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From Mexico to Argentina: Predicting the distribution of the invasive weed *Tithonia tubaeformis* beyond its native range using niche modelling

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Abstract

1. Biological invasions are a major driver of global change, affecting biodiversity, ecosystem functioning and agricultural productivity. *Tithonia tubaeformis* (Asteraceae) is a weed native to Mexico that has become invasive in several regions worldwide, including Argentina, where it threatens crop systems. Here, we compared species distribution models trained with native- and invaded-range occurrences to estimate the potential distribution of *T. tubaeformis* in Argentina. We also developed an invasion risk map to support prevention and management strategies.

2. Environmental predictors included 19 bioclimatic variables, elevation, and a Human Influence Index (HII). Models were calibrated using native- and invaded-range occurrences with MaxEnt, testing multiple regularisation multipliers and feature class combinations, with and without HII. The best-performing models were projected onto Argentina to estimate potential distribution and assess model transferability and environmental niche overlap between ranges.

3. Models showed good performance, and including HII improved model accuracy and explained a large portion of the predicted distribution. The native-trained model projected a broader potential range than the invasive-trained model, suggesting that *T. tubaeformis* has not yet occupied all suitable habitats in Argentina. Most invasive occurrences fell within the environmental space predicted using the native-trained model, although some records indicated a slight niche expansion under previously unoccupied conditions. The risk map identified northern Argentina as highly suitable for invasion, highlighting priority areas for monitoring and prevention.

4. Implications. Our findings demonstrate that native-range trained models can anticipate the spread of emerging weeds and that incorporating anthropogenic factors enhances predictive performance. These results contribute to understanding invasion processes and provide a practical tool for risk assessment and management planning in human-modified landscapes.

[Keywords: biological invasion, ecological niche, invasion risk, model transferability, species distribution models]

Resumen. De México a la Argentina: Prediciendo la distribución de la maleza invasora *Tithonia tubaeformis* más allá de su rango nativo utilizando modelado de nicho

1. Las invasiones biológicas afectan la biodiversidad, el funcionamiento de los ecosistemas y la productividad agrícola. *Tithonia tubaeformis*, maleza nativa de México, es invasora en varias regiones y amenaza los sistemas productivos en Argentina.

2. Comparamos modelos de distribución de especies calibrados con ocurrencias de los rangos nativo e invadido para estimar su distribución potencial en el país. También desarrollamos un mapa de riesgo de invasión para estrategias de prevención y manejo. Las variables ambientales incluyeron 19 bioclimáticas, la elevación y un índice de influencia humana (HII). Los modelos se calibraron con ocurrencias de los rangos nativo e invadido mediante MaxEnt, probando combinaciones de los diferentes parámetros, con y sin HII. Los modelos con mejor desempeño fueron proyectados sobre Argentina para estimar la distribución potencial, evaluar su transferibilidad y analizar el solapamiento del nicho entre rangos.

3. Los modelos tuvieron buen desempeño. Incluir el HII mejoró su precisión y explicó una porción significativa de la distribución predicha. El modelo entrenado con ocurrencias del rango nativo predijo una distribución más amplia que el entrenado con ocurrencias del rango invadido, sugiriendo que *T. tubaeformis* aún no ocupó todo el hábitat disponible. La mayoría de los puntos de presencia invasora se ubicaron dentro del espacio ambiental predicho por el modelo entrenado con ocurrencias del rango nativo, aunque algunos registros indicaron una leve expansión del nicho bajo nuevas condiciones ambientales. El mapa de riesgo identificó el norte de Argentina como altamente susceptible a la invasión, resaltando áreas prioritarias para el monitoreo y la prevención.

4. Implicancias. Los modelos entrenados con el rango nativo pueden anticipar la propagación de malezas, e incorporar factores antropogénicos mejora su desempeño predictivo. Estos resultados contribuyen a comprender las invasiones biológicas y proporcionan una herramienta práctica para evaluar riesgos y planificar la gestión de paisajes modificados por la actividad humana.

[Palabras clave: invasión biológica, modelos de distribución de especies, nicho ecológico, riesgo de invasión, transferibilidad de modelos]

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Introduction

Biological invasions are among the main drivers of global change resulting from human activities. The environmental and economic impacts of biological invasions have been widely documented across ecosystems worldwide. Invasive species can lead to biodiversity loss, community homogenization, disruption of ecosystem functioning and significant economic losses, particularly in productive systems (Vilà et al. 2011; Pyšek et al. 2020).

The introduction of organisms into environments outside their native range often occurs through deliberate human actions —for agricultural, economic, or ornamental purposes—, but can also result from unintentional transport. A species introduced to a new area by humans is considered alien, and if it becomes self-sustaining without direct human assistance it is termed naturalized, whereas if it spreads in the new environment over considerable distances —often producing numerous offspring— is considered an invasive species (Richardson et al. 2000). In agronomic contexts, invasive alien plants are often referred to as weeds due to their impact on crop systems since many invasive plant species can compete with crops and reduce yields (Richardson et al. 2000; Oerke 2006). However, invasive weeds of exotic origin often represent a higher ecological risk as they can also invade natural habitats surrounding productive lands. These species typically exhibit traits associated with invasiveness, such as rapid growth, both sexual and asexual reproduction and the absence of natural enemies, among others (Fan et al. 2018; Pyšek et al. 2020), although their invasion success also depends on the community context (D'Antonio 1993). In addition, disturbed environments, often resulting from land-use change, can facilitate the establishment of alien species while disadvantaging native communities (disturbance hypothesis) (Ricciardi et al. 2013). Consequently, species adapted to human-altered habitats may have a higher capacity to establish, spread and expand their distribution, highlighting the key role of human activities in shaping invasion patterns (González-Moreno et al. 2014; Ren et al. 2025).

Species distribution models (SDM) have become an essential tool for understanding how environmental conditions shape the geographic range of species. By correlating known occurrences with environmental variables, SDM can predict areas of suitable habitat and estimate a species' potential distribution (Peterson 2003). This has multiple applications for invasive species management, including identifying areas where the species is not yet established, guiding monitoring and building invasion risk maps that support early detection for action planning (Srivastava et al. 2021). SDM can also allow researchers to explore the relative importance of environmental predictors associated with a species' spread (Fan et al. 2018). Based on the concept of ecological niche, these models operate under the assumption that a species' niche is conserved (i.e., the environmental conditions that support viable populations remain constant across space and time), which enables the projection of models across new landscapes and even future climate change scenarios (Peterson 2003; Guisan and Thuiller 2005; Thapa et al. 2018). However, niche shifts can sometimes occur during invasions, highlighting the importance of selecting ecologically relevant predictors and evaluating model transferability (i.e., the ability of a model calibrated in one geographic range to predict species distribution in another range) (Fan et al. 2018; Srivastava et al. 2020).

One of the most widespread and resilient weeds associated with croplands in northwestern Argentina is *Tithonia tubaeformis*, a tall herbaceous Asteraceae species native to Mexico and Central America that was introduced accidentally to Argentina in the 1950s (Novara and Gutiérrez 2010). Known as gigantón in its native range, the species was colloquially renamed pasto cubano in Argentina. Today, it occupies vast areas (particularly in warm agricultural regions) where it thrives in disturbed habitats such as roadsides, cultivated fields, recently cleared lands and other human-disturbed habitats, often forming dense monospecific patches (Larenas-Parada et al. 2004; Novara and Gutiérrez 2010). *Tithonia tubaeformis* behaves as a troublesome weed in several extensive crops such as soybean, common bean, sugarcane, maize and tobacco in northwestern Argentina (De Andrada et al. 1995; Sánchez-Ducca et al. 2019; Berruezo et al. 2023). Along with two other congeners, the species has also become problematic in several sub-Saharan African countries, including South Africa and Zambia, where it threatens agricultural productivity and has even led to the abandonment of arable lands in some cases (Mashele et al. 2017; Witt et al. 2019). The invasive potential of *T. tubaeformis*

is enhanced by several traits that make it highly competitive: allelopathic properties (Juárez and Cazón 2003), rapid growth, early reproduction, high regrowth capacity and the ability to produce a persistent soil seed bank (Mashele et al. 2017; Huarte et al. 2025). In its native range, *T. tubaeformis* is also considered a weed of crops such as maize (Fonteyne et al. 2022). Since its introduction in Argentina, the species has expanded its distribution considerably, particularly toward the southern regions, colonizing new areas with contrasting climatic conditions. However, it remains unclear whether the species has reached the limits of its potential distribution, and there is still no comprehensive understanding of the environmental factors that define its ecological niche. This species thus represents an ideal case study to explore the feasibility of transferring SDM from one environment to another.

In this context, we aimed to evaluate the usefulness of SDM for predicting the distribution of *T. tubaeformis* as an invasive plant in Argentina. Specifically, we compared models calibrated with native- and invaded-range occurrences, and assessed the contribution of the Human Influence Index (HII) to model performance. Based on the best-performing models, we then estimated the potential distribution of the species and built a risk map identifying areas that could potentially be invaded.

Materials and Methods

Species under study

Tithonia tubaeformis (Jacq.) Cass. (Asteraceae) is an annual herbaceous plant native to Central America. It is a robust species, commonly reaching about 4 m in height but capable of growing up to 7 m. It bears large yellow capitula with ligulate florets 20-35 mm long, and its fruits are achenes of ~5 mm. Its seeds are sticky and have been proposed to exhibit epianthropochory, meaning they are dispersed by humans (Vibrans 1999). In addition to its wide distribution in its native range (i.e., Mexico, Honduras, Guatemala and El Salvador) (Global Biodiversity Information Facility —GBIF—, gbif.org), the species has been recorded in South America (in Argentina) (Larenas-Parada et al. 2004; Novara and Gutiérrez 2010; De Andrada et al. 1995; Sánchez-Ducca et al. 2019; Berruezo et al. 2023) and Africa (in South Africa, Zambia, Zimbabwe, Eswatini and Mozambique) (Mashele et al. 2017; Witt et al. 2019). Some databases also report introduced populations in Bolivia and Madagascar (e.g., GBIF).

In Argentina, *T. tubaeformis* behaves as a weed in many landscapes. It is believed that the species arrived in the country accidentally in the 1950s with seeds of the ornamental plant *Hibiscus cisplatinus* imported from Panama to the Jujuy province, and later expanded its distribution, likely facilitated by agricultural machinery (Novara and Gutiérrez 2010). It was officially declared a national pest by Resolution No. 283/1983 of the Secretariat of Agriculture and Livestock of Argentina, and included in the list of invasive, potentially invasive and cryptogenic alien species by Resolution No. 109/2021 (MAyDS 2021). Despite being considered problematic, the species is used as forage for livestock (both in its native and exotic ranges), as well as for medicinal, ceremonial and religious purposes (Zepeda-Bastida et al. 2019; Díaz-Medina et al. 2021).

Occurrence data

Native-range occurrence records of *T. tubaeformis* were obtained from GBIF, resulting in 2670 points. These records were carefully screened to remove doubtful, duplicate and misidentified records. A spatial thinning procedure was applied at a 10-km resolution to reduce sampling bias by excluding points located less than 10 km apart.

Invasive-range records were restricted to Argentina. These were compiled from our own field surveys (conducted over a five-year period across northwestern Argentina, covering a wide range of environmental conditions and land-use types), reports provided by local farmers, technical reports (including information obtained via email consultation with members of the Red de Restauración Ecológica Argentina) and published literature. The latter was identified through a bibliographic search in Google Scholar using the terms "Tithonia" AND ("tubaeformis" OR "tubiformis"), complemented by screening the reference lists of the retrieved articles. This resulted in a total of 42 occurrence points. Additionally, the limited GBIF records available for Argentina were individually verified and only those that could be visually confirmed using Google Street View imagery during the flowering period of the species were incorporated into the dataset. After data cleaning, the final

dataset comprised 844 occurrence points from the native range and 66 points from the invasive range.

Environmental data

The environmental variables used in our models included the 19 bioclimatic variables and an elevation layer from WorldClim version 2.1 (Fick and Hijmans 2017), which are widely employed in species distribution modelling. These variables represent different combinations of temperature and precipitation, all available at a 30 arc-sec resolution (~1 km^2) (Supplementary Material 1-Table S1).

Given that the presence of *Tithonia tubaeformis* has been frequently associated with highly disturbed environments, both in other invaded regions (López-Camal et al. 2021) and in Argentina (Gorostiague personal observation), we incorporated a variable reflecting human influence, as human-altered habitats may facilitate the establishment and proliferation of alien species (Ricciardi et al. 2013; Ren et al. 2025). For this purpose, we used the global human influence index (HII), a global dataset at 1-km resolution that integrates several indicators of human pressure, including population density, land use, infrastructure and accessibility features such as roads (WCS and CIESIN 2005).

Environmental layers were processed to define two modelling backgrounds: one restricted to the native range (i.e., Mexico, Honduras, Guatemala and El Salvador), and one covering the entire territory of Argentina as the invaded range. To eliminate multicollinearity among predictors, we excluded highly correlated variables, a common practice in species distribution modelling to avoid overparameterization and improve model interpretability (Guisan and Thuiller 2005; Aguirre-Gutiérrez et al. 2013). For this, we assessed pairwise correlations of variables in both ranges (independently for each background) using the remove highly correlated variables tool in SDM Toolbox 2.5 for ArcGIS (Brown et al. 2017). This tool evaluates the correlations among all input environmental data and then removes layers that are correlated at a specified level. We retained variables with correlation coefficients below 0.8, resulting in 10 predictors for the native range (Bio2, Bio3, Bio9, Bio10, Bio12, Bio15, Bio18, Bio19, elevation and HII) and 11 predictors for Argentina (Bio2, Bio3, Bio4, Bio9, Bio11, Bio14, Bio15, Bio16, Bio19, elevation and HII).

Model calibration

Models to estimate the distribution of *T. tubaeformis* were built using the MaxEnt algorithm v.3.4.1 (Phillips et al. 2006), as this approach has been widely recognized for its accuracy and robustness in ecological studies of invasive species (Phillips and Dudík 2008; Aguirre-Gutiérrez et al. 2013). Each model was trained with 10000 background points generated within a convex polygon surrounding the occurrence points, buffered by 50 km to approximate the accessible area and restrict the background to the sampled region. This approach avoids including environmentally unrealistic regions and reduces the bias associated with broad background extents, thereby minimizing the risk of overestimating model predictive performance (Radosavljevic and Anderson 2014).

Models were calibrated using a range of regularization multiplier values (0.5, 1, 1.5, 2, 2.5, 3 and 4) and different feature class combinations (L, LQ, LQH, H and LQHPF), which cover a broad set of parameterizations that have proven to be effective in other studies (Radosavljevic and Anderson 2014). For each combination, a spatial jackknife procedure was applied, splitting occurrence points into three geographically distinct groups to evaluate predictive ability across space (Brown et al. 2017). The best-performing model was selected based on a composite metric combining the area under the curve (AUC) and the prediction rate, calculated as 1-omission rate, and the model with the highest combined value of these metrics was retained. While omission rate was evaluated independently for each spatial partition, AUC was calculated for the entire study area, making both measures complementary indicators of model performance. This calibration process was performed using the modelling tools available in SDM Toolbox 2.5 (Brown et al. 2017), for both the native and invaded ranges. Also, given that the inclusion of human disturbance predictors can give significantly different results (Ren et al. 2025), models were created both including and excluding the HII environmental variable in order to test whether this index affects model performance. In addition, the contribution and permutation importance of predictor variables were calculated to assess the

relevance of incorporating HII. This was done in MaxEnt using a jackknife test, which trains the model with each variable first omitted and then used in isolation. Once the optimal configuration for each scenario was identified, models were rerun with the selected feature classes and regularization settings using five cross-validated replicates, and the average prediction map was retained. At this stage, two types of models were developed: 1) a native-to-invasive model, trained in the native range and projected onto Argentina (through the projection layers' function in Maxent), and 2) an invasive-to-invasive model, trained exclusively with exotic records in Argentina.

Continuous model outputs were converted into binary predictions using two threshold criteria: the maximum test sensitivity plus specificity threshold (based on predictive performance), and the 10th percentile training presence threshold (which excludes the lowest 10% of occurrence probabilities).

Spatial analysis

Once the best model for each scenario was finalized, we analysed differences between them to evaluate model transferability. Binary predictions for each threshold and projection (native-to-invasive vs. invasive-to-invasive) were compared by calculating the proportion of shared and non-shared presence, using the difference between binary SDM tool in SDM Toolbox 2.5 (Brown et al. 2017). In addition, niche similarity between models was assessed using Schoener's D index, which ranges from 0 (no overlap) to 1 (complete overlap).

Model performance was further evaluated using the 66 occurrence points from Argentina, by calculating the proportion of correctly predicted presences for each model. The area that could potentially be occupied by *T. tubaeformis* was calculated projecting the binary maps using Albers Conic Equal-Area projection for continental South America.

Environmental analysis

We characterized the values of all environmental variables at native and invasive occurrence sites, assessing their degree of overlap. To further explore environmental differentiation, a principal component analysis (PCA) was performed using all environmental variables associated with occurrence points from both the native range and exotic range in Argentina. The PCA was used to characterize the environmental space occupied by native and invasive occurrences independently of the predictor selection used for model calibration. Significant differences in PCA scores between native and exotic occurrences were tested using a MANOVA using Wilks' lambda, which ranges between 0 and 1 (values close to 1 indicate groups are similar, while values close to 0 indicate groups are different). This test was conducted on the first principal components that explained more than 90% of the total variance. Additionally, ANOVA was applied to each component to compare groups. All analyses were performed in R v.3.6.3 (R Core Team 2021).

Projected potential distribution and invasion risk

Finally, a risk map was developed for Argentina to represent environmentally suitable habitat for the establishment of *T. tubaeformis*. For this purpose, we averaged the predictions of the best-performing native-to-invasive and invasive-to-invasive models including HII. This approach was used to integrate the complementary information provided by the two modelling strategies: the native-to-invasive model provides information on potential environmental suitability beyond the currently occupied range, whereas the invasive-to-invasive model reflects environmental suitability associated with the species' current distribution in Argentina. We then calculated two complementary metrics of suitability within each political unit: 1) the mean suitability across all pixels, and 2) the maximum suitability value recorded within each unit. Argentina is divided into 24 provinces and each of them contains smaller political units called departments, with a total of 527 units. The mean suitability values were used to classify each department into invasion risk categories (using Jenks' natural breaks in ArcMap 10.2) as no risk, low risk, mid risk, high risk or maximum risk of invasion, and to create a risk map. In addition, the maximum suitability criterion was used to identify departments containing one or more high-suitability pixels (>0.8), which were considered priority areas for potential invasion risk of the studied species.

Results

Overall, models showed strong performance and revealed both consistencies and differences between native- and invasive-based approaches. The best-performing native-to-

invasive model including the HII variable was obtained with a regularization multiplier (RM) of 3 and all feature classes, whereas the best model excluding HII used a RM of 2.5 with all feature classes. For the invasive-to-invasive approach, the optimal configuration including HII was obtained with an RM of 0.5 and linear features only, while excluding HII yielded the best results with an RM of 1 and four feature classes (Supplementary Material 2-Table S1). In both cases, when the HII was included as a predictor variable, it had a major contribution to the MaxEnt model, ranking as the most influential predictor (48.4% contribution for the native range and 56.8% for the invasive range) (Supplementary Material 3-Table S1). These four selected models were used for further analyses.

A comparison of presence-absence maps generated with different model settings revealed that both the modelling approach and the chosen threshold influenced the results. Overall, coincidence was higher when the HII was included (Supplementary Material 4-Table S1). Schoener's D index was used to compare continuous suitability maps between the native-to-invasive and invasive-to-invasive models. Including HII yielded a D value of 0.4503, while excluding HII gave 0.4982, indicating moderate niche similarity (Figure 1).

Model performance was consistently high, with relatively large AUC values across all models. Training and testing AUC values were similar, with the former slightly higher, suggesting good predictive ability without signs of overfitting (Table 1). In addition, the proportion of correctly predicted presences was higher under the 10th percentile threshold, as expected given that this less restrictive threshold includes lower suitability values and thus a broader predicted range. The inclusion of the HII improved AUC values in all cases, while the proportion of correctly predicted presences varied among models. The most accurate configuration (92% of presences correctly predicted) was the invasive-to-invasive model including HII, under the 10th percentile threshold.

Binary predictions for each threshold and projection (native-to-invasive vs. invasive-to-invasive) were also compared in terms of spatial overlap (Supplementary Material 4-Table S1) as well as the total area predicted as suitable (km²). Overlap among models ranged from ~1% to 74%, depending on the modelling approach and threshold (Supplementary Material 4-Table S1).

Environmental predictor values at invasive-range occurrence sites in Argentina fell largely within the range of values observed in the native range, suggesting that the species occupies a broader niche in its native distribution. The only exception was observed for Bio12 (mean annual precipitation), where two invasive records occurred below the native minimum. These outlier records (i.e., niche expansion) were also evident in the PCA (Figure 2) and correspond to the locality of Cachi (Salta province), an arid valley where cultivation relies on irrigation.

A MANOVA indicated that native and invasive occurrence groups were significantly different ($P<0.001$); however, the Wilks' lambda value (0.879) suggested that both groups are

Table 1. Model performance for the prediction of *Tithonia tubaeformis* presence in Argentina using different projection approaches and thresholds. AUC: area under the curve.

Tabla 1. Desempeño de los modelo para predecir la presencia de *Tithonia tubaeformis* en la Argentina utilizando diferentes enfoques de proyección y umbrales. AUC: área bajo la curva.

Model	Test AUC	Training AUC	Maximum test sensitivity plus specificity threshold			10th percentile threshold		
			Threshold value	Area (km²)	Correctly predicted occurrences	Threshold value	Area (km²)	Correctly predicted occurrences
native-to -invasive (with HII)	0.766	0.776	0.467	7201	50%	0.301	41442	79%
native-to -invasive (without HII)	0.716	0.731	0.583	1261	0%	0.334	225309	85%
invasive-to-invasive (with HII)	0.850	0.884	0.420	15447	74%	0.147	68061	92%
invasive-to-invasive (without HII)	0.796	0.881	0.458	19963	79%	0.251	56306	89%

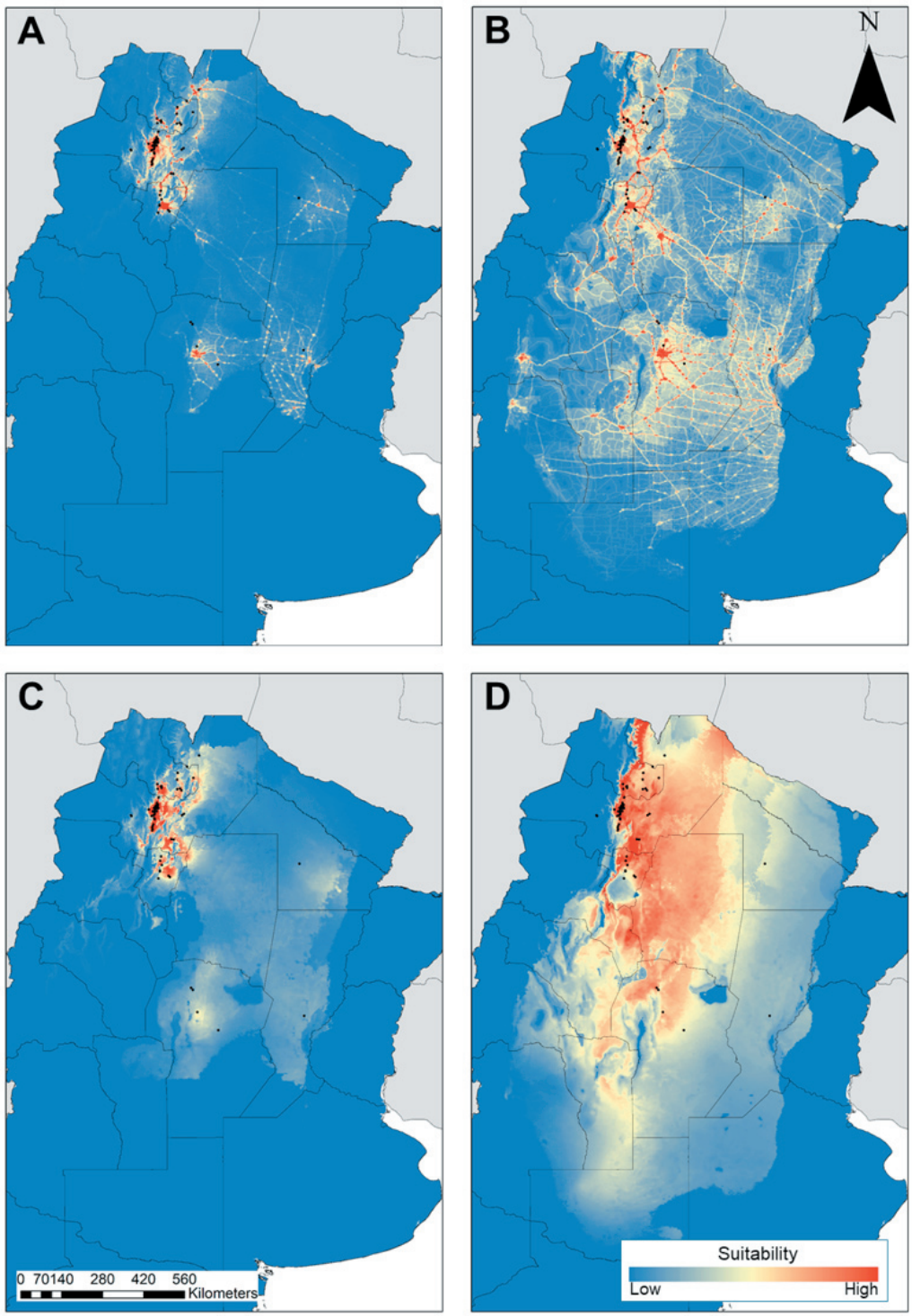

Figure 1. Mean species distribution models (SDM) showing the suitability for potential invasion range of *Tithonia tubaeformis* in Argentina, using the native-to-invasive (A, C) and invasive-to-invasive (B, D) approach, both including (A, B) and excluding (C, D) the human influence index as a predictor variable. Black dots indicate occurrence records.

Figura 1. Modelos promedio de distribución de especies (SDM) que muestran la idoneidad ambiental del rango potencial de invasión de *Tithonia tubaeformis* en Argentina, utilizando el enfoque nativo-a-invasivo (A, C) e invasivo-a-invasivo (B, D), ambos incluyendo (A, B) y excluyendo (C, D) el índice de influencia humana como variable predictora. Los puntos negros indican los registros de ocurrencia.

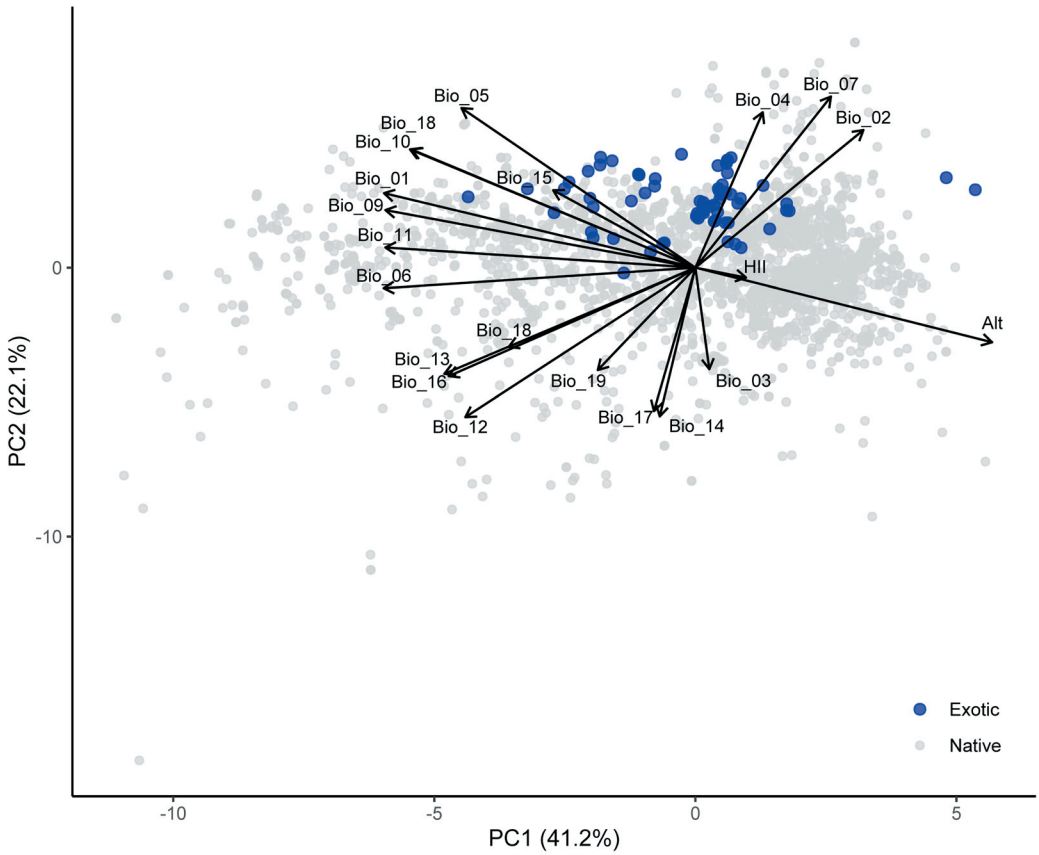

Figure 2. Principal components analysis showing the first two components and the proportion of variance explained, based on the environmental values of *Tithonia tubaeformis* occurrence points. Grey dots represent native-range occurrences, while blue dots correspond to occurrences in Argentina.

Figura 2. Análisis de componentes principales mostrando los dos primeros componentes y la proporción de varianza explicada, basado en los valores ambientales de los puntos de ocurrencia de *Tithonia tubaeformis*. Los puntos grises representan ocurrencias en el rango nativo, mientras que los puntos azules corresponden a ocurrencias en la Argentina.

overall very similar in their environmental conditions. The first five principal components explained 90.8% of total variance (PC1=41.2% of total variance; PC2=22.1%; PC3=14.8%; PC4=8.4% and PC5=4.4%). ANOVA performed on each principal component showed no significant differences between groups for PC1 (P=0.734), but significant differences for the other four components (P<0.001 in all cases).

For the risk map, suitability values were averaged across the raster files of the native-to-invasive and invasive-to-invasive models, both including HII given its strong contribution and positive effect on model performance. The map revealed that a large portion of northern Argentina is at considerable risk of invasion, particularly in the provinces of Jujuy, Salta, Tucumán, Chaco, Santiago del Estero, Córdoba, San Juan and Santa Fe (Figure 3). Among the 527 departments, 31 were classified as high or maximum risk based on their mean suitability values, located in the provinces of Salta, Tucumán, Jujuy, San Juan, Córdoba and Santiago del Estero (Supplementary Material 5-Table S1). Additionally, according to the maximum suitability recorded within each unit, 27 departments contained pixels with a predicted suitability higher than 0.8, concentrated in the same provinces, except for San Juan (Supplementary Material 5-Table S1).

Discussion

In this work, we used species distribution models to estimate the potential distribution of *Tithonia tubaeformis* in Argentina and to assess the performance of models trained in the native and invaded ranges. This approach allowed us to evaluate model

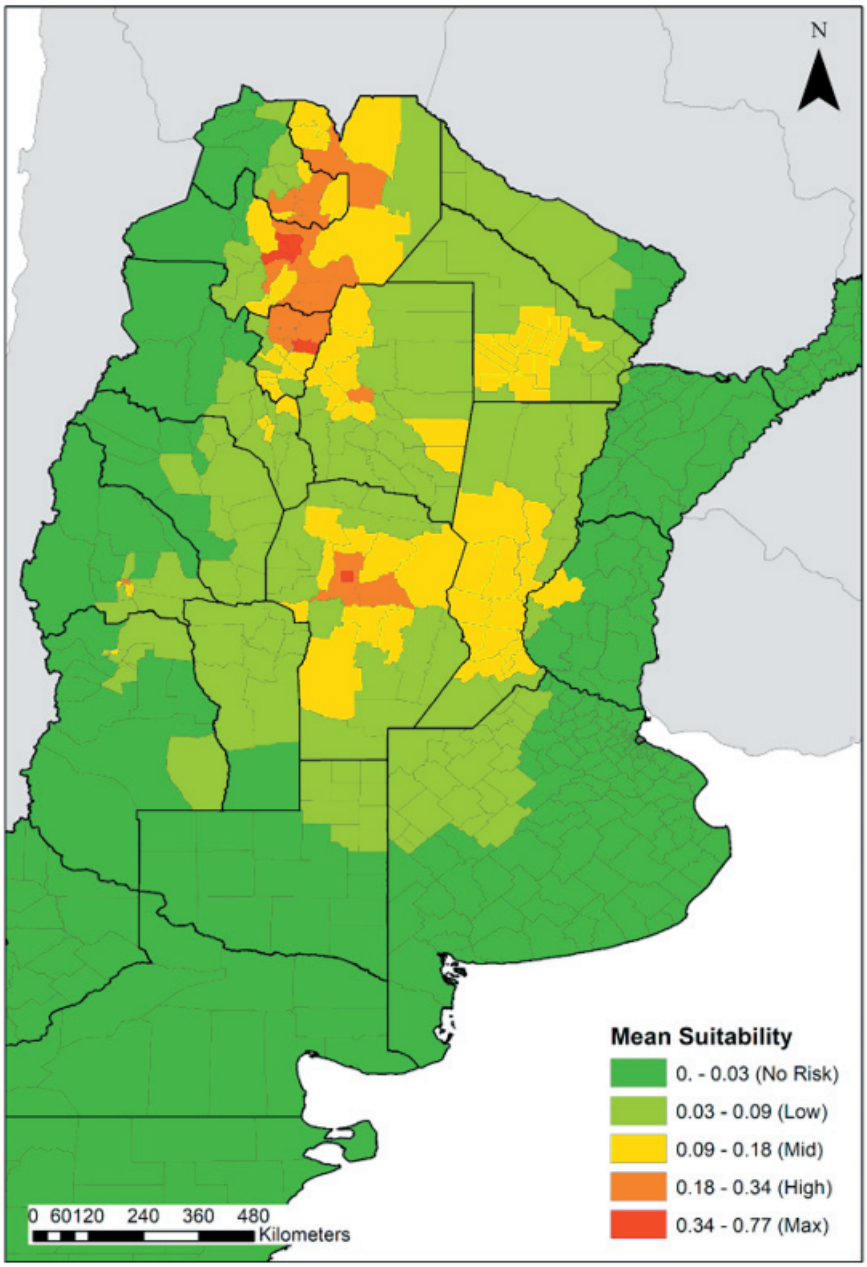

Figure 3. Risk map showing provinces and departments with high environmental suitability for invasion by *Tithonia tubaeformis* in Argentina.

Figura 3. Mapa de riesgo que muestra las provincias y departamentos con alta idoneidad ambiental para la invasión de *Tithonia tubaeformis* en la Argentina.

transferability and to generate a risk map that can guide prevention and management actions (Srivastava et al. 2021).

As expected, the invasive-to-invasive model showed the highest predictive performance for occurrence records within the invaded range, likely because it was calibrated using the same data. However, the native-to-invasive model also achieved a high prediction success under the less restrictive threshold (10th percentile), highlighting its capacity to identify suitable environments beyond the currently occupied range (Václavík and Meentemeyer 2012). Furthermore, differences between modelling approaches provide insights into the invasion process, particularly regarding the extent to which the species has filled its potential niche in the invaded region.

An important result was that the range obtained with the native-to-invasive approach was more extensive than the range predicted by the invasive-to-invasive models. This difference is likely related to the fact that native-range models were calibrated with a

large number of occurrence points that cover a wider set of environmental conditions, representing a more stable or equilibrated niche. In addition, models trained with the invasive distribution could reflect a species that is still expanding and has not yet occupied all suitable habitats in Argentina. Therefore, the native-to-invasive model can provide useful insights into the possible expansion of the species in this new environment. This agrees with previous findings that invasive niche models may give less robust predictions in early stages of invasion, when equilibrium has not yet been reached (Václavík and Meentemeyer 2012; Fan et al. 2018).

In Argentina, the distribution of *T. tubaeformis* is still not stable and continues to expand from north to south. The PCA analysis also showed that the species has not yet occupied all the suitable environmental conditions, reinforcing the idea that further spread is likely. This species behaves as a weed not only in its native range but also in invaded regions worldwide, posing risks to agricultural production (Vilà et al. 2011). The species occurs in croplands, roadsides, riversides, irrigation channels, rangelands, and other disturbed sites (Gorostiague personal observation), as has been observed in African countries (Witt et al. 2019). Its presence could therefore be associated with early stages of secondary succession, and it has not yet been recorded under the canopy of native forests. This may explain its rapid expansion in landscapes heavily altered by human activities, as seen in other invasive plant species (González-Moreno et al. 2014; Ren et al. 2025). In this sense, the high contribution of the HII in our models highlights that anthropogenic disturbance is a central component of the species' niche, both in its native and invaded ranges (Fan et al. 2018; Pyšek et al. 2020).

Although the MANOVA detected statistically significant differences between native and invasive occurrences, the high Wilks' lambda value indicates that these differences are relatively small in magnitude. This suggests that most of the environmental space occupied in the invaded range overlaps with that of the native range. Consistently, the first principal component (representing the main environmental gradient and 41% of the variance) did not differ between groups, while differences were restricted to secondary components. Together, these results support a pattern of overall niche conservatism with limited shifts along less dominant environmental dimensions. However, we also found evidence that the species can establish in new conditions not recorded in its native range. The records in Cachi (Salta province), located in an arid valley isolated by mountain ranges, represent a clear example. These points had precipitation values below the minimum observed in the native range, where the species would be able to persist near irrigated crop fields. It is very likely that the species reached this site through human-mediated dispersal, such as contaminated seeds. This highlights the risk of accidentally introducing invasive plants into cultivated areas, where favourable conditions can allow them to proliferate and persist (Srivastava et al. 2021). In Cachi, we observed populations of *T. tubaeformis* in vegetable fields (tomato and pepper) but also along roadsides (Gorostiague and Urtasun personal observation), where the species can already be considered naturalized (sensu Richardson et al. 2000).

The broad suitable area predicted by our models suggests that the expansion of *T. tubaeformis* represents a growing challenge for its management, being a competitive weed that tolerates a wide range of soil conditions (Larenas-Parada et al. 2004). Biological control has been explored in northern Argentina with the defoliating caterpillar *Chlosyne lacinia* saundersii (Gómez et al. 2020), and in Africa, attempts have been made to introduce natural enemies from the native range, such as *Zygogramma* spp. beetles, although establishment has often failed (Mawela and Simelane 2021). Chemical methods with pre- and post-emergence herbicides have proven to be effective in agroecosystems, but complementary actions are needed to prevent seed contamination and dispersal along roads and field margins (Sánchez-Ducca et al. 2019). Cultural practices should also be taken into account, considering the seed dormancy and light requirements for germination reported for the species (Huarte et al. 2025). Similar traits in other *Tithonia* species have been found in Africa, such as high seed production and dormancy, which have been shown to give them an advantage in colonizing croplands after harvest (Muoghalu and Chuba 2005).

Another aspect that should be noted is the presence of the congener *Tithonia rotundifolia* in northwestern Argentina (Novara and Gutiérrez 2010). This species naturally hybridizes with *T. tubaeformis* in their native range (López-Caamal et al. 2018), which could increase risks by enhancing allelopathic effects

or tolerance to abiotic stress (Juárez and Cazón 2003; López-Caamal et al. 2018). Since *T. rotundifolia* is also an invasive weed in Africa, representing a major cause of crop yield losses (Witt et al. 2019; Mawela and Simelane 2021), the possibility of hybridization and further expansion of these invasive species in Argentina deserves attention. Unfortunately, information on the occurrence and invasion status of this species in the region remains scarce.

A risk assessment can serve as a valuable tool for planning preventive measures in areas with a high probability of being occupied by invasive species (Pyšek et al. 2020). The risk map produced in this study could be used for prevention planning. It suggests that large areas in northern Argentina are highly suitable for the establishment of *T. tubaeformis*. The historical expansion from north to south is consistent with these projections: the species was introduced in Jujuy, the northernmost province, and was later recorded in Salta (Novara and Gutiérrez 2010) and further south in Tucumán (Sánchez-Ducca et al. 2019). This suggests that the species could continue to spread, so special attention should be paid to the provinces and departments identified as high-risk sites. One caveat is that the averaging of suitability at the level of political units may underestimate risk in large departments, and thus, the identification of high-suitability pixels within them provides complementary information. These areas should be prioritized to prevent the introduction of seeds and establishment of new populations.

Despite the insights provided by our models, many aspects of the biology of *T. tubaeformis* remain poorly understood, including its reproductive biology, dispersal mechanisms, and seed bank dynamics. Such knowledge would be crucial for designing effective strategies to control its expansion. In a broad sense, a deeper understanding of the ecological dynamics driving species invasions will enable more effective prevention and management plans, ultimately reducing their impact on both natural and productive ecosystems.

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References

Aguirre-Gutiérrez, J., L. G. Carvalheiro, C. Polce, E. E. van Loon, N. Raes, et al. 2013. Fit-for-purpose: species distribution model performance depends on evaluation criteria - Dutch hoverflies as a case study. PLoS ONE 8:e63708. https://doi.org/10.1371/journal.pone.0063708.

Berruezo, L., G. Cárdenas, C. Machado, and M. Galván. 2023. Diagnóstico de malezas, posibles hospederas de virosis en el cultivo de tabaco. IV Congreso Argentino de Malezas, Buenos Aires.

Brown, J. L., J. R. Bennett, and C. M. French. 2017. SDMtoolbox 2.0: the next generation Python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. PeerJ 5:e4095. https://doi.org/10.7717/peerj.4095.

D'Antonio, C. M. 1993. Mechanisms controlling invasion of coastal plant communities by the alien succulent *Carpobrotus edulis*. Ecology 74(1):83-95. https://doi.org/10.2307/1939503.

De Andrada, N., H. Robinet, O. Arce, B. Díaz, S. Guillen, et al. 1995. Relevamiento y determinación de la distribución de malezas frecuentes en la zona sojera del noreste de Tucumán. XII Congreso Latinoamericano de Malezas, Uruguay.

Díaz-Medina, L. K., V. Colín-Navarro, C. M. Arriaga-Jordán, L. Brunett-Pérez, B. R. Vázquez-de-Aldana, et al. 2021. In vitro nutritional quality and antioxidant activity of three weed species as feed additives for sheep in the Central Highlands of Mexico. Tropical Animal Health and Production 53(3):394. https://doi.org/10.1007/s11250-021-02819-8.

Gómez, G. C., M. L. F. Salinas, and M. J. Barrionuevo. 2020. Ciclo de vida de *Chlosyne lacinia saundersii* (Lepidoptera: Nymphalidae) sobre *Tithonia tubaeformis* (Jacq.) Cass. en condiciones controladas de laboratorio. Revista de la Sociedad Entomológica Argentina 79(4):31-38. https://doi.org/10.25085/rsea.790405.

González-Moreno, P., J. M., Diez, I. Ibáñez, X. Font, and M. Vilà. 2014. Plant invasions are context-dependent: multiscale effects of climate, human activity and habitat. Diversity and Distributions 20(6):720-731. https://doi.org/10.1111/ddi.12206.

Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters 8(9):993-1009. https://doi.org/10.1111/j.1461-0248.2005.00792.x.

Fan, J. Y., N. X. Zhao, M. Li, W. F. Gao, M. L. Wang, et al. 2018. What are the best predictors for invasive potential of weeds? Transferability evaluations of model predictions based on diverse environmental data sets for *Flaveria bidentis*. Weed Research 58(2):141-149. https://doi.org/10.1111/wre.12292.

Fick, S. E., and R. J. Hijmans. 2017. WorldClim 2: new 1 km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37(12):4302-4315. https://doi.org/10.1002/joc.5086.

Fonteyne, S., A. J. Leal González, L. Osorio Alcalá, J. Villa Alcántara, C. Santos Rodríguez, et al. 2022. Weed management and tillage effect on rainfed maize production in three agro-ecologies in Mexico. Weed Research 62(3):224-239. https://doi.org/10.1111/wre.12530.

Huarte, H. R., P. D. Vargas, G. D. Puglia, and A. Sánchez-Ducca. 2025. Seed dormancy release and germination ecophysiology of wild Mexican sunflower (*Tithonia tubaeformis*). Weed Science 73(e49):1-10. https://doi.org/10.1017/wsc.2025.19.

Juárez, V. D., and A. V. Cazón. 2003. Autotoxicity in *Tithonia tubaeformis* as a mechanism of invasion control. Ecología Austral 13(2):133-138.

Larenas-Parada, G., M. L. De Viana, T. Chafatinos, and N. E. Escobar. 2004. Relación suelo-especie invasora (*Tithonia tubaeformis*) en el sistema ribereño del río Arenales, Salta, Argentina. Ecología Austral 14(1):19-29.

López-Caamal, A., R. Reyes-Chilpa, and E. Tovar-Sánchez. 2018. Hybridization between *Tithonia tubaeformis* and *T. rotundifolia* (Asteraceae) evidenced by nSSR and secondary metabolites. Plant Systematics and Evolution 304(3):313-326. https://doi.org/10.1007/s00606-017-1478-8.

López-Caamal, A., and E. Tovar-Sánchez. 2021. Comparing the population history of Neotropical annual species: the role of climate change and hybridization between *Tithonia tubaeformis* and *T. rotundifolia* (Asteraceae). Plant Biology 23(6):962-973. https://doi.org/10.1111/plb.13313.

MAyDS (Ministerio de Ambiente y Desarrollo Sostenible de la Nación). 2021. Resolución 109/2021: Lista de especies exóticas invasoras, potencialmente invasoras y criptogénicas de la República Argentina. Boletín Oficial de la República Argentina. URL: shorturl.at/S8UfI.

Mashele, B., C. Mafuwane, M. C. Moshobane, and D. O. Simelane. 2017. Mexican sunflower (*Tithonia tubaeformis*): a new threat to food security in South Africa. SAPIA News 46:4-6.

Mawela, K. V., and D. O. Simelane. 2021. Biological control of *Tithonia* spp. (Asteraceae) in South Africa: challenges and possibilities. African Entomology 29(3):896-904. https://doi.org/10.4001/003.029.0896.

Muoghalu, J. I., and D. K. Chuba. 2005. Seed germination and reproductive strategies of *Tithonia diversifolia* (Hemsl.) Gray and *Tithonia rotundifolia* (P.M.) Blake. Applied Ecology and Environmental Research 3(1): 39-46. https://doi.org/10.15666/aeer/0301_039046.

Novara, L., and D. G. Gutiérrez. 2010. Asteraceae-Tribu 5. Heliantheae. Aportes Botánicos de Salta - Serie Flora 9(6): 1-201.

Oerke, E. C. 2006. Crop losses to pests. The Journal of agricultural science 144(1):31-43. https://doi.org/10.1017/S0021859605005708.

Peterson, A. T. 2003. Predicting the geography of species' invasions via ecological niche modelling. The Quarterly Review of Biology 78(4):419-433. https://doi.org/10.1086/378926.

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modelling of species geographic distributions. Ecological Modelling 190:231-259. https://doi.org/10.1016/j.ecolmodel.2005.03.026.

Phillips, S. J., and M. Dudík. 2008. Modelling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31(2):161-175. https://doi.org/10.1111/j.0906-7590.2008.5203.x.

Pyšek, P., P. E. Hulme, D. Simberloff, S. Bacher, T. M. Blackburn, et al. 2020. Scientists' warning on invasive alien species. Biological Reviews 95(6):1511-1534. https://doi.org/10.1111/brv.12627.

R Core Team. 2021. R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.

Radosavljevic, A., and R. P. Anderson. 2014. Making better Maxent models of species distributions: complexity, overfitting and evaluation. Journal of Biogeography 41(4):629-643. https://doi.org/10.1111/jbi.12227.

Ren, Z., Y. Ai, M. S. Heinz, J. Liu, X. Yuan, et al. 2025. Climatic, human-induced and biodiversity factors differently shape the suitable areas of *Bidens pilosa*. Journal of Plant Ecology 18(2):rtaf032. https://doi.org/10.1093/jpe/rtaf032.

Richardson, D. M., P. Pyšek, M. Rejmánek, M. G. Barbour, F. D. Panetta, et al. 2000. Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions 6(2):93-107. https://doi.org/10.1046/j.1472-4642.2000.00083.x.

Ricciardi, A., M. F. Hoopes, M. P. Marchetti, and J. L. Lockwood. 2013. Progress toward understanding the ecological impacts of nonnative species. Ecological monographs 83(3):263-282. https://doi.org/10.1890/13-0183.1.

Sánchez-Ducca, A., P. D. Vargas, S. Sabaté, M. López, and E. R. Romero. 2019. Pasto cubano: nueva maleza problema para Tucumán. Avance Agroindustrial 40(2):26-27.

Srivastava, V., W. Liang, M. A. Keena, A. D. Roe, R. C. Hamelin, et al. 2020. Assessing niche shifts and conservatism by comparing the native and post-invasion niches of major forest invasive species. Insects 11(8):479. https://doi.org/10.3390/insects11080479.

Srivastava, V., A. D. Roe, M. A. Keena, R. C. Hamelin, and V. C. Griess. 2021. Oh the places they'll go: improving species distribution modelling for invasive forest pests in an uncertain world. Biological Invasions 23(1):297-349. https://doi.org/10.1007/s10530-020-02372-9.

Thapa, S., V. Chitale, S. J. Rijal, N. Bisht, and B. B. Shrestha. 2018. Understanding the dynamics in distribution of invasive alien plant species under predicted climate change in Western Himalaya. PLoS ONE 13(4):e0195752. https://doi.org/10.1371/journal.pone.0195752.

Václavík, T., and R. K. Meentemeyer. 2012. Equilibrium or not? Modelling potential distribution of invasive species in different stages of invasion. Diversity and Distributions 18(1):73-83. https://doi.org/10.1111/j.1472-4642.2011.00854.x.

Vilà, M., J. L. Espinar, M. Hejda, P. E. Hulme, V. Jarošík, et al. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecology Letters 14(7):702-708. https://doi.org/10.1111/j.1461-0248.2011.01628.x

Vibrans, H. 1999. Epianthropochory in Mexican weed communities. American Journal of Botany 86(4):476-481. https://doi.org/10.2307/2656808.

Wildlife Conservation Society (WCS), and Center for International Earth Science Information Network (CIESIN) - Columbia University. 2005. Last of the Wild Project, Version 2, 2005 (LWP-2): Global Human Influence Index (HII) Dataset (Geographic). Palisades, NY: ESDIS. https://doi.org/10.7927/H4BP00QC.

Witt, A. B. R., R. T. Shackleton, T. Beale, W. Nunda, and B. W. Van Wilgen. 2019. Distribution of invasive alien *Tithonia* (Asteraceae) species in eastern and southern Africa and the socio-ecological impacts of *T. diversifolia* in Zambia. Bothalia 49(1):a2356. https://doi.org/10.4102/abc.v49i1.2356.

Zepeda-Bastida, A., M. Ayala Martínez, and S. Soto-Simental. 2019. Carcass and meat quality of rabbits fed *Tithonia tubaeformis* weed. Revista Brasileira de Zootecnia 48:e20190074. https://doi.org/10.1590/rbz4820190074.