicate that ports-adjacent areas are likely to remain high-risk hotspots for non-native reef fish through the end of the century under both emissions scenarios. These persistent hotspots require sustained strategies that combine removal, monitoring and coordinated outreach (Figure 3).

A first priority is targeted removal in persistent hotspots, where feasible, coupled with approaches that increase participation and sustained effort. In Hawai'i, fishing holds cultural significance for subsistence and community sharing (Goto, 1986; Vaughan & Ayers, 2016), and events such as the 'Invasive Species Round-up' (Angler's Atlas) can contribute to local reductions. Where appropriate, removal programmes can be paired with initiatives that encourage utilization of non-native catch (Giakoumi et al., 2019), analogous to market-based efforts used to curb the population of the invasive lionfish in the Caribbean and Western Atlantic (Chapman et al., 2016; Green et al., 2014). In Hawai'i, commercial uptake may be constrained by preferences for native species and toxicity concerns for some taxa (e.g. *C. argus*; Bienfang et al., 2012). Alternative uses may provide complementary pathways, such as fish-skin leather applications reported for *L. kasmira* (To'au) through efforts piloted by Conservation International (CI press release, 14 April 2025).

Beyond removal, long-term management benefits from coordinated monitoring and community engagement (Westbrooks & Eplee, 2011). Public awareness and community science reporting can improve detection, while education and outreach can increase support for sustained interventions (Hart & Larson, 2014). Overall, managing persistent hotspots is most likely to succeed through integrated strategies that combine targeted removal, feasible commercialization that leverages traditional practices and continuous monitoring supported by cross-agency coordination.

4.3 | Emergence and disappearance of hotspots over time, necessitating tailored management actions

Projected environmental change may alter suitable habitats for non-native fish, particularly in densely populated coastal areas and near ports (Figure 2). Under both emissions pathways (SSP1-2.6 and

13652664, 2026, 6, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2664.70452, Wiley Online Library on [28/09/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

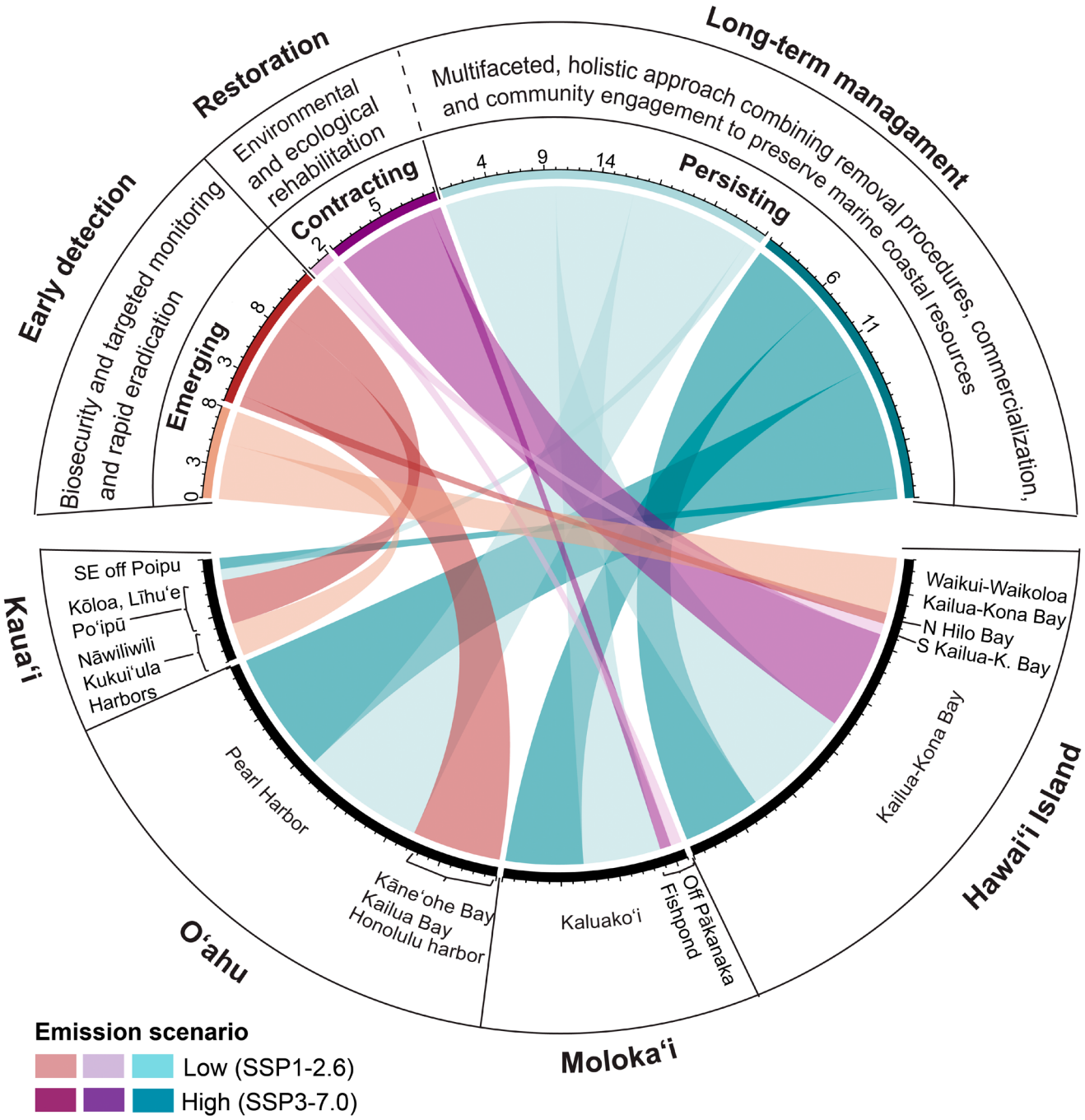


FIGURE 3 Conceptual diagram illustrating the temporal dynamics of non-native fish species hotspots across four Hawaiian Islands, linked to corresponding management phases, from early detection through restoration to long-term management. Coloured bands illustrate the projected changes in hotspot distribution under two future emission scenarios (low SSP1-2.6 and high SSP3-7.0). Graduated lines represent the number of hotspots per scenario and types of hotspots, including persisting (stable), emerging and contracting (disappearing) hotspots, requiring different targeted, area-specific management strategies.

SSP3-7.0), new hotspots emerge by mid-century on Kauaʻi (Poʻipū; Kukuiʻula to Nawiliwili; between Līhuʻe and Kōloa) and Oʻahu (Kāneʻohe and Kailua; Honolulu Harbour; Figure 2). These shifts are consistent with the expectation that changes in temperature, salinity and productivity can enhance suitability for some non-native taxa, particularly those that exploit modified environments (Bradley & Wilcove, 2009; Song et al., 2024).

Kāneʻohe Bay is frequently cited as one of the most heavily invaded marine systems in Hawaiʻi, with ~200 non-native species reported (Coles et al., 2002), and yet it was detected as a hotspot only in future projections. This discrepancy may reflect gaps in publicly digitized records (particularly for cryptic and/or low-density taxa), taxonomic misidentification or local drivers not captured at our predictor resolution. In emerging hotspots (Figure 3), strengthening

13652664, 2026, 6, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2664.70452, Wiley Online Library on [28/09/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

EDRR protocols is critical and can start with biosecurity measures that include both ballast water (e.g. filtration, chemical treatment) and biofouling management (e.g. antifouling coating, physical barriers, and ultrasonic technologies; Westbrooks & Eplee, 2011). EDRR efforts should also incorporate community science initiatives, where local agencies and grassroots organizations help monitor for new incursions using tools like online databases and standardized reporting systems (Azzurro et al., 2013; Clements et al., 2021).

In contrast, Hawai'i Island exhibits more variable hotspot trajectories. Under the high emission scenario (SSP3-7.0), some western coastal hotpots diminish, whereas under the low emission pathway (SSP1-2.6), they re-emerge by late century. These contrasting trends suggest sensitivity to conditions that can exceed non-native species' physiological tolerances, leading to localized extirpation (Comte & Olden, 2017). While temperature exhibited the largest projected change, shifts in pH, salinity, productivity and current velocity may also influence suitability by altering metabolic constraints, resource availability or dispersal conditions (Figure S4). Similar declines are projected for parts of southern Kailua-Kona and a small area in southern Moloka'i (Figures 2 and 3). Areas projected to decline in suitability for non-natives may represent opportunities for environmental rehabilitation focused on reducing local stressors (e.g. pollution, habitat degradation) and improving resilience through coral transplanting or building artificial reefs (Hoegh-Guldberg, 2014). Where native communities have declined due to interacting environmental and ecological stressors, additional restoration strategies may eventually be needed, potentially including assisted gene flow or translocation of resilient genotypes to support adaptations (Bradley et al., 2009).

4.4 | Recognizing indigenous knowledge in non-native species management

While this study uses Western scientific timelines and management framing, Indigenous knowledge systems offer nuanced, place-based perspectives on stewardship. This is exemplified by Māori communities in Aotearoa New Zealand, whose documentation of introduced species following 19th-century colonization provides a long-term ecological record that predates and enriches standard Western datasets (Mercier et al., 2022; Wehi, 2006). Scientific terms in western science, such as 'invasive', 'introduced' or 'naturalized', emphasize origin and ecological stage, whereas Indigenous languages are centred around relationships, place and responsibility (Wehi et al., 2023). In 'Ōlelo Hawai'i, descriptors such as *malihini* (newcomer), *lawe 'ia mai* (brought here) or *mai nā 'āina 'ē* (from other lands) provide relational language (Pukui & Elbert, 1986). This framing does not minimize ecological harm but rather situates management within cultural histories and responsibilities (Kealiikanakaoleohaililani et al., 2018; Kimmerer, 2020; Tadaki et al., 2023).

We suggest treating Indigenous and scientific perspectives as distinct but overlapping knowledge systems that can inform inclusive, adaptive management. Māori-led biosecurity initiatives provide models of integrated approaches (Black et al., 2019), and analogous collaborations can be explored in Hawai'i. Efforts that honour Indigenous language, values and decision-making authority alongside scientific tools can strengthen non-native species management in culturally grounded and ecologically effective ways.

5 | CONCLUSION

As marine ecosystems shift away from historical environmental baselines while facing intensifying local human pressures, the challenge of managing non-native species grows increasingly urgent. Our results revealed persistent hotspots near ports and developed areas, validating these locations as primary introduction foci that will likely maintain their high-risk status under future conditions. By integrating SDMs with hotspot analyses, we provide a scalable, spatially explicit EDRR framework to prioritize prevention, early monitoring and rapid intervention in emerging hotspots and sustained strategies (removal, rehabilitation and long-term planning) in persistent ones. Effective management also requires social engagement and cultural grounding beyond ecological modelling. Integrating place-based Indigenous knowledge alongside Western science can promote community-inclusive approaches for non-native species management in Hawai'i, yielding long-term results.

AUTHOR CONTRIBUTIONS

Laura Gajdzik and Kisei R. Tanaka both conceived the main ideas and contributed to the analysis and writing process.

ACKNOWLEDGEMENTS

We thank all those who contributed in situ data and acknowledge the open-source data providers, including GBIF, OBIS and Bio-ORACLE, whose resources made this analysis possible. We also thank Dr. Andrew Shantz for reviewing the paper and providing valuable feedback. This work was funded by the National Oceanic and Atmospheric Administration (NOAA) Coral Reef Conservation Program (CRCP).

CONFLICT OF INTEREST STATEMENT

All authors declare no competing interests.

DATA AVAILABILITY STATEMENT

All data and R codes are available on GitHub (https://github.com/krtanaka-NOAA/dynamic-reef-hotspots) and Zenodo https://doi.org/10.5281/zenodo.20336687 (Tanaka, 2026).

ORCID

Laura Gajdzik https://orcid.org/0000-0001-6781-9625
Kisei R. Tanaka https://orcid.org/0000-0002-1901-6972

REFERENCES

Assis, J., Araújo, M. B., & Serrão, E. A. (2018). Projected climate changes threaten ancient refugia of kelp forests in the North Atlantic. *Global Change Biology*, *24*(1), e55–e66. https://doi.org/10.1111/gcb.13818

13652664, 2026, 6, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2664.70452, Wiley Online Library on [28/09/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Assis, J., Fernández Bejarano, S. J., Salazar, V. W., Schepers, L., Gouvêa, L., Fragkopoulou, E., Leclercq, F., Vanhoorne, B., Tyberghein, L., Serrão, E. A., Verbruggen, H., & De Clerck, O. (2024). Bio-ORACLE v3.0. Pushing marine data layers to the CMIP6 earth system models of climate change research. *Global Ecology and Biogeography*, *33*(4), e13813. https://doi.org/10.1111/geb.13813

Azzurro, E., Broglio, E., Maynou, F., & Bariche, M. (2013). Citizen science detects the undetected: The case of *Abudefduf saxatilis* from the Mediterranean Sea. *Management of Biological Invasions*, *4*, 167–170.

Bax, N., Williamson, A., Aguero, M., Gonzalez, E., & Geeves, W. (2003). Marine invasive alien species: A threat to global biodiversity. *Marine Policy*, *27*(4), 313–323. https://doi.org/10.1016/S0308-597X(03)00041-1

Bienfang, P., DeFelice, S., Laws, E., & Wallsgrove, N. (2012). Ciguatoxicity in the main Hawaiian Islands, spatial and temporal variability in the introduced reef carnivore *Cephalopholis argus*. *Journal of Research in Environmental Science and Toxicology*, *1*, 47–57.

Black, A., Mark-Shadbolt, M., Garner, G., Green, J., Malcolm, T., Marsh, A., Ropata, H., Waipara, N., & Wood, W. (2019). How an Indigenous community responded to the incursion and spread of myrtle rust (**Austropuccinia psidii**) that threatens culturally significant plant species—A case study from New Zealand. *Pacific Conservation Biology*, *25*(4), 348–354. https://doi.org/10.1071/PC18052

Bradley, B. A., Oppenheimer, M., & Wilcove, D. S. (2009). Climate change and plant invasions: Restoration opportunities ahead? *Global Change Biology*, *15*(6), 1511–1521. https://doi.org/10.1111/j.1365-2486.2008.01824.x

Bradley, B. A., & Wilcove, D. S. (2009). When invasive plants disappear: Transformative restoration possibilities in the Western United States resulting from climate change. *Restoration Ecology*, *17*(5), 715–721. https://doi.org/10.1111/j.1526-100X.2009.00586.x

Calabrese, J. M., Certain, G., Kraan, C., & Dormann, C. F. (2014). Stacking species distribution models and adjusting bias by linking them to macroecological models. *Global Ecology and Biogeography*, *23*(1), 99–112. https://doi.org/10.1111/geb.1210

Cariton, J. T., & Geller, J. B. (1993). Ecological roulette: The global transport of nonindigenous marine organisms. *Science*, *261*(5117), 78–82. https://doi.org/10.1126/science.261.5117.78

Carlton, J. (1985). *Transoceanic and interoceanic dispersal of coastal marine organisms: The biology of ballast water*. (No. 23:313–371). Oceanography and Marine Biology, An Annual Review.

Carlton, J. (1987). Patterns of transoceanic marine biological invasions in the Pacific Ocean. *Bulletin of Marine Science*, *41*, 452–465.

Carlton, J. (1999). Molluscan invasions in marine and estuarine communities. *Malacologia*, *443 41(2)*, 439–454.

Chamberlain, S., Barve, V., Mcglinn, D., Oldoni, D., Desmet, P., Geffert, L., & Ram, K. (2024). Rgbif: Interface to the global biodiversity information facility API. R package version 3.8.1, https://CRAN.R-project.org/package=rgbif. [Computer software].

Chamberlain, S. A., & Boettiger, C. (2017). *R python, and ruby clients for GBIF species occurrence data* (No. e3304v1). PeerJ Inc. https://doi.org/10.7287/peerj.preprints.3304v1

Chapman, J. K., Anderson, L. G., Gough, C. L. A., & Harris, A. R. (2016). Working up an appetite for lionfish: A market-based approach to manage the invasion of *Pterois volitans* in Belize. *Marine Policy*, *73*, 256–262. https://doi.org/10.1016/j.marpol.2016.07.023

Chaudhary, C., Alfaro-Lucas, J. M., Simões, M. V. P., Brandt, A., & Saeedi, H. (2023). Potential geographic shifts in the coral reef ecosystem under climate change. *Progress in Oceanography*, *213*, 103001. https://doi.org/10.1016/j.pocean.2023.103001

Clements, K. R., Karp, P., Harris, H. E., Ali, F., Candelmo, A., Rodríguez, S. J., Balcázar-Escalera, C., Fogg, A. Q., Green, S. J., & Solomon, J. N. (2021). The role of citizen science in the research and management of invasive lionfish across the Western Atlantic. *Diversity*, *13*(12), 12. https://doi.org/10.3390/d13120673

Coles, S., DeFelice, R., & Eldredge, L. (2002). *Non-indigenous marine species in Kane'ohe Bay, O'ahu, Hawai'i* (Bishop Museum Technical Report N No. 24). Bernice Pauahi Bishop Museum Hawai'i Biological Survey. http://hbs.bishopmuseum.org/pdf/kbay-report.pdf

Coles, S. L., Kandel, F. L. M., Reath, P. A., Longenecker, K., & Eldredge, L. G. (2006). Rapid assessment of nonindigenous marine species on coral reefs in the Main Hawaiian Islands. *Pacific Science*, *60*(4), 483–507. https://doi.org/10.1353/psc.2006.0026

Coles, S. L., Reath, P. R., Skelton, P. A., & Eldredge, L. G. (2004). Rapid assessment of nonindigenous marine species on coral reefs in the Main Hawaiian Islands. *Pacific Science*, *58*(2), 281–303. https://doi.org/10.1353/psc.2004.0013

Comte, L., & Olden, J. D. (2017). Climatic vulnerability of the world's freshwater and marine fishes. *Nature Climate Change*, *7*(10), 718–722. https://doi.org/10.1038/nclimate3382

Couce, E., Ridgwell, A., & Hendy, E. J. (2012). Environmental controls on the global distribution of shallow-water coral reefs. *Journal of Biogeography*, *39*(8), 1508–1523. https://doi.org/10.1111/j.1365-2699.2012.02706.x

Dierking, J., Williams, I., & Walsh, W. (2009). Diet composition and prey selection of the introduced grouper species peacock hind (*Cephalopholis argus*) in Hawai'i. *Fishery Bulletin*, *107*, 464–476.

Doney, S. C., Busch, D. S., Cooley, S. R., & Kroeker, K. J. (2020). The impacts of ocean acidification on marine ecosystems and reliant human communities. *Annual Review of Environment and Resources*, *45*, 83–112. https://doi.org/10.1146/annurev-environ-012320-083019

Eldredge, L. G., & Carlton, J. T. (2002). Hawaiian marine bioinvasions: A preliminary assessment. *Pacific Science*, *56*(2), 211–212.

Elith, J., & Graham, C. H. (2009). Do they? How do they? Why do they differ? On finding reasons for differing performances of species distribution models. *Ecography*, *32*(1), 66–77. https://doi.org/10.1111/j.1600-0587.2008.05505.x

Ester, M., Kriegel, H.-P., Sander, J., & Xu, X. (1996). A density-based algorithm for discovering clusters in large spatial databases with noise. Proceedings of the Second International Conference on Knowledge Discovery and Data Mining, 226–231.

Förderer, M., Rödder, D., & Langer, M. R. (2018). Patterns of species richness and the center of diversity in modern Indo-Pacific larger foraminifera. *Scientific Reports*, *8*(1), 8189. https://doi.org/10.1038/s41598-018-26598-9

Franklin, E. C., Gray, A. E., & Mundy, B. C. (2019). Three New Records of Coastal Fishes in the Hawaiian Islands. https://doi.org/10.5281/ZENODO.3572888

Friedlander, A. M., Brown, E. K., Jokiel, P. L., Smith, W. R., & Rodgers, K. S. (2003). Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. *Coral Reefs*, *22*(3), 291–305. https://doi.org/10.1007/s00338-003-0317-2

Friedlander, A. M., Donovan, M. K., DeMartini, E. E., & Bowen, B. W. (2020). Dominance of endemics in the reef fish assemblages of the Hawaiian Archipelago. *Journal of Biogeography*, *47*(12), 2584–2596. https://doi.org/10.1111/jbi.13966

Friedlander, A. M., & Parrish, J. D. (1998). Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *Journal of Experimental Marine Biology and Ecology*, *224*(1), 1–30. https://doi.org/10.1016/S0022-0981(97)00164-0

Gaither, M. R., Aeby, G., Vignon, M., Meguro, Y., Rigby, M., Runyon, C., Toonen, R. J., Wood, C. L., & Bowen, B. W. (2013). An invasive fish and the time-lagged spread of its parasite across the Hawaiian Archipelago. *PLoS One*, *8*(2), e56940. https://doi.org/10.1371/journal.pone.0056940

García Molinos, J., Halpern, B. S., Schoeman, D. S., Brown, C. J., Kiessling, W., Moore, P. J., Pandolfi, J. M., Poloczanska, E. S., Richardson, A. J., & Burrows, M. T. (2016). Climate velocity and the future global

13652664, 2026, 6, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2664.70452, Wiley Online Library on [28/09/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

redistribution of marine biodiversity. *Nature Climate Change*, *6*(1), 83–88. https://doi.org/10.1038/nclimate2769

Giakoumi, S., Katsanevakis, S., Albano, P. G., Azzurro, E., Cardoso, A. C., Cebrian, E., Deidun, A., Edelist, D., Francour, P., Jimenez, C., Mačić, V., Occhipinti-Ambrogi, A., Rilov, G., & Sghaier, Y. R. (2019). Management priorities for marine invasive species. *Science of the Total Environment*, *688*, 976–982. https://doi.org/10.1016/j.scitotenv.2019.06.282

Giddens, J., Friedlander, A., Conklin, E., Wiggins, C., Stamoulis, K., & Donovan, M. (2014). Experimental removal of the invasive peacock hind (roi) *Cephalopholis argus*, in Puakō, Hawai'i: Methods for assessing and managing marine invasive species. *Marine Ecology Progress Series*, *511*, 209–221. https://doi.org/10.3354/meps10919

Global Fishing Watch. (2020). www.globalfishingwatch.org

Goto, A. (1986). *Prehistoric ecology and economy of fishing in Hawaii: An ethnoarchaeological approach*. (PhD Dissertation) Department of Anthropology.

Green, S. J., Dulvy, N. K., Brooks, A. M. L., Akins, J. L., Cooper, A. B., Miller, S., & Côté, I. M. (2014). Linking removal targets to the ecological effects of invaders: A predictive model and field test. *Ecological Applications*, *24*(6), 1311–1322. https://doi.org/10.1890/13-0979.1

Guisan, A., Thuiller, W., & Zimmermann, N. E. (2017). *Habitat suitability and distribution models: With applications in R*. Cambridge University Press. https://doi.org/10.1017/9781139028271

Hart, P. S., & Larson, B. M. H. (2014). Communicating about invasive species: How "driver" and "passenger" models influence public willingness to take action. *Conservation Letters*, *7*(6), 545–552. https://doi.org/10.1111/conl.12109

Hoegh-Guldberg, O. (2014). Coral reef sustainability through adaptation: Glimmer of hope or persistent mirage? *Current Opinion in Environmental Sustainability*, *7*, 127–133. https://doi.org/10.1016/j.cosust.2014.01.005

Johnson, C. H., Zhao, C., Xu, Y., & Mori, T. (2017). Timing the day: What makes bacterial clocks tick? *Nature Reviews Microbiology*, *15*(4), 232–242. https://doi.org/10.1038/nrmicro.2016.196

Kealiikanakaoleohaililani, K., Kurashima, N., Francisco, K. S., Giardina, C. P., Louis, R. P., McMillen, H., Asing, C. K., Asing, K., Block, T. A., Browning, M., Camara, K., Camara, L., Dudley, M. L., Frazier, M., Gomes, N., Gordon, A. E., Gordon, M., Heu, L., Irvine, A., … Yogi, D. (2018). Ritual + sustainability science? A portal into the science of aloha. *Sustainability*, *10*(10), 10. https://doi.org/10.3390/su10103478

Kimmerer, R. (2020). *Braiding sweetgrass: Indigenous wisdom, scientific knowledge and the teachings of plants*. Penguin Books.

Li, X., Liu, X., Kraus, F., Tingley, R., & Li, Y. (2016). Risk of biological invasions is concentrated in biodiversity hotspots. *Frontiers in Ecology and the Environment*, *14*(8), 411–417. https://doi.org/10.1002/fee.1321

Maciolek, J. A. (1984). *Exotic fishes in Hawaii and other islands of Oceania*. 131–136.

Manes, S., Costello, M. J., Beckett, H., Debnath, A., Devenish-Nelson, E., Grey, K.-A., Jenkins, R., Khan, T. M., Kiessling, W., Krause, C., Maharaj, S. S., Midgley, G. F., Price, J., Talukdar, G., & Vale, M. M. (2021). Endemism increases species' climate change risk in areas of global biodiversity importance. *Biological Conservation*, *257*, 109070. https://doi.org/10.1016/j.biocon.2021.109070

Mercier, O., Palmer, S., & King-Hunt, A. (2022). Hoha riha: Pest insect control in Maori tradition. *The Journal of the Polynesian Society*, *131*, 261–288.

Metz, C. E. (1978). Basic principles of ROC analysis. *Seminars in Nuclear Medicine*, *8*(4), 283–298. https://doi.org/10.1016/S0001-2998(78)80014-2

Molnar, J. L., Gamboa, R. L., Revenga, C., & Spalding, M. D. (2008). Assessing the global threat of invasive species to marine biodiversity. *Frontiers in Ecology and the Environment*, *6*(9), 485–492. https://doi.org/10.1890/07006

O'Donnell, J., Gallagher, R. V., Wilson, P. D., Downey, P. O., Hughes, L., & Leishman, M. R. (2012). Invasion hotspots for non-native plants in Australia under current and future climates. *Global Change Biology*, *18*(2), 617–629. https://doi.org/10.1111/j.1365-2486.2011.02537.x

Ord, J. K., & Getis, A. (1995). Local spatial autocorrelation statistics: Distributional issues and an application. *Geographical Analysis*, *27*(4), 286–306. https://doi.org/10.1111/j.1538-4632.1995.tb00912.x

Pearson, R. G., Raxworthy, C. J., Nakamura, M., & Townsend Peterson, A. (2007). Predicting species distributions from small numbers of occurrence records: A test case using cryptic geckos in Madagascar. *Journal of Biogeography*, *34*(1), 102–117. https://doi.org/10.1111/j.1365-2699.2006.01594.x

Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, *190*(3), 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026

Pickens, B. A., Carroll, R., Schirripa, M. J., Forrestal, F., Friedland, K. D., & Taylor, J. C. (2021). A systematic review of spatial habitat associations and modeling of marine fish distribution: A guide to predictors, methods, and knowledge gaps. *PLoS One*, *16*(5), e0251818. https://doi.org/10.1371/journal.pone.0251818

Pittman, S. J., & Brown, K. A. (2011). Multi-scale approach for predicting fish species distributions across coral reef seascapes. *PLoS One*, *6*(5), e20583. https://doi.org/10.1371/journal.pone.0020583

Pukui, M., & Elbert, S. (1986). *Hawaiian dictionary, revised & enlarged edition*. University of Hawaii Press.

Randall, J. E. (1987). Introduction of marine fishes to Hawaiian Islands. *Bulletin of Marine Science*, *41*, 490–502.

Randall, J. E. (2007). *Reef and shore fishes of the Hawaiian Islands*. Sea Grant College Program, University of Hawai'i. https://cir.nii.ac.jp/crid/1130000795985626752

Reaser, J. K., Burgiel, S. W., Kirkey, J., Brantley, K. A., Veatch, S. D., & Burgos-Rodríguez, J. (2020). The early detection of and rapid response (EDRR) to invasive species: A conceptual framework and federal capacities assessment. *Biological Invasions*, *22*(1), 1–19. https://doi.org/10.1007/s10530-019-02156-w

Roy, H. E., Pauchard, A., Stoett, P. J., Renard Truong, T., Meyerson, L. A., Bacher, S., Galil, B. S., Hulme, P. E., Ikeda, T., Kavileveettil, S., McGeoch, M. A., Nuñez, M. A., Ordonez, A., Rahlao, S. J., Schwindt, E., Seebens, H., Sheppard, A. W., Vandvik, V., Aleksanyan, A., … Ziller, S. R. (2024). Curbing the major and growing threats from invasive alien species is urgent and achievable. *Nature Ecology & Evolution*, *8*(7), 1216–1223. https://doi.org/10.1038/s41559-024-02412-w

Salimi, P., Creed, J. C., Esch, M. M., Fenner, D., Jaafar, Z., Levesque, J. C., Montgomery, A. D., Alidoost Salimi, M., Edward, J. K. P., Raj, K. D., & Sweet, M. (2021). A review of the diversity and impact of invasive non-native species in tropical marine ecosystems. *Marine Biodiversity Records*, *14*(1), 11. https://doi.org/10.1186/s41200-021-00206-8

Schumacher, B. D., & Parrish, J. D. (2005). Spatial relationships between an introduced snapper and native goatfishes on Hawaiian reefs. *Biological Invasions*, *7*(6), 925–933. https://doi.org/10.1007/s10530-004-2983-6

Seebens, H., Gastner, M. T., & Blasius, B. (2013). The risk of marine bioinvasion caused by global shipping. *Ecology Letters*, *16*(6), 782–790. https://doi.org/10.1111/ele.12111

Seebens, H., Meyerson, L. A., Rahlao, S. J., Lenzner, B., Tricarico, E., Aleksanyan, A., Courchamp, F., Keskin, E., Saeedi, H., Tawake, A., & Pyšek, P. (2024). IPBES invasive alien species assessment: Chapter 2. Trends and status of alien and invasive alien species. *Zenodo*. https://doi.org/10.5281/zenodo.10677067

Semmler, R. F., Martineau, G., Schiettekatte, N. M. D., Pratchett, M. S., Berumen, M. L., Parravicini, V., & Casey, J. M. (2025). Marine

13652664, 2026, 6, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2664.70452, Wiley Online Library on [28/09/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

heatwaves imperil emblematic reef fishes by altering the energetic landscape of coral reefs. *Journal of Animal Ecology*, *94*, 1553–1568. https://doi.org/10.1111/1365-2656.14238

Simberloff, D., Martin, J.-L., Genovesi, P., Maris, V., Wardle, D. A., Aronson, J., Courchamp, F., Galil, B., García-Berthou, E., Pascal, M., Pyšek, P., Sousa, R., Tabacchi, E., & Vilà, M. (2013). Impacts of biological invasions: What's what and the way forward. *Trends in Ecology & Evolution*, *28*(1), 58–66. https://doi.org/10.1016/j.tree.2012.07.013

Song, T., Huang, Y., Fang, L., Li, Y., Li, J., & Chang, J. (2024). Non-native species in marine protected areas: Global distribution patterns. *Environmental Science and Ecotechnology*, *22*, 100453. https://doi.org/10.1016/j.ese.2024.100453

Syfert, M. M., Smith, M. J., & Coomes, D. A. (2013). The effects of sampling bias and model complexity on the predictive performance of MaxEnt species distribution models. *PLoS One*, *8*(2), e55158. https://doi.org/10.1371/journal.pone.0055158

Tadaki, M., Clapcott, J., Holmes, R., MacNeil, C., & Young, R. (2023). Transforming freshwater politics through metaphors: Struggles over ecosystem health, legal personhood, an invasive species in Aotearoa New Zealand. *People and Nature*, *5*(2), 496–507. https://doi.org/10.1002/pan3.10430

Tanaka, K. (2026). Data and R codes for 'Persisting, emerging, and contracting: The dynamic nature of non-native hotspots and their implications for management'. *Zenodo*. https://doi.org/10.5281/zenodo.20336687

Toonen, R. J., Andrews, K. R., Baums, I. B., Bird, C. E., Concepcion, G. T., Daly-Engel, T. S., Eble, J. A., Faucci, A., Gaither, M. R., Iacchei, M., Puritz, J. B., Schultz, J. K., Skillings, D. J., Timmers, M. A., & Bowen, B. W. (2011). Defining boundaries for ecosystem-based management: A multispecies case study of marine connectivity across the Hawaiian archipelago. *Journal of Marine Sciences*, *2011*(1), 460173. https://doi.org/10.1155/2011/460173

Tyberghein, L., Verbruggen, H., Pauly, K., Troupin, C., Mineur, F., & De Clerck, O. (2012). Bio-ORACLE: A global environmental dataset for marine species distribution modelling. *Global Ecology and Biogeography*, *21*(2), 272–281. https://doi.org/10.1111/j.1466-8238.2011.00656.x

U.S. Geological Survey. (2025). *Nonindigenous aquatic species database*. http://nas.er.usgs.gov

Valavi, R., Elith, J., Lahoz-Monfort, J. J., & Guillera-Arroita, G. (2023). Flexible species distribution modelling methods perform well on spatially separated testing data. *Global Ecology and Biogeography*, *32*(3), 369–383. https://doi.org/10.1111/geb.13639

Vaughan, M. B., & Ayers, A. L. (2016). Customary access: Sustaining local control of fishing and food on Kaua'i's north shore. *Food, Culture & Society*, *19*(3), 517–538. https://doi.org/10.1080/15528014.2016.1208339

Venette, R. C., Gordon, D. R., Juzwik, J., Koch, F. H., Liebhold, A. M., Peterson, R. K. D., Sing, S. E., & Yemshanov, D. (2021). Early intervention strategies for invasive species management: Connections between risk assessment, prevention efforts, eradication, and other rapid responses. In T. M. Poland, T. Patel-Weynand, D. M. Finch, C. F. Miniat, D. C. Hayes, & V. M. Lopez (Eds.), *Invasive species in forests and rangelands of the United States: A comprehensive science synthesis for the United States forest sector* (pp. 111–131). Springer International Publishing. https://doi.org/10.1007/978-3-030-45367-1_6

Wehi, P. (2006). *Harakeke (Phormium tenax) ecology and historical management by Māori: The changing landscape in New Zealand* [PhD thesis]. University of Waikato.

Wehi, P. M., Kamelamela, K. L., Whyte, K., Watene, K., & Reo, N. (2023). Contribution of Indigenous Peoples' understandings and relational frameworks to invasive alien species management. *People and Nature*, *5*(5), 1403–1414. https://doi.org/10.1002/pan3.10508

Westbrooks, R. G., & Eplee, R. E. (2011). Early detection and rapid response (Simberloff, D. & M. Rejmanek).

Whiting, P., Savović, J., Higgins, J. P. T., Caldwell, D. M., Reeves, B. C., Shea, B., Davies, P., Kleijnen, J., & Churchill, R. (2016). ROBIS: A new tool to assess risk of bias in systematic reviews was developed. *Journal of Clinical Epidemiology*, *69*, 225–234. https://doi.org/10.1016/j.jclinepi.2015.06.005

Wiens, J. A., Stralberg, D., Jongsomjit, D., Howell, C. A., & Snyder, M. A. (2009). Niches, models, and climate change: Assessing the assumptions and uncertainties. *Proceedings of the National Academy of Sciences*, *106*, 19729–19736. https://doi.org/10.1073/pnas.0901639106

Work, T., Rameyer, R., Takata, G., & Kent, M. (2003). Protozoal and epitheliocystis-like infections in the introduced bluestripe snapper *Lutjanus kasmira* in Hawaii. *Diseases of Aquatic Organisms*, *57*, 59–66. https://doi.org/10.3354/dao057059

Zizka, A., Silvestro, D., Andermann, T., Azevedo, J., Duarte Ritter, C., Edler, D., Farooq, H., Herdean, A., Ariza, M., Scharn, R., Svantesson, S., Wengström, N., Zizka, V., & Antonelli, A. (2019). CoordinateCleaner: Standardized cleaning of occurrence records from biological collection databases. *Methods in Ecology and Evolution*, *10*(5), 744–751. https://doi.org/10.1111/2041-210X.13152

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. List of non-native taxa in Hawai'i with additional information regarding pathway of introduction, region of origin, habitat association in native and introduced ranges, and potential impacts.

Table S2. Number of occurrence records for non-native (and native) reef fishes in Hawai'i from two open-source databases—GBIF (Global Biodiversity Information Facility) and OBIS (Ocean Biodiversity Information System)—and corresponding AUC values from Maxent distribution models. Occurrence records reflect the total number of georeferenced specimens or observations available. AUC values (>0.9 indicate strong predictive performance) were obtained after filtering, cleaning and modelling each species' distribution.

Figure S1. Predicted habitat suitability for 27 non-native reef fish species across the Main Hawaiian Islands under baseline conditions (2000–2020), based on Maxent models. Suitability values range from 0 (unsuitable) to 1 (highly suitable), with warmer colours indicating more favourable conditions. Species exhibit distinct spatial patterns, reflecting differences in ecological preferences and environmental tolerances.

Figure S2. Mean predicted non-native reef fish richness (left) and associated uncertainty (right) across the Main Hawaiian Islands under baseline conditions (2000–2020). Richness values represent the sum of occurrence probabilities across 27 species, with darker shades indicating higher species richness. Uncertainty is represented by the standard deviation of richness values across bootstrap replicates, highlighting spatial variation in model confidence. Higher uncertainty was generally observed in areas of elevated richness near populated coastal zones.

Figure S3. Distance to port across the main Hawaiian Islands, based on the Global Fishing Watch anchorage dataset (Global Fishing

13652664, 2026, 6, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2664.70452, Wiley Online Library on [28/09/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Watch., 2020. Distance from Port, Version 1.0.). Port labels highlight key commercial, military and regional harbour facilities. Overlaid points (yellow circles) indicate statistically significant invasive species hotspots, identified using Getis-Ord Gi analysis.

Figure S4. Distribution of six oceanographic variables across three time periods under two SSP scenarios: Baseline (2000–2020), 2050s (mid-century) and 2090s (end-of-century). Values represent nearshore conditions within 5 km of the coast across Hawai'i. Data are from Bio-ORACLE v3.1.

Figure S5. Human population density across the main Hawaiian Islands, representing the average density from 2000 to 2020 based on the Gridded Population of the World, Version 4.11 (GPWv4) dataset from NASA's Socioeconomic Data and Applications Center (SEDAC) (CIESIN. 2018). The colour scale shows population density (persons per km^2) on a logarithmic scale. Overlaid points (pink squares) indicate statistically significant population hotspots, identified using Getis-Ord Gi analysis.

How to cite this article: Gajdzik, L., & Tanaka, K. R. (2026). Persisting, emerging and contracting: The dynamic nature of non-native hotspots and their implications for management. *Journal of Applied Ecology*, *63*, e70452. https://doi.org/10.1111/1365-2664.70452

13652664, 2026, 6, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2664.70452, Wiley Online Library on [28/09/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License