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Geographical patterns in the distribution of naturalized plants in Central America

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Abstract

Non-native plant species are increasing globally, yet their distribution patterns and environmental drivers remain poorly understood in biodiversity-rich but understudied regions like Central America. In this region, non-native species increasingly affect biodiversity, ecosystem integrity, and conservation efforts, especially when they become invasive. We analyzed the spatial distribution of 751 naturalized plant species using over 42,000 occurrence records across the seven countries in Central America. We evaluated the influence of environmental variables, human population density, protected areas, and life zones on both occurrence and species richness. Human population density emerged as the strongest predictor of naturalized species occurrence and richness, highlighting the role of human activity in facilitating invasions. Annual precipitation was positively associated with occurrences, while species richness declined with increasing temperature and biodiversity integrity. Tropical rainforests and other humid life zones had more naturalized species than expected by chance. Protected areas had fewer naturalized species overall, but a higher species ratio per observation, indicating both conservation value and vulnerability. Rare species were found outside protected zones, particularly in disturbed and urbanized areas. Our findings highlight the need for early detection, targeted management, and strengthened protection strategies, especially in mid-elevation zones and densely populated areas. By identifying key environmental and anthropogenic drivers, this study provides actionable insights for conservation planning and invasive species management in one of the world’s most biodiverse and socio-environmentally vulnerable regions.

Keywords: Invasive Species, Biodiversity, Protected Areas, Central America, Population Density

Introduction

Naturalized plant species, those that establish self-sustaining populations outside their native range, play a complex and growing role in affecting global change and biodiversity conservation (IPBES 2023). When naturalized species become invasive, they can severely impact ecosystem function, economic stability, food and water security, human health, and even cultural identities

(Pimentel et al. 2001; Clements et al. 2021; Heringer et al. 2021; Bacher et al. 2023). Understanding naturalized species' drivers and distribution patterns is essential for developing effective management strategies for biodiversity conservation and ecological resilience. Despite substantial progress in invasion ecology, significant knowledge gaps remain, particularly regarding the interplay between environmental factors and human activities in shaping naturalization patterns.

Central America is a biodiversity hotspot with exceptional species richness and endemism (Coates 1999). However, the region also faces a high degree of ecological and socioeconomic vulnerability, shaped by a long history of colonialism, political instability, inequality, poverty, inadequate use of territory, and rapid unplanned urbanization (Morales-Marroquín et al. 2022). These pressures are exacerbated by limited investment in scientific research, weak conservation policies, and poor regulation of activities that affect native ecosystems (Harvey et al. 2005). For instance, managing non-native invasive and naturalized species is rarely addressed in environmental regulations and policies across Central American countries (Chacón-Madrigal et al. 2022). Thus, empirical research on plant invasions in the region remains scarce compared to other regions.

Recent studies have begun to address long-standing knowledge gaps in our understanding of plant invasions in Central America (see Avalos et al. 2021; Chacón-Madrigal et al. 2022; Rojas-Sandoval et al. 2022; MacVean and Zinn 2023). These efforts have provided valuable baseline data, such as species inventories, introduction pathways, and invasion histories, and emphasize the pressing need for more coordinated, region-wide research on plant invasions. A persistent challenge identified across these studies is the lack of updated herbarium records, and systematic botanical surveys focused specifically on non-native species. For example, our previous work documented 1,228 species in the alien flora of Central America, including 835 naturalized species and 393 casuals (Rojas-Sandoval et al. 2022). That study also identified major introduction pathways, economic uses, and country-specific patterns. However, this region still has limited fine-scale analyses of distributions of species and the environmental and human factors influencing their spread. Addressing these gaps is crucial, as they constrain the capacity of this region to develop predictive tools and proactive strategies for managing invasive species and mitigating their ecological and socioeconomic impacts.

In this study, we evaluate the distribution patterns of naturalized species across Central America in relation to key environmental and anthropogenic factors. Specifically, we assess the distribution of these species across ecosystems and life zones, protected areas vs. unprotected areas, gradients of human population density, and climatic variables such as annual mean temperature and precipitation. By identifying the ecological and socioeconomic drivers of naturalized species distributions, we aim to conduct future research, guide policy development, and support evidence-based management strategies. Our findings provide crucial insight into the role of protected areas in buffering against biological invasions and maintaining biodiversity, as well as the vulnerability of disturbed landscapes and the potential for climatic and demographic trends to shape future invasions. Finally, this research contributes to the scientific understanding of biological invasions in the tropics and offers practical guidance for preserving the ecological integrity of diverse landscapes in a region of global conservation significance.

Methods

Study site

We analyzed seven countries in Central America: Belize, Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua, and Panama. These countries cover a total area of 525,300 km^2 (World Bank 2022) and encompass a complex and diverse geography, including mountain ranges, volcanoes, plains, and significant bodies of water. Elevation ranges from sea level to 4,220 m a.s.l. at Tajumulco Volcano in Guatemala. The mean annual temperature is 24 °C, with average minimum temperatures ranging from 0°C during the coldest month in the highlands and maximum temperatures around 30°C during the hottest month in the lowlands (Taylor and Alfaro 2005). Annual rainfall varies widely due to topographic and elevational gradients. For instance, El Salvador and specific parts of Guatemala, Honduras, and Nicaragua receive less than 1,000 mm annually. In contrast, other regions in Guatemala, Panama, and Costa Rica receive more than 2,500 mm. The region has distinct wet and dry seasons, with the wet season typically extending from May to November (coinciding with increased hurricanes and tropical storm activity), while the dry season extends from December to April. The Caribbean coast is generally more humid and receives more rainfall than the Pacific coast (Taylor and Alfaro 2005).

Central America is a narrow land bridge connecting North and South America and separating the Pacific Ocean from the Caribbean Sea. As a corridor between two major biogeographical regions, it harbors ca. 7 % of the world's plant and animal species (Greenheck 2002). Despite its rich biodiversity and abundant natural resources, the region faces significant environmental challenges. It is considered a threatened biological hotspot with high conservation priority due to habitat degradation, soil erosion, water pollution, and climate change (Harvey et al. 2005). Deforestation, driven primarily by agriculture, is a major concern. Large portions of the forest have been cleared for cattle ranching, palm oil plantations, and other agricultural activities. Estimates suggest that less than 20% of the region retains dense forest cover, and much of the remaining forest is highly fragmented or at risk of conversion (Hoang and Kanemoto 2021).

The population of Central America is ca. 50 million people. The country with the highest population is Guatemala, and the smallest is Belize. The region has a high population growth rate, along with accelerating urbanization and migration. Economically, Central America relies heavily on agriculture, with coffee, bananas, sugarcane, and other crops as key exports (Grau and Aide 2008). However, recent years have shifted towards manufacturing and service industries, particularly in Costa Rica and Panama. According to the World Bank, nearly 30% of the population lives below the poverty line, with rural areas and indigenous communities especially vulnerable. The region is highly vulnerable to climate change due to its geographic location, socioeconomic inequalities, agricultural dependence, low educational levels, and weak infrastructure. Expected impacts of climate change include more frequent and intense hurricanes, floods, landslides, and droughts (Hannah et al. 2017; Donatti et al. 2019), leading to potential loss of life, displacement, and economic disruption. Rising sea levels may threaten coastal communities and infrastructure, and growing water scarcity could further exacerbate food insecurity (Hagen et al. 2022).

Due to its strategic geographic position, Central America is one of the most important global trade routes (e.g., the Panama Canal). As a result, the region is undergoing rapid economic development and increased international trade (Kerf 2021), which have ecological consequences, including pollution, resource degradation, and overexploitation. Infrastructure expansion, such as roads, ports, and urban areas, further contributes to environmental disturbances (ECLAC 2015) and may facilitate the introduction and spread of non-native species.

Data collection and analysis

This study builds on an open-access dataset of 1,228 non-native plant species occurring across Central America compiled by Rojas-Sandoval et al. (Rojas-Sandoval et al. 2022) as part of the FINCA Project (Flora Introduced and Naturalized in Central America: https://finca.collaboration.uconn.edu/). In the FINCA dataset, species were classified as either casuals or naturalized. We revised and expanded the original dataset for this study, incorporating updated information for invasion status. Following Richardson et al. (2000) and Blackburn et al. (2011), species were reclassified as cultivated, casual, naturalized, or invasive. For those species classified as naturalized or invasive, we searched for occurrence records in the Global Information Biodiversity Facility (GBIF: https://www.gbif.org/). For all the records in the dataset, we applied the workflow by Seebens and Kaplan (2022), which includes data-cleaning procedures to eliminate errors in geographic coordinates. Finally, we restricted our search to records of each species in the country listed in the FINCA dataset.

We conducted correlation analyses between the number of occurrences and species by country and three national-level variables: land area (km^2), population size (people), and Gross Domestic Product (GDP) (Billions US$) for the year 2022. Country-level data were obtained from the World Bank Data (World Bank 2022, 2025a, b). We calculate Pearson correlation coefficients using R software (R Development Core Team 2022).

For independent variables, we use annual mean temperature (AMT), annual precipitation (AP), human population density (human population), and a biodiversity integrity index. Climate data (AMT and AP) at 5-minute resolution were obtained from WorldClim (Fick et al. 2017). Human population density data were obtained from WorldPop Hub (2020) at 1 km resolution (https://hub.worldpop.org/). Biodiversity integrity data were derived from Gassert et al. (2022). All datasets were *resampled* to obtain the same resolution using bilinear interpolation with *R*'s *raster* package (Hijmans 2023). Species occurrence data were rasterized at a 5-minute resolution to estimate both the number of naturalized species records and the number of different species per cell. We used a mixed-effect regression model to assess the influence of independent variables on the number of records. Latitude and longitude were included as random effects using a Matérn correlation matrix to control spatial autocorrelation. The country was included as a fixed effect. We used the *fitme* function from the package *spaMM* (Rousset and Ferdy 2014). Species richness was analyzed with a similar model, incorporating the number of records as an additional fixed effect. We generated maps of predicted records and predicted richness for each model.

To evaluate whether life zones influence the number of occurrences of naturalized species, we used a contemporary map of life zones from Elsen et al. (2021). We calculated the number of raster cells per life zone and the number of cells with naturalized species. The proportion of occupied cells was compared to a random distribution by sampling the map 1,000 times and estimating mean and 95% confidence intervals. We plotted differences between observed and expected proportions per life zone. We also use the *climenv* package (Tsakalos et al. 2023) to visualize species occurrences within a climatic space diagram compared to the overall availability in Central America.

Vector *shapefile* of protected areas for each Central American country were obtained (Supplementary Information Table 1), and a 1 km^2 resolution raster map of protected areas was created. We calculated the number of observations and species inside and outside protected areas and determined the number of cells with naturalized species for each category (i.e., with and without protection). Proportions were compared using a chi-square test with Yates's correction. We also used rarefaction analysis with Hill numbers of order 0, 1, and 2 to compare species richness between protected and unprotected cells (Chao et al. 2014) using the *iNEXT* package (Chao et al. 2014). All the analyses were conducted in *R* (R Development Core Team 2022).

Results

We compiled 42,658 occurrence records for 751 naturalized plant species across Central America. The number of records was positively associated with the number of species (SI. Fig. 1). However, records were unevenly distributed among countries; Costa Rica accounted for the highest number of species (19,179), while Belize had the fewest (909; Table 1). Neither the number of occurrence records nor the number of species per country was correlated with land area, population size, or GDP (SI Fig. 2).

At the spatial cell level, population density and annual precipitation significantly explained the number of occurrence records (Table 2). Cells with higher population density and precipitation levels had more occurrences of naturalized species. In contrast, AMT and the biodiversity integrity index did not significantly affect the number of records (Table 2). The species richness of naturalized plants was significantly influenced by population density, AMT, and biodiversity integrity index (Table 2). Specifically, species richness increased with population density, while it decreased in areas with higher AMT and higher biodiversity integrity values (Table 2).

When comparing life zones, we found no significant deviation from random expectations in the proportion of cells observed with naturalized species for tropical moist, tropical dry, and premontane moist forests (Figs. 2 and 3). In contrast, all other life zones showed a higher-than-expected proportion of cells with naturalized species. The tropical rainforest had the largest positive deviation from random expectations (Figs. 2 and 3), with nearly 4% more occupied cells than expected. These findings are consistent with the spatial model results.

Regarding protected areas, we found 33,211 occurrences of naturalized species outside protected areas, compared to 8755 observations inside. In total, 729 naturalized species were recorded outside protected areas, while 540 were found within protected areas (Fig. 4). Most species occurring exclusively outside protected areas were observed at low frequencies (Fig. 4). No significant differences were observed in the number of common or frequent species between protected and unprotected areas (Fig. 4). The proportion of cells with naturalized species was significantly different between protected and unprotected areas ($\chi^2 = 296$, df = 2, $p > 0.001$), with higher numbers of naturalized species occurring outside protected areas (0.029) than inside (0.019). However, the observation density was similar, with ca. 6.9 records per 100 km^2 outside protected areas versus ca. 6.5 records per 100 km^2 inside. Interestingly, the ratio of species to observations was higher within protected areas, averaging ca. six species per 100 records compared to ca. two species per 100 records outside protected areas.

Discussion

Our findings reveal a clear pattern in the spatial distribution of naturalized plant species in Central America, offering insight into future management of invasive species and the prevention of biological invasions. Among all predictors, human population density emerged as a strong determinant of both the number of occurrences and the richness of naturalized species. This is consistent with global (Essl et al. 2019) and regional studies, e.g., China (Liu et al. 2005), South Africa (Spear et al. 2013), and supports hypotheses linking invasion patterns to propagule pressure (Simberloff 2009; De Jong and Fowler 2018), disturbance (Lozon and MacIsaac 1997;

González-Moreno et al. 2015), and deliberate or accidental human-mediated introductions (Zimmermann et al. 2014).

While herbarium records are known to be spatially and temporally biased, favoring urban centers and accessible areas, our models accounted for this by including both sampling effort (number of occurrences) and country as fixed effects. Even after this correction, population density remained a significant predictor, highlighting its robust association with invasion patterns. The tendency for early records of non-native species to appear near urban areas (Aikio et al. 2012) may reflect higher propagule pressure and the role of ornamental plant use in urban landscapes (Mayer et al. 2017; van Kleunen et al. 2018; Abonyo and Oduor 2025). Our rarefaction analysis reinforces the pattern. Species richness was higher outside protected areas, although there was no difference in the number of common or frequent species between protected and unprotected areas. This suggests that less frequent species are more likely to be found in disturbed, non-protected regions. These areas should be prioritized for early detection and rapid response strategies to prevent the spread of potentially invasive plants into natural or protected ecosystems. The negative association between species richness and biodiversity integrity index also supports the idea that degraded environments, often associated with human activity and high propagule pressure, are more susceptible to invasions (Marvier et al. 2004; Rojas-Sandoval and Ackerman, 2021; Rojas-Sandoval et al. 2024).

Interestingly, regions with high population density are not necessarily of low conservation value. Many urban adjacent protected areas, such as Braulio Carrillo National Park (Costa Rica), La Tigra National Park (Honduras), and El Boquerón National Park (El Salvador), safeguard critical ecosystems and deliver essential services, including water supply, air filtering, and biodiversity protection (Torres-Miranda et al. 2011, McDonald et al. 2008, Brassard et al. 2021). Although our results show more naturalized species outside protected areas, the ratio of species per observation was higher within protected areas. This suggests that protected areas support relatively diverse non-native floras despite lower propagule pressure and reduced anthropogenic disturbance, highlighting their vulnerability to biological invasions (Ackerman et al. 2017).

We also found that the physical environment played an important role in shaping the number of occurrences and species richness of naturalized species. Annual precipitation was positively associated with the number of occurrence records but not species richness, while mean annual temperature had a weak negative effect on species richness alone. These findings align with broader global patterns (Essl et al. 2019). A similar trend emerged from our life zone analysis: life zones characterized by higher humidity and temperature, such as tropical rainforests and tropical wet forests, contained more occupied cells than expected under a random distribution. This pattern likely reflects regional biogeographic conditions, as much of Central America lies in humid tropical life zones, where water availability strongly limits plant establishment (Ratcliffe et al. 2024, Engelbrecht et al. 2007). Although the effect of precipitation on invasive species abundance has been observed in some regions (Ratcliffe et al. 2024), it is not globally consistent. In our study, Central America's tropical setting may explain the positive association between precipitation and the occurrence of naturalized species. Many naturalized plants in Central America originate from tropical zones (Rojas-Sandoval et al. 2022, MacVean and Zinn 2023), making them well-adapted to high rainfall environments where high solar radiation increases transpiration, making water availability a critical filter for plant survival. Historical colonization patterns may partially explain the weak negative effect of temperature on species richness. During the Spanish conquest and colonial period, most villages and towns were established in mid-elevation zones in areas with climates more like those in Europe (Heckadon-Moreno 1997). As a result, plant species introduced during that time became established in these mid-elevations. These historical introduction patterns likely continue to influence the current distribution of naturalized species across the region.

Conclusions

Our study highlights the strong influence of population density on the occurrence and the spread of naturalized species in Central America. These findings call for integrating conservation strategies into urban planning, focusing on green spaces, early detection systems, and public awareness of the risks associated with invasive species. Because densely human-populated areas support high species richness and higher occurrences of naturalized species, management strategies must balance biodiversity conservation and invasive species control. The associations between annual precipitation and naturalized plant occurrences emphasize the importance of considering climatic suitability in invasion risk assessments. Similarly, mid-elevation areas with moderate temperatures, likely reflecting ecological and historical introduction patterns, may act as hotspots for naturalized plants and should be prioritized for targeted monitoring and management.

This study also emphasizes the importance of early detection in disturbed, non-protected areas, which are likely entry points for invasive species. At the same time, protected areas, especially those near urban centers, play a vital role in maintaining native biodiversity and providing ecosystem services. Conservation strategies should include strengthened protection and proactive management of these areas to ensure long-term sustainability for people and natural ecosystems.

Addressing sampling bias in herbarium records and increasing data collection in underrepresented or remote regions will improve our understanding of the geographic and ecological dynamics of plant invasions. Equally important is the involvement of local communities in monitoring, education, and invasive control efforts. A holistic, multidisciplinary approach combining ecological research, urban planning, policy development, and public participation is essential for effectively managing naturalized plant species and safeguarding biodiversity throughout Central America.

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Table 1. Geographical and socioeconomic data of the Central American countries. Land area (km^2), human population (people), Gross Domestic Product 2022 (GDP), number of occurrence records, and naturalized plant species.

Country	**Land area (km^2)**	**Population**	**GDP (Billions US$)**	**Occurrences**	**Species**
Belize	22299.42	405272	2.8305	909	138
Costa Rica	51144.33	5180829	69.244	19179	545
El Salvador	20539.22	6336392	31.989	3261	364
Guatemala	108811.24	17357886	95.003	2904	273
Honduras	112236.73	10432860	31.426	3416	283
Nicaragua	128691.43	6948392	15.65	5373	287
Panama	74530.31	4408581	76.523	7616	286

Table 2. Coefficients of the mixed-effect regression model predicting the number of occurrences and the species richness of naturalized species in Central America using as predictors human population, annual mean temperature, annual precipitation, and biodiversity integrity index (see methods).

Variable	**Estimate**	**SE**	**Sq-Mean**	**Num df**	**Den df**	**F-value**	**Pr (>F)**
Number of occurrences							
(Intercept)	-15.399	24.477					
Population density	0.118	0.004	210.303	1	1520.1	804.155	<0.001***
Annual mean temperature	-0.683	0.612	0.326	1	460.34	1.247	0.265
Annual precipitation	0.008	0.003	1.329	1	94.6	5.083	0.026*
Biodiversity integrity	19.281	19.479	0.256	1	973.03	0.980	0.323
Species richness							
(Intercept)	22.441	5.321					
Population density	0.019	0.001	1.0817	1	1669.8	525.337	<0.001***
Annual mean temperature	-0.509	0.132	0.0308	1	808.24	14.980	<0.001***
Annual precipitation	0.001	0.001	0.0039	1	215.58	1.913	0.16805
Biodiversity integrity	-10.065	4.023	0.0128	1	1411.5	6.258	0.01247*

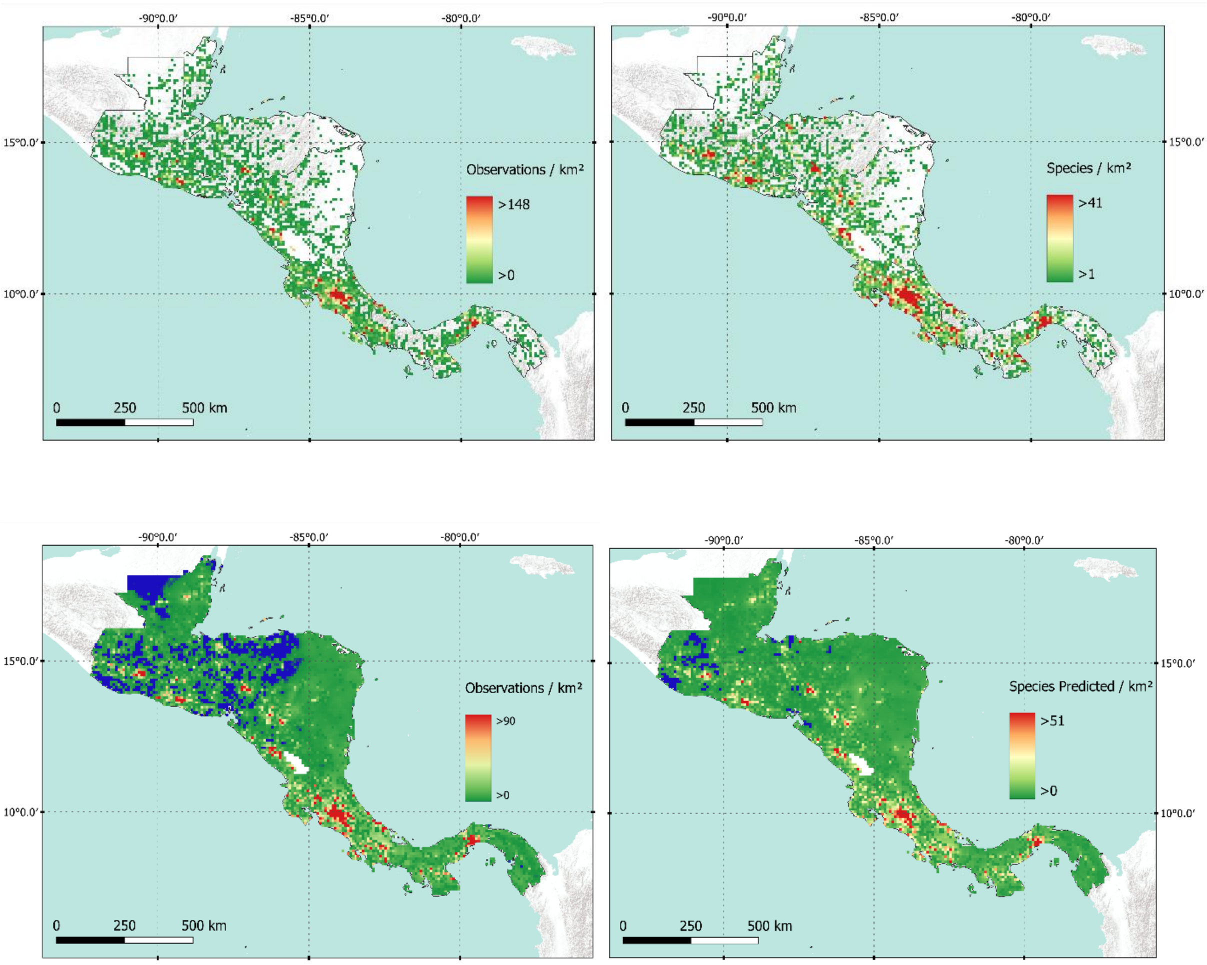

Figure 1. Maps of the number of occurrence records of naturalized species (above-left) and species richness (above-right). Map of the number of occurrences predicted (below-left), according to population density and precipitation, and map of species richness (below-right) predicted according to population density, temperature, and biodiversity integrity with a fixed number of 300 occurrences.

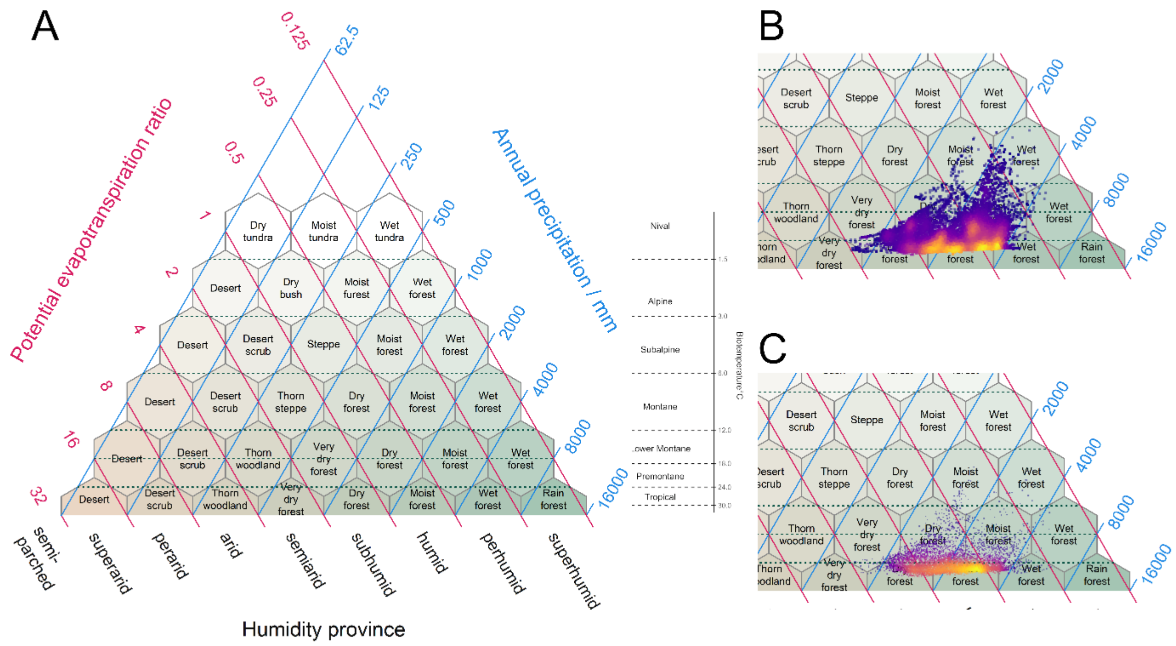

Fig. 2. Holdridge life zones scheme based on biotemperature, annual precipitation, and potential evapotranspiration ratio (A). (B) Environmental space is available within the Central American Region within the dimensions of the Holdridge life zone variables. (C) Environmental space where naturalized species have been recorded within the dimensions of the Holdridge life zones. The blue points represent low-density points, and the yellow points are high-density points.

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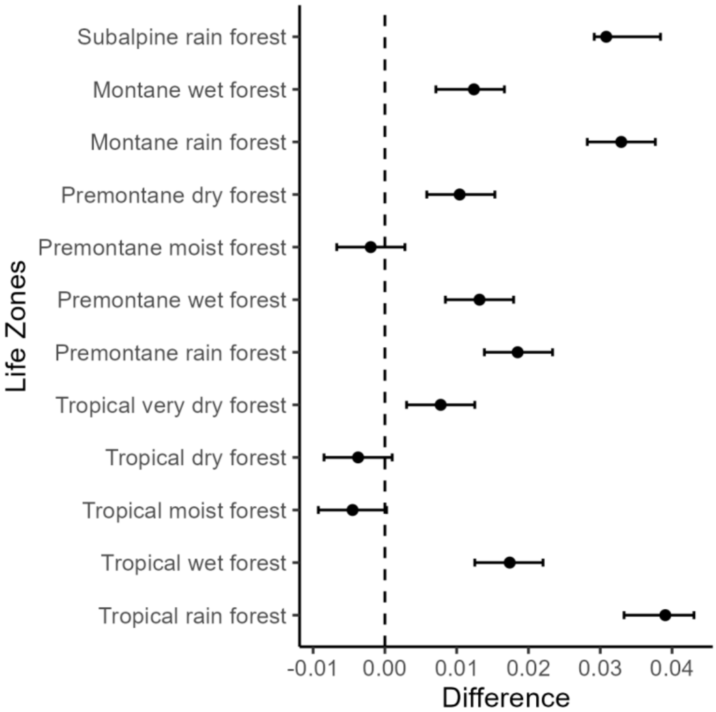

Fig. 3. Difference between the observed and expected proportion of cells with naturalized species across each Holdridge life zone in Central America. The observed proportion represents the number of cells per life zone, while the expected proportion was generated by randomly assigning the same number of occupied cells (n = 14,125) across all life zones randomized 1,000 times. The error bars represent the standard error of the expected distribution.

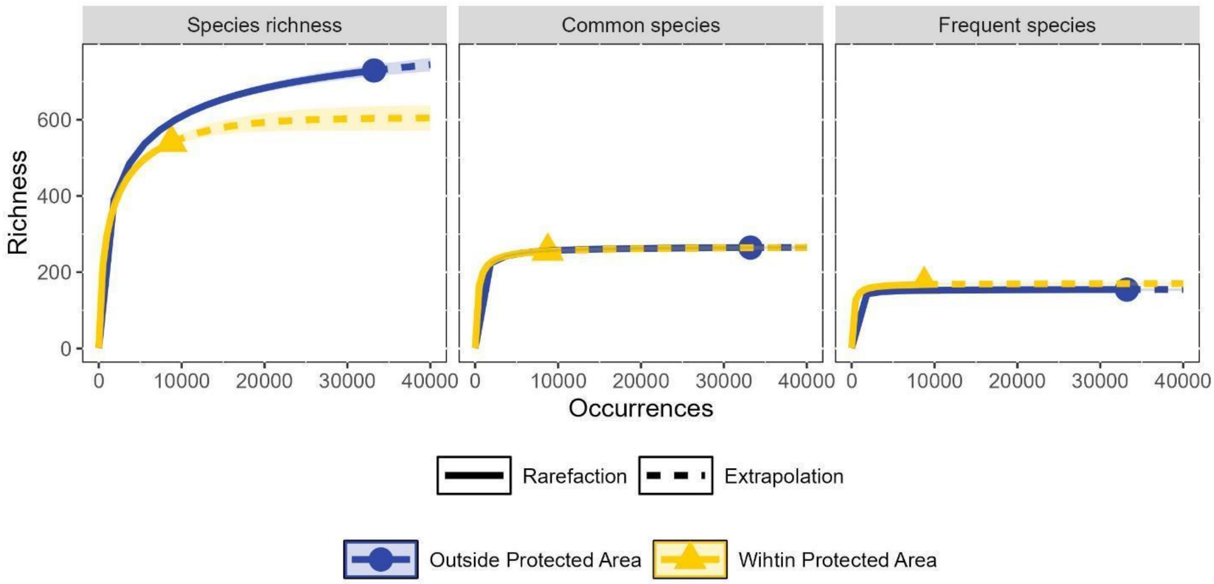

Fig. 4. Rarefaction curves of the naturalized plant species in Central America occurring within and outside protected areas based on Hill’s numbers 0 (species richness), 1 (common species), and 2 (frequent species). Curves represent the estimated diversity for each category, allowing a comparison of species accumulation and community structure between protected and unprotected areas.

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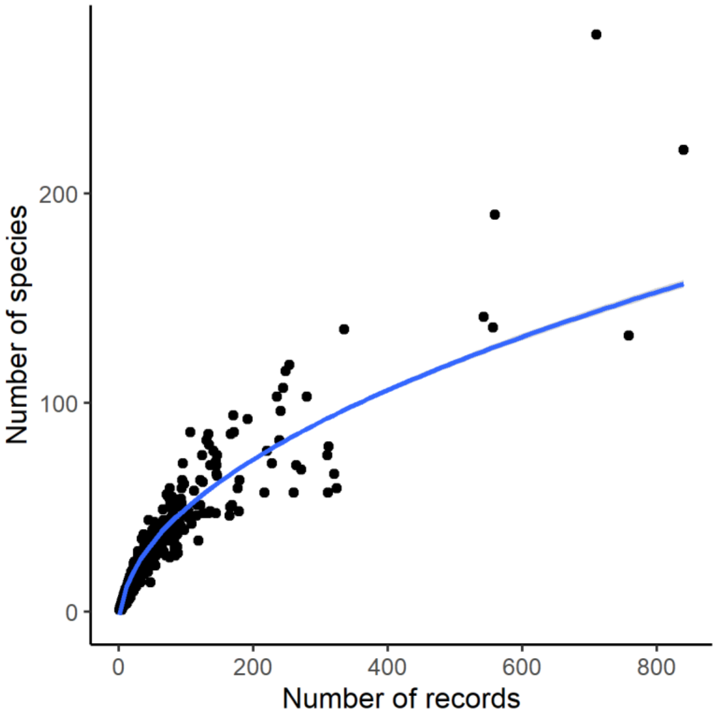
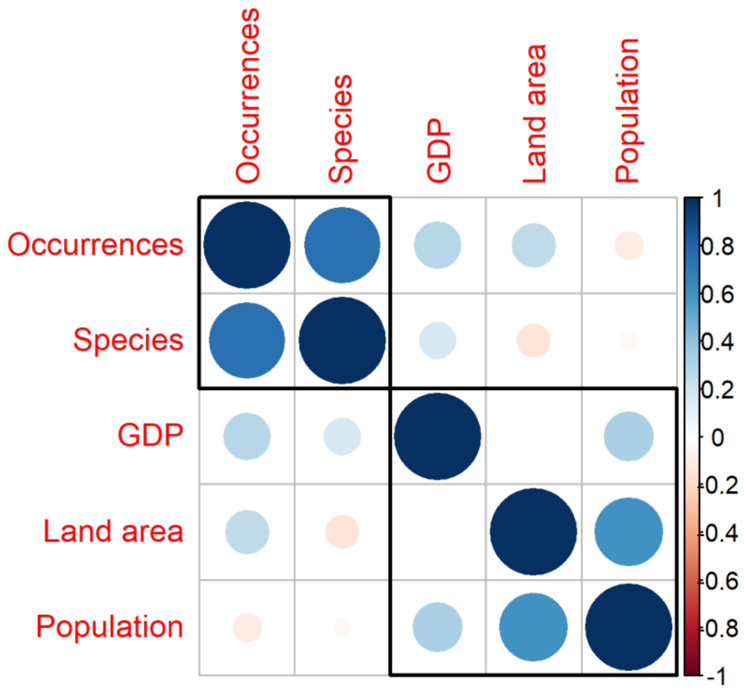
Supplementary Information.



SI. Fig. S1 Relationship between the number of occurrence records in the Global Biodiversity Information Facility (GBIF database and the number of naturalized plant species across Central America. Regression model: $y = 11.48 \pm 0.16 + (1,377.25 \pm 8.69)\ x = -233.57 \pm 8.69)\ \chi^2$, d.f. = 2868, $p < 0.001$, $r^2 = 0.9$.



SI. Fig 2. Correlation between the number of occurrence records of naturalized species and land surface, human population (2022), and Gross Domestic Product (GDP, 2022) across Central American countries.

SI. Table 1. Sources of layers of Protected Areas for each Central American country used in the analysis.

Country	**Source**
Belice	Meerman, J.C. (2019) Bm-Belize-Central America-all protected areas. Caribbean Marine Atlas. EPSG:26716. https://www.caribbeanmarineatlas.net/layers/cma_geonode_data:geonode:belize_protected_areas_all
Costa Rica	SINAC (2024) Areas silvestres protegidas. Sistema Nacional de Areas de Conservación. EPSG:5367. http://geos1pne.sirefor.go.cr/wfs
El Salvador	World Bank Data (2009) Protected natural areas in El Salvador. EPSG:32616 https://datacatalog.worldbank.org/search/dataset/0042341/Protected-Natural-Areas-in-El-Salvador
Guatemala	Cuque,D. Pérez, G. Unidad de datos e información estratégica. (2023). Mapa del sistema guatemalteco de áreas protegidas de la República de Guatemala. [mapa digital]. Guatemala. INVERSE(ESRI):103598. https://sie.url.edu.gt/capas-geograficas/
Honduras	Universidad Nacional Autónoma de Honduras (2020) Límite de áreas protegidas de acuerdo a la base de datos del Instituto de Conservación y Desarrollo Forestal. EPSG:32616. https://territoriosenriesgo.unah.edu.hn/layers/geonode:areas_protegidas
Nicaragua	UNEP-WCMC and IUCN (2025), Protected Planet: The world database on protected areas (WDPA) and world database on other effective area-based conservation measures (WD-OECM) [Online], January 2025, Cambridge, UK: UNEP-WCMC and IUCN.
Panama	Solano, M. (2022) Comprehensive Panama protected areas dataset (2022) Smithsonian Institution. https://stridata-si.opendata.arcgis.com/datasets/9c7deb2cb1e24dcc89214e6194f16fe3_0/about

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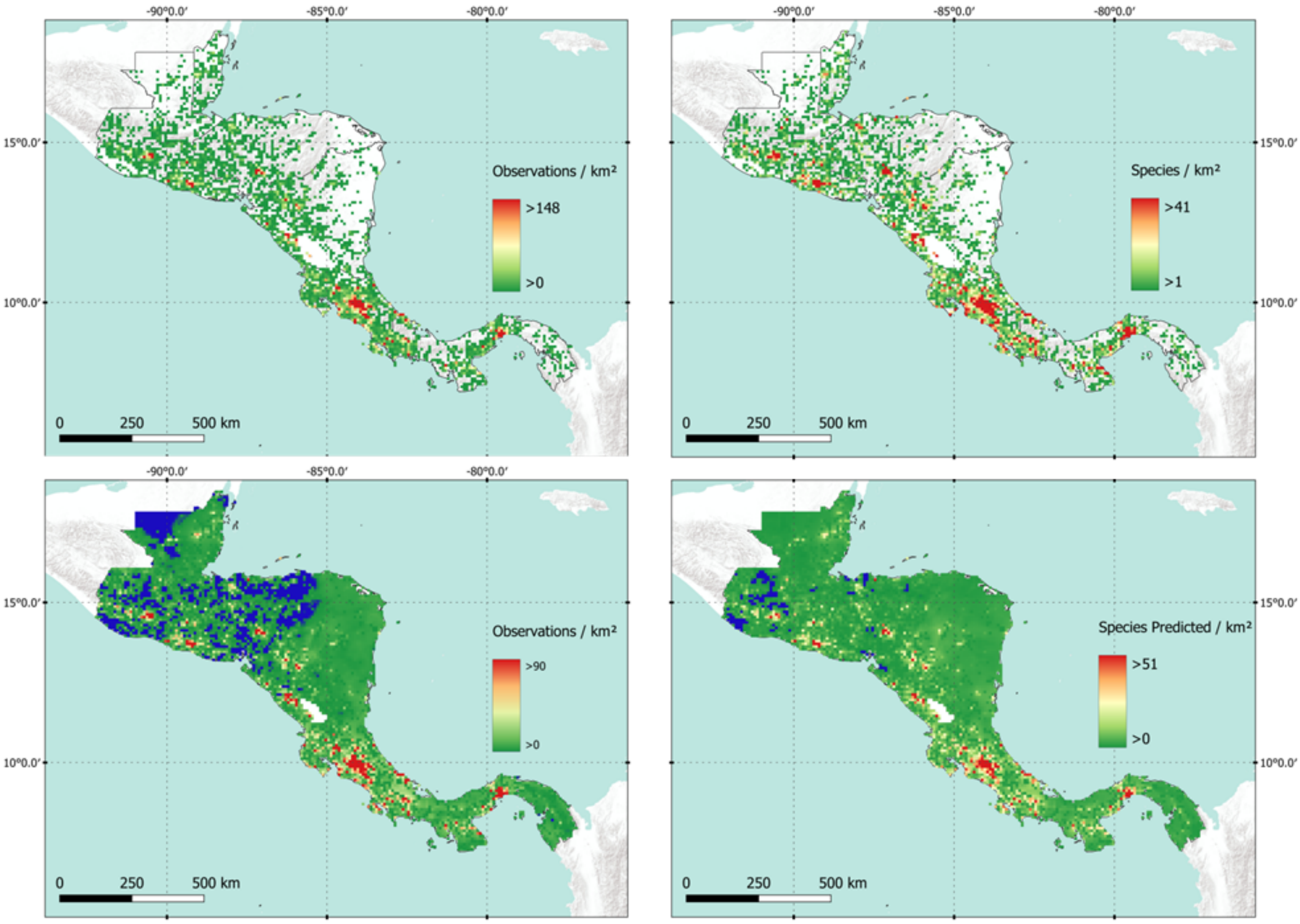
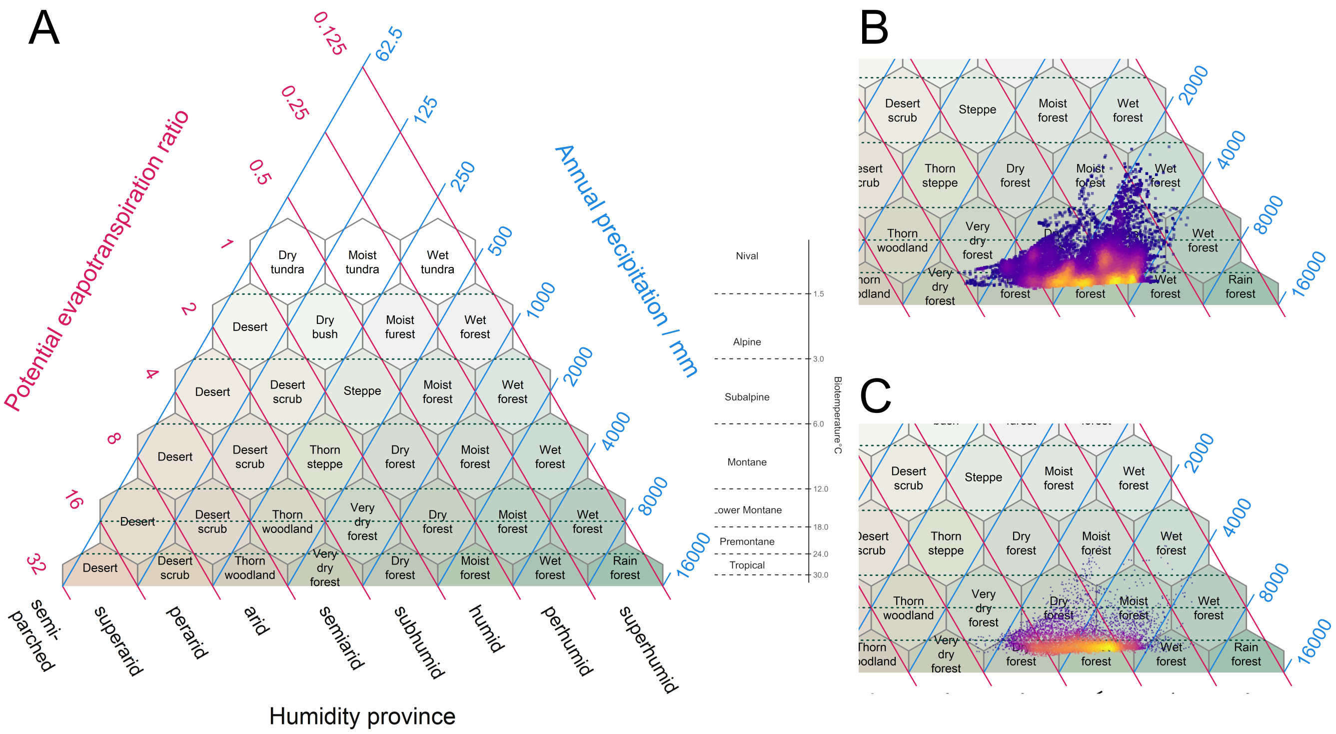
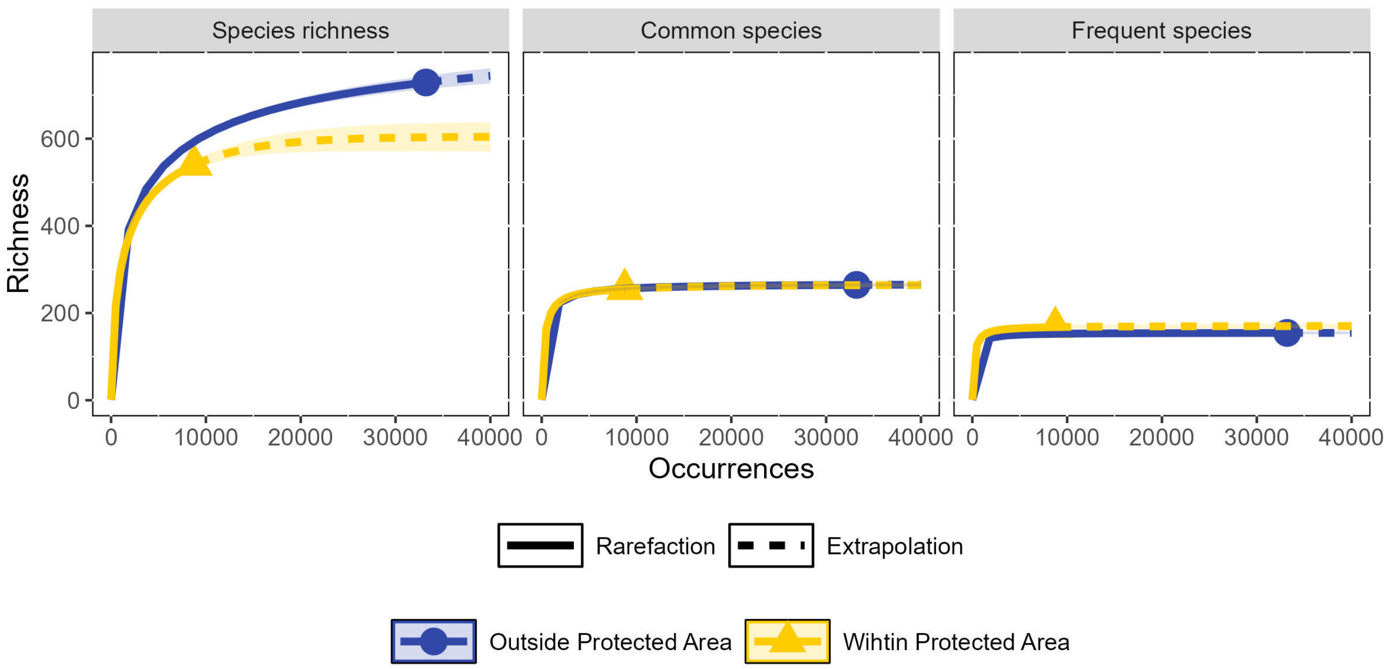



A
B
C
Potential evapotranspiration ratio
Annual precipitation / mm
Humidity province
Biotemperature °C


Species richness
Common species
Frequent species
Richness
0
200
400
600
0
10000
20000
30000
40000
Occurrences
Rarefaction
Extrapolation
Outside Protected Area
Wihtin Protected Area

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