invasimapr

A Workflow to Assess Site Invasibility and Species & Trait Invasiveness

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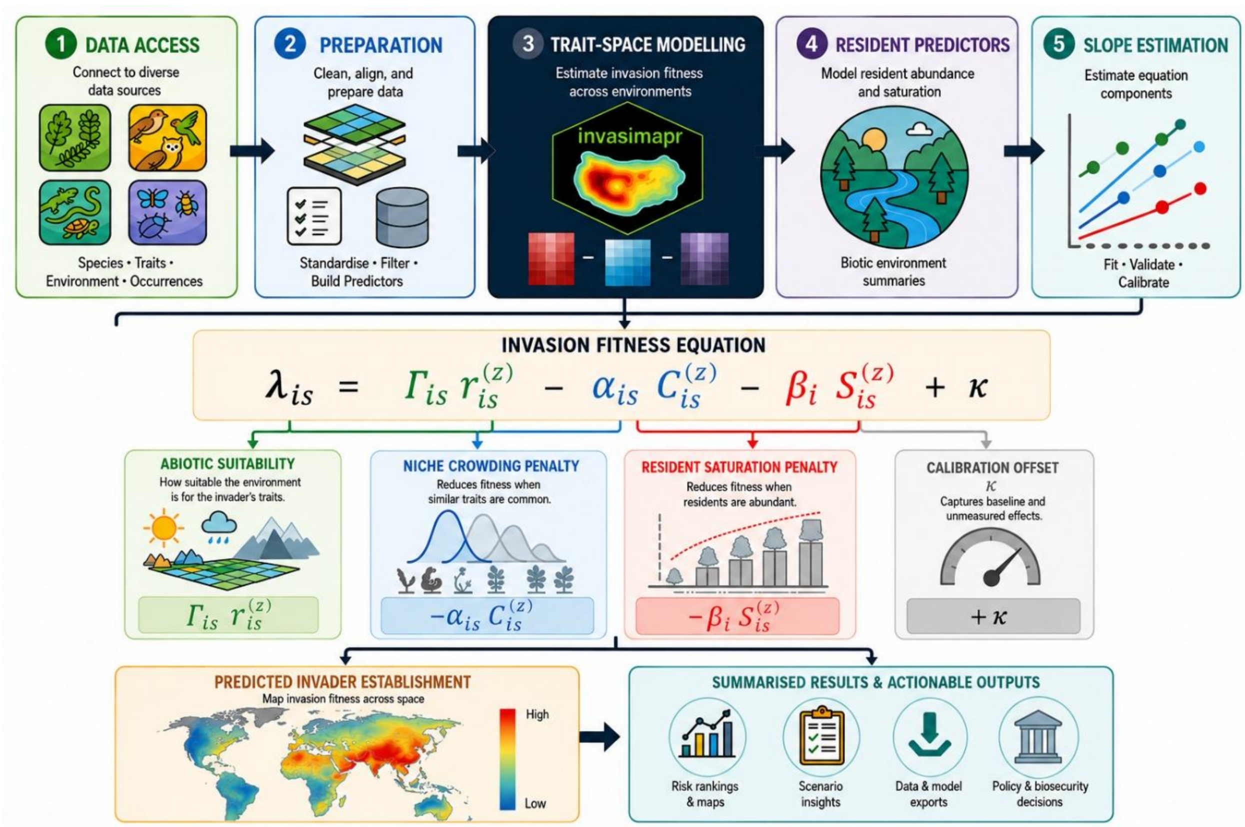

What is `invasimapr`?

The **Invasibility Cube** provides a unified, transparent, and reproducible framework for quantifying the potential of invasive alien species (IAS) to establish across sites and landscapes. Biological invasions rank among the leading drivers of biodiversity loss worldwide, yet invasion outcomes depend on the interplay of three key components: the functional traits of candidate invaders, the abiotic suitability of local environments, and the biotic resistance offered by resident communities. Despite substantial advances in invasion ecology, most existing risk assessment tools address only one or two of these axes at a time, limiting the ability of researchers and decision-makers to anticipate where invasions will succeed and which species pose the greatest threat.

invasimapr is an open-source R package that integrates all three components into a single multidimensional structure, resolving invasion fitness at the scale of individual species and sites. At its core, the package models intrinsic growth potential through trait-environment relationships, quantifies competitive penalties imposed by resident communities (incorporating both trait overlap and environmental filtering), and combines these into a site-specific and species-specific fitness surface. By embedding ecological mechanisms directly into the analytical pipeline, invasimapr moves beyond correlative approaches toward a process-based understanding of invasion risk.

The framework converts complex invasion ecology into decision-ready indicators that identify which invaders are most likely to establish, where invasions are most likely to occur, and which ecological mechanisms drive that risk. These outputs support surveillance planning, species prioritisation, and management interventions by highlighting invasion hotspots and high-risk species-trait combinations. Because the workflow is modular and fully scripted, analyses are reproducible across taxa, geographic regions, and policy scenarios.

This integrated framework enables researchers and policymakers to address several complementary objectives: conducting mechanistic risk assessments by identifying species-trait combinations with high establishment potential; supporting conservation planning by flagging vulnerable ecosystems and invasion hotspots across landscapes; and guiding ecosystem management by anticipating how community structure may reorganise under invasion pressure. The package thus bridges the gap between theoretical invasion ecology and the practical needs of biodiversity monitoring and policy.

The Invasion Fitness Concept

At the heart of invasimapr is the concept of **invasion fitness**, a quantity that captures whether a species can successfully establish at a given site once local environmental conditions and resident community structure are taken into account. Formally, invasion fitness represents the per-capita growth rate of a rare invader introduced into a resident community at ecological equilibrium. When this growth rate is positive, the invader can increase from low density and is predicted to establish; when it is negative, the invader is expected to decline and fail. This threshold-based logic provides a clear, ecologically grounded criterion for distinguishing successful from unsuccessful invasions.

The framework decomposes invasion fitness into three mechanistic components, each corresponding to a distinct ecological process:

- **Abiotic suitability:** the degree to which the invader's functional traits are matched to local environmental conditions. This component captures the "opportunity" dimension of invasion, reflecting habitat quality, climatic tolerances, and resource availability at the target site.
- **Niche crowding:** the extent to which the invader's traits overlap with those of resident species in a shared trait-environment space. High niche crowding indicates that the invader occupies a similar ecological strategy to many residents, intensifying competitive interactions and reducing the likelihood of establishment.
- **Resident competition:** the overall density and dominance of native species already occupying the site. Even when niche overlap is modest, a site saturated with abundant residents may resist invasion simply through numerical dominance and resource pre-emption.

When abiotic benefits outweigh competitive penalties, a species attains positive invasion fitness and a correspondingly higher probability of successful establishment. The probability of invasion success can be expressed via a logistic or probit transformation of predicted fitness values, providing a continuous and interpretable measure of risk. The coefficients weighting these three components may vary across species and sites, allowing for heterogeneity in invasion responses and accommodating context-dependent dynamics. This trait-centred, community-aware approach links ecological theory directly to spatial prediction, enabling researchers to move from abstract fitness concepts to mapped invasion risk surfaces.

Shared Trait-Environment Space

The shared trait-environment space provides a geometric representation of how invaders interact with resident communities and their abiotic surroundings. In this multidimensional space, each axis corresponds to a functional trait or environmental variable, and each species occupies a position determined by its trait values and ecological tolerances. The resident community collectively forms a "cloud" in trait space, whose shape, density, and spatial extent describe the diversity of ecological strategies present at a site. The geometry of this cloud is central to the invasimapr framework, because the relative position of an incoming invader within or outside this cloud governs the strength and nature of competitive interactions.

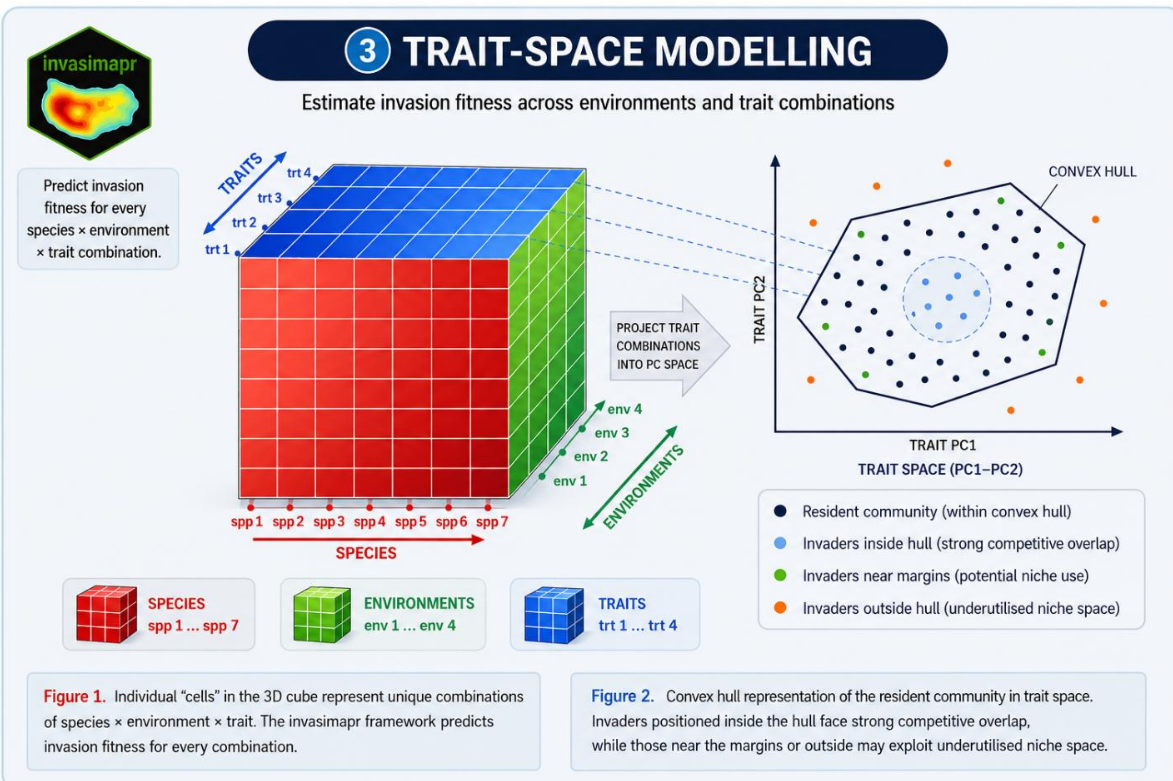

Figure 1. Trait-space modelling framework for estimating invasion fitness: A three-dimensional species x environment x trait cube is used to predict invasion fitness across all combinations. Trait combinations are projected into principal component trait space, where the convex hull defines the resident community.

Three geometric properties of the trait-environment space govern invasion outcomes. First, **abiotic suitability** reflects the alignment between the invader's trait vector and local environmental conditions, capturing how well-suited the invader is to the physical and climatic characteristics of the site. Second, **niche crowding** measures the overlap between the invader and the resident community's trait distribution, quantifying the intensity of the competitive neighbourhood. Third, **resident competition** accounts for the density and dominance of resident species in nearby trait space, reflecting the degree to which available niche space is already occupied.

The compute_trait_space() function constructs this shared space by applying Gower distance and principal coordinates analysis (PCoA) to the combined trait matrix of residents and invaders. The resulting ordination places all species on common axes, and the compute_centrality_hull() function then computes the convex hull of the resident community. The figure below shows this construction: the hull boundary separates regions of strong competitive overlap (inside) from less crowded niche space (outside), while species positions relative to the centroid indicate the intensity of competitive interactions they are likely to face.

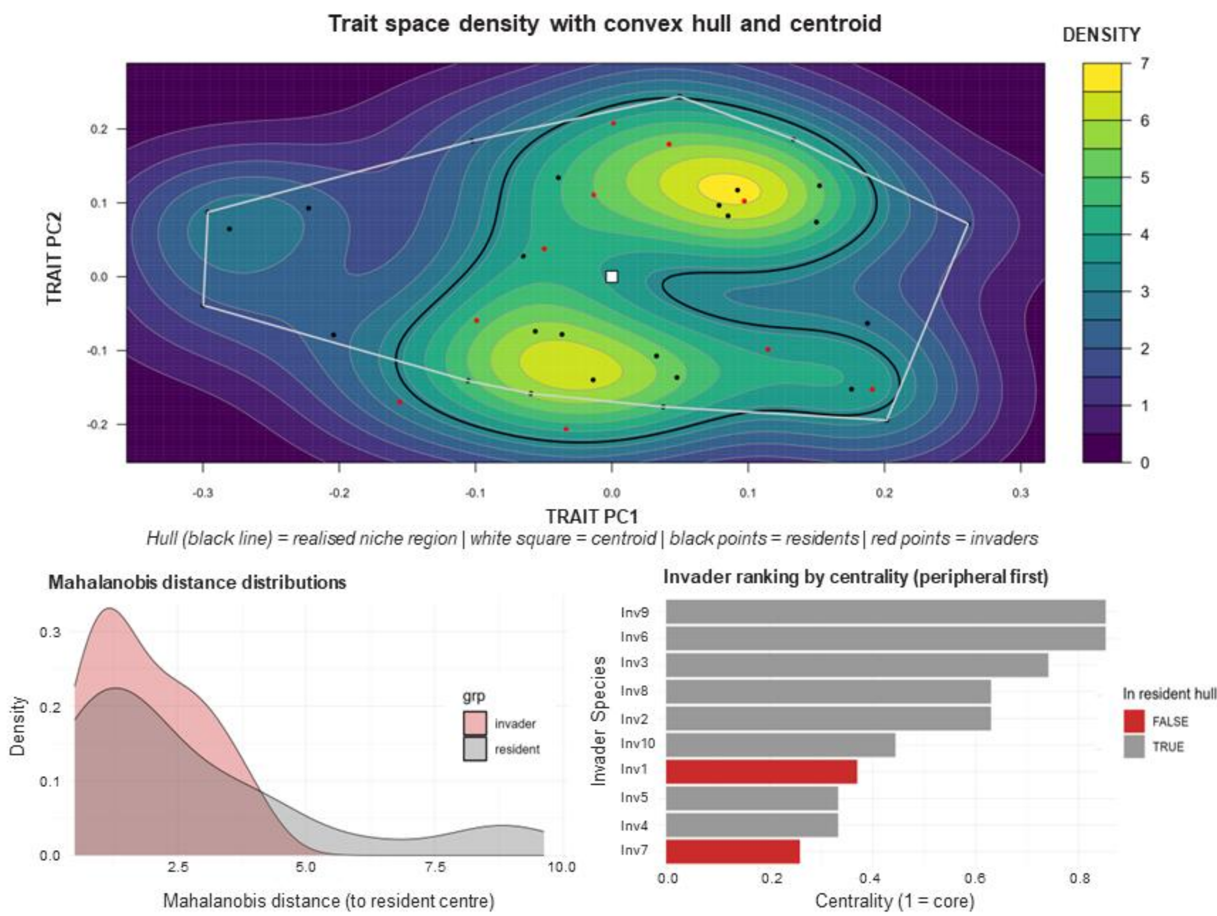

Figure 2. Trait-space density heatmap illustrating variation in competitive pressure across the shared trait-environment space, with marginal diagnostics for individual trait axes.

Together, these properties formalise invasion as a spatial problem in trait space, in which invasion success depends on an invader's position relative to the geometry of the resident community. Invaders near the centroid of the resident trait cloud experience strong competitive pressure from multiple resident species occupying similar strategies; conversely, those positioned toward the margins or outside the convex hull may find less crowded niche space and face reduced biotic resistance. This geometric perspective provides an intuitive and quantitative basis for understanding why certain invaders succeed at particular sites: invasion fitness emerges from the interplay of environmental opportunity and the competitive landscape defined by resident trait distributions.

The compute_resident_crowding() function quantifies the competitive neighbourhood experienced by each species at each site, using a Hellinger-composition and Gower-Gaussian trait kernel to measure local density in trait space. The resulting density surface, visualised as a heatmap below, reveals where in the trait-environment space competitive pressure is concentrated. High-density regions (warm colours) indicate trait combinations shared by many resident species, while low-density regions (cool colours) represent underexploited niche space where invaders may face less resistance. Marginal distributions along each trait axis provide additional diagnostic information about which functional dimensions most strongly structure the competitive landscape.

The `invasimapr` Workflow

The invasimapr workflow is modular, transparent, and fully reproducible, progressing from standardised ecological inputs to decision-ready outputs. It is built around eight wrapper functions that guide users through the complete analytical pipeline, from data acquisition through to invasion fitness computation and indicator derivation. Each function encapsulates a well-defined analytical step, and the pipeline can be run end-to-end with minimal user intervention or customised at any stage to accommodate specific research questions or data configurations.

Phase 1: Inputs and Setup

The first phase encompasses setup, library loading, and data acquisition. Users begin by assembling three core data matrices: a **site-environment matrix** describing the abiotic conditions at each site (climate, soil, topography, and related variables); a **site-resident matrix** recording the occurrence or abundance of resident species across sites; and a **species-trait matrix** containing functional trait measurements for both resident and candidate invader species. The package includes tools for trait data retrieval and harmonisation, drawing on standardised trait databases. Invader profiles can be imported directly or generated using the *simulate_invaders()* function, which creates synthetic invader profiles spanning the trait space to explore hypothetical invasion scenarios.

Phase 2: From Data to Invasion Fitness

The second phase transforms raw ecological data into estimates of invasion fitness. This begins with the construction of a standardised trait space, in which traits are rescaled and a joint trait-environment space is assembled for both resident and candidate invader species. Crowding indices are computed to quantify the competitive neighbourhood experienced by each invader at each site. The package then fits **generalised linear mixed models (GLMMs)** linking resident species occurrence or abundance to environmental predictors and trait-based covariates. These models provide the coefficients needed to estimate how trait-environment interactions shape the intrinsic growth potential of an invader. Sensitivity estimation procedures allow both trait-varying and site-varying responses, capturing the fact that the importance of individual traits may differ across environmental gradients and community contexts.

Phase 3: Prediction and Indicators

The third phase generates predictions and derives summary indicators. Invasion fitness is computed for every combination of invader species and site, producing a full species-by-site fitness matrix. These fitness values are then transformed into **establishment probabilities** via logistic or probit functions, providing a directly interpretable measure of invasion risk. The pipeline summarises results into three families of indicators: **site invasibility** (how open a site is to newcomers), **species invasiveness** (how broadly a species can establish across sites), and **trait-level diagnostics** (which functional attributes most strongly influence invasion outcomes). The package produces maps, plots, and tabular summaries that can be used directly for reporting and decision support.

It is worth noting that invasimapr integrates tightly with **dissmapr** for biodiversity data acquisition and spatial gridding, ensuring that input data are standardised, spatially explicit, and ready for analysis within the shared B-Cubed data infrastructure.

Derived Indicators

The cube structure at the core of invasimapr enables invasion outcomes to be summarised across hierarchical ecological levels, collapsing a high-dimensional fitness surface into interpretable indicators that serve different analytical and policy needs. By marginalising across species, sites, or traits, the framework produces three complementary families of indicators, each illuminating a different facet of invasion risk.

Species Invasiveness

Species invasiveness quantifies the propensity of a given species to establish across multiple sites, aggregating fitness predictions over the full set of target locations. Species with high invasiveness scores possess trait combinations that confer broad establishment potential under diverse environmental and competitive conditions. This indicator is particularly valuable for prioritisation, as it identifies the invaders most likely to succeed across a wide range of community contexts and can guide watchlists, early detection programmes, and border biosecurity efforts.

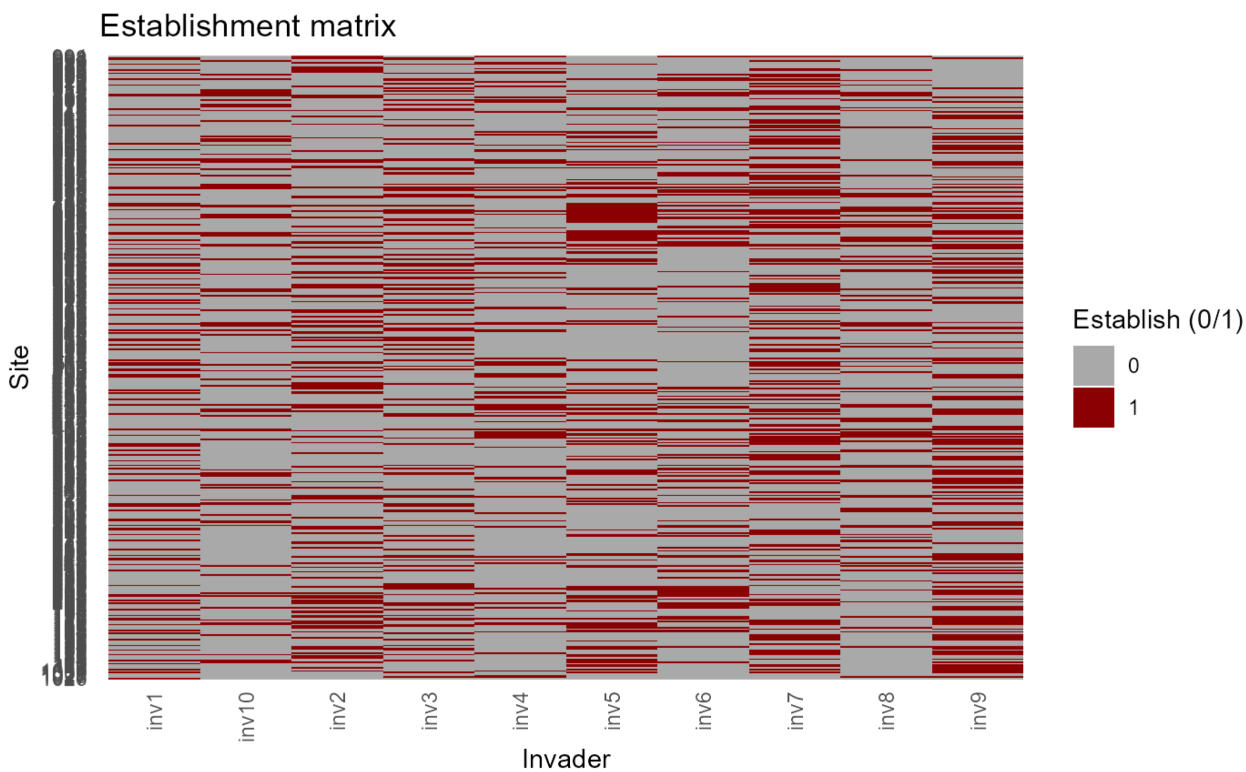

Figure 3: Spatial and invader-specific structure of establishment likelihood. Rows correspond to sites and columns to invaders, with cells showing binary establishment outcomes. The sparse but structured pattern indicates that invasion is constrained by both species identity and site context.

The predict_establishment() function computes establishment probabilities for every species-site combination and the summarise_results() function aggregates these into the heatmap shown below. Each row represents a site and each column an invader, with cells coloured according to binary establishment outcomes. The sparse but structured pattern of successful establishments reveals that invasion is not uniformly distributed but is instead constrained by the interplay of species identity and local site conditions, with certain invaders succeeding broadly while others are confined to narrow environmental windows.

To visualise how individual invaders distribute across the landscape, the package maps binary establishment outcomes for each candidate species separately. The panel maps below show the predicted geographic footprint of each invader across South Africa, with red cells indicating sites where establishment is predicted and dark grey cells where it is not. Comparing panels reveals species-specific spatial signatures: some invaders are predicted to establish across broad climatic envelopes, while others are restricted to particular biomes or environmental niches. These maps support targeted surveillance by identifying which regions are at risk from specific invader species.

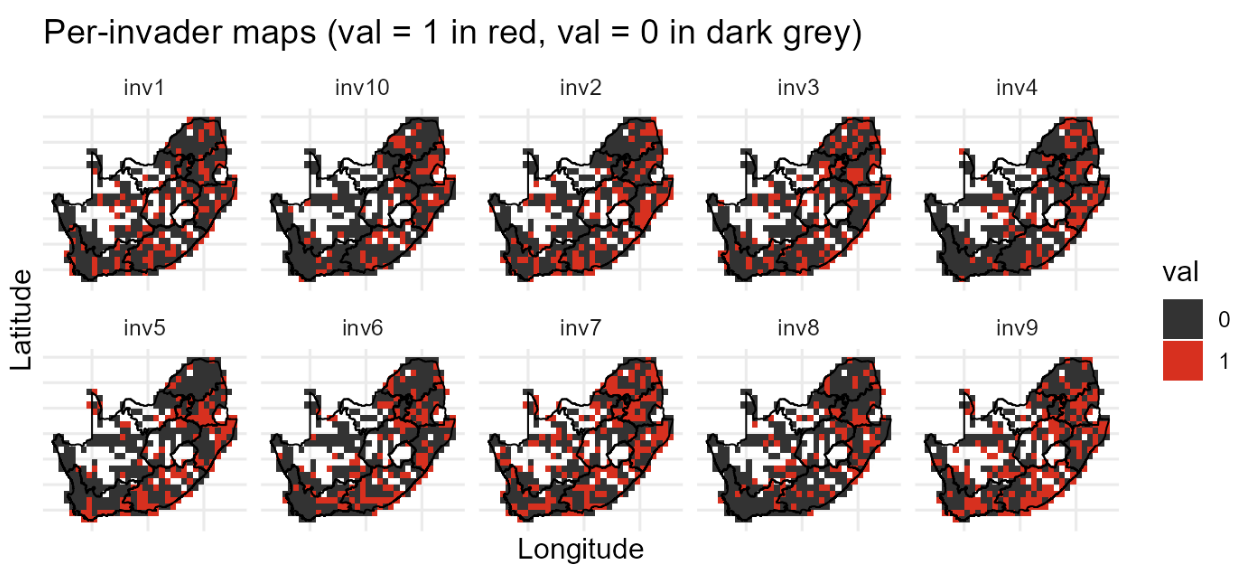

Figure 4: Per-invader maps of binary establishment across South Africa. Each panel is one invader; red cells indicate establishment (1) and dark grey non-establishment (0). Common grid and coastline enable direct comparison of spatial patterns among invaders.

Trait Invasiveness

Trait invasiveness isolates the contribution of individual functional attributes to overall invasion success. It is computed as the variance in species invasiveness explained by a single trait, providing a measure of how strongly each trait dimension influences establishment potential. By decomposing invasiveness along individual trait axes, this indicator reveals the mechanistic basis of invasion risk: for example, whether high specific leaf area, rapid growth rate, or broad thermal tolerance is the dominant driver in a given system. This information supports both ecological understanding and practical management, by identifying the trait syndromes that monitoring programmes should target.

The lollipop plot below, produced by the summarise_results() function, ranks individual traits by their association with mean establishment probability. Continuous traits are tested for significant linear relationships with invasiveness, while categorical and ordinal traits are assessed via group-level comparisons. A small number of continuous traits dominate the signal (with several showing statistical significance at $p < 0.05$), indicating that specific functional axes systematically raise or lower invasion success. Categorical and ordinal traits contribute more modestly, pointing to ecologically relevant but weaker thresholds or trait syndromes.

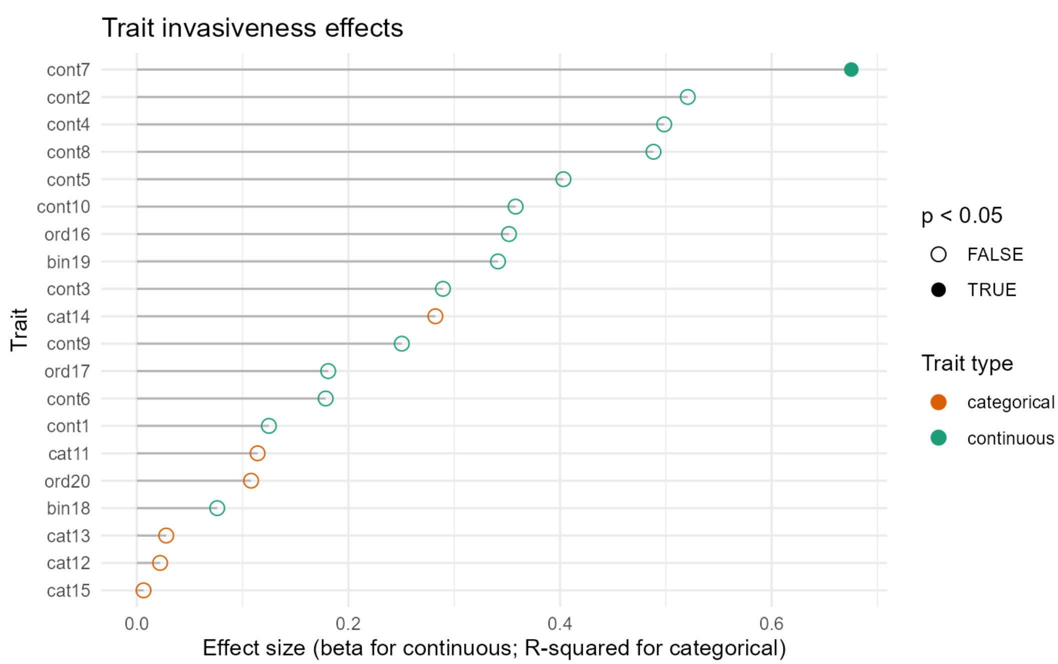

Figure 5: Trait invasiveness effects view with a lollipop plot ranking traits by their association with mean establishment probability for continuous traits. A small set of continuous traits dominate the signal, implying that functional axes captured by those traits systematically raise or lower invasion success.

Site Invasibility

Site invasibility captures the openness of a community to newcomers given its current structure and environmental setting. It is derived by aggregating invasion fitness across all candidate invaders for a given site, yielding a single measure of how vulnerable that location is to colonisation by novel species. Sites with high invasibility may be characterised by low resident diversity, underutilised niche space, or environmental conditions that favour a broad range of invader strategies. Conversely, sites with low invasibility harbour diverse, competitive communities that leave little ecological opportunity for newcomers. This indicator directly supports spatial planning by identifying invasion "hotspots" and distinguishing resistant communities from those requiring intervention.

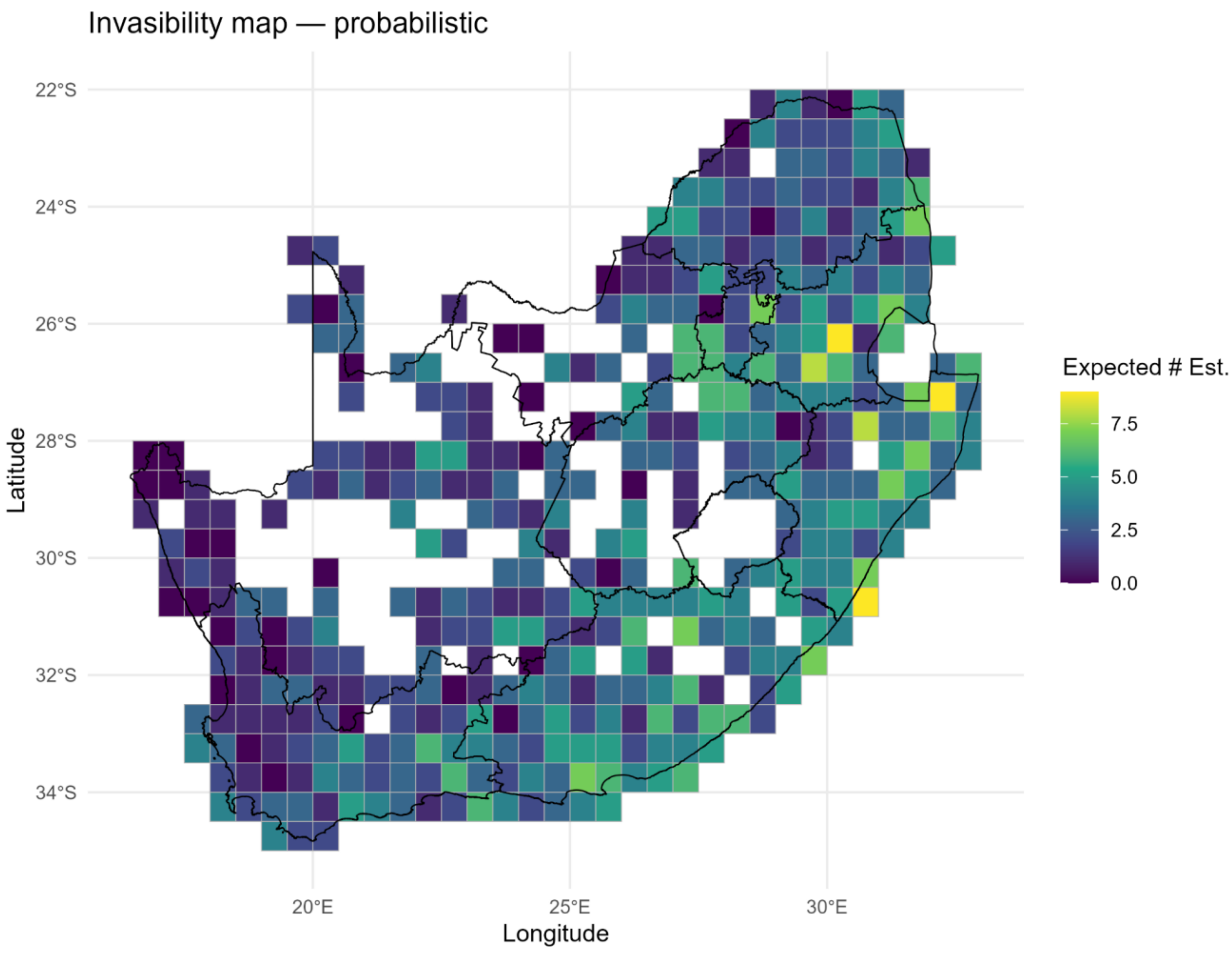

Figure 7. Invasibility map of South Africa, illustrating spatial variation in community openness to invasion based on trait-environment interactions and resident community structure.

The summarise_results() function aggregates establishment probabilities across all candidate invaders for each site, producing the invasibility surface mapped below. Warmer colours indicate sites with higher mean establishment probability across the invader pool, while cooler colours indicate communities that are more resistant to invasion. In the South African case study shown here, clear spatial gradients emerge, with certain biomes and climatic zones showing systematically higher openness to novel species. These patterns can be cross-referenced with existing protected-area boundaries, land-use maps, and conservation priorities to identify where targeted surveillance and management efforts are most urgently needed.

Together, these three indicator families provide mechanistic and spatially explicit measures of invasion risk that can inform conservation prioritisation, management strategies, and policy formulation at scales ranging from individual sites to national landscapes.

Key Outputs

The invasimapr package generates a comprehensive suite of outputs that span the full analytical chain, from raw fitness estimates to publication-ready visualisations. Each output type is designed to be immediately usable for research reporting, policy communication, or further analysis within the B-Cubed data infrastructure.

- **Invasion-fitness matrices:** Full species-by-site matrices of predicted invasion fitness values, capturing the per-capita growth rate of each candidate invader at every target site.
- **Establishment probabilities:** Logistic or probit transformations of invasion fitness into continuous probability estimates, ranging from zero to one.
- **Trait-space diagnostics:** Visualisations and summary statistics describing the geometry of the shared trait-environment space, including convex hull plots, density heatmaps, crowding indices, and marginal trait distributions.
- **Species-level indicators:** Ranked lists and summary scores of species invasiveness, identifying which candidate invaders possess trait combinations conferring the broadest establishment potential.
- **Site-level indicators:** Mapped and tabulated measures of site invasibility, highlighting which locations are most open to colonisation by novel species.
- **Maps and plots:** Spatial maps of invasion risk, trait-space visualisations, and summary plots that can be exported for reporting, publication, or integration with GIS platforms.

The resulting outputs allow direct exploration of invasion dynamics across scales, linking trait-environment interactions to local establishment potential and landscape-level vulnerability. Because all outputs are generated programmatically, they can be updated as new data become available, enabling iterative refinement of invasion risk assessments over time.

Applications

The Invasibility Cube supports a wide range of applications in invasion ecology, conservation biology, and environmental policy. Because the workflow is modular and reproducible, it enables consistent comparison across taxa, geographic regions, and policy scenarios, making it suitable for both targeted local assessments and broad-scale strategic planning.

Risk Assessment

The framework provides a mechanistic basis for invasion risk assessment by identifying species-trait combinations with high establishment potential and mapping the sites where those species are most likely to succeed. Unlike correlative species distribution models, which rely on observed occurrence records, invasimapr generates predictions grounded in ecological processes (abiotic filtering, niche overlap, and competitive exclusion). This process-based approach is particularly valuable for assessing species that have not yet been introduced or for which occurrence data are sparse, supporting proactive rather than reactive risk management.

Conservation Planning

Site invasibility maps produced by the package directly inform spatial conservation planning by identifying vulnerable ecosystems and invasion hotspots across landscapes. Protected area managers can use these maps to prioritise surveillance effort, allocate monitoring resources, and design early detection networks that target the most invasion-prone locations. The trait-level diagnostics further support conservation planning by revealing which functional attributes make communities susceptible to invasion, guiding restoration and management strategies aimed at strengthening biotic resistance.

Ecosystem Management

By anticipating how community structure may reorganise under invasion pressure, invasimapr supports forward-looking ecosystem management. Managers can explore scenarios in which different invader profiles are introduced to different sites, evaluating the likely consequences for resident communities and identifying tipping points at which invasion may trigger cascading ecological change. The modular design of the workflow makes it straightforward to incorporate updated trait data, revised environmental layers, or new candidate invader lists as management priorities evolve.

Policy and the B-Cubed Framework

Within the broader B-Cubed project, invasimapr operates alongside the **Suitability Cube** and the **Dissimilarity Cube (dissmapr)**, forming an integrated suite of tools for biodiversity assessment under the Horizon Europe programme. Together, these three cubes provide complementary perspectives on species distributions, community composition, and invasion risk, enabling policymakers to make evidence-based decisions that account for multiple dimensions of biodiversity change. The standardised data flows and shared analytical infrastructure ensure interoperability across cubes and facilitate integration with European and international biodiversity reporting frameworks.

Package Functions

The invasimapr package quantifies and visualises invasion fitness from occurrence and trait data. It computes trait centrality, maps trait dispersion, and estimates interaction strength. It assesses site-level invasibility and community openness to new invasions, produces interaction matrices and trait-specific invasion risk indicators, and aligns with the framework of Hui et al. (2023), integrating traits, propagule pressure, and environment. The package is organised around seven high-level wrapper functions and 18 core functions.

Wrapper Functions

`prepare_inputs()` Prepare inputs (assemble and align core tables)

`prepare_trait_space()` Prepare trait space and resident crowding

`model_residents()` Resident GLMM and construction of standardised predictors

`learn_sensitivities()` Learn sensitivities (alpha, beta, theta/gamma) and optional site-varying parameters

`predict_invaders()` Build standardised invader predictors (r, C, S)

`predict_establishment()` Compute invasion fitness and optional establishment probability

`summarise_results()` Summarise invasiveness and invasibility (tables, maps, rankings)

Core Functions

`get_trait_data()` Scrape and analyse trait data for a species

`assemble_matrices()` Assemble community matrices for invasion-fitness workflows

`simulate_invaders()` Simulate hypothetical invader trait profiles from a resident trait pool

`standardise_model_inputs()` Standardise model inputs (no leakage) for residents and invaders

`compute_trait_space()` Shared trait-space construction (Gower + PCoA), resident hull, centroid, and density plot

`compute_centrality_hull()` Compute trait-space centrality (robust Mahalanobis) and hull status

`compute_resident_crowding()` Resident crowding via Hellinger composition and Gower-Gaussian trait kernel

`build_model_formula()` Flexible formula constructor for residents-only trait-environment models

`prep_resident_glmm()` Build residents-by-sites long table and fit the residents-only GLMM

`standardise_by_site()` Standardise a site-by-species matrix by site (row-wise z)

`compute_site_saturation()` Compute site-only saturation and global z-score

`fit_auxiliary_residents_glmm()` Auxiliary GLMM for trait-varying and site-varying slopes

`derive_sensitivities()` Derive trait-varying sensitivities and abiotic slope

`site_varying_alpha_beta_gamma()` Site-varying alpha and gamma with trait-dependent beta

`build_invader_predictors()` Build standardised invader predictors (r, C, S)

`compute_invasion_fitness()` Compute invasion fitness for multiple model options

`compute_establishment_probability()` Probabilistic establishment from invasion fitness

`summarise_invasiveness_invasibility()` Summaries of invasion fitness: species invasiveness, trait effects, and site invasibility

Resources

Package and Documentation

- R package documentation: invasimapr.b-cubed.eu
- GitHub repository: github.com/b-cubed-eu/invasimapr
- B-Cubed project documentation: b-cubed.eu

Citation

MacFadyen, S., Yahaya, M.M., Trekels, M., Kumschick, S., Landi, P., Hui, C. (2025). *invasimapr: A Novel Framework to Visualise Trait Dispersion and Assess Invasibility*. R package version 0.1.0.

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