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Modelling the invasive trajectory of *Calotropis procera* in South America: new records and climate-driven distribution projections

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Abstract

Biological invasions are increasingly modulated by global climate change. *Calotropis procera*, a resilient and drought-tolerant shrub, has emerged as an aggressive invader across South American drylands. While static distribution models predict an overall range contraction for this species under future climates, we hypothesize that regional aridification interacts with local habitat degradation to severely accelerate the invasion front in specific vulnerable biomes. To test this, we integrated an optimized ensemble of Ecological Niche Models (CMIP6, SSP2-4.5) with a novel discrete-time kinematic framework. This approach allowed us to move beyond static suitability maps by quantitatively classifying the velocity, acceleration, and dynamic topology of the species' climatic niche through 2070. Our projections reveal a strongly polarized invasion trajectory. We forecast a continuous climatic retraction in the southern Gran Chaco; however, a runaway expansion and asymptotic saturation are projected for northern equatorial corridors, including the Brazilian Caatinga, Venezuela, and Colombia. Furthermore, over 300 new field records from Paraguay confirm that highly plastic phenology (continuous year-round reproduction) and wind-driven seed dispersal in degraded soils actively catalyze its current local spread. Our dynamic topological framework improves invasion forecasting, prioritizing immediate management in emerging ecological hotspots.

Keywords: *Calotropis procera*, Biological Invasions, Geographic Expansion, South America, suitable areas.

1 Introduction

Biological invasions represent one of the most significant environmental threats to natural ecosystems worldwide. Some exotic species exhibit aggressive growth and expansion in regions outside their native distribution range, often displacing native flora and fauna. Climate change may further facilitate the expansion of certain invasive alien species into areas that are currently free of their presence. Anticipating the potential expansion of these species is essential for the development of effective regional control and management strategies.

Calotropis procera (Aiton) Dryand, a member of the Apocynaceae family, also known as the "Sodom apple," is notable for its incredible adaptability and resistance to adverse conditions [1]. Although the species is native to arid and semi-arid regions

of Africa and Asia, it has expanded and become an invasive species in several parts of the world, including South America [2].

The Apocynaceae family, according to specialists, is composed of numerous genera and species. Ezcurra et al. [3] mention approximately 170 genera and 1,800 species, while Endress et al. [4] mention 37 genera and about 5,300 species. It is a family that develops in pantropical regions and very little in temperate areas. In Paraguay, 16 native genera and 49 species have been described so far [3]. It is characterized by being trees, shrubs, herbs and lianas; in general, the species have beautiful flowers, many of them being used as ornamentals in Paraguay, so they are often found cultivated in gardens, patios, sidewalks, parks, and central walks (such as *Allamanda*, *Nerium*, *Plumeria* and *Thevetia*) [3], while others are already considered adventitious as in the case of *Catharanthus roseus* [5].

C. procera develops into a small tree, reaching heights of about 6 m or more, with a short stem that typically grows to approximately 2.5 m. It is very branched and produces abundant latex. It is characterised by a fibrous bast trunk and corky and very cracked bark, as well as opposite leaves, sessile, oval up to 30 × 16 cm, cordate base, greyish green, pubescent, wide midrib, the young ones covered with fine white hairs. Its flowers are grouped in axillary cymes, subumbelliform, white to red-brownish-pinkish; corolla 2-3 cm, petals five, pinkish-violet. The fruits are convex, soft, and green, with ovoid capsules up to 10 cm long, featuring spaced and spongy pulp. It has numerous small, flat seeds with a tuft of hairs at one end [6]. The species is widely distributed on almost all continents, including Africa, Asia, South America (northern Argentina, Brazil, Colombia, Ecuador, Peru, Venezuela), and Europe (Cape Verde Islands, Canary Islands and the Caribbean) [7].

Some authors present it as an exotic invader [8]. Its rapid expansion in different biomes and ecoregions of Latin America occurs in very favourable areas, both in terms of climate and soils, colonising savannas, Cerrado and dry forests [6, 9, 10]. According to Goncalvez-Oliveira et al. [11], numerous authors consider that this species was introduced in the Neotropics in the 20th century; Barbosa et al. [12] mention it as one of the 205 exotic species introduced in the Brazilian Caatinga, as Sousa Sobrinho et al. [13] who also mention its extension in the Brazilian Caatinga; Gracia et al. [14] mention that it was found in the dunes of the Atlantic coast, in Colombia and Brazil, and finally note that it is in the process of naturalisation in disturbed areas.

C. procera (Ayton), in Paraguay known as "tuja bola" and elsewhere as "Sodom's apple tree", was mentioned as adventitious to the Paraguayan flora and collected for the first time in the central Paraguayan Chaco [21°22'00" S, 61°29'00" W] in 1991 [15]. The specimens correspond to the centre of this natural region known as the Chaco Seco ecoregion [16], in an area characterised as semi-arid and covered by seasonal dry forests [17, 18] and modified by anthropogenic actions [19].

How did *C. procera* reach the semi-arid Chaco region (Argentina, Bolivia and Paraguay)? Due to the plant characteristics, especially the seeds, it could have arrived without human help. It is mentioned that the seeds of the species were dragged by the trade winds from the equatorial zones to the subtropical zones, falling in appropriate areas for rooting (personal comments written on herbarium labels of the specimen of *C. procera* collected in the centre of the Paraguayan Chaco, 1994 and deposited in

the CTES Herbarium by Mr. Saravia Toledo, C.). The same author mentions that the introduction to the South American continent took place in the Caribbean region via ships transporting merchandise and enslaved people from the African continent. The latter propagation was due to successive changes in the use of the soils covered by the dry forest region, which were mainly modified for agriculture and livestock.

C. procera has been extensively studied from many points of view in many places due to its invasive nature, causing concern in the areas where it is established [8, 9, 11, 13, 20–30]. However, no one has addressed the advancement of the species and the problems it is already causing in the dry forest of the regional Chaco, especially in the Paraguayan Chaco, which is composed of very fragile ecosystems. Changes in land use are widespread in this territory, which is undergoing rapid development [31].

Species Distribution Models (SDM) have been widely used in recent decades to understand the potential invasiveness of invasive alien species. These models help understand the spread and establishment of species, which is crucial for assessing the potential invasion of invasive alien species [32]. In the case of *C. procera*, a wind-dispersed species that forms extensive populations, reducing the productivity of grazing lands, Mengue et al. [33] used Maximum Entropy-based models to understand the potential distribution and drivers of the species' spread in Australia. Other authors have employed similar approaches with the same species, such as *C. gigantea* (L.) W. T. Aiton, in different regions [34]. In South America, Goncalvez-Oliveira et al. [11] assessed the vulnerability of dry biomes in the region to *C. procera* invasion and how climate change favours the spread of this species, mainly in arid biomes. These authors have concluded that the predicted invasion biomes did not change under a climate change scenario and that conditions in suitable areas increased under climate change.

The biological success of *C. procera* is largely attributed to a highly drought-tolerant physiology and a remarkably plastic leaf morphology that enables it to thrive in rapidly changing and harsh environments [1]. Furthermore, *C. procera* utilizes wind for highly efficient seed dispersal, allowing its propagules to travel long distances across open and degraded terrains [33]. Collectively, recent literature underscores that human activity, land-use changes, and soil disturbances strongly facilitate the propagation of this shrub, consolidating it as a persistent threat to environmental conservation and regional ecosystems [2].

Current modeling studies indicate that, although climate change could potentially reduce the total absolute area occupied by this species across South America as a whole, habitat suitability is projected to severely intensify in specific vulnerable zones, thereby accelerating its local establishment [11]. Based on these eco-physiological and spatial observations, our core hypothesis is that climate change —specifically the processes driving the advancement and intensification of arid zones— will govern a significant expansion in the climatic niche of the species.

Consequently, this study addresses the following central research question: *How do climate-driven shifts in regional aridity interact with local habitat degradation to govern the spatial expansion and dynamic topology of the C. procera invasion front in South America through the 21st century?*

Within this context, our specific contributions are as follows: (i) we provide new occurrence records (mainly from the western Paraguayan Chaco) ogether with observations on the species' natural history, update its distribution in the Chaco, and report the onset of its expansion into eastern Paraguay; (ii) we describe the environmental conditions in which the species establishes and persists; (iii) we analyze why *C. procera* does not colonize certain degraded environments adjacent to its current distribution in the Paraguayan Chaco; (iv) we model its present, potential, and future distribution in South America; (v) we apply spatial partitioning methods to minimize sampling bias and spatial autocorrelation in the modeling process; and implement statistical and machine-learning optimization criteria to reduce overfitting in future projections; and (vii) we apply a finite-difference kinematic framework to evaluate the dynamic topology of the species' climatic suitability, estimating the velocity and acceleration of niche expansion and contraction.

By bridging macro-climate projections with fine-scale landscape degradation, this dynamic framework provides actionable decision-support tools to mitigate land degradation and biodiversity loss in fragile drylands, directly advancing Sustainable Development Goal 15 (Life on Land).

2 Results

In this section, we present a comprehensive assessment of the invasive trajectory of *C. procera* across multiple spatial and temporal scales. First, we detail recent occurrence records, geographic expansion patterns, and field observations within Paraguay (Section 2.1). Next, we define the baseline ecological niche and current habitat suitability across South America based on the optimized model ensemble (Section 2.2). We then project these baseline models under the SSP2-4.5 climate scenario to identify macro-regional expansion and contraction trends up to the year 2070 (Section 2.3). Finally, we apply our finite-difference kinematic framework to quantitatively classify the evolutionary phases and dynamic topologies of the invasion front over the course of the century (Section 2.4).

2.1 Occurrence and Expansion of *C. procera* in Paraguay

Field monitoring and georeferencing efforts yielded over 300 new occurrence records for *C. procera* in Paraguay (detailed in Supplementary Table S3). The species is predominantly established in the northern region of the country, transitioning between the ecological Dry Chaco and the Cerrado formations (originating from Bolivia and Brazil), roughly between 20° and 23° S latitude and 58° to 62° W longitude. Conversely, occurrences are markedly less frequent in the southern ranges (23°–24°50′ S; 57°–60° W) (Fig. 2A).

Initially observed in the central boreal Chaco [19], the invasion front has systematically advanced across the Dry Chaco ecoregion into the northern Cerrado (Departments of Alto Paraguay, Boquerón, Presidente Hayes, and Concepción). Ecologically, the species exhibits a strong affinity for highly modified habitats, specifically colonizing degraded soils devoid of native vegetation cover. It has not been recorded within the interior of intact or even moderately degraded forest matrices.

Morphologically, individuals predominantly occur as shrubs ($\leq$ 3 m height; $\leq$ 10 cm trunk diameter), establishing either as solitary plants, small clusters ($\leq$ 10 individuals), or dense populations exceeding 300 individuals, primarily distributed along roadsides (Supplementary Fig. S1). Phenologically, populations across the western departments and the eastern department of Concepción, Paraguay have maintained a consistent reproductive pattern for over 30 years, exhibiting continuous flowering, fruiting, and seed dispersal throughout the year.

2.2 Ecological Niche Modeling and Current Suitability

Hyperparameter optimization via the composite scoring system (C) identified the `fc.LQH_rm.1.5` model as the most robust fit (lowest AICc and optimal discrimination/overfitting balance; see Fig. 1 and Fig. SA.2).

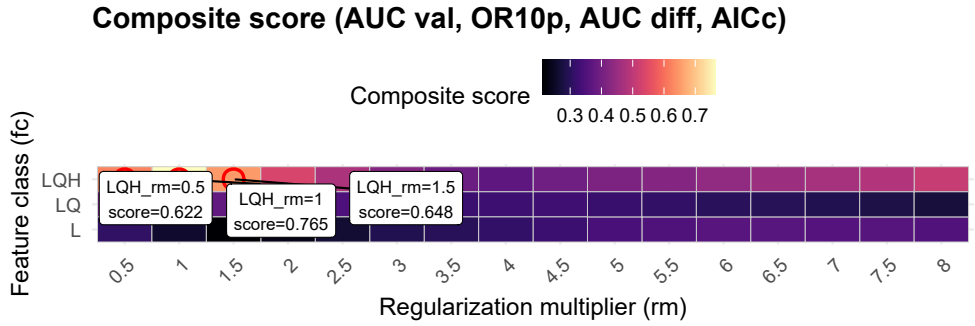


Fig. 1 Hyperparameter tuning heatmaps for the *C. procera* Maxent model. The selected model (`fc.LQH_rm.1.5`) balances validation AUC, omission rates, and AICc criteria to prevent spatial overfitting.

The projected baseline distribution (Fig. 2B) delineates two primary regions of high climatic suitability in South America. The first macro-region encompasses the Caatinga in northeastern Brazil, interconnected by fragmented corridors of medium-to-low suitability extending into the Brazilian and Paraguayan Cerrado. The second core region covers the ecological Gran Chaco, dominating northern Paraguay and southern Bolivia. Secondary, highly suitable, yet geographically restricted areas occur along the arid Pacific coast (Peru–Bolivia border) and the extreme northern tips of Colombia and Venezuela. Conversely, the Andean mountain ranges and the southern cone of the continent exhibit zero suitability for the species. Suitable areas are also observed in central Chile.

2.3 Climate-Driven Expansion and Contraction Trends

Under the SSP2-4.5 moderate mitigation scenario, the habitat suitability for *C. procera* undergoes pronounced geographic shifts. During the mid-century period

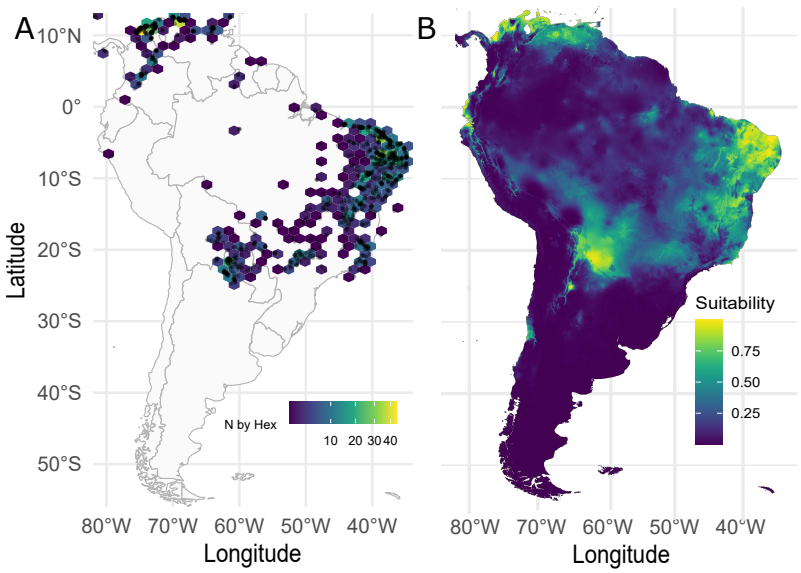


Fig. 2 A) Geographic distribution of *C. procera* occurrences. B) Baseline potential habitat suitability (1970–2000) modeled via the optimal Maxent configuration (`fc.LQH_rm.1.5`).

(2041–2060, Fig. 3A), climatic suitability intensifies significantly along the northeastern coast of South America. This drives a projected expansion from the Brazilian Caatinga northward into French Guiana, Suriname, and Guyana. Concurrently, localized suitability increases are projected across the northern territories of Venezuela and Colombia. In stark contrast, notable climate-driven habitat degradation (negative suitability change) emerges along the Paraguay-Bolivia border and the western coastal plains of Ecuador and Peru.

By the late-century projection (2061–2080, Fig. 3A), these divergent spatial trajectories consolidate. The northern expansion merges into a continuous high-suitability corridor spanning the continent's northeastern edge. Suitability also increases within the transitional ecotones linking the Caatinga, the Brazilian Cerrado, and the Amazonian fringes. Conversely, the climatic niche within the core Gran Chaco (southern Bolivia and northern Paraguay) is projected to undergo sustained, progressive degradation, rendering this historically invaded region increasingly less suitable for the species.

2.4 Kinematic Evolution and Dynamic Invasion Topology

Applying finite difference operators to the ensemble sequence revealed significant, nonlinear shifts in the invasion dynamics of *C. procera* (Fig. 4). The spatial configuration of the five topological regimes varied significantly across the century (Likelihood-ratio G-test: $G = 91855.1$, $df = 8$, $p < 0.001$).

During the initial projected phase (mid-period 2030.5), the invasion is dominated by *Asymptotic saturation* (41.5% of the masked suitable area) and *Runaway expansion* (30.1%), indicating a rapid but decelerating colonization of available ecological space.

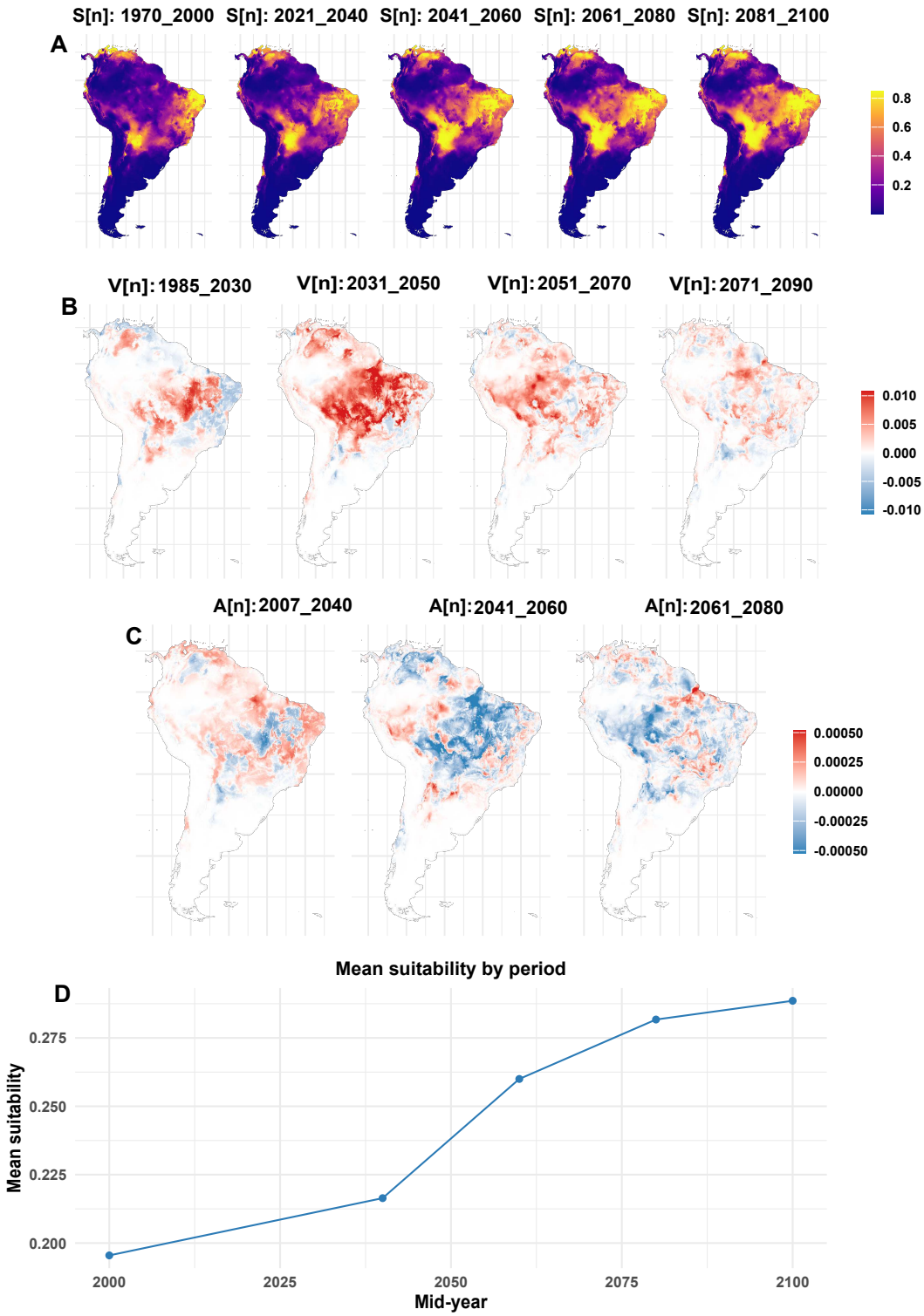


Fig. 3 Future climate-driven projections for *C. procera* under the SSP2-4.5 ensemble. A) Potential habitat suitability for 2040 to 2100. B) Annual rates of suitability change ($V[n] = \Delta\text{Suitability}/\Delta t$), representing niche suitability velocity in environmental phase space rather than physical dispersal speed (ΔSuitability), highlighting geographic areas of potential expansion (warm colors) and contraction (cool colors). C) acceleration in the coming decades in South America. D) Trajectory of average suitability in South America from the present to 2100.

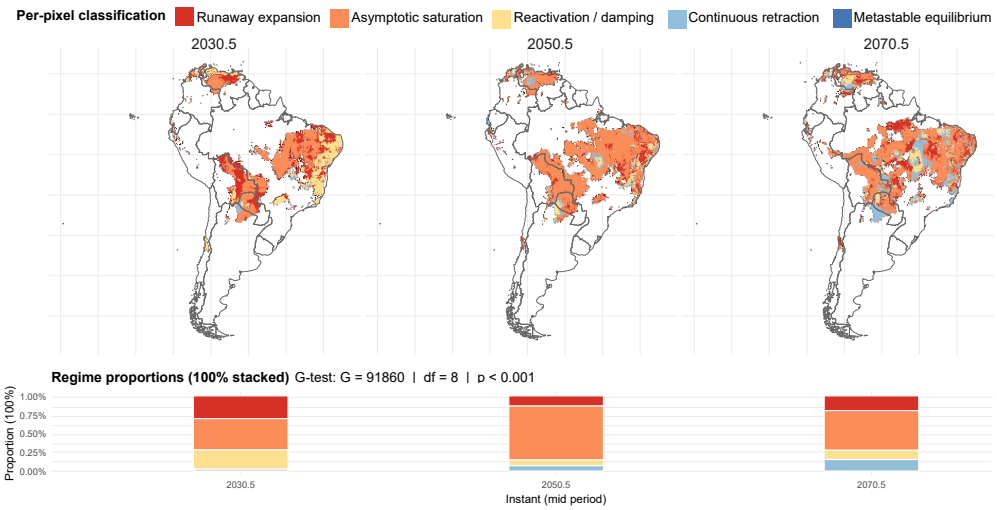


Fig. 4 Spatio-temporal kinematics of the *C. procera* invasion front. Upper panels: Spatial distribution of dynamic regimes (velocity-acceleration phase space) for the mid-periods 2030.5, 2050.5, and 2070.5. Lower panel: Stacked proportions demonstrating the temporal evolution of the invasion topologies (G-test $p < 0.001$).

However, by mid-century (2050.5), the area experiencing *Asymptotic saturation* surges to 69.2%, while *Runaway expansion* halves (13.1%), and *Continuous retraction* triples from 2.6% to 7.1%. This indicates that the species is rapidly reaching its climatic carrying capacity in regions like the Caatinga, while simultaneously losing optimal habitat in the Chaco.

By the end of the projection (2070.5), the invasion enters a highly polarized phase. *Continuous retraction* expands dramatically to encompass 15.5% of the species' range (primarily in the Gran Chaco and western coasts), indicating severe climatic exclusion. Simultaneously, *Runaway expansion* rebounds to 19.5%, and *Reactivation/damping* increases to 12.3%, underscoring a late-century surge in invasion pressure along the northern South American coast (Venezuela, Colombia, and the Guianas).

3 Discussion

Our findings robustly support the central hypothesis that climate change—acting synergistically with localized land degradation—governs a significant, yet spatially polarized, expansion of the *C. procera* invasion front across South America. By transforming static distribution models into a dynamic kinematic framework, we demonstrate that while the total continental area suitable for the species may face local retractions, the intensity of the invasion will severely accelerate in specific northern arid and semi-arid zones.

The projected spatial shifts reveal a continent partitioned into divergent invasion topologies. The rapid transition towards *Asymptotic saturation* and *Runaway expansion* in northeastern Brazil (Caatinga), French Guiana, Suriname, Venezuela, and

Colombia underscores the species' high ecophysiological affinity for intensifying aridification. The biological success of *C. procera* under these extreme climate scenarios is largely driven by its drought-tolerant physiology and remarkable foliar plasticity, which allow it to maintain high photosynthetic performance even under high vapor pressure deficits and severe soil water scarcity [1]. As climate change exacerbates arid conditions in these northern equatorial and sub-equatorial corridors, the species rapidly approaches—and colonizes—new climatic carrying capacities.

Conversely, our kinematic models project a *Continuous retraction* of climatic suitability within the core Gran Chaco (northern Paraguay and southern Bolivia) by the late 21st century (2070). This suggests that while *C. procera* is highly resilient, the future interplay of extreme thermal anomalies and altered precipitation regimes in the southern cone may eventually exceed its optimal physiological thresholds, pushing its fundamental niche strictly northward.

Despite the projected late-century climatic retraction in the Gran Chaco, the current empirical reality in Paraguay demonstrates an aggressive, ongoing invasion. This apparent paradox is explained by the catalytic role of human activity and soil disturbance. Our field observations confirm that *C. procera* acts as a pioneer species predominantly in highly modified environments, —such as fallow agricultural plots, cleared lands, and roadsides— where native vegetation has been eradicated [28].

The absence of organic matter and native canopy in these degraded zones exposes the soil to direct, intense solar radiation. The resulting high surface temperatures accelerate seed scarification and germination. Once established, the species' deep root systems and vegetative reproduction make it incredibly costly and difficult to eradicate. Furthermore, the species exploits the predominant North-Northeast winds of the Chaco territory, —amplified by the Venturi effect between the Cerro León and the pre-Andean ranges— to maximize its anemophilous seed dispersal across open, deforested terrains [33].

However, natural edaphic barriers remain. While *C. procera* readily invades the Dry Chaco (characterized by sandy-loam cambisols and luvisols), it has entirely failed to penetrate the adjacent Humid Chaco. The latter ecoregion features gleysols and planosols with exceptionally high clay content that become impermeable, sticky, and highly prone to prolonged flooding [35]. This confirms that while climate sets the macro-ecological boundaries, fine-scale edaphic properties and anthropogenic landscape opening ultimately dictate the local invasion topology.

This multi-scale decoupling underscores a classic niche hierarchy: while our SDM grid utilizes bioclimatic predictors to delineate the macro-climatic fundamental niche across South America, local establishment is ultimately governed by landscape-level realized niche filters. Specifically, fine-scale edaphic properties (e.g., clay content in hydromorphic soils) and physical dispersal vectors (wind-driven anemochory facilitated by local topographies) act as deterministic filters that either restrict or catalyze local colonization within macro-climatically suitable cells.

A critical intrinsic factor facilitating the aggressive dynamics of *C. procera* in South America is its exceptional phenological plasticity. In its native African and Asian ranges, or in other invaded regions like Israel and Saudi Arabia, the species

exhibits restricted reproductive windows, halting flowering drastically due to seasonal temperature fluctuations [36, 37].

In stark contrast, our 30-year monitoring in the Paraguayan Chaco reveals that the species has adapted to flower, fruit, and disperse seeds continuously throughout the entire year. With mature shrubs capable of releasing upwards of 35,000 highly viable seeds (over 80% germination success) [8], this continuous, uninterrupted propagule pressure ensures a constant supply of recruits ready to colonize any newly degraded land [13]. This continuous reproductive output, likely a plastic response to the currently favorable and relatively stable warm climates of the South American dry biomes, underscores why *C. procera* remains a persistent and growing threat to regional biodiversity and agroecosystems.

The massive expansion of *C. procera* across South America's dry biomes is driven by the synergistic effects of environmental degradation, highly plastic phenology, and currently favorable climatic conditions. Our kinematic projections reveal a future polarization in the invasion dynamics: while climate change will force an ecological contraction of the species in the Gran Chaco by 2070, it will simultaneously trigger runaway expansion and saturation in northern equatorial regions such as the Brazilian Caatinga, Venezuela, and Colombia.

Locally, the species' ability to flower and fruit year-round, coupled with efficient wind dispersal, has allowed it to aggressively colonize fallow crop plots, roadsides, and desolate environments. Notably, in Paraguay, the invasion has breached the Paraguay River into the Eastern region, where it now threatens critical conservation areas including the Médanos del Chaco, Paso Bravo, and Serranía San Luís National Parks. Ultimately, our dynamic topological framework demonstrates that anticipating the trajectory of *C. procera* requires accounting for both macro-climatic shifts and fine-scale anthropogenic landscape disturbances. Immediate, targeted management strategies are urgently needed to mitigate its socioeconomic and ecological impacts, particularly in newly suitable northern corridors and currently vulnerable protected areas.

Beyond theoretical niche modeling, our findings directly align with SDG 15 (Life on Land), specifically Targets 15.3 (combating desertification and restoring degraded land) and 15.8 (preventing and reducing the impact of invasive alien species). Quantifying the velocity and acceleration of the invasion front enables environmental authorities to transition from reactive control to proactive, target-specific interventions in vulnerable hotspots such as the Caatinga and Latin American dryland corridors.

4 Materials and Methods

In this section, we provide the core data and methodological description necessary to ensure the reproducibility of our results. Extended mathematical formalisms, computational workflows, and detailed data processing protocols are provided in Supplementary Information A (SA) and Supplementary Information B (SB).

4.1 Ecological context and species description

The environmental conditions characterizing *Calotropis procera* occurrences are primarily semi-arid to sub-humid, with annual rainfall ranging between 350 and 600 mm, occasionally exceeding these values during wet summer seasons. These habitats are subject to extreme solar radiation, frequent cloudy conditions, and persistent winds (northeastern to southeastern) [38]. The regional landscape, recognized as the Seasonal Dry Forest (Dry Chaco), supports vegetation on luvisol and cambisol soil types [17, 18, 35]. The canopy is defined by isolated emergents such as *Aspidosperma quebracho-blanco*, *Schinopsis lorentzii*, and *Ceiba chodatii*, while the understory is dominated by cacti, bromeliads, and various lianas [39, 40].

4.2 Occurrence data, spatial filtering, and background sampling

Presence records for *C. procera* were aggregated from 1993 to present, incorporating precise georeferencing. A global dataset was established by combining records from GBIF (https://www.gbif.org/) using the `spocc` R package [41] (n=2005), the speciesLink network from Brazil (n=516), and new botanical records from Paraguay (n=55) and Argentina [42] (n=48). Data were processed using tidy data principles [43]. Duplicate records and occurrences lacking precise geographic coordinates were removed.

As detailed in SA, to minimize environmental over-representation and spatial autocorrelation caused by sampling bias, we applied a spatial thinning algorithm using the `spThin` package [44]. Following a Nearest Neighbor Analysis (NNA) utilizing `spatstat` [45] to assess baseline spatial aggregation, records were thinned to ensure a minimum separation distance of 10 km, consistent with the species' natural dispersal capacity. For background sampling, we constrained the calibration area to a 900 km buffer around occurrences using the `sf` package [46] (projected in Eckert IV) to avoid historically inaccessible regions, extracting 10,000 random background points.

4.3 Environmental predictors and dimensionality reduction

Baseline climate data (1970–2000) were obtained from WorldClim v2.1 [47] at a high spatial resolution of 2.5 arc-minutes (`wc2.1_2.5m`, ≈ 5 km). To mitigate dimensionality issues and prevent multicollinearity from inflating model variance, we performed a rigorous collinearity analysis (Dimensionality Reduction). Bioclimatic variables exhibiting high Variance Inflation Factors (VIF) or Pearson's correlation coefficients $|r| > 0.90$ were systematically excluded, yielding a final set of 10 non-collinear predictors (see SA for the complete list).

To interpret climate-driven scenarios, future projections for 2050 (2041–2060) and 2070 (2061–2080) were assessed using a multi-model ensemble from the Coupled Model Intercomparison Project Phase 6 (CMIP6) [48]. The ensemble incorporates four Global Circulation Models (ACCESS-CM2, MPI-ESM1-2-HR, MRI-ESM2-0, and UKESM1-0-LL) under the SSP2-4.5 pathway [49], representing a standard mid-range mitigation scenario. All future climate layers were strictly pre-processed to match the `wc2.1_2.5m` resolution via bilinear resampling in the `terra` package [50], guaranteeing topological

congruence with the baseline grid. Further details on Climate Models and Scenario Interpretation are available in SA.

4.4 Ecological Niche Modeling and Composite Selection

Potential distribution was modeled using the maximum entropy algorithm (`maxnet`) [51]. Hyperparameter tuning was performed via the `ENMeval` package [52] using a block spatial cross-validation method to further penalize spatial autocorrelation. As described in SA, we evaluated a comprehensive grid of hyperparameters, testing Feature Classes (L, LQ, LQH) and Regularization Multipliers (RM) ranging from 0.5 to 8.0 in 0.5 increments.

Model selection was driven by a normalized composite scoring system (C) to strictly balance discrimination capacity against overfitting risk:

$$C = w_{\text{auc}}\hat{A}_{\text{val}} + w_{\text{or}}(1 - \hat{O}_{10}) + w_{\text{diff}}(1 - \hat{\Delta}_{\text{auc}}) + w_{\text{aicc}}(1 - \hat{\text{AICc}}) \tag{1}$$

where $\hat{A}_{\text{val}}$, $\hat{O}_{10}$, $\hat{\Delta}_{\text{auc}}$, and $\hat{\text{AICc}}$ represent the min-max normalized validation AUC, 10% training omission rate, training-validation AUC difference (overfitting penalty), and corrected Akaike Information Criterion, respectively. Weights were assigned as $w_{\text{auc}} = 0.40$, $w_{\text{or}} = 0.20$, $w_{\text{diff}} = 0.20$, and $w_{\text{aicc}} = 0.20$, prioritizing cross-validation discrimination capacity while evenly weighting omission error, spatial generalization, and model parsimony.

4.5 Dynamic Topology

Beyond static suitability projections mapped with the *cloglog* link function, we implemented a dynamic analysis framework. Following the theoretical principles established in Supplementary Information B (SB), the habitat suitability sequence $\mathbf{R}[n]$ derived from the ensemble median was analyzed via finite difference operators. To ensure the kinematic analysis evaluated only ecologically probable occurrences rather than marginal habitats, a dynamic binary mask was applied to each projected period utilizing the 10th-percentile training presence threshold.

The suitability velocity ($\mathbf{V}[n]$) and acceleration ($\mathbf{A}[n]$) matrices were then calculated to quantify the rate and curvature of the spatial shift. Modeling through discrete state variables allows us to analytically project future habitat suitability by assuming kinematic conservation. In matrix form, the state update equation is expressed as:

$$\mathbf{R}[n+1] = \mathbf{R}[n] + T \cdot \mathbf{V}[n] + \frac{1}{2}T^2 \cdot \mathbf{A}[n] \tag{2}$$

where T represents the temporal sampling interval. The suitability velocity ($V[n]$) and acceleration ($A[n]$) matrices were calculated to quantify the rate of change and curvature of environmental suitability through time. Importantly, $V[n]$ quantifies the rate of shift in environmental suitability space ($\Delta\text{Suitability}/\Delta t$, expressed in dimensionless suitability units per decade) rather than representing the physical dispersal velocity ($\text{km} \cdot \text{yr}^{-1}$) of organismal propagules across geographic space.

To prevent boundary truncation artifacts along the dynamic invasion front, finite difference calculations ($V[n]$ and $A[n]$) were evaluated across continuous suitability layers prior to applying the dynamic binary mask $M[n]$ (see Supplementary Information SA for full computational details).

By defining a strict asymptotic stability threshold ($\epsilon = 1 \times 10^{-6}$), pixels were classified into a topological regime $\mathcal{R}$ based on the phase-space tensor $[S(\mathbf{V}[n]), S(\mathbf{A}[n])]$. This enables the categorization of the **Ecological Denomination (Front Dynamics)**, identifying critical invasion states: *Runaway expansion* (increase in suitability with positive acceleration), *Asymptotic saturation* (suitability increases at a decreasing rate), *Reactivation / damping* (suitability loss slowing down), *Continuous retraction* (accelerated collapse of suitability), and *Metastable equilibrium* (propagation within a constant niche). Extended mathematical formalisms are provided in SB.

Additionally, shifts in the spatial proportions of these dynamic regimes across different time instants were statistically evaluated using a likelihood-ratio G-test. Finally, to quantify the epistemic uncertainty across the ensemble of M Global Climate Models, the stochastic classification per pixel was defined by the empirical mode $\mathcal{C}^* = \text{Mo}(\mathcal{R}_1, \ldots, \mathcal{R}_M)$. The spatial certainty of the front dynamics was modulated through the Absolute Agreement Index (U):

$$U = \sum_{m=1}^{M} \mathbb{I}(\mathcal{R}_m = \mathcal{C}^*) \tag{3}$$

where $\mathbb{I}$ is the indicator function representing the consensus among models (SB).

Supplementary information. **Supplementary Information A (SA):** Ecological Niche Modeling and Spatio-Temporal Dynamics Workflow (data preprocessing, spatial thinning, collinearity analysis, and hyperparameter tuning). **Supplementary Information B (SB):** Dynamic Topology of Expansion in CMIP6 Ensembles of Ecological Niche Models (mathematical definitions of velocity and acceleration finite difference operators, state-space equations, and regime classifications). **Supplementary Figures:** Supplementary Fig. S1 (Field record and growth habit of *C. procera* along Paraguayan roadsides) and Supplementary Fig. SA2 (ENMeval hyperparameter tuning heatmaps across feature classes and regularization multipliers). **Supplementary Tables:** Supplementary Table SA1 (CMIP6 Global Climate Models included in the ensemble) and Supplementary Table S3 (Geographic coordinates for new occurrence records in Paraguay).

Data Availability Statement. To ensure reproducibility of the results, the datasets analyzed during the current study, along with the R scripts for niche modeling and kinematic analyzes, are available in the repository under the placeholder DOI https://doi.org/10.5281/zenodo.23092901.

Ethical statements. The authors declare that they have no conflicts of interest.

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