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Biological invasions in Morocco: First national inventory and management prioritization

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Abstract

Biological invasions pose a growing threat to biodiversity and economic stability, yet accurate risk assessments in the Global South are hampered by severe data gaps. Positioned at a biogeographical crossroads between the Mediterranean and Atlantic, Morocco lacks a unified national inventory to guide biosecurity. This study presents the first comprehensive, expert-validated inventory and functional analysis of invasive alien species (IAS) in Morocco. Integrating multi-source data, we documented 604 IAS across ecosystems, dominated by vascular plants (63.4%) and terrestrial arthropods (19.4%). Spatial modeling of 3,963 occurrences identified the Tangier-Rabat-Casablanca axis as the primary invasion corridor, driven by maritime trade and urbanization. We prioritized species into four management categories by integrating spatial occupancy, literature-inferred invasion statuses, expert consensus, and InvaCost economic data. Our analysis reveals a mismatch between local spatial footprint and global economic risk. While widespread species require long-term containment, the highest potential costs align with the 239 early detection and rapid response (EDRR) candidates. Furthermore, high-cost ecosystem engineers like *Acacia mearnsii* remain in the Latent Risk category due to missing local impact assessments. This reliance on global proxies highlights a hidden liability where high-risk species remain under-prioritized. We propose a strategic shift toward proactive EDRR strategies. This baseline enables Morocco to meet Target 6 of the Kunming-Montreal Global Biodiversity Framework and serves as a replicable model for prioritizing biological invasions in data-deficient regions of the Global South.

Keywords: Biological Invasions, Biosecurity, EDRR, Morocco, Global South, InvaCost, Kunming-Montreal Target 6.

Résumé

Les invasions biologiques constituent une menace croissante pour la biodiversité et la stabilité économique. Toutefois, dans les pays du Sud, l'évaluation précise des risques se heurte à de sévères lacunes en matière de données. Situé à un carrefour biogéographique entre la Méditerranée et l'Atlantique, le Maroc manque d'un répertoire national unifié pour orienter sa biosécurité. Cette étude présente le premier inventaire exhaustif des espèces exotiques envahissantes (EEE) au Maroc, validé par des experts et assorti d'une analyse fonctionnelle. En intégrant des données de sources multiples, nous avons recensé 604 EEE à travers divers écosystèmes, dominées par les plantes vasculaires (63,4 %) et les arthropodes terrestres (19,4 %). La modélisation spatiale de 3 963 occurrences a identifié l'axe Tanger-Rabat-Casablanca comme le principal corridor d'invasion, façonné par le commerce maritime et l'urbanisation. Nous avons hiérarchisé les espèces en quatre catégories de gestion en croisant l'occupation spatiale nationale, les statuts d'invasion déduits de la littérature, le consensus d'experts et les données économiques de la base InvaCost. Notre analyse révèle un décalage marquant entre l'empreinte spatiale locale et le profil de risque économique mondial. Alors que les espèces largement répandues nécessitent un confinement à long terme, les coûts potentiels les plus élevés sont associés aux 239 espèces candidates à une détection précoce et réaction rapide (EDRR). Par ailleurs, des espèces ingénieuses de l'écosystème à fort impact économique, comme *Acacia mearnsii*, restent reléguées dans la catégorie des risques latents faute d'évaluations d'impact à l'échelle locale. Ce recours à des extrapolations mondiales pour évaluer le risque local met en évidence

une vulnérabilité cachée, où des espèces à haut risque demeurent sous-priorisées. Nous proposons une réorientation stratégique vers des mesures EDRR proactives. Cet état de référence permet au Maroc de répondre à la Cible 6 du Cadre mondial de la biodiversité de Kunming-Montréal et offre un modèle reproductible pour la priorisation des invasions biologiques dans les régions du Sud souffrant d'un déficit de données.

Mots-clés : Invasions biologiques, Biosécurité, EDRR, Maroc, Pays du Sud, InvaCost, Cible 6 de Kunming-Montréal

Introduction

The unprecedented expansion of global trade and transport networks has effectively eroded natural biogeographical barriers, facilitating the spread of species beyond their native ranges at rates never before recorded (Seebens et al. 2021). It acts as a primary vector for biological invasions, recognized as a major driver of global biodiversity loss and ecosystem disruption (Pyšek et al. 2020; IPBES 2019). Beyond their ecological footprint, biological invasions (and Invasive Alien Species, IAS) impose staggering economic burden. Global costs were recently estimated to exceed US\$ 423 billion annually, having quadrupled every decade since 1970 (IPBES 2023). However, these global estimates often suffer from pronounced geographic and taxonomic biases, with significant data gaps remaining for Africa and the Global South (Diagne et al. 2021). This lack of data is often exacerbated by language barriers in scientific literature (Angulo et al. 2021), hinders accurate risk assessment and delays the implementation of effective biosecurity measures in developing nations (Bang et al. 2022).

To mitigate these escalating impacts, international frameworks emphasize early detection, pathway management, and rapid response as the most cost-effective strategies (Ahmed et al. 2022; Cuthbert et al. 2022). The Kunming-Montreal Global Biodiversity Framework, adopted in 2022, explicitly targets a 50% reduction in the rate of IAS introduction and establishment by 2030 (Target 6). Achieving this ambitious target requires robust, standardized national baselines to accurately track progress and prioritize management actions. As highlighted by the IPBES assessment report on biological invasions (IPBES 2023), there is an urgent need for these comprehensive national inventories. This call to action has very recently been embraced by the scientific community, with several journals launching special issues (including *NeoBiota*, *African Biodiversity & Conservation*, and *Biological Invasions*), dedicated to standardizing protocols and mobilizing data in the Global South. In consequence, several nations and regions have recently published robust standardized baselines, such as Brazil (Zenni et al. 2024), the Philippines and Southeast Asia (Abreo et al. 2025), and South Africa (Zengeya et al. 2026). Without comprehensive national inventories, countries remain reactive rather than proactive, often incurring massive economic costs despite widespread knowledge gaps (Bang et al. 2022).

Morocco, situated at the biogeographical crossroads of the Mediterranean and the Atlantic, is highly vulnerable to biological invasions due to its extensive maritime trade, tourism, and diverse climate zones. Recent assessments underscore the severity of this threat, estimating that biological invasions could inflict an annual economic burden ranging from US\$ 1.14 billion to US\$ 5.13 billion annually (El Jamaai et al. 2026). These costs are projected to be driven largely by damage to agriculture and public health rather than management, highlighting the urgent need for preventive biosecurity measures rather than curative responses (Ahmed et al. 2022).

Despite these projected economic risks, Morocco's response has historically been fragmented. While the issue is incorporated into the National Biodiversity Strategy and Action Plan (NBSAP), the country lacks a unified, dynamic national inventory of IAS. Existing data are scattered across taxonomic-specific checklists (e.g., Menioui 2021; Taybi et al. 2023 for freshwater; Mghili et al. 2024 for marine), grey literature, and other lists (Sahara and Sahel Observatory 2020). This fragmentation prevents a holistic understanding of invasion hotspots, pathways, and overall threat prioritization.

To address this critical national baseline gap and facilitate proactive management, this study presents the first comprehensive, expert-validated national inventory and detailed taxonomic analysis of invasive alien species in Morocco. Specifically, (1) we synthesized data from global repositories and regional literature, applying a stratified protocol to distinguish established species with recognized invasive status; (2) we analyzed their taxonomic and ecological characteristics; and (3) we mapped species distributions to identify invasion hotspots. The resulting baseline is essential for supporting the national strategy for biodiversity and aligning Morocco's biosecurity framework with the ambitious targets of the Kunming-Montreal Global Biodiversity Framework, as well as to serve as a model for data mobilization in data-deficient regions of the Global South.

Methods

Compilation of the invasive species inventory

A comprehensive inventory of invasive alien species (IAS) in Morocco was compiled from multiple national and international sources. The global databases consulted included the Global Invasive Species Database (GISD; <http://www.iucngisd.org/gisd/>), the Global Register of Introduced and Invasive Species (GRIIS; <http://griis.org/>), and the Standardizing and Integrating Alien Species (SinAS) workflow (Seebens et al. 2020). These were supplemented by regional reference works, including the *Terrestrial Invasive Alien Species in the Arab Maghreb* report (Sahara and Sahel Observatory, 2020), and recent taxonomic checklists for terrestrial (Menioui 2021), freshwater (Taybi et al. 2023), marine ecosystems (Mghili et al. 2024), as well as the forthcoming "Alien Flora of Morocco" (Canavan et al. in prep). To supplement these datasets, systematic literature searches were conducted via Web of Science, Google Scholar, and Google Search to retrieve relevant peer-reviewed and grey literature. In addition, we engaged with national and international experts and stakeholders to validate records and provide access to unpublished or locally archived data. This approach ensured that the inventory listed both well-documented IAS and those less visible in formal databases.

Data filtering and taxonomic verification

To ensure data accuracy and reliability, we applied a multi-step filtering and stratification process to the initial database (see Fig. 1). We first performed a taxonomic standardization. Species names were first verified against authoritative databases including CABI and the Catalogue of Life. The list was then standardized using the Global Biodiversity Information Facility (GBIF) Backbone Taxonomy (Chamberlain et al. 2025). We retrieved accepted

names, taxonomic statuses, and unique GBIF backbone taxon ID. Synonyms were automatically resolved by replacing them with their accepted names. Entries identified only at the genus or subspecies level were removed to maintain consistency at the species level. Duplicate records were cross-checked and eliminated by filtering based on taxon keys.

We then verified the native status of the species. Species confirmed as native to Morocco were excluded. The non-native status was validated by experts from relevant taxonomic groups: Pr. Ahmed Taheri (Formicidae), Pr. Nard Bennis (Freshwater fauna), Dr. Sabour Brahim (Algae), Dr. Sergi Trocoli (Coleoptera), Pr. Susan Canavan (Flora), Pr. Yousra Banyahia (Arthropoda), and Pr. Kettani Kawtar (Diptera). When direct expert input was unavailable, we consulted additional authoritative sources including GRIN Global (Germplasm Resource Information Network, <https://www.grin-global.org/>), AlgaeBase (<https://www.algaebase.org/>), Avibase (<https://avibase.bsc-eoc.org/>), INRA (Institut national de la recherche agronomique, <https://www.inra.org.ma/>), Doris (<https://doris.ffessm.fr/>), CIESM (Commission Internationale pour l'Exploration Scientifique de la Méditerranée, <https://ciesm.org/>), IUCN Red List (International Union for Conservation of Nature, <https://www.iucnredlist.org/>), World Spider Catalog (<https://wsc.nmbe.ch/>), FAO (Food and Agriculture Organization, <https://www.fao.org/home>), Molluscabase (<https://www.molluscabase.org/>), SeaLifeBase (<https://www.sealifebase.se/>), AnimalDiversity (<https://animaldiversity.org/>), Florabase (<https://florabase.dbca.wa.gov.au/>), NISIC (USDA National Invasive Species Information Center, <https://www.invasivespeciesinfo.gov/>), WoRMS (World Register of Marine Species, <https://www.marinespecies.org/>), and relevant literature. The final dataset preserves original source information, taxonomic details, native/alien status, and expert-reviewed comments, forming a robust reference for IAS in Morocco (Supplementary Material Table 1).

Finally, to account for differences in data availability and introduction pathways between taxa, we applied specific filtering protocols: we first filtered alien flora. Given the high prevalence of agricultural introductions, the plant dataset underwent a rigorous two-step filtering process: (1) Exclusion of cultivated taxa: We manually reviewed botanical records to identify and exclude taxa present in Morocco solely under cultivation (e.g., *Triticum* spp., *Hordeum* spp., *Olea europaea*). These were removed from all spatial analysis to prevent agricultural land use from confounding the assessment (Supplementary Material Table S1, spreadsheet Excluded_Taxa). (2) Stratification by evidence level: The remaining non-cultivated alien plants were classified into two categories: (a) Recognized invasive plants: Taxa classified as “invasive” in GRIIS-Morocco or validated by local experts as established and spreading; (b) Naturalized / Uncertain: Taxa confirmed as established in the wild in Morocco but lacking sufficient evidence of invasive spread. These were included in the taxonomic analysis but excluded from density mapping to avoid false positives.

We then validated the alien fauna. Animal species were compiled from recent authoritative checklists (e.g., Taybi et al. 2023; Mghili et al. 2024) and supplemented by direct validation from taxonomic experts (e.g., for terrestrial invertebrates). As these records were pre-screened by experts to include only invasive species, and do not suffer from the same agricultural confounding factors as plants, all verified animal records were classified as recognized invasive animal species.

Taxonomic and ecological characterization

To facilitate impact assessments and management prioritization, we characterized the complete national inventory, including recognized invasive plant species, naturalized plants, as well as recognized invasive fauna species, using taxonomic, functional and pathway criteria.

In the taxonomic classification, all species were assigned to hierarchical ranks (i.e., Kingdom, Phylum, Class, Order, Family) using the standardized nomenclature retrieved from the GBIF Backbone Taxonomy.

To characterize the ecological strategies of the invasive biota, we assigned functional traits and environment types (mainly terrestrial, marine, and freshwater) (Supplementary material Table S1) using a hierarchical protocol based on standardized ecological classifications and expert-curated databases. For plants, we used plant growth forms, categorized into seven classes following Engemann et al. (2016). Functional traits were assigned based on taxonomic affiliation (Class, Family, and Genus) using a rule-based approach derived from Plants of the World Online (POWO 2026; <https://powo.science.kew.org>) and the World Flora Online (WFO 2026; <https://www.worldfloraonline.org>). Species were classified based on their dominant life form in the Mediterranean region: trees, shrubs, herbs and vines.

We assigned trophic guilds to animals (herbivore, predator, omnivore, detritivore) using a stratified approach. For vertebrates, trophic data for birds and mammals were aligned with EltonTraits 1.0 (Wilman et al. 2014). Fish traits were retrieved from FishBase (Froese and Pauly 2023) using the “rfishbase” package (Boettiger et al. 2012). For invertebrates, due to the high taxonomic diversity and data scarcity for specific insect traits, we applied a Hierarchical Inference Method (e.g., Tachet et al. 2010; Gossner et al. 2015). Species were first matched against the *AnimalTraits* database (Herberstein et al. 2022) and standard freshwater ecology keys (e.g., Tachet et al. 2010). To maintain analytical rigor, taxa belonging to families with highly variable or ambiguous feeding strategies (e.g., Staphylinidae, Miridae) were classified as “Diverse/Unknown” rather than assigning a low-confidence guild.

Spatial description and hotspot detection

We explored the spatial structure of biological invasions in Morocco by modeling the density of occurrences for the recognized invasive species from the inventory.

Data acquisition and cleaning: Occurrence records were searched for all 344 recognized invasive alien species in the Global Biodiversity Information Facility database (GBIF, <https://doi.org/10.15468/dl.9j6th7>; Supplementary Material Table S2). To ensure the analysis reflected genuine invasion pressure rather than agricultural land use or historical cultivation, the data was subjected to a two-step filtering process (see Fig.1). First, a new taxonomic filtering was applied to exclude widespread archaeophytes (i.e., non-native plant species introduced in ancient times, typically prior to 1500 CE) and traditional crops that were not detected in the first step (we explicitly filtered out two main crops: *Ficus carica* and *Punica granatum*) that are often recorded in biodiversity databases but do not represent “true” ecological invasions in the modern context. Second, spatial cleaning was performed using the “sf” package in R. Records with high coordinate uncertainty (>10km) and duplicate coordinates per species were removed. We performed a spatial intersection with the official 12

Administrative Regions of Morocco (2015 territorial division) to exclude erroneous coordinates falling in the Atlantic Ocean or neighboring countries. This process resulted in a final dataset of 3,963 verified occurrence records representing 177 species (51.4% of the recognized list). Taxa without digital occurrence records (N=167) were excluded from the spatial modeling but retained in the taxonomic and ecological analysis.

Hotspot analysis and species-specific distributions: Spatial patterns of invasion were analyzed using the accumulated occurrence data. To identify high-intensity invasion zones, a 2D Kernel Density Estimation (KDE) was performed on the aggregated occurrence points using the “stat_density_2d” function from the “ggplot2” package in R (Wickham 2016). This allowed the visualization of an invasion intensity gradient without imposing a rigid grid. To visualize distinct dispersal strategies, occurrence maps were generated for the 12 most widespread confirmed species, illustrating the contrast between broadly distributed taxa and localized specialists. All visualizations were produced using the “ggplot2” and “sf” packages in R (Wickham 2016; Pebesma 2018; Pebesma and Bivand 2023).

Management classification, potential economic impact, and introduction pathways

Management prioritization: Species were stratified into four operational management categories based on invasion status (Blackburn et al. 2011), environment type, and current spatial extent (verified GBIF occurrences) (Supplementary Material Table S3). The first category, *Latent Risk (Naturalized/Uncertain)*, comprises alien species established in the wild but not currently confirmed as spreading invasively, encompassing both latent invaders in a lag phase and taxa for which national status data is lacking due to research gaps. The second group identifies *EDRR candidates*, defined as known invaders with restricted distributions (fewer than 50 verified occurrences), representing optimal candidates for Early Detection and Rapid Response (EDRR) and potential eradication. Widespread known invaders (more than 50 occurrences) in terrestrial systems were classified as *Containment (Terrestrial)* category; these species are established beyond feasible eradication levels, and require long-term suppression strategies. Finally, the *Containment (Aquatic)* category includes all confirmed aquatic and marine invaders regardless of abundance. Given the high connectivity and low eradication success rates in aquatic systems (Giakoumi et al. 2019), these species require site-specific biosecurity measures to protect high-value ecosystems such as Ramsar wetlands and coastal lagoons.

Economic cost assessment: To estimate the potential economic risk associated with the identified species, we analyzed global cost data from the *InvaCost* global database (V4.1; Diagne et al. 2020; <https://doi.org/10.6084/m9.figshare.12668570>). We restricted the analysis to cost estimates classified as “observed” and “high” reliability, excluding potential or extrapolated costs, and further filtered for entries defined at “Country” or “Site” spatial scales. To standardize costs across varying timeframes, we implemented a year repair protocol to correct incomplete duration data and expanded the costs yearly. We then calculated the Mean Annual Cost (USD) for each species. This metric, derived from 115 species in the inventory that matched these robust criteria, serves as a proxy for the potential financial liability these species pose to national agriculture, infrastructure, and ecosystem services.

Introduction pathways: Introduction pathways were assessed for the full national inventory (N=604) by strictly cross-referencing species with two global standard datasets: Saul et al. (2017) and Turbelin et al. (2022). These databases harmonize pathway information from the IUCN Global Invasive Database (GISD), DAISIE, and InvaCost according to the Convention on Biological Diversity (CBD) classification scheme, which categorizes introductions into six primary vectors: release in nature (e.g., biological control, erosion control); escape from confinement (e.g., ornamental horticulture, agriculture, forestry); transport-contaminant (e.g., contaminants of nursery material or seed); transport-stowaway (e.g., hull fouling, ballast water); corridor (e.g., Lessepsian migrants via the Suez Canal); unaided (natural dispersal across borders). A hierarchical assignment strategy was used: species were first matched against Saul et al. (2017). For species not found, the Turbelin et al. (2022) database was queried to fill gaps, particularly for economically important invasive species. For species absent from both global datasets, a single biophysical inference rule was applied: marine species restricted to submerged habitats were assigned to “transport-stowaway” (hull fouling/ballast) due to the absence of alternative vectors in the region. All remaining species were classified as “data deficient” to explicitly quantify the gap in biosecurity knowledge.

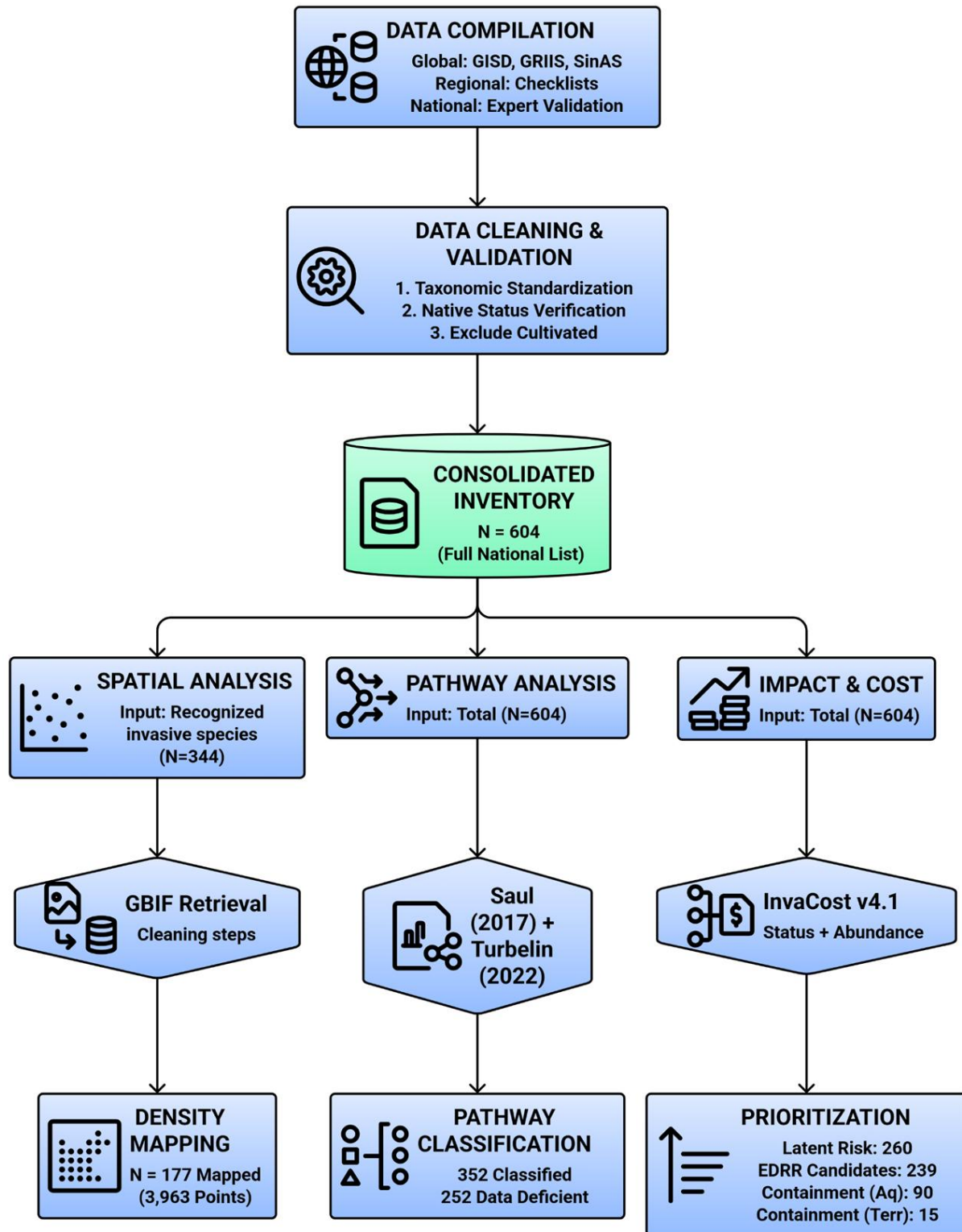


Fig. 1 Methodological workflow used to compile and analyze the Moroccan Invasive Alien Species Inventory. The process integrates global and national data sources, filtered through expert validation to remove native and strictly cultivated taxa. The final inventory (N = 604) was subjected to three parallel descriptive analyses: (1) Spatial analysis, utilizing GBIF occurrence data for recognized invasive species to model invasion hotspots; (2) Management and impact assessment, integrating invasion status, spatial abundance, and global economic costs to stratify species into priority management categories; and (3) Pathway classification, using global databases to identify introduction pathways. Numbers refer to the number of species, unless specified otherwise

Results

Taxonomic composition of IAS in Morocco

The national inventory documented a total of 604 invasive alien species. The assemblage spans five kingdoms, 14 phyla, 29 classes, 94 orders, and 197 families (Fig. 2).

The inventory is numerically dominated by the kingdom Plantae (N=383; 63.4%) followed by Animalia (N=204; 33.8%). Minor contributions were recorded from Fungi (N=11; 1.8%), Chromista (N=5; 0.8%), and Bacteria (N=1; 0.2%). At the phylum level, all plant species were classified within Tracheophyta (vascular plants). The animal kingdom was dominated by Arthropoda (insects, crustaceans, arachnids) and Chordata (vertebrates).

Among the alien flora, the class Magnoliopsida (dicots) was the most prevalent (N= 313), accounting for the vast majority of flowering plants, followed by Liliopsida (monocots, N=63) and Pinopsida (N=5). At the order level, the most frequent plant orders were Caryophyllales (N=58), Fabales (N=42), and Asterales (N=38). Other prominent orders included Solanales (N= 38) and Poales (N=30). The most species-rich plant families were Fabaceae (N=42), Asteraceae (N=38), and Solanaceae (N=30). Poaceae and Amaranthaceae were the next most represented families, with 28 and 26 species, respectively.

Among the alien fauna, the class Insecta was the most represented group (N=96). Other well-represented animal groups included Malacostraca (crustaceans; N=12) and Gastropoda (snails; N=8). The animal orders were led by Coleoptera (beetles; N=33) and Hymenoptera (ants, wasps, bees; N=25). Within Hymenoptera, the family Formicidae (ants) was the most diverse (N=17). Vertebrate orders were dominated by freshwater fish, specifically Cypriniformes (carps; N=14) and Perciformes (N=12). The family Cyprinidae (carps) was the most diverse. Other notable animal families included Bostrichidae (N=11), Curculionidae (N=9), and Centrarchidae (N=8).

Regarding the distribution of IAS in different ecosystems, terrestrial ecosystems hosted the vast majority of IAS (N=452; 74.8%), while marine and freshwater or inland aquatic components ecosystems supported N=47 and N=42 species, respectively. Additionally, N=1 species was documented spanning both terrestrial and freshwater systems, N=3 were classified as host-associated, while N=60 species (9.9%) lacked definitive environmental classification.

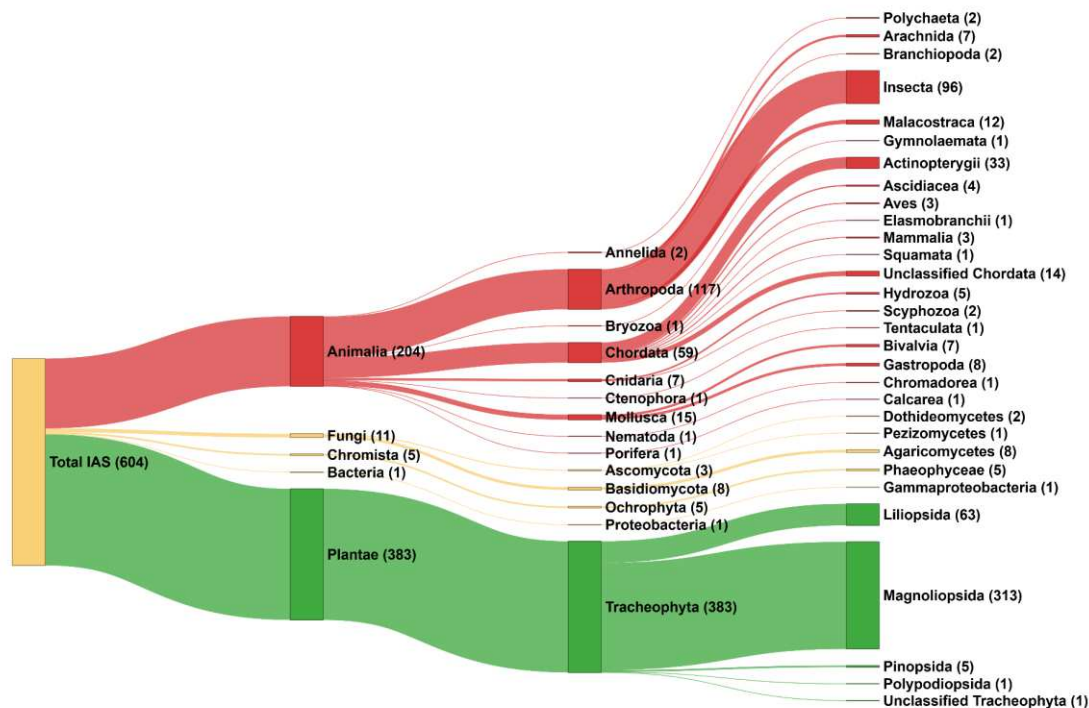


Fig.2 Taxonomic flow and composition of the invasive alien species of Morocco (N=604). The Sankey diagram visualizes species diversity patterns across Kingdom, Phylum, and Class levels. The width of flows is proportional to the number of species. Flows are color-coded by kingdom: Plantae (green) and Animalia (red), other (yellow)

Functional group and habitat type composition

Terrestrial ecosystems hosted the vast majority of the recorded alien biota, reflecting the numerical dominance of vascular plants and terrestrial arthropods. While aquatic environments supported a smaller but taxonomically distinct assemblage.

Among the alien flora (N=383 species), the functional spectrum was overwhelmingly dominated by herbs (N=317; 82.8%), encompassing widespread ruderal weeds and annual grasses adapted to disturbed agricultural landscapes. Woody perennials constituted a significant secondary group, with shrubs (N=28 species; 7.3%) and trees (N=27 species; 7.0%) accounting for forestry introductions (e.g., *Acacia*) and ornamental escapes. Specialized growth forms, including vines and lianas represented a minor functional cluster (N=11 species; 2.9%).

Trophic guilds were successfully assigned for 49.5% of the animal species (N=101), while the remaining 103 taxa (50.5%, mostly highly diverse invertebrate families) remained unclassified under the “Unknown” category. Among the assigned fauna, the invasive community is dominated by herbivores (N=42; 41.6% of assigned taxa), consisting mainly of phytophagous insects that pose risks to crops and agriculture. Omnivores (N=33; 32.7% of assigned taxa) formed the second largest guild, a group driven by ecologically plastic taxa such as invasive ants (Formicidae) and freshwater carps (Cyprinidae). Predators comprised 16 species (15.8% of assigned taxa), followed by specialized groups such as filter-feeders (N=7; 6.9%), parasites (N=2; 2.0%), and detritivores (N=1; 1.0%). These heterotrophic guilds were prominent in aquatic systems, reflecting the introduction of biocontrol agents (e.g., the mosquitofish *Gambusia holbrooki*) and marine invertebrates (e.g., the ascidian *Botrylloides niger*).

The relationship between taxonomic groups, habitats, and ecological characteristics (Fig. 3) reveals distinct ecological partitions. The terrestrial ecosystems are functionally dominated by autotrophic producers (herbaceous plants) and primary consumers (insect herbivores). Conversely, aquatic ecosystems (Marine and Freshwater) are characterized by a shift toward heterotrophy, dominated by omnivores (e.g., *Cyprinus carpio*) and predators (e.g., *Micropterus salmoides*). Marine environments specifically highlighted the distinct role of filter-feeders and predators among introduced crustaceans and mollusks, illustrating an invasion dynamic contrasting with the terrestrial realm.

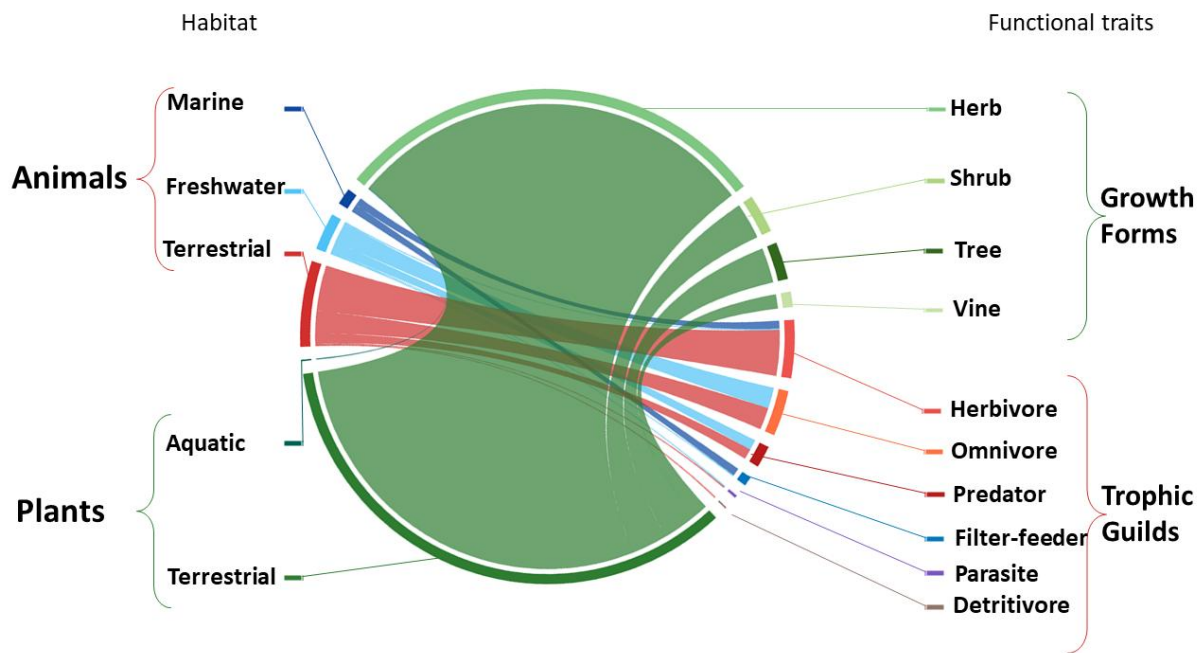


Fig. 3 Functional and environmental composition of invasive alien species in Morocco (N = 604). The chord diagram visualizes the flow from taxonomic-environmental groups (left semicircle) to ecological characteristics (right semicircle). The width of each chord is proportional to the number of species

Spatial analysis

The spatial analysis, based on 3,963 verified occurrence records representing 177 recognized invasive species (51.4% of the recognized inventory), reveals a distribution pattern linked to anthropogenic corridors and specific bioclimatic zones (Fig. 4a).

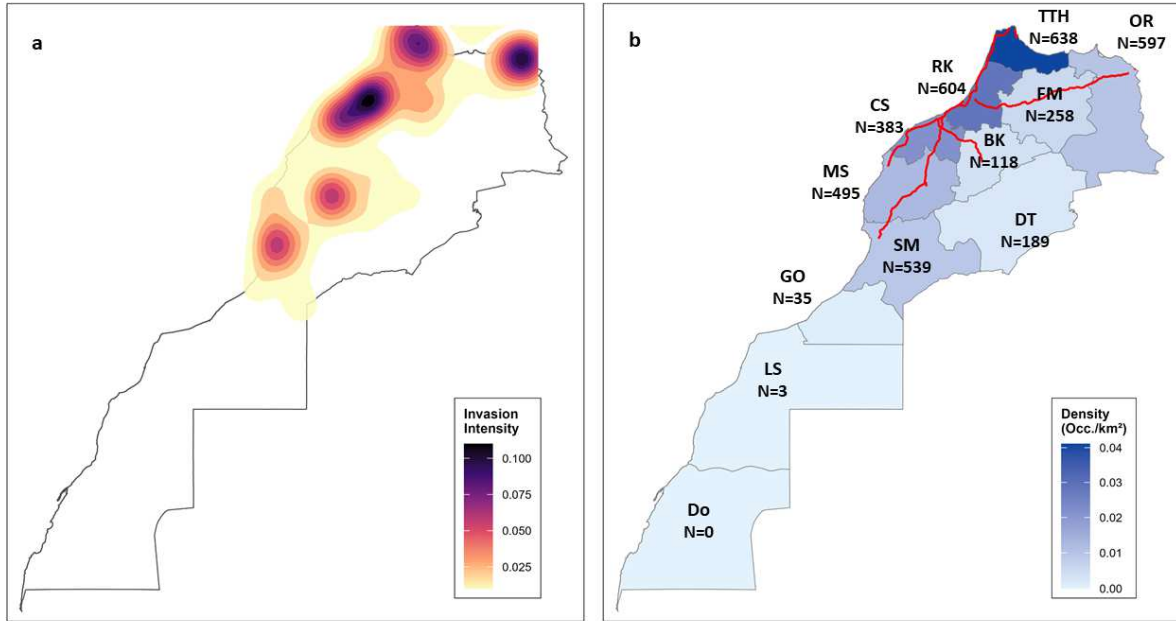


Fig. 4 Spatial analysis of biological invasions in Morocco. **(a)** Hotspots of biological invasion illustrating the intensity of invasion pressure (using the Kernel density estimation) based on 3,963 verified occurrence records. **(b)** Invasion density by administrative region displaying the number of records per km² across the 12 official administrative regions. Density values are log-transformed ($\log(x+1)$) to visualize gradients. Region codes: **BK** Béni Mellal-Khénifra; **CS** Casablanca-Settat; **DO** Dakhla-Oued Ed-Dahab; **DT** Drâa-Tafilalet; **FM** Fès-Meknès; **GO** Guelmim-Oued Noun; **LS** Laâyoune-Sakia El Hamra; **MS** Marrakech-Safi; **OR** Oriental; **RK** Rabat-Salé-Kénitra; **SM** Souss-Massa; **TTA** Tanger-Tétouan-Al Hoceïma. The national motorway network is overlaid in red

Analysis by administrative region (Fig. 4b, Supplementary Table S2, spreadsheet 5_Regional_Statistics) highlights distinct accumulation zones for invasive taxa. The highest proportion of invasive records was documented in the Tanger-Tétouan-Al Hoceïma region (16.1% of total occurrences), followed by Rabat-Salé-Kénitra (15.2%) and the Oriental region (15.1%). The Souss-Massa-Draâ region ranked fourth (13.6%), yet reflects a critical hub for intensive horticulture and tourism, facilitating the spread of widespread ruderal invaders such as *Nicotiana glauca* (N=129 in this region alone) and *Ricinus communis* (N=67). In contrast, the high recording in the Oriental region is driven largely by marine invasions in coastal lagoons (e.g., Nador), dominated by the ascidian *Botrylloides niger* (N=160) and the polychaete *Branchiomma luctuosum* (N=62).

When corrected for surface area, the Tanger-Tétouan-Al Hoceïma region exhibits the highest invasion density (0.041 occurrences/km²), confirming its role as the primary gateway for biological introductions via the Strait of Gibraltar. It is followed by Rabat-Salé-Kénitra (0.029 occurrences/km²) and Casablanca-Settat (0.022 occurrences/km²), underscoring the correlation between invasion pressure, urbanization, and road infrastructure. The Kernel Density Estimation (KDE) identified three primary invasion hotspots (Fig. 4a). First *the northern gateway*, a high-density cluster surrounding the Tangier-Tetouan axis, driven by maritime connectivity with Europe. Then *the coastal Atlantic axis*, a continuous band of invasion pressure connecting the economic capitals (Kenitra-Rabat-Casablanca), strongly overlapping with the national motorway network and urban growth (Fig. 4b). And finally, the *Agadir hub*, a distinct hotspot in the Sous-Massa basin, associated with disturbed agro-ecosystems and semi-arid climate favoring subtropical invasive flora.

Species-specific mapping (Fig. 5) illustrates the prevalence of the top invaders. *Nicotiana glauca* (N=459) and *Ricinus communis* (N=338) emerge as the most widespread taxa, exhibiting broad ecological amplitude across

disturbed habitats in the northern and central regions. *Oxalis pes-caprae* (N=272) remains a dominant agricultural weed. In contrast, region-specific dominance is observed for *Verbesina encelioides* (N=35 in Souss-Massa) and marine specialists like *Botrylloides niger* (N=161) in the Mediterranean.

It is notable that 167 recognized invasive species (48.5% of the inventory) were excluded from the spatial modeling. This subset consists of 165 species for which accessible georeferenced data are currently unavailable in global repositories. The remaining two species, *Ficus carica* and *Punica granatum*, were excluded as widespread cultivated crops.

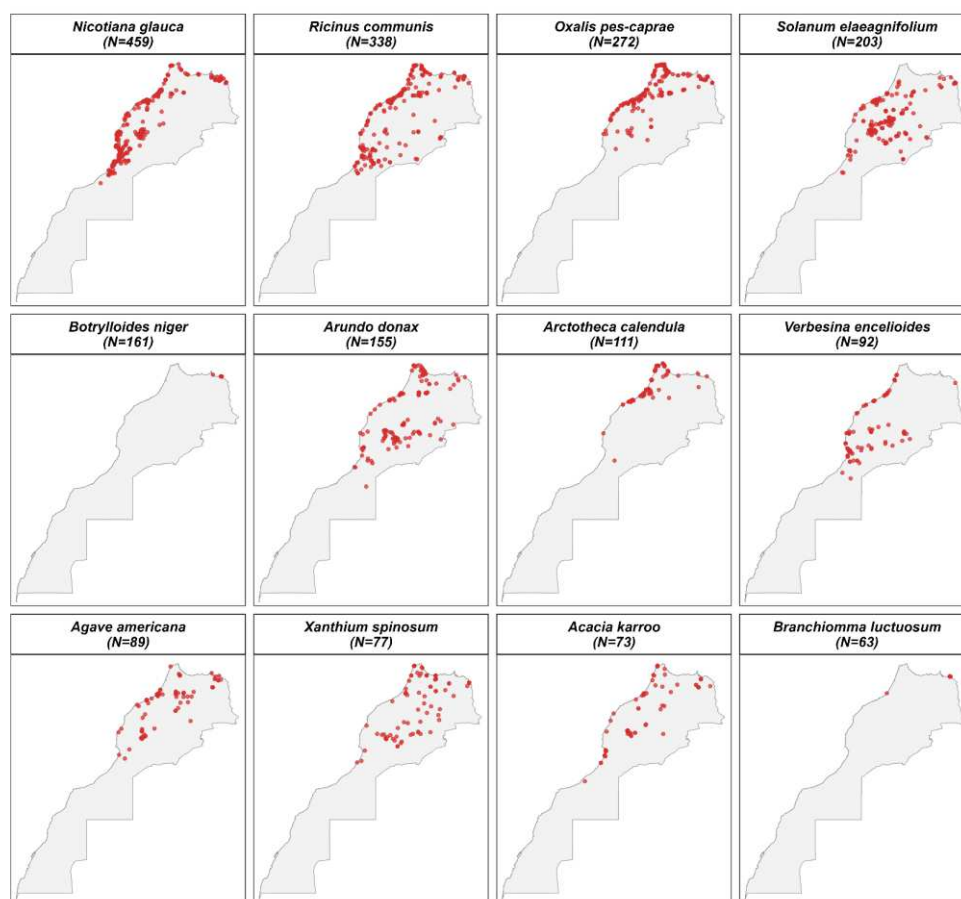


Fig. 5 Distributions of the top 12 widespread invasive species. Panels are sorted by decreasing abundance, with the total number of occurrences (N) indicated for each species

Introduction pathways, management classification and potential economic impact

To reconstruct invasion dynamics and prioritize mitigation efforts, we analyzed the links between introduction pathways, management status categories of invasive alien species, and potential economic risks.

We successfully classified the introduction pathways for 58.3% IAS of the inventory (N=352 species), while 252 IAS remain data deficient. The dominant pathway for introduction was escape from confinement (N=272 IAS), primarily driven by the ornamental plant trade and horticulture. Species introduced via this pathway often remain localized near urban centers or agricultural zones and typically fall into the *Latent Risk* category. In contrast, the transport-stowaway pathway (N=66 IAS), while less frequent, is strongly linked to the *Containment (Aquatic)*

category. This pathway is particularly critical for marine and aquatic invasions where species introduced via hull fouling and ballast water rapidly establish populations that are difficult to contain (Fig. 6).

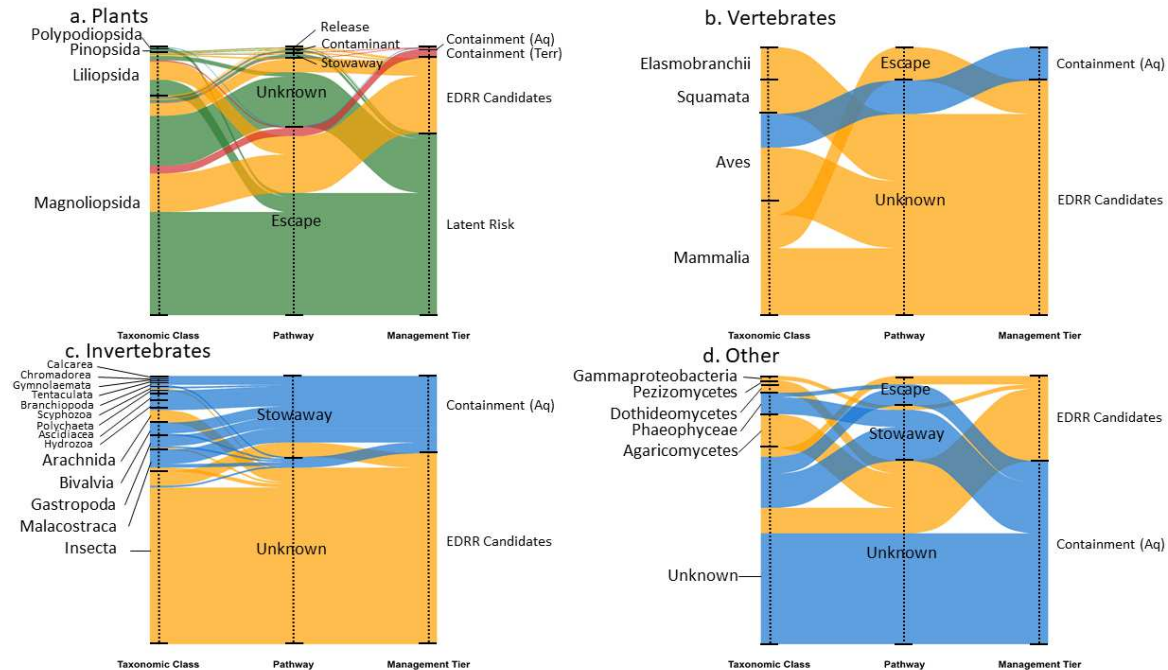


Fig. 6 Flow of invasive species across three dimensions: taxonomic class (left), introduction pathways (center) to their current management classification (right). To enhance readability, the diagram is divided into four separate panels representing the broad taxonomic groups (Plants, Invertebrates, Vertebrates, and Other). The width of the flows is proportional to the number of species. Colors represent species management categories

Regarding the four operational management categories for prioritization of species (Supplementary Material Table S3), we identified 15 terrestrial species for the *Containment (Terrestrial)* group, representing established, widespread terrestrial invaders that require long term suppression or control (e.g., *Acacia saligna*, *Ricinus communis*). While 90 aquatic and marine species were assigned to the *Containment (Aquatic)* group (e.g., the marine acadian *Botrylloides niger* and freshwater species like *Pontederia crassipes* and *Cyprinus carpio*).

In addition, we identified 239 species as *EDRR Candidates*. This group is characterized by limited confirmed occurrences (≤ 50 records) and includes confirmed terrestrial invaders that have not yet spread widely. These taxa represent the most cost-effective targets for rapid eradication before populations start to spread (e.g., the yellow fever mosquito *Aedes aegypti* and the Mediterranean fruit fly *Ceratitis capitata*). The remaining 260 species fall into the *Latent Risk* category. This group includes species flagged as invasive globally but for which national data on spread and impact is currently insufficient to confirm their invasive status (e.g., *Acacia mearnsii*, *Lantana camara*).

While specific national costs are under-documented, the species currently present in the Moroccan national inventory have caused substantial economic damage globally (Fig. 7). The economic distribution was highly uneven among the four operational management categories, with the *EDRR Candidates* category representing the most significant potential financial burden. This category included the species with the single highest mean annual cost, the yellow fever mosquito *Aedes aegypti* (US\$ 828.0 million), followed by the codling moth *Cydia pomonella* (US\$ 444.3 million) and the Mediterranean fruit fly *Ceratitis capitata* (US\$ 362.4 million). The *Containment (Aquatic)* category also reflected major economic burdens, led by the water hyacinth *Pontederia crassipes* (US\$

68.8 million) followed by the common carp *Cyprinus carpio* (US\$ 14.3 million). For the species classified as *Latent Risk*, the black wattle *Acacia mearnsii* recorded the highest mean annual cost (US\$ 153.8 million), while *Lantana camara* accounted for US\$ 5.0 million. In contrast, the *Containment (Terrestrial)* category showed lower reported costs, with the highest values attributed to *Acacia saligna* (US\$ 760,000) and *Ricinus communis* (US\$ 116,000).

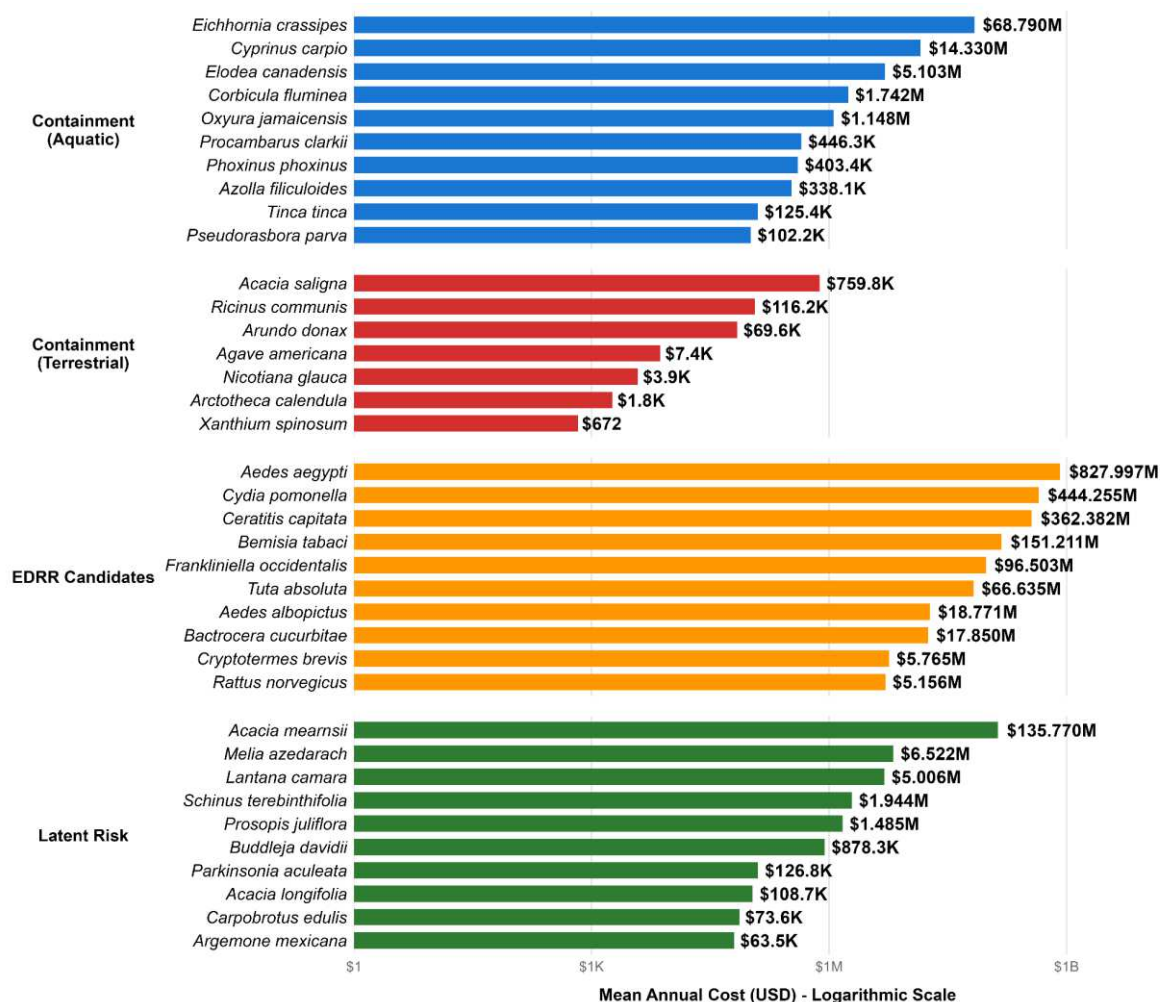


Fig. 7 Annual mean of economic costs (USD 2017) outside Morocco of the top-ten invasive species present in the Moroccan National Inventory grouped by the four operational management categories of prioritization: Containment (Aquatic), Containment (Terrestrial), EDDR Candidates, Latent Risks. M for million, K for thousand

Discussion

The first comprehensive baseline inventory

This study presents the first unified, functionally stratified inventory of invasive alien species (IAS) in Morocco, documenting 604 taxa across terrestrial, freshwater, and marine ecosystems. In contrast to previous fragmentary checklists, this dataset results from a standardized workflow that strictly filters native and cultivated taxa, while simultaneously integrating available data on species distribution and potential economic costs. We used a hybrid approach, combining digital mining with local expert knowledge, which helped address the scarcity of digital biodiversity data often characterizing the Global South. By excluding species lacking verifiable spatial data and

strictly classifying management status, we move beyond a simple species count to provide an operational tool for biosecurity (McGeoch et al. 2010). The resulting inventory reflects a distinct taxonomic profile, numerically dominated by vascular plants (63.4%) and terrestrial arthropods (19.4%), a pattern consistent with invasion profiles in Southern Europe and the wider Mediterranean Basin (Arianoutsou et al. 2013; Roques et al. 2010; Pyšek et al. 2017), where agricultural history, landscape fragmentation, and climate convergence favor the establishment of ruderal specialists (Gaertner et al. 2009).

This methodological approach directly aligns with a growing, coordinated effort across the Global South to standardize biological invasion data. Highlighted as a critical need in the recent IPBES global assessment on invasive alien species, developing nations are increasingly moving from isolated biodiversity checklists to dynamic databases. For instance, recent initiatives pioneered by researchers like John Wilson and the South African National Biodiversity Institute (SANBI) have generated comprehensive triennial national status reports, stimulating a wave of structured national checklists across the continent. Recent examples published in dedicated special issues, such as the updated alien flora checklist for Zimbabwe (Mayori 2026), demonstrate that standardizing national inventories is a foundational step for unlocking evidence-based biosecurity policy in developing economies.

Functional shifts and ecosystem vulnerability

The functional trait analysis reveals a distinct contrast in how invasions alter Moroccan ecosystems. Terrestrial invasions are primarily driven by resource competition, and are dominated by invasive herbs (78.1% of alien flora) that thrive in disturbed agro-ecosystems (Gaertner et al. 2009). In contrast, freshwater invasions are characterized by trophic restructuring. The prevalence of omnivores (e.g., *Cyprinus carpio*) and predators (e.g., *Micropterus salmoides*) suggests a significant threat to endemic amphibian and invertebrate diversity through direct predation and competition (Gallardo et al. 2016; Cucherousset and Olden 2011). In the same way, the marine invasion profile, defined by filter-feeders and crustaceans, reflects the strong influence of marine traffic (Seebens et al. 2013). This contrast highlights that while terrestrial management must often focus on habitat restoration to reduce ruderal dominance (Hulme 2006), aquatic management requires urgent control of specific high-impact trophic guilds introduced via hull fouling and ballast water (Molnar et al. 2008).

Spatial accumulation and spatial bias

The spatial analysis identifies the Tanger-Rabat-Casablanca axis as the primary area of accumulation for biological invasion in Morocco. Linking it to the anthropogenic corridor connecting the Strait of Gibraltar to the economic capital, effectively acting as a conduit for species introduction (Lockwood et al. 2005). This concentration confirms Morocco's role as a biogeographical crossroad, facilitating both the southward spread of Palearctic invaders and the northward expansion of Afrotropical taxa into Europe, a process expected to accelerate under climate change. This phenomenon is increasingly driven by climate-induced range shifts such as topicalization, where warm-water species (e.g., the bluespotted cornetfish *Fistularia commersonii*) expand into historically temperate marine ecosystems (Vergés et al. 2014). And borealization, where temperate and boreal taxa expand into higher latitudes and cooler biomes (Campana et al. 2020). Within this broad invasion corridor, however, distinct distribution patterns emerge. The contrast found in our results between widespread generalists and regional specialists

illustrates how local environment filters (e.g., aridity in Souss-Massa) and introduction pathways (e.g., maritime traffic in the Strait of Gibraltar) shape distribution ranges. The high invasion density in the Tanger-Tétouan-Al Hoceïma region (0.041 occurrences/km²) is consistent with the hypothesis that trade volume and transport connectivity are the strongest predictors of invasion success (Seebens et al. 2017; Sardain et al. 2019). However, urban and population density likely influence these geographic results, as higher human presence typically leads to more invasive species records (Meyer et al. 2016). In this sense, the data gaps in arid interior and the Atlas Mountains likely reflect a lack of digitization rather than true ecological resistance (Beck et al. 2014). The fact that 48.5% of the recognized inventory lacks accessible georeferenced data highlights a critical gap in spatial knowledge regarding species distributions. This deficiency is particularly pronounced for historical agricultural weeds and terrestrial invertebrate taxa. As frequently reported in other national lists across the Global South (e.g., in Zimbabwe; Maroyi 2026), taxonomic bias in South Africa and the broader Global South heavily favors agriculturally significant pests and weeds over environmental threats, a trend documented in national surveillance and listing (Faulkner et al. 2020). Recent studies, including work by Zengeya et al. (2026), highlight that while progress is being made, significant gaps remain for invertebrates and non-agricultural species due to these historically and economically driven monitoring frameworks. This reveals the need for increased digitization of national collections to improve predictive modeling for remote but biodiversity-rich ecosystems (Hortal et al. 2015; Meyer et al. 2016).

Hidden economic liabilities and data deficiencies

Our economic analysis reveals a disparity in potential costs across management categories. While the containment in aquatic environments includes conspicuous invaders like *Pontederia crassipes* (US\$ 68.8 million mean annual cost), the *EDRR candidates* (i.e., taxa with limited confirmed occurrences, ≤ 50 records, that have not yet spread widely but pose severe impact risks) represent the most significant financial liability, driven by high-impact taxa such as *Aedes aegypti* (US\$ 828.0 million) and *Cydia pomonella* (US\$ 444.3 million). Furthermore, the *Latent Risk* category serves as a reservoir for major economic threats; for instance, the invasive tree *Acacia mearnsii* (US\$ 153.8 million) is classified here due to data deficiencies, despite potentially exceeding the costs of many established pests. This classification does not imply that these populations have no impact; rather, it stems from a lack of local ecological impact assessments. In the absence of targeted field studies, these species (such as severe ecosystem engineers like *Acacia mearnsii* and the widespread shrub *Lantana camara*) remain in lower priority categories by default, potentially masking an invasion that has not been already detected or assessed (Crystal-Ornelas and Lockwood 2020; McGeoch et al. 2016). This suggests that Morocco, like other countries of the Global South, faces an enormous knowledge gap where available national data fails to reflect the true threat potential. The dominance of the escape from confinement pathway (almost 45% of the species of the national inventory) as the driver of this category implicates the ornamental and nursery trade as the primary economic sectors (van Kleunen et al. 2018; Hulme et al. 2018). If these species bridge the gap from naturalized to widespread invasive, potentially triggered by climate change or relaxed biosecurity controls (Hellmann et al. 2008), the economic liability could shift from potential to realized. Therefore, a cost-effective national strategy would involve not merely containing for established species, but prioritizing the surveillance of the high-cost species pool identified in the *EDRR* and *Latent Risk* categories (Bradley et al. 2012).

To evaluate this risk, we employed global cost data from the invaCost database as a proxy for the intrinsic economic hazard posed by each species. While a recent study (El Jamaai et al. 2026) applied socio-economic scaling (PPP adjustment) and climatic adjustment to model specific national costs for Morocco (estimating US\$ 1.14 - US\$ 5.13 billion annually), their analysis was based on a preliminary version of the national inventory. This substantial difference in species coverage, combined with their specific modeling adjustments, explains why direct comparisons are inappropriate. However, the alignment of high-impact species present in both datasets confirms the threat posed by major agricultural and public health threats. Notably, the codling moth *Cydia pomonella* and the Mediterranean fruit fly *Ceratitis capitata* consistently rank among the costliest invaders in both assessments, with El Jamaai et al. (2026) further identifying the cassava mealybug *Phenacoccus madeirensis* as the top national economic threat. Our inventory captures major economic threats that were absent from the previous dataset, most notably the water hyacinth *Pontederia crassipes* (syn. *Eichhornia crassipes*) and the black wattle *Acacia mearnsii*. The inclusion of such high-cost ecosystem engineers demonstrates that previous national models underestimated the total economic costs of invasive alien species by missing key taxa in the *Latent Risk* and *Aquatic Containment* categories.

The Watchlist as a management tool

The identification of 239 species on the early detection and rapid response management type represents a clear policy opportunity. While these species currently have limited distributions (≤ 50 records), they include high impactful invaders such as the yellow fever mosquito *Aedes aegypti* and the codling moth *Cydia pomonella*, which are associated with massive economic burdens globally (Bradshaw et al. 2016; Roiz et al. 2024). The return on investment for eradicating species at the early detection stage is exponentially higher than long-term containment of widespread taxa (Leung et al. 2002; Ahmed et al. 2022). However, the high proportion of data deficient species (41.7% of the inventory) regarding introduction pathways remains a vulnerability. The inability to assign pathways to nearly half the inventory hampers preventive biosecurity (Essl et al. 2015). This reveals the need to transition from passive biodiversity lists to active, pathway-based monitoring, particularly for the under-documented invertebrate fauna which likely enters undetected as contaminants of agricultural commodities (Roques 2010).

Conclusion

This study establishes the first verified, functionally stratified national inventory of invasive alien species in Morocco, documenting 604 taxa, prioritizing their management based on their pathways of invasion, and revealing a complex invasion landscape driven by trade, urbanization, and agricultural disturbance. Beyond the taxonomic description of the national inventory, three critical patterns emerge with significant implications for the Global South and the Maghreb region. First, the identification of the primary invasion corridor along the north-western coast highlights Morocco's strategic role as a biogeographical bridge. As a transit hub between Europe and Africa, effective biosecurity in the Tangier-Casablanca axis would provide a regional public good, acting as a dual buffer: shielding the wider Maghreb and Sahelian ecosystems from the southward expansion of Palearctic invaders, while simultaneously mitigating the northward spread of Afrotropical species into Europe, a phenomenon likely to accelerate as climate change facilitates meridional range expansions. Platforms of environmental surveillance, such as the one in Cotonou Seaport in Benin (Adamjy et al. 2024), dedicated to monitoring and managing invasive

alien species inside an African seaport, represent an innovative, science-guided initiative that could be reproduced in the Tanger-Casablanca seaports to prevent new invasions entering through this corridor.

Second, the disconnect between invasion status and potential economic impact reveals a significant hidden liability and potential costs. The finding that high-cost ecosystem engineers like *Acacia mearnsii* remain in the *Latent Risk* category due to data deficiencies, while national resources are absorbed by established agricultural pests, illustrates a vulnerability common to developing economies. For instance, widely established agricultural pests represent a massive financial drain; the tomato leafminer (*Tuta absoluta* syn *Phthorimaea absoluta*), for example, is responsible for up to US\$ 1.15 billion in annual economic losses across the African continent (Diagne et al. 2021). Without resources for effective control across the board, a cost-effective strategy for Morocco is to pivot toward early detection and rapid response (EDRR) management strategies, specifically targeting the 239 species identified in this category before they transition into unmanageable, high-cost burdens.

Finally, this study outlines a workflow for addressing prioritization in data-scarce regions. By integrating global risk proxies with local expert validation, we circumvented the lack of national impact data to generate actionable biosecurity priorities. As nations strive to meet Target 6 of the Kunming-Montreal Global Biodiversity Framework, this model offers a blueprint for other Global South nations to transition from passive checklists to risk-based management.

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