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Original Article

Factors explaining species richness of invasive plants in Neotropical forests

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ABSTRACT

Tropical forests are biologically significant ecosystems, yet they face increasing pressure from human activities, which has led to the introduction of invasive plant species. Despite this, much of the existing literature on plant invasions in tropical forests focuses on Old World forests and grasses, leaving Neotropical forests relatively understudied. To address this gap, we aimed to investigate patterns of woody plant invasions in Neotropical forests with different levels of leaf deciduousness and identify the key factors that explain the richness of invasive woody plants. We conducted a systematic review of floristic surveys in Neotropical forests, gathering data on climate, environmental, and anthropogenic variables for each study site. Our analysis revealed that the richness of invasive plants increased with greater temperature seasonality, higher accessibility, and elevated per capita gross domestic product, while it decreased with increased canopy cover. Higher temperature seasonality and accessibility were strong positive predictors of invasive plant richness. Subtropical Neotropical forests are more susceptible to the establishment of invasive species due to the higher temperature seasonality. In addition, factors such as leaf deciduousness and increased human accessibility further contribute to the susceptibility of these forests to the arrival and establishment of invasive woody plants.

Keywords: The Caribbean, Central America, deciduousness, forest invasion, South America, systematic review, tropical forest, woody invaders

Introduction

Climatic variables are important filters for the establishment of non-native species. Interrelated climatic variables, such as temperature and precipitation, correlate with patterns of plant invasions around the world (González-Moreno *et al.*, 2014; Vinogradova *et al.*, 2018). Regions with mild temperatures tend to harbour a higher richness of invasive non-native (hereafter "invasive") plants (Ohlemüller *et al.*, 2006; Marini *et al.*, 2012; Gallardo & Vilà, 2019). For instance, in China, invasive species diversity increases with temperatures between 1 °C and 25 °C, suggesting that stable climates within this temperature range are conducive to higher invasive plant richness (Shi *et al.*, 2010). However, human influence can change, interact, or override these climatic variables (González-Moreno *et al.*, 2014). For

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example, biomes characterized by limiting environmental conditions, such as periods of rain scarcity, may host higher invasive species richness when in proximity to areas densely populated (Spear *et al.*, 2013; Dimitrakopoulos *et al.*, 2017). In addition, human-modified habitats function both as sources of disturbance (Dimitrakopoulos *et al.*, 2017) and as pathways for the introduction and spread of invasive species propagules (Vilà *et al.*, 2007; Vicente *et al.*, 2010; Essl *et al.*, 2019).

Socioeconomic variables, such as *per capita* gross domestic product (GDP), extensive land use for agriculture, and population density, are positively associated with the presence and richness of invasive species in non-urbanized areas worldwide (Essl *et al.*, 2019). Anthropogenic disturbance drives increases in the richness and abundance of invasive plants in tropical forests, including grasses (*e.g. Megathyrsus maximus*, *Urochloa brizantha*) and trees (*e.g. Artocarpus heterophyllus*) (Abreu & Rodrigues, 2010; Veldman & Putz, 2011). In temperate regions, roads serve as pathways that allow invasive species to reach adjacent natural areas (Joly *et al.*, 2011; Lemke *et al.*, 2019), as vehicles act as long-distance vectors for propagule spread, even without specific seed or fruit adaptations for this kind of dispersal (Taylor *et al.*, 2012; Von der Lippe *et al.*, 2013; Lemke *et al.*, 2019). However, studies showing the influence of roads on the spread of invasive plants in tropical forests are limited (Döbert *et al.*, 2018, but see Padmanaba & Sheil, 2014; Veldman & Putz, 2010). Additionally, human occupation in forest regions often leads to fragmentation and gap formation, altering local environmental conditions. Increased light availability due to forest degradation is one factor that explains the higher number of invasive species along forest edges or in gaps compared with the forest interior (Laurance *et al.*, 2002; Green *et al.*, 2004).

Non-anthropogenic disturbance, such as gap openings caused by falling trees and branches, can also affect forests. These stochastic events may or may not be combined with deterministic events associated with deciduousness cycles (Gandolfi *et al.*, 2007; 2009). Both types of gaps play an important role in maintaining native species richness in these ecosystems, as the varying light conditions under the canopy create microhabitats that filter the establishment of plants (Gandolfi *et al.*, 2007; 2009). The dynamics of canopy openness in forests may be an important factor influencing the arrival and establishment of invasive plants (Spear *et al.*, 2013; Dechoum *et al.*, 2015), as dense forest canopies not only reduce light incidence but also act as physical barriers to propagule entry (Hansen & Clevenger, 2005).

Tropical forests have historically been considered less susceptible to invasion than tropical open ecosystems or temperate forests (Rejmánek, 1996; Teo *et al.*, 2003). This perception is partly due to the limited documentation of biological invasions in these regions and a relatively recent history of species introductions and habitat loss compared with temperate forests (Denslow & DeWalt, 2008; Chong *et al.*, 2021). Additionally, low light availability may restrict the establishment of invasive species, although some species can establish and survive in the understory (Fine, 2002; Martin *et al.*, 2009; Dechoum *et al.*, 2015). Deciduousness in tropical forests varies with climatic characteristics (Pennington & Lavin, 2016), with some closed-canopy forests occurring in humid climates (Fine *et al.*, 2005), while seasonal forests are found in areas with prolonged dry periods in tropical or subtropical regions characterized by low winter temperatures (Malhi *et al.*, 2009).

The Neotropical region spans from southern South America to central Mexico, encompassing diverse ecosystems, such as moist and dry broadleaf forests, grasslands, savannas, deserts, and xeric shrublands (Olson *et al.*, 2001). It harbours the highest richness of animal and plant species on the planet and contains five of the world's 24 biodiversity hotspots (Myers *et al.*, 2000). However, Neotropical forests have been negatively impacted by anthropogenic disturbances, including deforestation, fire, and biological invasions, compounded by climate change effects such as prolonged droughts and rising temperatures (*e.g.* Carvalho *et al.*, 2001; Rowland *et al.*, 2015; Gomes *et al.*, 2019; Faria *et al.*, 2021). The Neotropics are one of the fastest developing regions in the world, with over 81% of the population living in urban areas, and one of the highest global rates of forest conversion to pasture and monoculture (Wassenaar *et al.*, 2007; Curtis *et al.*, 2022). Anthropogenic disturbances, in particular, are significant drivers of invasive species establishment and invasion across tropical and temperate environments (Brooks, 2007; Vicente *et al.*, 2010).

This study addresses a significant gap in the literature by focusing on the underexplored area of invasion biology in tropical and subtropical forests, particularly within the Neotropics. Existing research has predominantly emphasized Old World forests (Africa and Asia) and herbaceous species (grasses) (Fine, 2002; Chong *et al.*, 2021), leaving a need for understanding woody invaders in Neotropical forests. We conducted an extensive literature review to identify studies documenting invasive species in vegetation surveys in the Neotropics. For each study site, we obtained anthropogenic, environmental, and climatic variables from various sources to model which factors best explain the richness of invasive woody plants across forests. We aimed to answer the following question: which anthropogenic, climatic, and environmental factors best explain the richness of invasive woody plants in Neotropical forests? Our findings are expected to identify key factors influencing invasive woody plants and contribute to a broader understanding of invasion processes in highly diverse ecosystems.

Material and methods

Data search and selection criteria

We conducted a systematic review of floristic surveys carried out in Neotropical forests between 1945 and 2019 using the *Web of Science* database. The terms used in the search were combined for (a) study type: *floristic* OR *phytosociology* OR *flora* AND; (b) forest type: *deciduous forest* OR *semideciduous forest* OR *evergreen forest* OR *rain forest* AND; (c) country where the study was carried out: *Argentina* OR *Belize* OR *Bolivia* OR *Brazil* OR *Chile* OR *Colombia* OR *Cuba* OR *Costa Rica* OR *Dominican Republic* OR *Ecuador* OR *El Salvador* OR *French Guiana* OR *Guatemala* OR *Guyana* OR *Haiti* OR *Honduras* OR *Jamaica* OR *Mexico* OR *Nicaragua* OR *Panama* OR *Paraguay* OR *Peru* OR *Puerto Rico* OR *Suriname* OR *Trinidad and Tobago* OR *Uruguay* OR *Venezuela*. The search terms had to appear in the publication title, abstract, or keywords.

The mention of invasive shrubs or trees in the articles was verified by searching for the words exotic, non-native, non-indigenous, invasive, alien, and naturalized throughout the text. In the absence of such words, a search of the species lists was conducted to verify whether the species were non-native and invasive or native in the region where the survey was carried out. Global and national databases were used to verify this information (CABI - Invasive Species Compendium, 2020; GISD - Global Invasive Species Database, 2020; I3N - Brazil National Invasive Alien Species Database Base, 2020; CONABIO - Mexico Commission for the Knowledge and Use of Biodiversity, 2020). Author names for the species listed (Table S2) were checked on The Plant List (2020). The names of the invasive species were standardized based on World Flora Online (WFO, 2019). We considered the articles that mentioned the size of the sampling area and complete species lists. The data obtained from these articles were coordinates of the sampling sites, sampling area (in hectares), number of invasive species, and total number of species recorded. Articles covering more than one site, more than 5 km apart, with separate species lists for each site, were considered individual surveys. Articles with surveys in more than one site that did not provide separate species lists were discarded. The location of the sampling area in articles with more than one sampling site less than 5 km apart was marked as the centroid of the group of sampling areas. The centroid was calculated using QGIS *Development Team* software (2020).

Explanatory variables – climatic, environmental, and anthropogenic

We defined eight climatic variables (mean annual temperature, temperature seasonality, maximum temperature of the hottest month, minimum temperature of the coldest month, annual rainfall, rainfall of the wettest month, rainfall of the driest month, rainfall seasonality); two environmental variables (canopy cover; relative range of normalized difference vegetation index - NDVI); and seven anthropogenic variables (accessibility, population density, index of human influence, Gross Domestic Product *per capita* (GDP), parity of purchasing power – GDP-PPP, human development index - HDI, and night light development index - NLDI) (Table 1). The variables were obtained from matrix files (raster) of global databases. The QGIS software was used to delimit a 1 km radius buffer for the geographic coordinates of each sampling site or the centroid of each group of sampling sites. The mean value for each buffer was calculated for each vectorial/raster layer.

Climate variables were obtained considering monthly average data from 1970 to 2000 (Fick & Hijmans, 2017).

Canopy cover refers to the density of soil cover by the crowns of trees higher than 5 m in the sampling area in the year 2000 (Hansen *et al.*, 2013). The normalized difference vegetation index (NDVI) is an indicator of photosynthetically active biomass on each site and can show changes in canopy cover due to climate seasonality (Alcaraz-Segura *et al.*, 2009). A possible limitation of using this variable is the impossibility of determining whether the canopy cover variation occurred due to leaf deciduousness or deforestation. The NDVI values computed for each article refer to the RREL-NDVI (Relative Range of NDVI), which maintains the biological significance of NDVI variation between the dry and rainy seasons but is standardized using the average between these seasons (Alcaraz-Segura *et al.*, 2006; 2009). High RREL-NDVI values indicate a higher degree of change in the canopy between seasons, while low RREL-NDVI values indicate a low change in the canopy between seasons. We used the geographic coordinates where each study was conducted to obtain the NDVI value for that specific location. We used NASA's Application for Extracting and Exploring Analysis Ready Samples (AppEEARS, 2023) to obtain a sample for each geographic coordinate over a 20-year timespan (2002–2022). The months of December, January, and February, contrasting with June, July, and August, were used to represent seasonal variation. We only kept pixels tagged as 'high quality' with low aerosol quantity. Additionally, pixels with NDVI values less than 0.2 were discarded since they are unlikely to reflect vegetation.

Accessibility refers to travel time (in minutes) by land (roads) or water (navigable rivers or ocean) to the nearest city with more than 50,000 inhabitants (Nelson, 2008). It is derived from a distance algorithm that calculates the cost of travelling between two areas on a raster – the "cost" measured in time. The accessibility map developed by Nelson (2008) is available from the *Forest Resources and Carbon Emissions* website (IFORCE, 2021).

Population density refers to the estimate of human habitation (number of persons per km^2) based on national censuses and population records for 2010 (CIESIN, 2020a).

Table 1. Climatic, environmental, and anthropogenic variables were obtained for each sampling area in each study. Variables in bold were used to build the models after the variance inflation factor (VIF) was calculated. Resolution: measure of pixel size (Unit: kilometers).

Variables	Variable type	Resolution	Unit
Climatic			
bio1: Mean annual temperature	Raster	0.9	°C
bio4: Temperature seasonality	Raster	0.9	SD annual temp. x 100
bio5: Maximum temperature of the hottest month	Raster	0.9	°C
bio6: Minimum temperature of the coldest month	Raster	0.9	°C
bio12: Annual precipitation	Raster	0.9	Millimeters
bio13: Rainfall of the wettest month	Raster	0.9	Millimeters
bio14: Rainfall of the driest month	Raster	0.9	Millimeters
bio15: Rainfall seasonality	Raster	0.9	Coefficient of variation
Environmental			
Canopy cover	Raster	0.03	Percentage (%)
RREL– NDVI	Raster	0.25	Index (-1 to 1)
Anthropogenic			
Accessibility	Raster	0.9	Minutes
Population density	Raster	0.9	People/km²
Human development index – HDI	Raster	10	Index (0-1)
Human influence index – HII	Raster	0.9	Index (0-64)
***Per capita* GDP**	Raster	10	Billion US$/2011
GDP (PPC)	Raster	10	Billion US$/2011
Night lights	Raster	0.9	Index (1-63)

The Global Human Influence Index (HII) measures human influence on terrestrial ecosystems. It was developed using raster files of human settlements (population density, built-up area), accessibility (roads, railroads, navigable rivers, access to the ocean), land-use change (land use and cover), and energy infrastructure (night lights). HII values vary between 0 and 64, with values close to zero indicating low human influence and values close to 64 indicating high human influence (CIESIN, 2020b). The data used refers to the year 2005.

GDP *per capita* (gross domestic product) represents the mean *per capita* production per year in a specific administrative unit (base year 2015) in billions of US dollars, *i.e.*, it is a measure of economic performance (Bregar *et al.*, 2008; Kummu *et al.*, 2020). The parity of purchasing power (GDP-PPP) is calculated from the dollar purchasing power of each country and takes into consideration the cost of living and inflation rate (Bregar *et al.*, 2008; Kummu *et al.*, 2020). The Human Development Index (HDI) measures basic human development calculated from health, education, and income data based on 2015. This index varies between 0 and 1, with values ≥ 0.8 in regions with high development, 0.8 to 0.5 with moderate development, and ≤ 0.5 with low human development (PNUD, 2012).

The measure of night lights refers to 2013 and represents lights in cities and other areas with constant artificial illumination. Short-lived events like fires are not considered (NOAA, 2020). The data are derived from an aggregation of pixels – a number varying from 1 (dark spot) to 63 (light spot) is attributed to each pixel (Addison & Stewart, 2015). This variable is positively correlated with the degree of urbanization, estimated from population density and GDP (Mellander *et al.*, 2013).

The raster and vector files were obtained from the global databases *WorldClim* (bio1, bio4, bio5, bio6, bio12, bio13, bio14, bio15) (Fick & Hijmans, 2017), *Global Forest Watch* (forest cover) (Hansen *et al.*, 2013), *Earth Resources Observation and Science* - EROS (NDVI), *Forest Observation* (accessibility) (Nelson, 2008), *Center for International Earth Science Information Network* (population density, human influence index) (CIESINa, CIESINb), NOAA - *National Centers for Environmental Information* (night lights) (NOAA, 2020), and *Dryad* (PIB, PIB PPC, IDH) (Kummu *et al.*, 2020).

Data analyses

We built a generalized linear model (GLM) using the proportion of invasive plants in relation to the total

number of species recorded at each site to verify which anthropogenic, climatic, and environmental variables influenced the richness of invasive woody plants and the degree of their impact. Before building the model, collinearity was checked by excluding explanatory variables with variance inflation factor (VIF) >4 (Zuur *et al.*, 2009). As a result, five variables were excluded: mean annual temperature, minimum temperature of the coldest month, rainfall of the wettest month, rainfall of the driest month, and night lights. Therefore, twelve explanatory variables were used in the full model (Table 1). The full model underwent a backward simplification process in which we eliminated non-significant variables progressively, one at a time until a final model containing only significant variables was achieved. This stepwise approach allowed for a more focused and interpretable model, as it removed variables that did not contribute significantly to the predictive power of the model. By iteratively assessing the statistical significance of each variable and discarding those with negligible impact, the resulting simplified GLM captured the essential relationships between the dependent and independent variables, providing a clearer understanding of the underlying dynamics influencing the outcome of interest. We assumed a binomial distribution once the response variable varied between 0 and 1, *i.e.*, it represents the proportion of non-native species in relation to the total number of species recorded at each site. As the sampling area varied in each study, we used the sampling area as an offset term in the models (log-transformed to correspond to the scale of the response variable). The model was validated using residual diagnostics through a simulation-based approach. We used Nagelkerke's R^2 (Nagelkerke, 1991) to verify the goodness of fit of the final model. An analysis of dominance was conducted to verify the relative importance of variables in the final model (Azen & Traxel, 2009). The analyses were conducted in R software (R Development Core Team, 2014) using the packages *car* (Fox & Weisberg, 2019) to verify variable collinearity, *DHARMa* (Hartig, 2021) for model validation, *visreg* (Breheny & Burchett, 2017) to view the relation between explanatory variables in the response variable, and *dominanceanalysis* (Navarrete & Soares, 2020) for analysis of dominance.

Results

We found 1,116 articles published between 1988 and 2019, of which 97 (Fig. 1, Table S1) were selected for our analyses. The total number of sites considered for this study was 121 (some studies had more than one site sampled) (Fig. 1, Table S1).

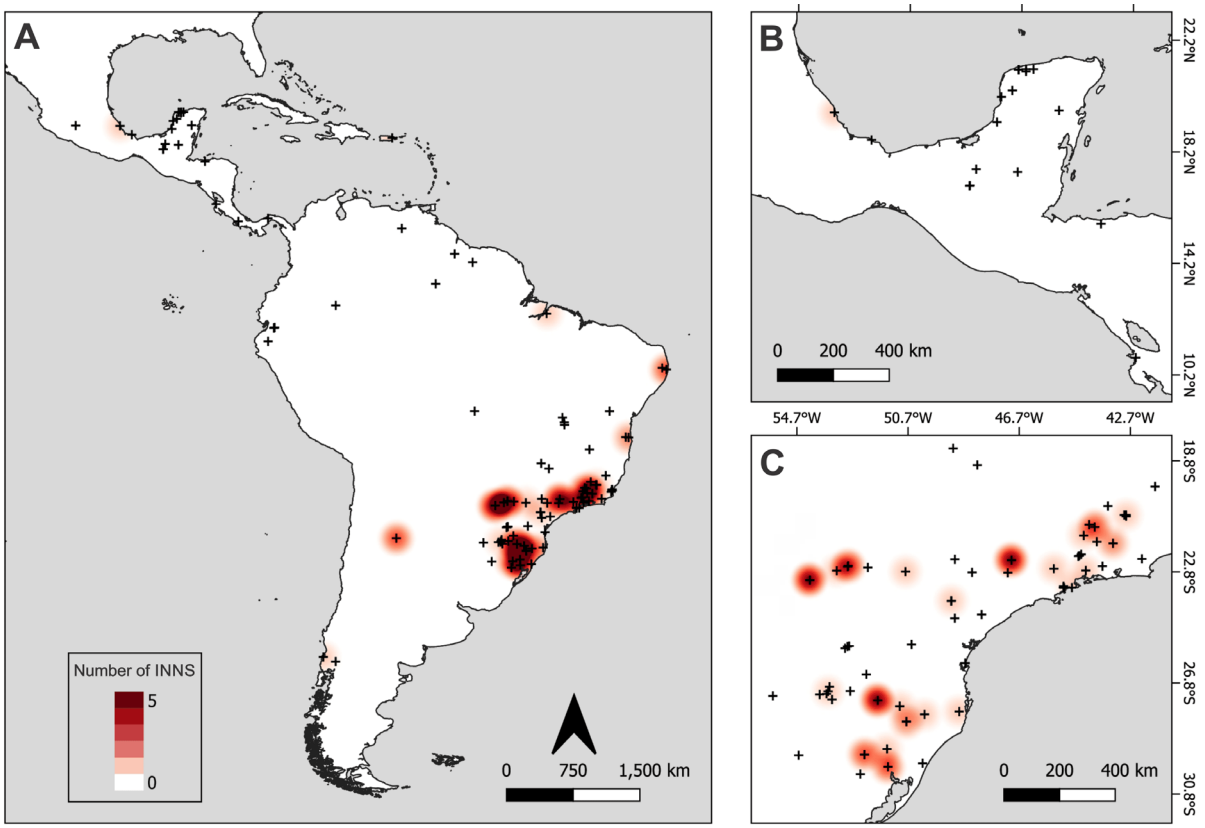

Figure 1. Heatmap representing the Neotropical region, with the location of the 121 sites considered in our study. Darker regions indicate the recording of a greater number of invasive woody plants. Figures B and C are an enlargement of the image (A) to visualize Central America and southern South America better, respectively. INNS: invasive species.

Among the 1,019 articles discarded, 140 focused on other biological groups (109 on animals, 18 on bryophytes, five on lichens, four on fungi, three on algae, and one on cyanobacteria); 313 articles focused on vascular plants but did not contain floristic data; 348 articles on floristic surveys did not provide complete species lists, but only the list of species with higher importance values, and/or did not indicate the size of the sampling area; 113 articles were reviews (used other floristic studies or databases to compile species lists); and 123 floristic survey articles focused on non-forest vegetation. Some papers were excluded due to a combination of the abovementioned categories.

Thirty-two (26.4%) of the 121 sites contained at least one invasive woody plant species. A list of 23 invasive woody plant species was compiled from the articles reviewed (17 trees and six shrubs) (Table S2).

Which anthropogenic, climatic, and environmental factors best explain the richness of invasive woody plants in different types of Neotropical forests?

The model that explained the proportion of invasive woody plants in relation to the total number of species contained four variables: accessibility, canopy cover, GDP *per capita*, and temperature seasonality (Table 2). The final model explained 49% of data variation ($R^2_{Nagelkerke} = 0.49$).

The results of the dominance analysis showed that temperature seasonality and accessibility were the variables with higher general dominance in the final model, explaining 20% and 16% of data variation, respectively (Table 2). The variables canopy cover and GDP *per capita* explained 9% and 4% of data variation, respectively (Table 2).

The proportion of invasive species increased with higher temperature seasonality (temperature variation throughout the year) and GDP *per capita* (Figs. 2A and 2C, respectively; Tab. 2). On the other hand, the proportion of invasive species decreased with increasing canopy cover and decreasing accessibility (distance to urban areas with more than 50,000 inhabitants) (Figs. 2B and 2D, respectively).

Discussion

Climatic (temperature seasonality), environmental (forest cover), and anthropogenic (accessibility and gross domestic product *per capita* - GDP) factors explained the major proportion of richness of invasive non-native woody plants in Neotropical forests with different deciduousness levels. The richness of invasive plants increased with higher temperature seasonality, accessibility, and GDP and decreased with the increase of canopy cover. Temperature seasonality and accessibility had the most significant effect on data variation.

There is a higher proportion of invasive woody plants in areas with higher temperature variations throughout the year (higher seasonality). Higher temperature seasonality is common in subtropical regions, where the mean annual temperature may vary between 20° and 35°C (Meteoblue, 2021). In these regions, deciduousness in seasonal forests is due to cold winters (monthly mean ≤ 15°C), determining partial foliage loss by some tree species. Higher temperature seasonality gives invasive plants a competitive advantage over native species (Castro *et al.*, 2021). In subtropical climates in the Neotropical region, for instance, some invasive grasses and herbs such as *Arundo donax* L. and *Tradescantia zebrina* Bosse, grow faster or increase seed germination rates when temperatures begin to drop in early autumn. This is a period when many native species are slowing down their metabolic processes (Decruyenaere & Holt, 2005; Castro *et al.*, 2021). Therefore, conditions provoked by lower temperatures, such as lower rates of competition for resources and herbivore pressure (Mari & Galassin, 2010; Castro *et al.*, 2021), are potential explanations for the higher proportion of invasive species in areas with higher temperature seasonality. Additionally, partial foliage loss by some species during cold winters in subtropical decidual forests leads to the formation of clearings that facilitate the arrival and establishment of invasive plants (Gandolfi *et al.*, 2009; Spear *et al.*, 2013; Dechoum *et al.*, 2015).

The richness of invasive plants was higher in areas of greater accessibility (*i.e.*, closer to cities) and in areas with

Table 2. Result of the relation between explanatory variables of the model selected and their influence on the response variable. General contributions were calculated using Nagelkerke's pseudo R^2. Significant p values are in bold.

Explanatory variable	Estimate	Std. Error	z	p	General contribution
Temperature seasonality	$7.914e^{-3}$	$1.465e^{-3}$	5.40	**< 0.001**	0.20
Canopy cover	$-3.506e^{-2}$	$5.513e^{-3}$	-6.36	**< 0.001**	0.09
Per capita GDP	$9.665e^{-10}$	$1.782e^{-10}$	5.42	**< 0.001**	0.04
Accessibility	$-6.256e^{-3}$	$2.111e^{-3}$	-2.96	**0.003**	0.16

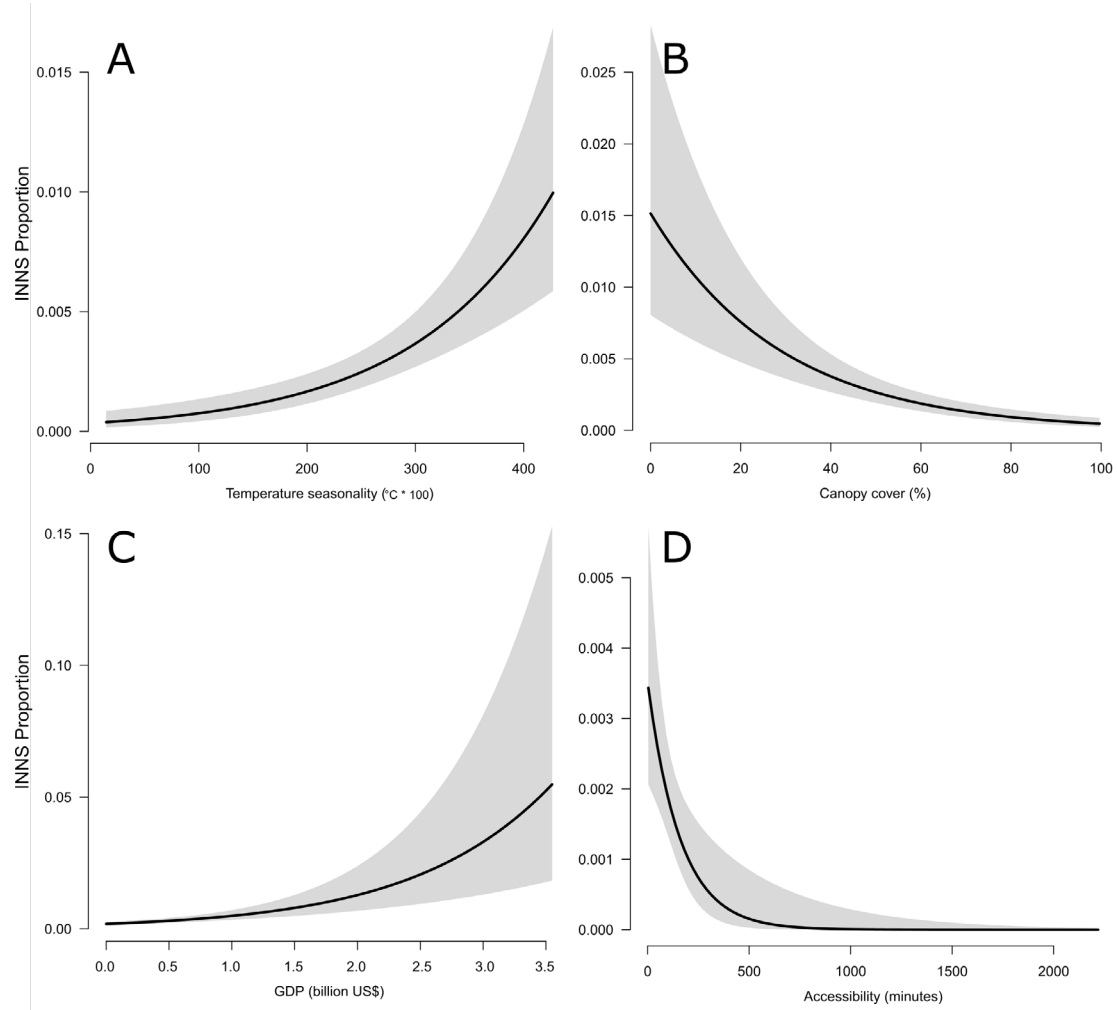

Figure 2. Proportion of invasive species (INNS) in relation to temperature seasonality (A), canopy cover (B), GDP *per capita* (C), and accessibility (D) in neotropical forests. The black line represents the linear adjustment of the selected model, and the shaded areas represent the 95% confidence interval of the adjustment.

elevated *per capita* gross domestic product. This result shows the importance of anthropogenic influence on the increase of invasive plant richness, corroborating research that showed how invasive plant richness was higher in more densely populated areas, along roads, or in areas with higher GDP (*e.g.* Spear *et al.*, 2013; Dimitrakopoulos *et al.*, 2017; Essl *et al.*, 2019; Gallardo & Vilà, 2019; Mungi *et al.*, 2021). Areas closer to cities or roads are also more prone to the arrival of propagules (Veldmam & Putz, 2010; 2011; Padmanaba & Sheil, 2014; Davis *et al.*, 2016; Gallardo & Vilà, 2019). Several studies have shown that the likelihood of invasive species occurrence increases with proximity to propagule sources. For example, widely commercialized species used for ornamental purposes in residential areas, such as *Ligustrum sinense* Lour., *Heptapleurum arboricola* Hayata (Davis *et al.*, 2016; Padayachee *et al.*, 2017; Marciniak *et al.*, 2020), and *Quercus rubra* L. (Woziwoda *et al.*, 2018), may be dispersed by animals to adjacent areas.

Proximity to roads is also an efficient dispersal pathway to surrounding natural tropical areas, as large amounts of propagules can be transported long distances adhered to tires or through the flux of air generated by vehicles (Veldmam & Putz, 2010; Padmanaba & Sheil, 2014). Road margins also function as habitats for invasive plants as disturbance favours the establishment of many species (Joly *et al.*, 2011). The absence of trees or shrubs along roads due to disturbance caused by frequent road maintenance generates conditions of lower competition and higher resource availability compared with natural areas (Joly *et al.*, 2011; Speziale *et al.*, 2018; Woziwoda *et al.*, 2018; Khaniya & Sherestha, 2020).

Canopy cover has also influenced non-native invasive plant richness. The higher the cover, the lower the richness, corroborating other research on tropical forests in Asia (Khaniya & Shrestha, 2020; Mungi *et al.*, 2021) and Central America (Lopez, 2012). This variable might also be related

to accessibility/road opening, considering that proximity to roads plays a fundamental role in the opening of areas for exploitation of forest resources, hunting, mining, and deforestation in tropical regions in South America and Asia (Laurence *et al.*, 2002; Wilkie *et al.*, 2000). Moreover, openings in the forest canopy can facilitate the entry of non-native invasive species propagules once the physical barrier posed by the canopy is broken (Joshi *et al.*, 2015). Such clearings are important even for shade-tolerant species, which grow better at higher light rates despite surviving in low light conditions in the forest interior (Martin *et al.*, 2010; Schuster *et al.*, 2020).

Subtropical forests in the Neotropics are more susceptible to the establishment of invasive woody plants than tropical forests, primarily due to their higher temperature seasonality. The deciduous nature of these forests may further promote the arrival of invasive plant propagules by reducing the physical barrier of the canopy as well as by increasing light availability. Forests with greater accessibility are also more prone to invasion as roads facilitate the spread of invasive species and increase the likelihood of propagules arriving from cultivated areas nearby. Neotropical forests are currently in a critical state of threat from anthropogenic impacts, including habitat loss, forest fragmentation, and climate change. Given the combined effects of human activities and the rising presence of invasive species, a further increase in invasive species richness is inevitable without effective management. Urgent action is needed through management policies at international, national, and regional levels to mitigate the threat posed by invasive species and promote the conservation of Neotropical forests.

Limitations

This review of floristic surveys revealed a significant gap in the inclusion of invasive species, with only 26.4% of the surveys reporting them. Notably, widely recognized invasive species in Neotropical forests, such as *Pittosporum undulatum, Spathodea campanulata*, and *Syzygium cumini*, were absent from the reviewed studies. This suggests that floristic and phytosociological surveys, as well as regional and state flora catalogues, may deliberately omit invasive species from their compiled lists, as pointed out by Moro *et al.* (2012). We emphasize the importance of including invasive species in floristic survey lists to enhance the accuracy of review studies and to provide managers with crucial information about their presence. Mapping invasive species improves distribution data and helps subsidize management in protected areas and other areas of relevance for biodiversity conservation (Moro *et al.*, 2012).

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Author contributions

AAC, MSD, PF, and RBS delineated the study; AAC, RBS, and GMS reviewed the articles and derived the variables used in the study; AAC and RBS conducted the analyses; AAC, RBS, PF, and MSD wrote the text.

Conflicts of interest

The authors have no conflicts of interest to declare.

Supplementary material

The following online material is available for this article:

Table S1. List of the 121 sites considered for the statistical analyses. Articles repeated in the list had more than one sampled sites that were more than 5km apart.

Table S2. Names of the 23 invasive non-native woody plant species compiled from the articles reviewed.

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