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Non-native and invasive tree species are abundant in neotropical secondary forest but decline over time

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Non-native and invasive species are among the leading causes of global biodiversity loss and could therefore compromise the recovery of native forests after disturbance, such as on abandoned agricultural lands. Here we evaluated how the relative density and richness of non-native woody species (NNS) change across secondary tropical forest succession, determined whether they vary between dry and moist forests and identified the underlying environmental and social drivers of these changes. We used data from 1,561 forest plots and 58 chronosequences from ten neotropical countries. We classified 3,735 woody species by origin and invasiveness. Our analyses and conclusions focus on NNS, whereas native (potentially) invasive groups were examined separately. NNS were widespread, occurring in 81% of the chronosequences and comprising 18% of dry and 41% of moist forest plots. We recorded 11 non-native invasive species, most of which were multifunctional trees associated with human activity. In early succession (the first 10–20 years), NNS reached high relative density and richness, accounting for 28% of stems and 22% of species in moist forests, and 9% of stems and species in dry forests. Both metrics declined considerably during the same period but were still present in late succession, mirroring the successional trajectory of native pioneer species, probably due to canopy closure and increased shading. Spatially, NNS richness increased with the Human Development Index. However, both density and richness were negatively affected by increasing surrounding forest cover, agricultural proximity and precipitation, while soil organic carbon generally favoured NNS retention. Our findings suggest that naturally regrowing forests and maintaining relatively intact forest landscapes provide nature-based solutions to control NNS, thereby protecting native biodiversity, ecosystem integrity and local livelihoods.

Biological invasions are among the five most important drivers of biodiversity and ecosystem services loss in the Anthropocene[1,2]. Locally, biological invasions can lead to biotic homogenization, species extinctions and even ecosystem collapse[3]. Non-native woody species (NNS) are abundant in human-modified landscapes, and most are useful species initially introduced and cultivated by humans[4]. After being established, non-native species can potentially become invasive since many are fast-growing pioneers, thriving in open and disturbed environments[5–8]. However, some shade-tolerant NNS can persist for a longer time in the system[9]. NNS may have substantial negative impacts on tropical ecosystems[10,11] by negatively affecting the native species that are adapted to stable environments. As NNS have escaped their natural enemies and have high propagule pressure, high fecundity and/or fast growth rates[12,13], they can effectively outcompete native species. Since NNS are abundant in agricultural landscapes, they could negatively[3] or positively impact ecosystem restoration and the recovery

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of secondary tropical forests regrowing naturally on abandoned agricultural fields[14–16]. This study therefore aims to evaluate how many NNS are found in neotropical secondary forests, how their relative density and richness change during secondary forest succession and how NNS are affected by socio-ecological drivers such as human development, land use, climate and soil conditions.

Biological invasion is the result of (un)intentional human transport, introduction, establishment and spread of a species outside the area where it naturally occurs[3]. Such species are introduced due to their provision of ecosystem services to society, by having social, cultural and economic value[4,17,18]. After they arrive in new territories, the establishment and spread of NNS are determined by the interaction between environmental drivers, such as land use and climate change, and the intrinsic traits of the species themselves[19,20]. Once outside its natural range, a species becomes 'non-native' (also called alien or exotic), and after establishing in or adapting to the new environment, it is considered 'naturalized'. It is called 'invasive' only after being recognized to cause damage to people and nature, notably when affecting agricultural practices. Non-native species can outcompete native plant species and rapidly spread into new environments without natural enemies. By replacing the role of one or more native species in the ecosystem and changing other properties such as soil-nutrient cycling, invasive species can modify trophic networks and functional, structural and biological diversity[21,22].

About 6% of the established non-native species are considered invasive globally[3]. Around 200 new invasive species are recorded annually worldwide, a collateral effect of globalization[3], with islands especially prone to biological invasions[23]. Among the global negative impacts, the food supply is the most severely affected, resulting in a loss of around US$280 billion annually. The costs of invasive species are unevenly distributed among regions[24] and are mainly related to the damage to nature's contribution to people and quality of life, rather than invasive management[3,25]. The perceived benefits of invasive species are therefore inadequate to counterbalance the negative impacts[3], although this has not been extensively studied in tropical forests.

Scientific and civil societies are trying to build knowledge on how NNS perform in different situations and across time and space. Few studies have assessed the long-term effects of longer-lived NNS, such as trees, on succession in forest ecosystems[9,26]. Since tropical forests are crucial for safeguarding the planet's stability[27], secondary forests regrowing on deforested lands play a vital role in recovering biodiversity and ecosystem services typical of the original forest ecosystems[28–30]. Over time, tropical forests tend to undergo sustained growth, changing from initial states formed by colonizing pioneer species that are well adapted to sunny and harsh conditions, which are gradually replaced by more shade-tolerant, later-successional tree species[31,32]. NNS may interfere with the trajectory of forest regeneration and negatively affect biodiversity recovery and the provision of ecosystem services[8,20].

The spread of NNS may vary between contrasting forest climates in the lowland Neotropics, such as dry and moist forests. Despite being heavily affected by plant invasion (for example, by herbaceous *Lantana camara* and grasses)[33,34], dry forests may be less prone to colonization and invasion by NNS because they present a seasonally harsh environment in which non-native, unadapted plants can thrive less easily. Moreover, many dry forest species produce large belowground storage organs, enabling them to resprout vigorously after aboveground damage caused by drought or fire. As a result, resprouting is a dominant mode of regeneration in early successional dry forests[35,36], which provides fewer opportunities for fire-sensitive NNS to establish from seed or to compete effectively with native vegetation. However, dry forests remain comparatively understudied, and current understanding is biased towards a limited set of geographies and systems, such as Hawaii and India[34]. Further research is needed to clarify the mechanisms underlying NNS dynamics in these systems. Because of their inherently fast growth rates, NNS may be better adapted to thrive in productive moist forests, where high resource availability supports their rapid growth and ruderal strategies, even after disturbances such as fragmentation[13,37]. Additionally, global change drivers such as habitat fragmentation and climate change may facilitate biological invasions by increasing ecosystem invasibility[38–41].

This study aims to understand the abundance, richness and degree of spread of NNS in neotropical secondary forests. We classified 3,735 tropical tree species according to their distribution and degree of invasiveness into groups: non-native non-invasive, non-native potentially invasive (that is, species reported as invasive elsewhere) and non-native invasive. The three non-native groups were also analysed together as NNS. For comparison, the native species (excluding non-invasive ones) were grouped as native (potentially) invasive species (N(P)IS), and the results are presented in the extended data figures. We used data from 1,561 secondary forest plots belonging to 58 chronosequences distributed across 10 neotropical countries to address the following three questions and corresponding hypotheses:

(1) What is the proportion of NNS groups found in neotropical secondary forests? We hypothesized that while non-native species are common, only a small proportion are invasive, and their distribution differs among forest types, with a preference for moist over dry forests. Moreover, we expected that the most common invasive species are useful, introduced non-native species, such as edible fruit trees[18].
(2) How do the density and richness of NNS groups change during succession? We hypothesized that NNS initially occur at high density and richness in early successional stages of secondary forests, as they are predominantly fast-growing, light-demanding pioneers with high dispersal capacity[42]. As shade-tolerant, long-lived species dominate the canopy during later-successional stages[43], we expected the relative density and richness of NNS to decrease over time.
(3) How do environmental (climate, landscape and soil) and social (Human Development Index (HDI)) drivers influence the density and richness of NNS groups? We hypothesized that, especially in moist areas, the density and richness of non-native species will increase with nearby agricultural (cropland and pastures) cover, because NNS thrive in open areas with repeated agricultural disturbances; with higher soil fertility, because most NNS are opportunistic ruderal species; and with a higher HDI, since land conversion will increase suitable habitat for NNS.

Using chronosequence data from the 2ndFor network, we analysed secondary forest plots ditributed across the tropical Americas (Fig. 1). We determined how the relative density and richness of non-native and/or invasive woody species change across successional and environmental gradients. All species were taxonomically standardized and classified by geographic origin and invasiveness status using established global databases. They were then categorized into groups on the basis of origin and invasiveness, and relative density and richness were calculated per plot. We fitted generalized linear mixed models (GLMMs) to test the effects of time since abandonment and seven socio-environmental variables (climate, soil properties, land cover and HDI) on these metrics.

Results

Quantifying non-native and/or invasive species

From all 3,735 species sampled across forest plots, there were 131 non-native non-invasive, 14 non-native potentially invasive (that is, species reported as invasive elsewhere) and 11 non-native invasive species. We also encountered 26 native potentially invasive species and five native invasive species (see Supplementary Information for N(P)IS). Combined, we found 156 NNS species (see

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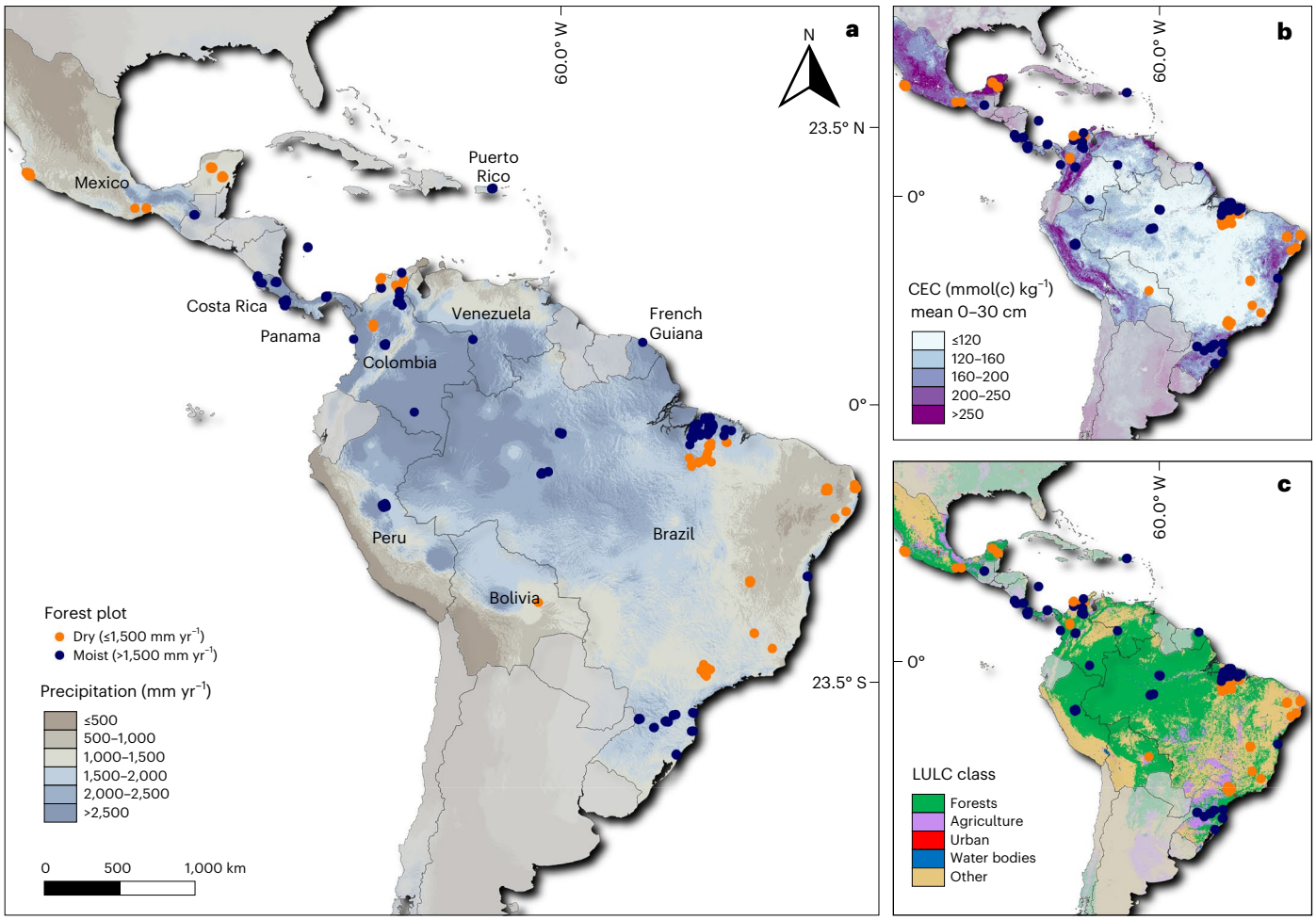

Fig. 1 | Distribution of the study plots and socio-ecological drivers. a–c, Studied countries, plot locations (dots) and maps of mean annual precipitation for the period 1979–2013[78] in dry sites (precipitation ≤1,500 mm yr^{-1}, orange symbols) and moist sites (precipitation >1,500 mm yr^{-1}, dark blue symbols) (**a**); cation exchange capacity (CEC, in mmol(c) kg^{-1}) based on SoilGrids[88] (**b**); and land use land cover (LULC) for 2019: temporary agriculture is coloured in pink, while permanent agricultural classes were not distinguished from 'forest', 'shrub' and 'herbaceous'; 'other' refers to bare soil, snow, ice and moss[79] (**c**).

Extended Data Table 1 for the country-level density of all non-native invasive species and N(P)IS found). Two non-native invasive species were encountered in two countries each, yielding 13 species–country combinations (Fig. 2). Non-native invasive species were found in three of the ten countries assessed (Brazil, Costa Rica and Puerto Rico) (Fig. 2 and Extended Data Table 1). Five native invasive species were encountered in three countries (Extended Data Fig. 1). The invasive species had, on average, four uses (ranging from two to seven), and according to the CABI Digital Library Compendium, they were mostly used for food, timber or fodder.

The non-native non-invasive species group was the most common, occurring in 29% of the 1,561 sampled plots, followed by non-native potentially invasive species (4%) and non-native invasive species (2.3%). The NNS were distributed differently over dry and moist forests, in terms of plot area per forest type (chi-squared test, $\chi^2 = 15.05$, d.f. = 1, $P < 0.001$) and number of plots ($\chi^2 = 93.69$, d.f. = 1, $P < 0.001$). All groups, except native invasive, occurred two to eight times more frequently in moist than in dry forests, although the sample sizes for some groups were very small (Table 1).

Density and richness change during forest succession

In dry and moist forests, the relative stem density of the groups declined with stand age (Fig. 3 and Extended Data Fig. 2), with stronger declines in moist forests. For all groups, the most substantial relative density decline occurred in the first 10–20 years. Relative stem density was used as a standardized indicator of numerical dominance, reflecting the proportional contribution of a species group within the woody community. In dry forests, the modelled relative stem density of NNS was 9% during the first 10 years of succession (with observed values reaching up to 30%) and declined to 5.5% or less after 20 years. In moist forests, modelled NNS relative stem density decreased from 28% to 10%, although observed values exceeded 90% in some plots younger than 20 years. However, after the steep decline, the numbers stabilized, and even after 50 years, the modelled relative density stayed over 4% in dry forests and 5% in moist forests.

Similarly to stem density, relative richness significantly declined with forest age (Fig. 4 and Extended Data Fig. 3), especially in moist forests. Relative richness expresses the proportional contribution of a species group to the total woody species diversity in each plot. The most considerable changes occurred during the first 20 years. In dry forests, the relative richness of NNS decreased in 20 years from 9% to 7% (the maximum observed was 23%), and in moist forests from 22% to 10% (the maximum observed was 99%). After the sharp drop, the numbers stabilized, with relative richness remaining above 6% (dry) and 7% (moist) after 50 years.

Influence of environmental and social drivers on density and richness

Five of seven drivers had strong effects on relative density in dry forests, with consistent responses across groups. A moderate and variable effect

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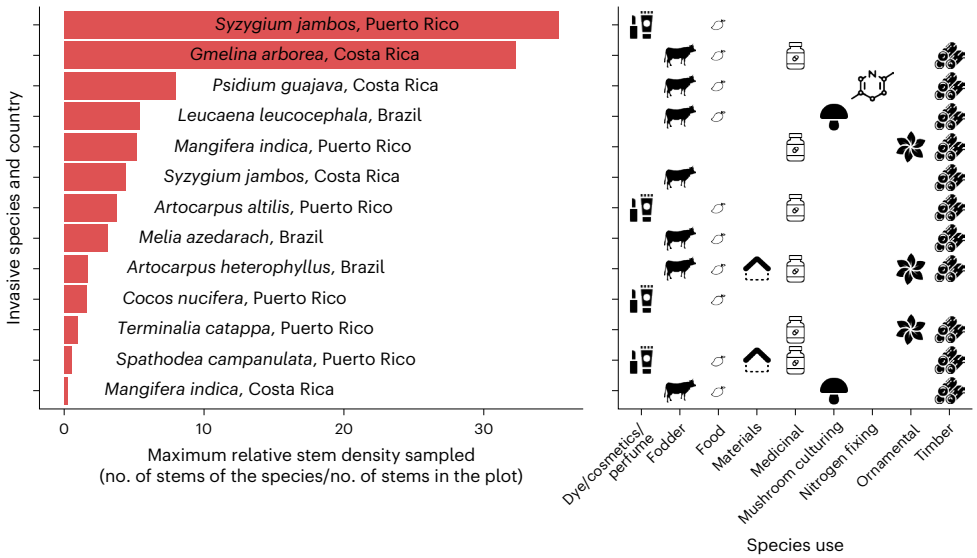

Fig. 2 | Non-native invasive species density. Thirteen species–country combinations representing 11 unique non-native invasive species (*Mangifera indica* and *Syzygium jambos* were encountered in different countries). Left: maximum relative stem density encountered in the country of occurrence. Right: human use of the species as reported by CABI[86]. All invasive species were introduced in their respective countries before 1913, except for *Gmelina arborea*, which was introduced in Costa Rica in 1966. References for each species are provided in the Supplementary References.

on relative density was detected in moist forests, and a weak effect on relative richness in moist forests (Fig. 5; see Extended Data Fig. 4 for native groups). In moist forests, the relative density and richness of most groups decreased with mean annual precipitation. For dry forests, and for most groups in moist forests, relative density and richness decreased with increasing surrounding forest and agricultural cover. The relative density and richness increased with soil organic carbon in both dry and moist forests. Finally, in moist forests, the relative density of non-native invasive species significantly increased with surrounding agricultural cover and HDI, whereas relative density decreased with precipitation.

Discussion

In this study, we assessed the importance of NNS in secondary forests and how they are affected by succession and other socio-ecological drivers. Eleven species were classified as invasive, and most of them are valuable, multipurpose tree species that may have spread by humans. NNS were widespread, occurring in 81% of the chronosequences and being significantly more common in moist than in dry forests (occurring in 41% versus 18% of the plots). Their relative density and richness decline exponentially in the first years of forest succession when the forest canopy closes and they are outshaded by the regrowing vegetation. Most NNS are disturbance-adapted pioneers, and as a result, their relative density and richness increase with human development and with decreasing surrounding forest cover.

Prevalence of non-native or invasive species in secondary forests

Of the 3,735 identified species, only 156 (4.2%) were classified as NNS in at least one country. Nevertheless, NNS covered a considerable relative density and richness in the early stage of succession, reaching 28% and 22%, respectively. Two NNS groups were relatively rare and found in only a few plots: non-native invasive and non-native potentially invasive species in dry forests. In dry areas, the low number of non-native (potentially) invasive species in our plots may be due to the lack of adaptation of these species to harsh hydrologic conditions, against the specialized local flora[13,44]. The seedling survival rate of moist-adapted species is strongly affected in seasonally dry forests[45].

Most of the NNS were non-native non-invasive (131 species), whereas 25 species were in the other two non-native groups combined; 31 other species were classified in native (potentially) invasive groups. While in the consulted databases some non-native species are not considered to be a threat in certain countries, our data show that they can be found at relatively high densities (species number of stems per total number of stems) in these countries. For example, several species listed as non-native but not as invasive accounted for more than 25% of stems in some areas, including *Croton glabellus* and *Leucaena leucocephala* in Colombia (Providencia Island), *Piper colonense* in Costa Rica, *Hovenia dulcis* in Brazil and *Lagerstroemia speciosa* in Panama (Supplementary Fig. 3 and Extended Data Table 1). Outdated databases are also a concern. We noted that *H. dulcis* in Brazil is already listed in the recently issued national list[46] but was not classified as 'invasive' in the international databases consulted.

In our study, 11 non-native species were classified as invasive, and two (that is, *Mangifera indica* and *Syzygium jambos*) were encountered in different countries (Fig. 2). The consulted databases' classifications on species invasiveness were mainly based on scientific literature, local reports and official country flora lists. In general, those databases list a relatively low number of non-native tree species as invasive, which might be due to a lack of floristic and ecological studies[47], or because it takes time before non-native species are detected and considered to be invasive. This can lead to some species being considered non-native in certain countries, even though they are possibly native, simply because they were never inventoried. In contrast, native invasive species (Extended Data Fig. 1) were recorded exclusively in the largest countries studied (Brazil, Colombia and Mexico). These nations encompass biologically distinct biomes, allowing species native to the political territory to be properly classified as invasive when spreading into different sub-regions or ecosystems.

We hypothesized and found that the most common invasive species in secondary forests are valuable introduced or cultivated species (Fig. 2), suggesting they were actively planted or passively seeded in the agricultural phase or the forest fallows. Most of these species are multipurpose trees with an average of four different uses, facilitating their human adoption, domestication and intentional or unintentional spread[4,18]. Half of the encountered invasive species produce edible fruits that are widely appreciated, such as *Syzygium jambos*, *Mangifera*

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Table 1 | Total number sampled and group percentages of chronosequences, plots, sampled area, species, stems and stems-per-species ratio

Group	Dry forest						Moist forest					
	Chron. (*n*)	Plots (*n*)	Area (ha)	Species (*n*)	Stem (*n*)	Stem/sp. (*n*)	Chron. (*n*)	Plots (*n*)	Area (ha)	Species (*n*)	Stem (*n*)	Stem/sp. (*n*)
Total	26[a]	682	33.2	1,234	46,466	39	44[a]	879	73.7	3,096	92,298	30
	Chron. (%)	Plots (%)	Area (%)	Species (%)	Stem (%)	Stem/spp. (*n*)	Chron. (%)	Plots (%)	Area (%)	Species (%)	Stem (%)	Stem/spp. (*n*)
Non-native non-invasive	57.69	17.30	18.30	2.19	0.93	16	84.09	36.63	58.59	3.65	2.87	23
Non-native potentially invasive	3.85	0.73	1.36	0.16	0.03	6	31.82	6.14	7.21	0.42	0.28	20
Non-native invasive	7.69	0.44	0.84	0.24	0.02	4	20.45	3.64	9.97	0.29	0.38	39
NNS	61.6	18.2	20.0	2.6	1.0	14	84.0	41.2	62.7	4.2	3.5	25
Native potentially invasive[b]	65.38	11.44	17.71	1.54	0.89	22	72.73	21.05	29.49	0.58	0.98	50
Native invasive[b]	42.31	8.06	6.69	0.41	0.67	63	13.64	1.25	0.49	0.10	0.03	10
Native non-invasive[c]	100.00	99.71	99.97	96.11	97.46	38	100.00	99.66	99.94	96.48	95.45	29

[a]Twelve chronosequences contain plots in both dry and moist forests. [b]The two groups with native species were analysed separately, and the results are presented in the Supplementary Results. [c]The native non-invasive group was not analysed; it was used only to compose the assembled community for calculating percentages, relative density and relative richness. The groups include native non-invasive, native potentially invasive, native invasive, non-native non-invasive, non-native potentially invasive, non-native invasive and NNS. There is an overlap of 595 species that occur in both climates, dry and moist. Chron, chronosequences; stem/sp., stems-per-species ratio.

indica and *Psidium guajava*. The non-edible species in our study are used for medicine, ornamental purposes or fodder. Non-fleshy fruits such as legume pods (for example, *Leucaena leucocephala*) are used only for fodder or reforestation ends (Fig. 2). Even though such species are considered useful, they can also pose a threat to the native flora and occur pervasively in high densities, such as *Syzygium jambos* in Puerto Rico[9] and *Artocarpus heterophylla* in Brazil[9,48]. It is worth mentioning that 6 out of 11 species classified as non-native invasive were found in Puerto Rico, which is expected, given the known high invasibility of small islands.

Changes in non-native and invasive species during succession

We hypothesized that NNS would be more abundant early in succession because most are light-demanding pioneers with high colonization ability, but they would decline with stand age because they cannot fully regenerate or survive in the shade. We indeed found that the relative stem density and relative richness of all groups decreased over time (Figs. 3 and 4). The strongest decline was observed during the first 10–20 years, which reflects rapid canopy closure and shading during the first years[49,50] and the short lifespans of many of these pioneer species[51]. This successional trajectory is not unique to NNS; it is characteristic of many light-demanding native pioneer species (Extended Data Figs. 2 and 3), regardless of their origin, and suggests NNS are being outcompeted by shade-tolerant, later-successional species, as expected. At the same time, NNS may persist to some extent; after 50 years, they still have an estimated relative density of 5% and relative richness of 7%, either because the maximum lifespan of established trees has not been reached yet, or because they persist through resprouting.

Another explanation for the successional decay of NNS is an increased 'biotic resistance' over time, when a more diverse native community builds up, which is better able to occupy all niches and resist biological invasion[52,53]. Indeed, the relative richness of NNS declined during the first 10–20 years, which means the community accumulated native diversity over time[29,30,54].

We hypothesized and found that NNS groups had consistently higher relative density and richness in moist than in dry forests, with differences reaching multiple-fold in some groups (Table 1). Most NNS are fast-growing ruderals that require high resource availability to sustain their rapid growth and metabolic rates, which is more characteristic of moist forests than of (seasonally) dry, resource-limited environments[13,37].

Environmental and social drivers that facilitate non-native and invasive species

Climate, landscape, soil and human modifications can all affect the occurrence and survival of NNS[20–23]. We hypothesized and found that the relative density and richness of NNS groups decrease with surrounding forest cover (Fig. 5), probably because NNS have higher seed production and perform better in open environments with repeated human disturbances[55,56]. Neighbouring forests facilitate the suppression of invasive species by reducing the openness of the landscape and creating better conditions for native species to compete[57].

Surprisingly, the relative density and richness of NNS generally declined with an increase in the surrounding agricultural area for dry forests, while the invasive subset in moist forests actually increased (or persisted) with nearby agriculture (Fig. 5). The mechanization and management of crop fields and more continuous crop cover may reduce the chances of NNS establishing or becoming mature and reproductive[23]. Instead, non-native and invasive species may increase in highly transformed and permeable human landscapes, with more constructed areas, such as buildings and roads[57]. Most secondary forests are part of successional mosaics, formed by a combination of slash-and-burn agriculture, extensive livestock farming (which often trespasses on the regenerating forest) and the exploitation of forest

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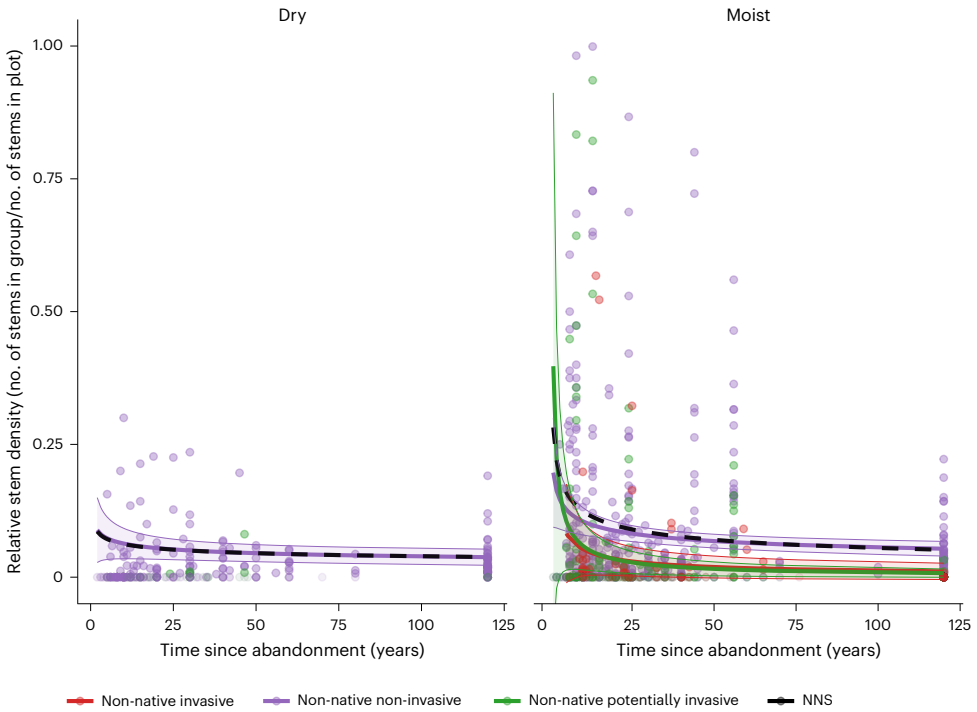

Fig. 3 | Relative stem density per group versus time since abandonment in dry and moist areas. The individual groups are represented in red for non-native invasive species, purple for non-native non-invasive species and green for non-native potentially invasive species. Their combination (non-native and/or invasive species—NNS) is shown as dashed black lines. The observed values (dots) represent the subset of plots where non-native species were present (n = 486 plots; 124 dry, 362 moist; note that a single plot may contain multiple species groups, resulting in multiple data points per plot). The regression lines (conditional mean predictions) and shaded areas (95% confidence intervals) represent the conditional component of the zero-inflated GLMMs fitted to the full analysed dataset (n = 1,349 unique plots; 559 dry, 790 moist).

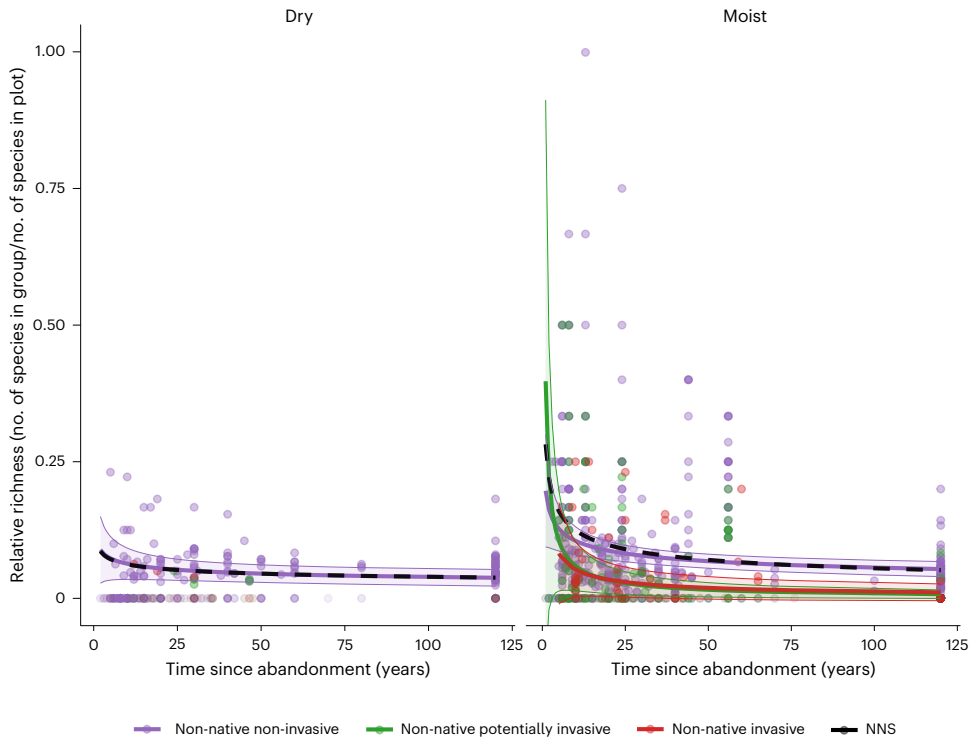

Fig. 4 | Relative species richness per group versus time since abandonment in dry and moist areas. The individual groups are represented in red for non-native invasive species, purple for non-native non-invasive species and green for non-native potentially invasive species. The combined NNS group is shown as dashed black lines. The observed values (dots) represent the subset of plots where non-native species were present (n = 486 plots; 124 dry, 362 moist; note that a single plot may contain multiple species groups, resulting in multiple data points per plot). The regression lines (conditional mean predictions) and shaded areas (95% confidence intervals) represent the conditional component of the zero-inflated GLMMs fitted to the full analysed dataset (n = 1,349 unique plots; 559 dry, 790 moist).

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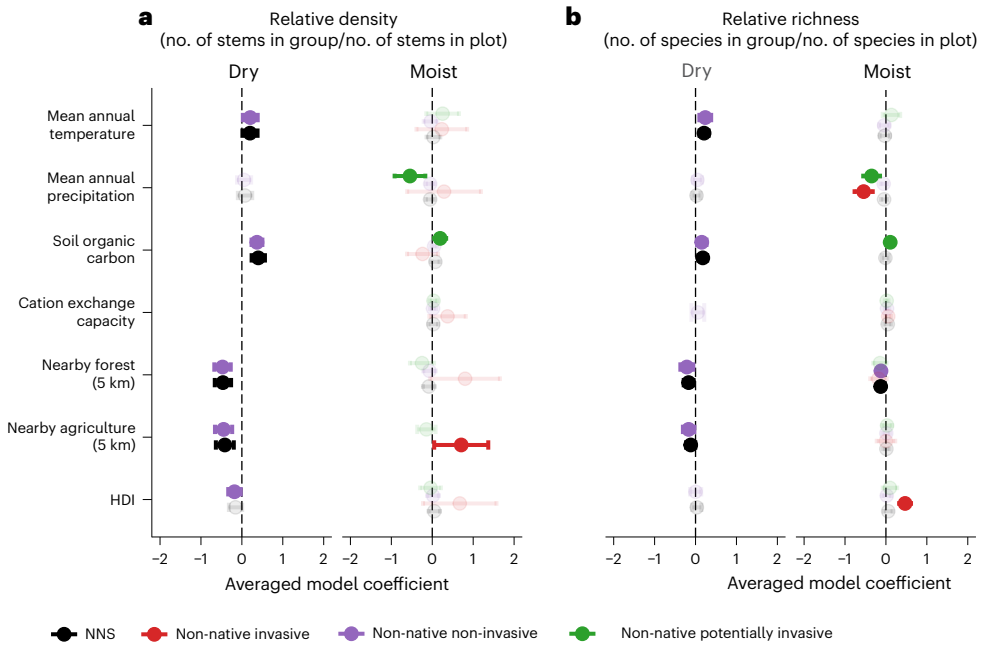

Fig. 5 | Effects of environmental and social drivers on NNS. a,**b**, Standardized regression coefficients (parameter estimates) and 95% confidence intervals for relative stem density (**a**) and relative richness (**b**) in dry (left plots) and moist forests (right plots). The points represent the model estimates, and the horizontal lines indicate the 95% confidence intervals. Individual groups are represented in red (non-native invasive species), purple (non-native non-invasive species), green (non-native potentially invasive species) and black (combined NNS). Negative relationships are shown to the left of the dashed vertical lines, and positive relationships to the right. Significant effects ($P < 0.05$) are indicated by vivid colours ($n = 1{,}349$ unique plots; 559 dry, 790 moist).

products such as firewood[58]. Thus, the simple metric of coverage of agricultural areas may not be a good predictor of disturbance or the creation of useful habitats for NNS.

We predicted that areas with a higher HDI and more urban and rural development would create more favourable conditions for the dispersal, arrival and growth of NNS in secondary forests. Humans are known to spread valuable species actively[59], and economic development is associated with increased disturbances, creating open sites for establishment[57,60]. The HDI indeed positively affected relative richness of non-native invasive species in moist forests, which is compatible with global studies[61]. The HDI is calculated by considering local populations' health, education and standard of living, and has been related to trade[62] and deforestation and land-use change[63]. These factors increase the introduction and establishment of non-native species due to increased propagule pressure[64], reduced competition by native vegetation and the creation of larger areas suitable for invasion[57].

We hypothesized that the relative abundance and richness of NNS would increase with higher soil fertility or soil water retention because most species are fast-growing, opportunistic and ruderal with high resource requirements. Relative density and richness increased with soil organic carbon content, which enhances soil water retention (Fig. 5). High soil water availability may be especially important for NNS to establish in dry areas, and it may be less relevant or inhibiting in moist forests, if soils become too wet, waterlogged or anoxic. Similarly, annual precipitation negatively affected the relative density and richness of NNS in moist forests (Fig. 5).

Limitations

In our study, we may have underestimated the impact of NNS. We focused only on woody trees with stem diameters >5 cm and did not analyse seedlings, saplings or herbaceous NNS. In tropical forests worldwide, invasive herbaceous ferns (for example, *Pteridium aquilinum*), climbing shrubs (for example, *Lantana camara*) and grasses (for example, *Imperata cylindrica*) lead to arrested succession or alternative states[65–68]. Despite our efforts to correct species names, some NNS classifications might be imprecise due to erroneous name determinations (for example, *Anisophyllea guianensis* and *Virola elongata* in Colombia). Additionally, about 50% of the data owners in our study reported avoiding the installation of forest plots in areas severely invaded by non-native species, such as *Gmelina arborea* in Costa Rica or *Acacia mearnsii* in Brazil. However, after field sampling, they found NNS species and kept the plots. Ten per cent of the plot owners reported intentionally sampling highly invaded areas, and 40% did not notice invasions a priori. Future studies could also use remote sensing techniques to detect and quantify the proportion of highly invaded areas in the landscape.

While our analysis accounts for spatial clustering, our findings reflect only successional dynamics at the plot level. These trends may not capture broader metacommunity dynamics, such as the limits on total community abundance driven by stochastic ecological drift described by neutral theory[69]. It remains possible that the surrounding anthropized landscape acts as a propagule source maintaining NNS regionally despite local decline[70]. Consequently, unmeasured dispersal rates could decouple local exclusion from regional persistence, a dynamic not explicitly quantified here[70].

Policy and management implications

There is a growing number of global targets on dealing with invasive species, such as the former Aichi Biodiversity Target 9 (ref. 3), Sustainable Development Goal 15 Target 8 and the Kunming-Montreal Global Biodiversity Framework Target 6 (ref. 3), aiming at preventing, eliminating, minimizing, reducing and mitigating the impacts of non-native invasive species on biodiversity and ecosystem services. The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services report on invasive species estimates that, despite 80% of countries having targets related to invasive species, only 17% have effective laws to deal with them[3]. In the Neotropics, Mexico[71] and Brazil[46] have national strategies for biological invasions. It should be acknowledged that NNS can also play a positive role in certain situations. As they dominate the beginning of forest succession, they may

improve the microclimate and soils and attract seed dispersers, thus facilitating succession[14,15]. They may also even form novel ecosystems, which occur in degraded areas where the native forest can no longer establish itself[16].

Despite many local and global warnings about the risks of non-native species[22], governments are usually not engaged in studying and actively controlling NNS. Puerto Rico has recognized many of the sampled NNS. In contrast, in the Colombian island of Providencia, invasive species such as *Leucaena leucocephala* are not reported as such, which might be critical due to the high vulnerability of islands[72]. Other small isthmian countries, such as Panama and Costa Rica, did not report dominant non-native species as invasive, as with *Lagerstroemia speciosa* and *Piper colonense*, respectively. Even large countries such as Brazil and Mexico fall short of detecting, studying and formally recognizing all the aggressive (or highly dominant) non-native species in their territories.

Conclusion

In this study, we found that, in terms of relative density and richness, the major threats from NNS to secondary forests are in the initial phases (10–20 years), which can be critical in cases of arrested succession[66,73]. Moreover, the high dominance of NNS in the initial phase and its reduction in the advanced phases can culminate in new communities formed by native species and NNS[16]. It is essential to note that early-development forests are widespread in dynamic, human-modified, tropical landscapes, such as large parts of the Amazonian and Atlantic Forests in Brazil[74,75]. Controlling invasive species substantially and positively impacts native biodiversity conservation[28].

Engaging with political leaders and local initiatives is essential to addressing invasions. Given the high costs of removing non-native species[76], regrowing forests and maintaining relatively intact forest landscapes provide nature-based solutions to control NNS. Additionally, assisted natural regeneration should control NNS to favour native trees. Campaigns should raise awareness among government agencies and local communities of the importance of choosing native over invasive species for cultivation, and provide incentives for local communities to harvest (potentially) invasive species and use their wood for fencing poles, firewood and construction. Overall, promoting the natural regeneration of invasion-resilient ecosystems is key to addressing environmental and societal challenges and reducing the threats posed by NNS to native biodiversity, ecosystem integrity and local livelihoods.

Methods

Study area and secondary forest data

We used the 2ndFor network database (https://sites.google.com/view/2ndfor/home) on secondary forests. We analysed 58 chronosequences from the tropical Americas and 1,561 forest plots (Fig. 1 and Extended Data Table 2). A chronosequence approach provides a long-term perspective on succession by using a space-for-time substitution and comparing secondary forest plots that differ in age since agricultural abandonment. Our plots' ages span from 1 to more than 120 years (old-growth plots were attributed 120 years). The chronosequence approach assumes that all plots experienced similar starting conditions and followed the same successional trajectory, which is not necessarily the case[73,77]. Therefore, during longer successional time frames, within-chronosequence variation in successional trajectories is smaller than between-chronosequence variation. Hence, by using a large dataset across the Neotropics, we can detect such drivers of regional differences in recovery. Only trees, palms and woody lianas ('woody species') were inventoried. Seedlings, saplings and non-woody herbaceous species were not included in this dataset. The minimum diameter at breast height was 5 cm in 54 chronosequences and 10 cm in the remaining 4. All individuals were botanically identified. Most chronosequences were inventoried using 0.1-ha plots (Extended Data Table 2). Differences in plot size and sampling design were accounted for by standardizing quantitative measurements (unrelated to floristic composition) to a per-hectare basis.

The 58 chronosequences are found in ten countries: Puerto Rico, Mexico, Costa Rica, Panama, Venezuela, French Guiana, Colombia, Peru, Brazil and Bolivia. The chronosequence sites span broad ranges in mean annual precipitation (850–6,400 mm yr^{-1}; BioClim Chelsa), mean annual temperature (14.8–27.7 °C, BioClim Chelsa[78]) and CEC (6.1–38.9 mmol(c) kg^{-1} in the 0–30 cm topsoil; SoilGrids). The chronosequences were established after land abandonment in multiple years, characterizing a natural experiment. The surrounding forest cover within a 5-km radius around each plot varies from 0% to 100%[79]. Additionally, at least 35% of all plots are surrounded by agricultural uses. Previous land use comprised abandoned crop fields for 29% of the plots and abandoned pastures for 27%; for 40% of our plots, it was a mix of the two, whereas the other 4% were on areas of high-intensity pasture or crop fields or were established right after forest clear-cut.

The plots were grouped into two major climatic regions: dry (up to 1,500 mm yr^{-1}, 682 plots) and moist (>1,500 mm, 879 plots). The plots were sampled by different research groups using different sampling designs and inclusion criteria (Extended Data Table 2). All sites have in common the chronosequence sampling approach, conventional fixed-sized plots and structure and floristics tree inventories (5–10 cm minimum diameter at breast height).

Species identification and geographic origin

We thoroughly checked for misspelled scientific names and replaced synonyms using R (version 4.5.2 (2025-10-31 ucrt)[80]), packages TNRS (version 0.3.6)[81] and flora (version 0.3.4)[82] (only for Brazil). After substituting synonyms, we ended up with 3,735 unique identifiers; 80% were identified to the species level and 15% to the genus level, and 5% were included as morphotypes.

To classify all species as native or non-native, we identified the original geographic distribution of each species (probable native range) at the country level rather than at the sub-country level, since most databases provide only country-level information. For this, we used the rWCVP package (version 1.2.4)[83], which provides the range of occurrence and indicates whether each species was introduced to the country where it was inventoried. Only nine species had no geographical distribution in the WCVP database; for those, we consulted their original distribution in the Kew (https://powo.science.kew.org/) and Flora do Brasil (https://floradobrasil.jbrj.gov.br/) databases. This step was performed in two tiers: the first considered only the species' complete names (genus and epithet), and the second considered only species identified at the genus level. Having only the genus can carry more uncertainty, so most morphotypes were classified as native if the genus is native to the target country. We considered a genus 'non-native' only if all species in that genus are considered non-native in the target country (for example, *Eucalyptus* spp.). A second reliable source of information on origin used was the Global Naturalized Alien Flora (GloNAF) database[84].

Invasiveness classification

Once the origin (native/non-native) was defined, we consulted three databases to classify each species according to its invasive/non-invasive status: GISD[85], GloNAF[84] and CABI[86]. The data search and download were performed in August 2023 with the most updated version of each database. Using the TNRS package in R, we first performed the same name check used in our data across the aforementioned databases to ensure a standardized nomenclature. We extracted all species-specific information from each database, enabling us to detect species status per country. We classified a species as invasive in the country where it was recorded only if it was listed as such in at least one database (for example, *Leucaena leucocephala* is listed as invasive in Brazil). We classified a species as potentially invasive if it was invasive in any

country other than where it was recorded, since a non-native species may already be invasive in some parts but not be reported (for example, *Leucaena leucocephala* is not listed as invasive in Colombia, but it is considered invasive in many other countries). Species with the status 'naturalized' or 'established' are also non-native but not officially reported or classified as invasive. In contrast, 'cryptogenic' species lack a well-defined origin, can be invasive and are usually considered non-native. Additionally, a species can be regarded as invasive in its country of origin if it invades regions outside its original range in that country (for example, *Leucaena leucocephala* was listed as native invasive in some parts of Mexico).

Origin–invasiveness classification

Before the analysis, we combined the two classifications cited above, grouping all species by origin (native or non-native) and reported invasiveness (invasive, potentially invasive or non-invasive). We then merged species into broader analytical groups for native and non-native species. For the analysis, we did not count the 'native non-invasive species' group since they were not focal, yielding five groups and two combinations (Extended Data Table 3). We ended up with the following groups: (1) non-native non-invasive, (2) non-native potentially invasive, (3) non-native invasive, (4) the combined NNS, (5) native potentially invasive, (6) native invasive and (7) the combined N(P)IS. The native non-invasive group was used only to represent the whole community as a basis for our analysis. Morphotyped individuals ($n = 599$) were classified as native non-invasive because they were rarely recorded and difficult to identify, unlike non-native invasive species, which could be easily identified.

Once we had the list of invasive species (native and non-native), we consulted their recognized uses in the CABI Digital Library Compendium (https://www.cabidigitallibrary.org/).

Response variables

After testing occurrence, basal area relative dominance, relative stem density and richness for all groups, we found that the last two variables are good descriptors for all groups in the chronosequences. We assessed the commonness of each group on the basis of relative density and richness quantified at the plot level, representing the proportional contribution of each group to the total within plots. Relative density is the number of stems of each group per the total amount of stems (per hectare). Relative richness represents the total number of species per group divided by the total number of species in each plot.

Drivers of non-native species

We considered time and seven spatial socio-environmental variables as drivers of the relative density and richness of non-native and/or invasive species groups. Time was defined as the number of years since land abandonment and represents forest successional age. We used the randomForest regression algorithm in R[87] to assess the initial 22 socio-environmental drivers that can potentially affect the density and richness of the target groups (see Supplementary Methods for the socio-environmental drivers screening). Only the seven most important variables were used. To keep the analysis straightforward, we used at least one representative layer for each group (climate, soil, land use land cover (LULC) and social), but no more than two.

We used two climate variables from Bioclim-Chelsa (years 1979–2013), annual mean temperature and annual precipitation, considering a 100-m buffer around each plot (https://www.chelsa-climate.org/datasets)[78]. The soil variables were also extracted considering a 100-m buffer around each plot and do not account for collection dates (https://soilgrids.org/) ref. 88. The 0–30 cm soil depth variables selected were soil CEC and organic carbon content in the fine earth fraction; their accuracy ranges from 30% to 70%. For LULC layers, we used the Copernicus Global Land Cover[79] for 2019. Agriculture and forest cover have the highest importance. After screening, we found a 5-km radius from each plot to be the most important scale (among buffers between 10 and 5,000 m; see Supplementary Methods for the socio-environmental drivers screening). For social drivers, only the HDI for 2015[89] at the sub-national level, when available, was highly important in our preliminary analysis. Most of our forest data were collected around 2010 (median), matching climate and soil data and differing by less than ten years from 85% of HDI and 60% of LULC observation dates. Although we used the best available layers, there are still limitations due to the coarse spatial resolution of all layers. For example, for LULC, many chronosequences probably cover a small geographic extent, with more than one plot buffer spatially overlapping, so the cover data are not independent. For climate variables, several plots within a chronosequence probably fall within the same pixel due to its coarse resolution.

Analysis

Of the 1,561 original plots, 40 plots from three chronosequences were not used in the analysis since they contained only native non-invasive species and none of the focal groups analysed here. This resulted in a filtered dataset of 1,521 plots across 55 chronosequences. Subsequently, two group-specific datasets were created for further analyses: the non-native species dataset comprised 1,349 plots across 47 chronosequences, whereas the native invasive/potentially invasive species dataset comprised 1,419 plots across 48 chronosequences. These datasets were not mutually exclusive, as non-native and native focal groups frequently co-occurred in the same plots.

We analysed the effects of time and socio-environmental drivers on relative stem density and richness using GLMMs with the glmmTMB package (version 1.1.13)[90] in R[80]. Chronosequence was included as a random effect to account for unmeasured regional and historical differences among systems, allowing inference on landscape and climatic drivers within chronosequences rather than across them. To account for the high proportion of zeros, we fitted zero-inflated models. In this study, we focused on the conditional component of the models, which quantifies the effects of environmental and socio-economic predictors on the relative frequency of invasive species given their presence.

To select the appropriate GLMM family, we identified the best-fitting distributions for each response variable (relative density and relative richness) of each group using the fitdistriplus R package (version 1.2-4)[91]. We then ran a series of GLMMs with beta (link logit), zi-gamma (link log) and log-normal (link log) distributions, all of which are suitable for continuous variables. We selected the best-fitting model on the basis of the lowest Akaike information criterion (AIC), Bayesian information criterion and deviance, and the highest log-likelihood[90]. Furthermore, the distribution of residuals was visually inspected, and the homogeneity of variance was assessed using the dispersion tests implemented in the DHARMa package (version 0.4.7)[92]. Dispersion models with the log of years since abandonment were also used to account for non-constant variances, which can lead to heteroscedasticity in which the variability of the response variable changes across the range of an independent variable[90].

To evaluate how species in each group were driven by macroclimate (mean annual temperature and annual precipitation), landscape context (the percentage of forest and agriculture cover within a 5-km radius), average 0–30 cm soil conditions (CEC and soil organic carbon content in the fine earth fraction) and HDI, a series of GLMMs were constructed. We used multiple models and an information-theoretic approach, which involves comparing models on the basis of their ability to explain the data to evaluate how different exploratory variables affect the response[26]. To avoid multicollinearity, any pairs of explanatory variables with a Pearson correlation coefficient of 0.7 or greater were included in separate models. We then ranked the models using AIC corrected for small sample sizes (AICc), since some groups had fewer than 30 samples. Models with $\Delta AICc \leq 2$ were considered to have strong explanatory power and biological significance. Mean parameter

estimates for the models were calculated by averaging the regression coefficients weighted by the AICc weights. The relative importance of exploratory variables was determined by summing the AICc weights of all averaged models that included each variable (see Supplementary Methods for more details).

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The minimum dataset required to interpret, verify and reproduce the findings of this study is provided in the paper and its Supplementary Information. A thorough description of each analysed species, including scientific name, group, presence and absolute density, is provided in Extended Data Table 1. Metadata on the chronosequences and plots used in this study are provided in Extended Data Table 2 (for Fig. 1). The detailed forest inventory data supporting the findings of this study are available from the 2ndFor network (https://sites.google.com/view/2ndfor/home) upon reasonable request, subject to approval by the data providers and compliance with the network's data-sharing policy and data use agreements. Publicly available datasets were analysed in this study. Taxonomic and invasiveness data are available from the World Checklist of Vascular Plants (https://powo.science.kew.org/), Flora do Brasil (https://floradobrasil.jbrj.gov.br/), the GloNAF database (https://esajournals.onlinelibrary.wiley.com/doi/full/10.1002/ecy.2542#support-information-section), the IUCN SSC Invasive Species Specialist Group list (GISD, https://doi.org/10.3391/mbi.2015.6.2.03) and the CABI Compendium (https://www.cabidigitallibrary.org/). Environmental data are available from CHELSA (https://www.chelsa-climate.org/datasets), SoilGrids (https://soilgrids.org/) and the Copernicus Global Land Cover (https://land.copernicus.eu/). Socio-economic data (HDI) are available via Dryad at https://doi.org/10.5061/dryad.dk1j0 (ref. 89). Source data are provided with this paper.

Code availability

The custom code used for data processing and the main analysis is available via Zenodo at https://doi.org/10.5281/zenodo.19593673 (ref. 93).

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Author contributions

The core team (A.F.R., L.P., F.B., R.C., G.H., I.H., C.C.J. and M.T.v.d.S.) conceived the study and contributed to the development of the research framework. A.F.R. and F.A.R.M. designed and performed the analyses, with support from L.P. and the core team. Data were collected or curated by all co-authors to build the 2ndFor network. A.F.R. curated the dataset and led the integration of the multi-site database for the current paper. A.F.R. led the writing of the manuscript. L.P., F.B., P.H.S.B., R.C., G.H., I.H., C.C.J. and M.T.v.d.S. contributed to the interpretation of results and critically revised the manuscript. All authors reviewed the manuscript, approved the final version and agree to be accountable for their contributions.

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Competing interests

P.H.S.B. is a partner at Re.green, a Brazilian forest restoration company. The other authors declare no competing interests.

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Extended Data Table 1 | Mean absolute density per target group per country

Group	Scientific name	Bolivia	Brazil	Colombia	Costa Rica	French Guiana	Mexico	Panama	Peru	Puerto Rico	Venezuela
Native Potentially Invasive	*Psidium guajava*	8	0	0	0	0	0	0	0	0	0
	Sterculia apetala	11	40	61	14	0	0	3	0	0	0
	Annona glabra	0	45	0	0	44	20	0	0	0	0
	Cedrela odorata	0	10	100	17	0	22	5	20	0	0
	Ceiba pentandra	0	25	79	4	0	20	3	10	0	0
	Eugenia uniflora	0	20	0	0	0	0	0	0	0	0
	Miconia calvescens	0	38	0	0	0	0	0	0	0	0
	Mimosa bimucronata	0	192	0	0	0	0	0	0	0	0
	Piper aduncum	0	552	0	25	0	0	12	0	0	0
	Schinus terebinthifolia	0	233	0	0	0	0	0	0	0	0
	Vachellia farnesiana	0	40	0	0	0	0	0	0	0	0
	Acanthocereus tetragonus	0	0	250	0	0	50	0	0	0	0
	Annona squamosa	0	0	15	0	0	40	0	0	0	0
	Castilla elastica	0	0	15	21	0	15	3	0	0	0
	Cecropia peltata	0	0	68	90	0	89	10	0	0	37
	Melicoccus bijugatus	0	0	208	0	0	0	0	0	0	0
	Samanea saman	0	0	100	22	0	0	0	0	0	0
	Tabebuia rosea	0	0	110	12	0	63	4	0	0	0
	Caesalpinia pulcherrima	0	0	0	0	0	52	0	0	0	0
	Carica papaya	0	0	0	0	0	140	0	0	0	0
	Chromolaena odorata	0	0	0	0	0	80	0	0	0	0
	Chrysobalanus icaco	0	0	0	0	0	4	0	0	550	0
	Haematoxylum campechianum	0	0	0	0	0	168	0	0	0	0
	Pithecellobium dulce	0	0	0	0	0	145	0	0	0	0
	Cecropia schreberiana	0	0	0	0	0	0	0	0	90	0
	Tabebuia heterophylla	0	0	0	0	0	0	0	0	338	0
Native Invasive	*Psidium guajava*	0	121	0	0	0	0	0	0	0	0
	Solanum mauritianum	0	185	0	0	0	0	0	0	0	0
	Prosopis juliflora	0	0	60	0	0	0	0	0	0	0
	Leucaena leucocephala	0	0	0	0	0	206	0	0	0	0
	Vachellia farnesiana	0	0	0	0	0	69	0	0	0	0
Non-native Non-invasive	*Acrocomia aculeata*	25	0	0	0	0	0	0	0	0	0
	Aiouea grandifolia	0	33	0	0	0	0	0	0	0	0
	Aralia excelsa	0	17	0	0	0	0	0	0	0	0
	Bauhinia melastomatoidea	0	20	0	0	0	0	0	0	0	0
	Calliandra houstoniana var. anomala	0	102	0	0	0	0	0	0	0	0
	Citrus sp.	0	44	0	24	0	0	0	0	0	0
	Clusia parviflora	0	167	0	0	0	0	0	0	0	0
	Dendropanax macropodus	0	10	0	0	0	0	0	0	0	0
	Derris trifoliata	0	10	0	0	0	0	0	0	0	0
	Eschweilera gigantea	0	40	0	0	0	0	0	0	0	0
	Eucalyptus sp.	0	33	0	0	0	0	0	0	0	0
	Geophila pilosa	0	10	0	0	0	0	0	0	0	0
	Hebepetalum humiriifolium	0	33	0	0	0	0	0	0	0	0
	Herrania cuatrecasasiana	0	45	0	0	0	0	0	0	0	0
	Hovenia dulcis	0	190	0	0	0	0	0	0	0	0
	Inga filiformis	0	17	0	0	0	0	0	0	0	0
	Lonchocarpus mutans	0	10	0	0	0	0	0	0	0	0
	Mabea caudata	0	27	0	0	0	0	0	0	0	0

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Extended Data Table 1 (continued) | Mean absolute density per target group per country

Group	Scientific name	Bolivia	Brazil	Colombia	Costa Rica	French Guiana	Mexico	Panama	Peru	Puerto Rico	Venezuela
	Maytenus tetragona	0	44	0	0	0	0	0	0	0	0
	Miconia symplectocaulos	0	40	0	0	0	0	0	0	0	0
	Myrcia huallagae	0	120	0	0	0	0	0	0	0	0
	Myrcia madida	0	20	0	0	0	0	0	0	0	0
	Myrcia servata	0	23	0	0	0	0	0	0	0	0
	Neea anisophylla	0	20	0	0	0	0	0	0	0	0
	Ouratea paruensis	0	60	0	0	0	0	0	0	0	0
	Persea americana	0	63	0	0	0	0	12	0	0	0
	Pouteria peruviensis	0	18	0	0	0	0	0	0	0	0
	Protium altissimum	0	64	0	0	0	0	0	0	0	0
	Quararibea turbinata	0	10	0	0	0	0	0	0	0	0
	Rinorea pubiflora var. pubiflora	0	40	0	0	0	0	0	0	0	0
	Sloanea tuerckheimii	0	15	0	0	0	0	0	0	0	0
	Syzygium sp.	0	22	0	0	0	0	0	0	0	0
	Zanthoxylum panamense	0	40	0	0	0	0	0	0	0	0
	Anisophyllea guianensis	0	0	60	0	0	0	0	0	0	0
	Bougainvillea glabra	0	0	100	0	0	0	0	0	0	0
	Calliandra harrisii	0	0	50	0	0	0	0	0	0	0
	Casearia oblongifolia	0	0	150	0	0	0	0	0	0	0
	Chrysophyllum cainito	0	0	100	3	0	0	0	0	0	0
	Combretum spinosum	0	0	100	0	0	0	0	0	0	0
	Cordia gerascanthus	0	0	400	0	0	0	0	0	0	0
	Croton glabellus	0	0	681	0	0	0	0	0	0	0
	Dendropanax arboreus	0	0	22	21	0	154	15	0	0	0
	Desmoncus orthacanthos	0	0	10	0	0	0	0	0	0	0
	Eugenia herrerae	0	0	400	0	0	0	0	0	0	0
	Ficus trigonata	0	0	138	0	0	0	0	0	0	0
	Guatteria grandiflora	0	0	10	0	0	0	0	0	0	0
	Homalolepis ferruginea	0	0	10	0	0	0	0	0	0	0
	Inga disticha	0	0	20	0	0	0	0	0	0	0
	Licania bracteata	0	0	60	0	0	0	0	0	0	0
	Marlimorimia pittieri	0	0	125	0	0	0	0	0	0	0
	Metopium brownei	0	0	433	0	0	0	0	0	0	0
	Moringa oleifera	0	0	50	0	0	0	0	0	0	0
	Myrcia loranthifolia	0	0	150	0	0	0	0	0	0	0
	Neea nigricans	0	0	140	0	0	0	0	0	0	0
	Oxandra laurifolia	0	0	167	0	0	0	0	0	0	0
	Phytelephas aequatorialis	0	0	20	0	0	0	0	0	0	0
	Pourouma herrerensis	0	0	20	0	0	0	0	0	0	0
	Senna fruticosa	0	0	100	0	0	0	0	0	0	0
	Sloanea schomburgkii	0	0	10	0	0	0	0	0	0	0
	Triplaris poeppigiana	0	0	100	0	0	0	0	0	0	0
	Vachellia collinsii	0	0	399	0	0	0	0	0	0	0
	Virola elongata	0	0	27	0	0	0	0	0	0	0
	Vochysia vismiifolia	0	0	120	0	0	0	0	0	0	0
	Alibertia dwyeri	0	0	0	3	0	0	0	0	0	0
	Anacardium occidentale	0	0	0	20	0	0	10	0	0	0
	Aspidosperma spruceanum	0	0	0	6	0	0	3	0	0	0
	Attalea butyracea	0	0	0	7	0	0	14	0	0	0

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Extended Data Table 1 (continued) | Mean absolute density per target group per country

Group	Scientific name	Bolivia	Brazil	Colombia	Costa Rica	French Guiana	Mexico	Panama	Peru	Puerto Rico	Venezuela
	Bombax ceiba	0	0	0	20	0	0	0	0	0	0
	Cananga odorata	0	0	0	2	0	0	0	0	0	0
	Castilla ulei	0	0	0	40	0	0	0	0	0	0
	Cestrum megalophyllum	0	0	0	11	0	0	0	0	0	0
	Chomelia barbata	0	0	0	20	0	0	0	0	0	0
	Chromolucuma rubriflora	0	0	0	2	0	0	0	0	0	0
	Citrus × aurantiifolia	0	0	0	40	0	0	0	0	0	0
	Citrus × aurantium	0	0	0	3	0	0	15	0	0	0
	Coccoloba venosa	0	0	0	10	0	0	0	0	0	0
	Compsoneura sprucei	0	0	0	40	0	0	0	0	0	0
	Damburneya salicifolia	0	0	0	4	0	0	0	0	0	0
	Diospyros acapulcensis subsp. nicaraguensis	0	0	0	13	0	0	0	0	0	0
	Diospyros salicifolia	0	0	0	10	0	0	0	0	0	0
	Dussia mexicana	0	0	0	3	0	0	0	0	0	0
	Eschweilera neei	0	0	0	2	0	0	0	0	0	0
	Euterpe oleracea	0	0	0	16	0	0	0	0	0	0
	Gonzalagunia rudis	0	0	0	40	0	0	0	0	0	0
	Lonchocarpus latisiliquus	0	0	0	3	0	0	0	0	0	0
	Matisia bracteolosa	0	0	0	9	0	0	0	0	0	0
	Nephelium ramboutan-ake	0	0	0	4	0	0	0	0	0	0
	Ormosia coccinea	0	0	0	2	0	0	0	0	0	0
	Perebea angustifolia	0	0	0	15	0	0	0	0	0	0
	Piper aequale	0	0	0	14	0	0	0	0	0	0
	Piper colonense	0	0	0	46	0	0	0	0	0	0
	Posoqueria coriacea subsp. maxima	0	0	0	11	0	0	0	0	0	0
	Protium aracouchini	0	0	0	3	0	0	0	0	0	0
	Protium copal	0	0	0	4	0	0	0	0	0	0
	Protium decandrum	0	0	0	22	0	0	0	0	0	0
	Pycnandra acuminata	0	0	0	2	0	0	0	0	0	0
	Qualea polychroma	0	0	0	9	0	0	0	0	0	0
	Stryphnodendron microstachyum	0	0	0	11	0	0	0	0	0	0
	Swartzia cubensis	0	0	0	16	0	0	0	0	0	0
	Tetrorchidium andinum	0	0	0	1	0	0	0	0	0	0
	Trichospermum mexicanum	0	0	0	88	0	0	0	0	0	0
	Virola surinamensis	0	0	0	11	0	0	8	0	0	0
	Vismia guianensis	0	0	0	20	0	0	0	0	0	0
	Ficus pallida	0	0	0	0	5	0	0	0	0	0
	Prunus myrtifolia	0	0	0	0	6	0	0	0	0	0
	Cassipourea guianensis	0	0	0	0	0	10	0	0	60	0
	Diospyros ferrea	0	0	0	0	0	106	0	0	0	0
	Eugenia buxifolia	0	0	0	0	0	110	0	0	0	0
	Ficus carica	0	0	0	0	0	27	0	0	0	0
	Geonoma pinnatifrons subsp. oxycarpa	0	0	0	0	0	6	0	0	0	0
	Guarea guidonia	0	0	0	0	0	14	0	0	0	0
	Melicoccus oliviformis	0	0	0	0	0	96	0	0	0	0
	Muellera torrensis	0	0	0	0	0	50	0	0	0	0
	Nectandra sanguinea	0	0	0	0	0	2	0	0	0	0

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Extended Data Table 1 (continued) | Mean absolute density per target group per country

Group	Scientific name	Bolivia	Brazil	Colombia	Costa Rica	French Guiana	Mexico	Panama	Peru	Puerto Rico	Venezuela
	Piper yzabalanum	0	0	0	0	0	4	0	0	0	0
	Byrsonima spicata	0	0	0	0	0	0	40	0	0	0
	Gmelina arborea	0	0	0	0	0	0	5	0	0	0
	Lindackeria laurina	0	0	0	0	0	0	6	0	0	0
	Miconia doriana	0	0	0	0	0	0	5	0	0	0
	Piper arboreum	0	0	0	0	0	0	3	0	0	0
	Piper schiedeanum	0	0	0	0	0	0	8	0	0	0
	Virola multiflora	0	0	0	0	0	0	6	0	0	0
	Vismia macrophylla	0	0	0	0	0	0	88	0	0	0
	Astrocaryum murumuru	0	0	0	0	0	0	0	30	0	0
	Protium nodulosum	0	0	0	0	0	0	0	10	0	0
	Schizolobium parahyba	0	0	0	0	0	0	0	20	0	0
	Solanum wrightii	0	0	0	0	0	0	0	50	0	0
	Tachigali chrysaloides	0	0	0	0	0	0	0	20	0	0
	Talisia cupularis	0	0	0	0	0	0	0	30	0	0
	Lindackeria paludosa	0	0	0	0	0	0	0	0	0	38
	Swartzia macrophylla	0	0	0	0	0	0	0	0	0	73
Non-native Potentially Invasive	*Mangifera indica*	0	27	214	0	0	15	8	0	0	0
	Rhaphiolepis bibas	0	11	0	0	0	0	0	0	0	0
	Samanea saman	0	160	0	0	0	0	0	0	0	0
	Cecropia schreberiana	0	0	15	0	0	0	0	0	0	0
	Cocos nucifera	0	0	200	2	0	0	0	0	0	0
	Eugenia uniflora	0	0	13	0	0	0	0	0	0	0
	Leucaena leucocephala	0	0	1488	0	0	0	0	0	0	0
	Opuntia ficus-indica	0	0	200	0	0	0	0	0	0	0
	Tamarindus indica	0	0	100	0	0	0	0	0	0	0
	Terminalia catappa	0	0	300	15	0	0	0	0	0	0
	Pithecellobium dulce	0	0	0	60	0	0	0	0	0	0
	Syzygium malaccense	0	0	0	6	0	0	0	0	0	0
	Lagerstroemia speciosa	0	0	0	0	0	0	180	0	0	0
	Psidium guajava	0	0	0	0	0	0	9	0	0	0
Non-native Invasive	*Artocarpus heterophyllus*	0	13	0	0	0	0	0	0	0	0
	Leucaena leucocephala	0	78	0	0	0	0	0	0	0	0
	Melia azedarach	0	33	0	0	0	0	0	0	0	0
	Gmelina arborea	0	0	0	161	0	0	0	0	0	0
	Mangifera indica	0	0	0	3	0	0	0	0	73	0
	Psidium guajava	0	0	0	19	0	0	0	0	0	0
	Syzygium jambos	0	0	0	28	0	0	0	0	202	0
	Artocarpus altilis	0	0	0	0	0	0	0	0	85	0
	Cocos nucifera	0	0	0	0	0	0	0	0	10	0
	Spathodea campanulata	0	0	0	0	0	0	0	0	10	0
	Terminalia catappa	0	0	0	0	0	0	0	0	10	0

Table presenting the mean density (number of stems per hectare) for all non-native and native (potentially) invasive species encountered in the studied countries (Bolivia, Brazil, Colombia, Costa Rica, French Guiana, Mexico, Panama, Peru, Puerto Rico, Venezuela).

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Extended Data Table 2 | Chronosequence metadata

Country	Chrono sequence	Lat	Long	Secondary forest plots (n)	Old- Growth plots (n)	Age SF (min-max)	Min DBH (cm)	Plot area (ha)	Climate type
Bolivia	BO1	−16.7	−61.9	10	0	5–50	10	0.6	dry
Brazil	BR1	−29.6	−50.2	20	9	6–45	5	0.03	dry/moist
	BR2	−7.0	−35.1	10	12	14–30	5	0.03	dry/moist
	BR3	−20.6	−42.1	8	2	5–80	5	0.09	dry/moist
	BR4	−9.6	−36.8	25	20	5–65	10	0.1	dry/moist
	BR5	−26.0	−48.8	20	0	4–40	5	0.01–0.02	moist
	BR6	−26.6	−53.3	17	0	3–35	5	0.01–0.02	moist
	BR7	−27.6	−48.8	63	0	2–55	5	0.01	moist
	BR8	−26.6	−50.9	38	0	2–50	5	0.01–0.02	dry/moist
	BR9	−27.3	−52.1	20	0	5–60	5	0.01–0.02	dry/moist
	BR10	−2.4	−59.9	13	0	5–31	5	0.03–0.06	moist
	BR11	−2.4	−59.9	15	0	2–25	5	0.01–0.06	moist
	BR12	−5.7	−61.4	26	8	6.5–30	5	0.025–0.1	moist
	BR13	−5.8	−61.4	26	8	5–30	5	0.025–0.1	moist
	BR14	−1.8	−47.9	15	0	2–70	5	0.025	moist
	BR15	−2.3	−47.6	25	12	5–40	5	0.025–0.25	moist
	BR16	−1.4	−48.0	3	0	8–10	5	0.025	moist
	BR17	−14.5	−39.1	27	15	10–40	5	0.06–0.1	moist
	BR18	−4.1	−47.6	15	8	5–25	5	0.025	dry/moist
	BR19	−19.3	−43.6	9	0	4–50	5	0.1	dry
	BR20	−22.4	−47.6	23	5	11–46.5	5	0.09	dry/moist
	BR21	−14.8	−44.0	12	6	12–42	5	0.1	dry
	BR22	−7.1	−37.5	15	0	20–62	5	0.1	dry
	BR23	−15.0	−43.9	6	3	14–27	5	0.1	dry
Colombia	CO1	10.6	−75.2	15	0	3.5–15	5	0.01	dry
	CO2	5.6	−77.5	3	1	3–35	5	0.1	moist
	CO3	8.8	−73.7	18	9	3–40	5	0.02	dry/moist
	CO4	11.2	−73.4	9	0	12.5–45	5	0.1	moist
	CO5	9.9	−75.2	9	0	17.5–35	5	0.1	dry/moist
	CO6	10.2	−73.6	12	4	8–32	5	0.02	dry/moist
	CO7	13.4	−81.4	100	0	6–56	5	0.01	moist
	CO8	−0.6	−72.4	4	1	7–30	5	0.04–0.05	moist
	CO9	5.1	−74.8	12	2	2–27.5	5	0.1	moist
	CO10	6.7	−75.8	10	2	0.5–17.5	5	0.1	dry/moist
	CO11	10.8	−75.1	21	0	5–32.5	5	0.01	dry
	CO12	10.6	−75.2	14	2	3.5–20	5	0.01	dry
Costa Rica	CR1	8.4	−83.3	8	3	10–40	5	0.5	moist
	CR2	8.8	−83.4	5	2	10–40	5	0.5	moist
	CR3	8.7	−83.2	6	0	5.5–55	5	0.05	moist
	CR4	8.7	−83.2	6	0	6–40	5	0.05	moist
	CR5	10.4	−84.1	6	2	10–41	5	1	moist
	CR6	10.4	−84.0	23	7	10–42	5	0.1	moist
	CR7	10.9	−85.6	22	0	5–70	10	0.1	moist
	CR8	10.8	−85.6	40	3	6–70	10	0.1	moist
	CR9	10.4	−85.3	19	0	7–60	10	0.1	moist
French Guyana	FG1	5.3	−53.1	5	0	3.5–28.5	5	0.0808–0.212	moist

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Extended Data Table 2 (continued) | Chronosequence metadata

Country	Chrono sequence	Lat	Long	Secondary forest plots (n)	Old- Growth plots (n)	Age SF (min-max)	Min DBH (cm)	Plot area (ha)	Climate type
Mexico	MX1	19.5	−105.0	8	3	3–15	5	0.1	dry
	MX2	19.3	−88.6	60	22	2–80	5	0.05	dry
	MX3	20.1	−89.5	274	17	3–70	5	0.02–0.04	dry
	MX4	16.7	−95.4	0	7	120–120	5	0.05	dry
	MX5	16.7	−95.1	12	14	7–60	5	0.04–0.05	dry
	MX6	16.1	−91.0	17	3	0–27	5	0.1–0.5	moist
	MX7	19.6	−105.0	46	11	0–42	5	0.05	dry
Panama	PN1	9.1	−79.8	8	2	20–100	5	0.32	moist
	PN2	9.2	−79.8	45	10	2–31	5	0.2	moist
Peru	PE1	−8.5	−74.9	14	0	5–30	5	0.1	moist
Puerto Rico	PR1	18.3	−65.8	12	3	9–76	5	0.1	moist
Venezuela	VZ1	5.5	−67.4	12	3	5–20	5	0.1	moist

Details of the 58 chronosequences analysed, including country codes, coordinates, number of secondary and old-growth plots, age ranges, minimum DBH sampled, plot area, and climate type classification (dry/moist).

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Extended Data Table 3 | Species group definitions

Num.	Group	Definition
1	Non-native non-invasive	Non-native woody species to the country in which it was encountered, with no register of invasiveness anywhere
2	Non-native potentially invasive	Non-native woody species to the country in which it was encountered, with at least one register of invasiveness elsewhere
3	Non-native invasive	Non-native woody species to the country in which it was encountered, with a record of invasiveness in that country
4	Non-native species - NNS	A combination of the three 'Non-native' groups above (groups 1-3)
5	Native potentially invasive	Native woody species in the country in which it was encountered, with at least one register of invasiveness elsewhere
6	Native invasive	Native woody species in the country in which it was encountered, with a record of invasiveness in another region of that country.
7	Native (potentially) Invasive - Combined N(P)IS	A combination of the two 'Native' groups above (groups5-6)

Definitions and criteria used to classify woody species into seven groups: Non-native non-invasive, Non-native potentially invasive, Non-native invasive, the Non-native species (NNS), Native potentially invasive, Native invasive, and the combined Native (Potentially) Invasive species (N(P)IS) group.

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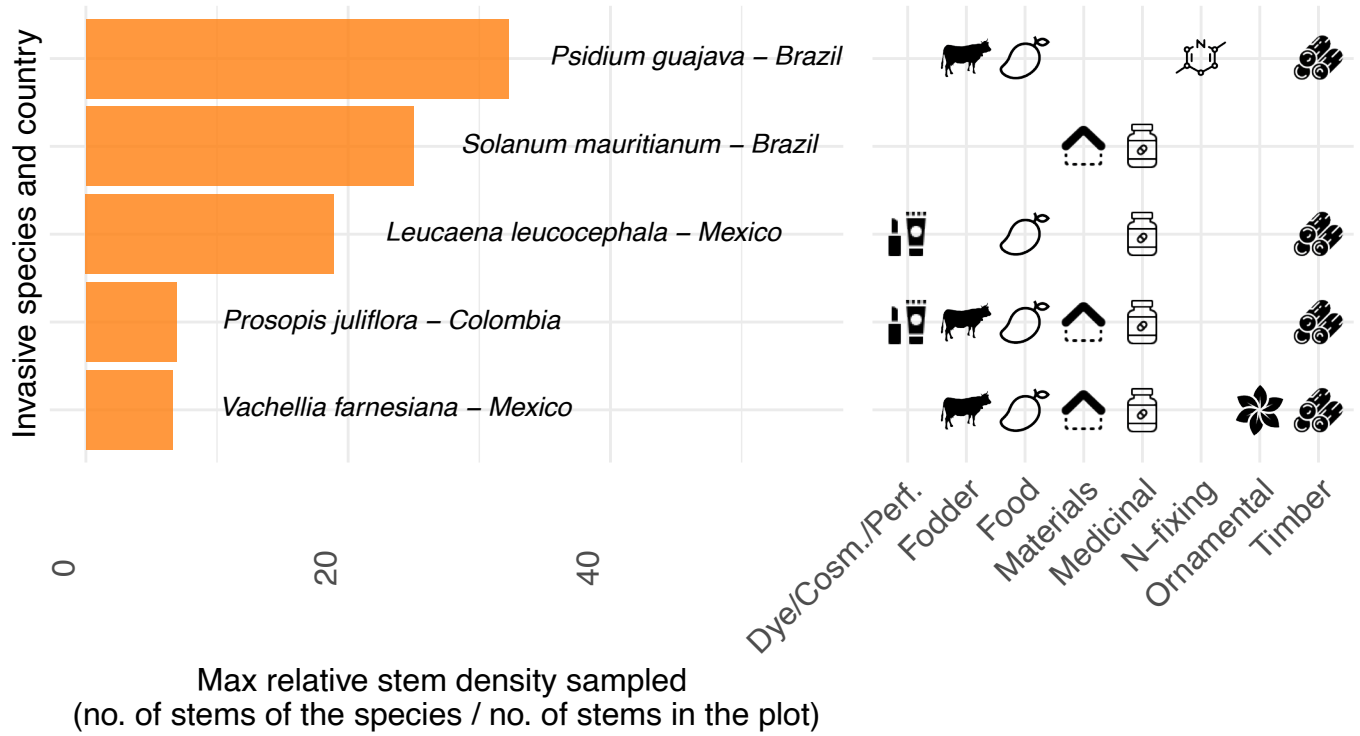
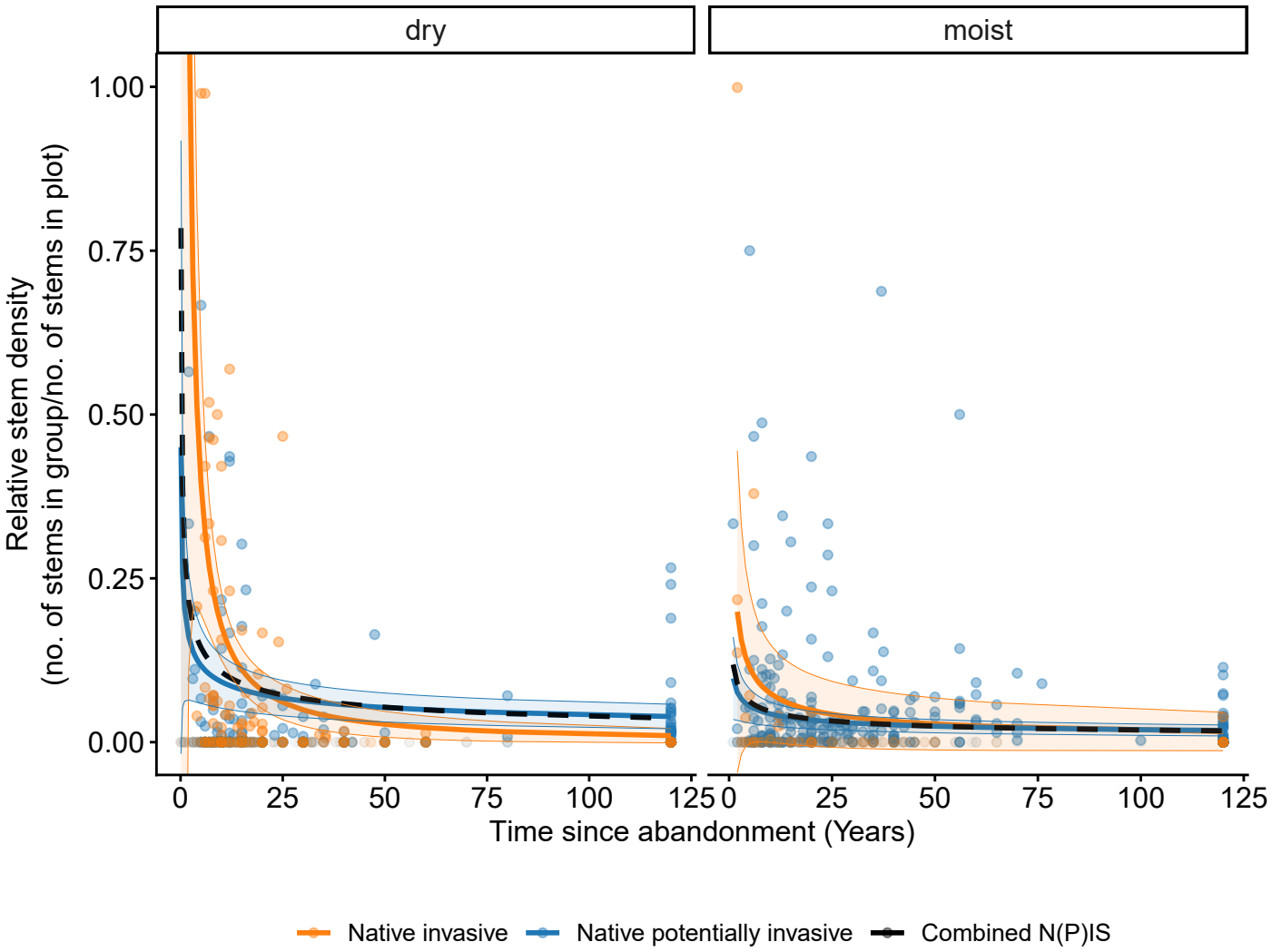


Extended Data Fig. 1 | Native invasive species density and uses. Maximum relative stem density and reported human uses for five native invasive species (including *Psidium guajava, Solanum mauritianum, Leucaena leucocephala, Prosopis juliflora*, and *Vachellia farnesiana*) in their country of occurrence.

https://doi.org/10.1038/s41477-026-02327-3



Extended Data Fig. 2 | Relative stem density of native species. Modelled relationships of relative stem density versus time since abandonment for native invasive species, native potentially invasive species, and the combined group (N(P)IS) in dry and moist forests. Dots represent observed values. Lines represent model predictions (conditional mean), and shaded areas indicate 95% confidence intervals. Colours indicate groups: native invasive (orange), native potentially invasive (blue), and combined N(P)IS (black). Models were fitted using the native-group dataset (n = 1,419; dry = 651, moist = 768).

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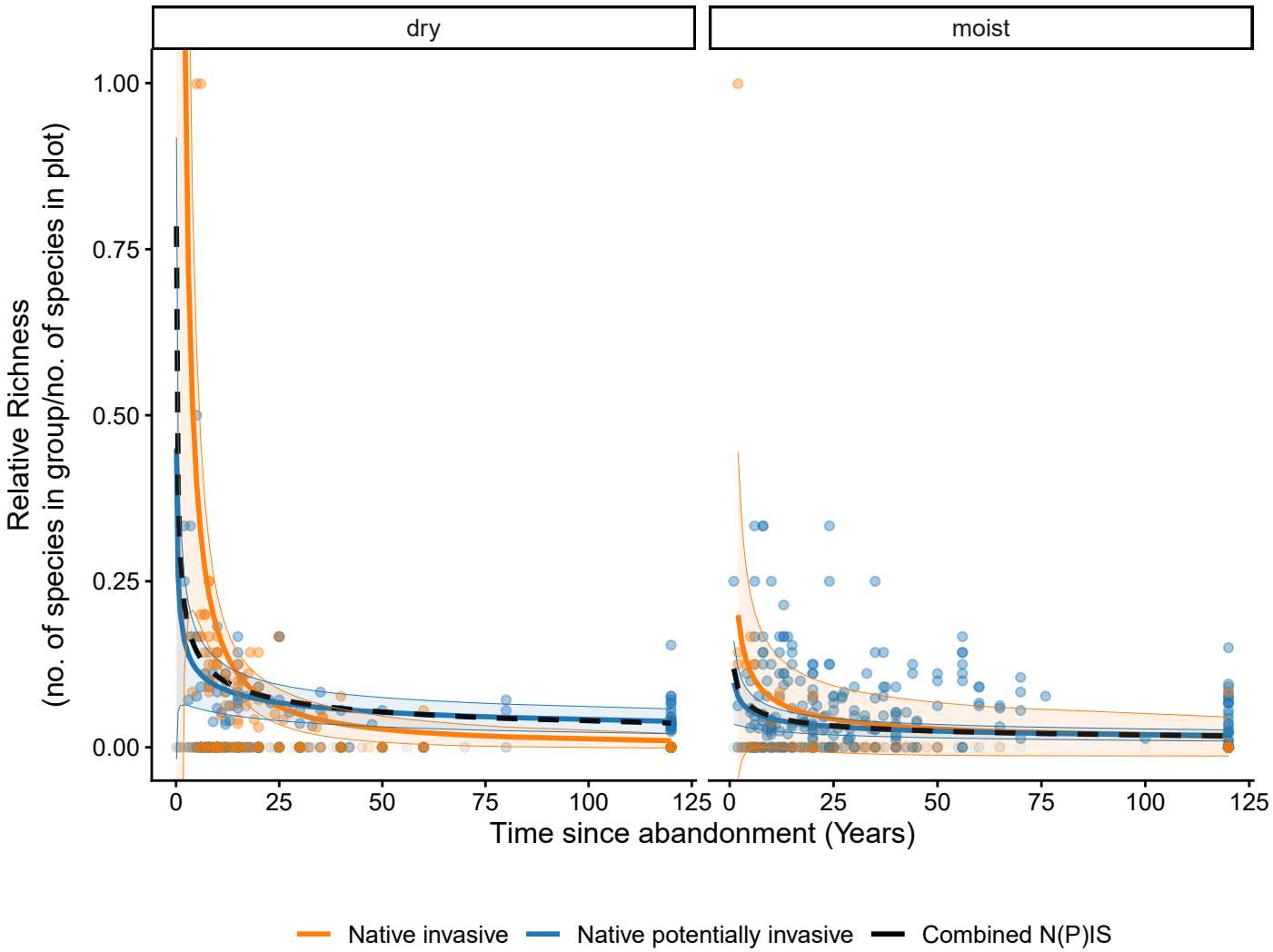
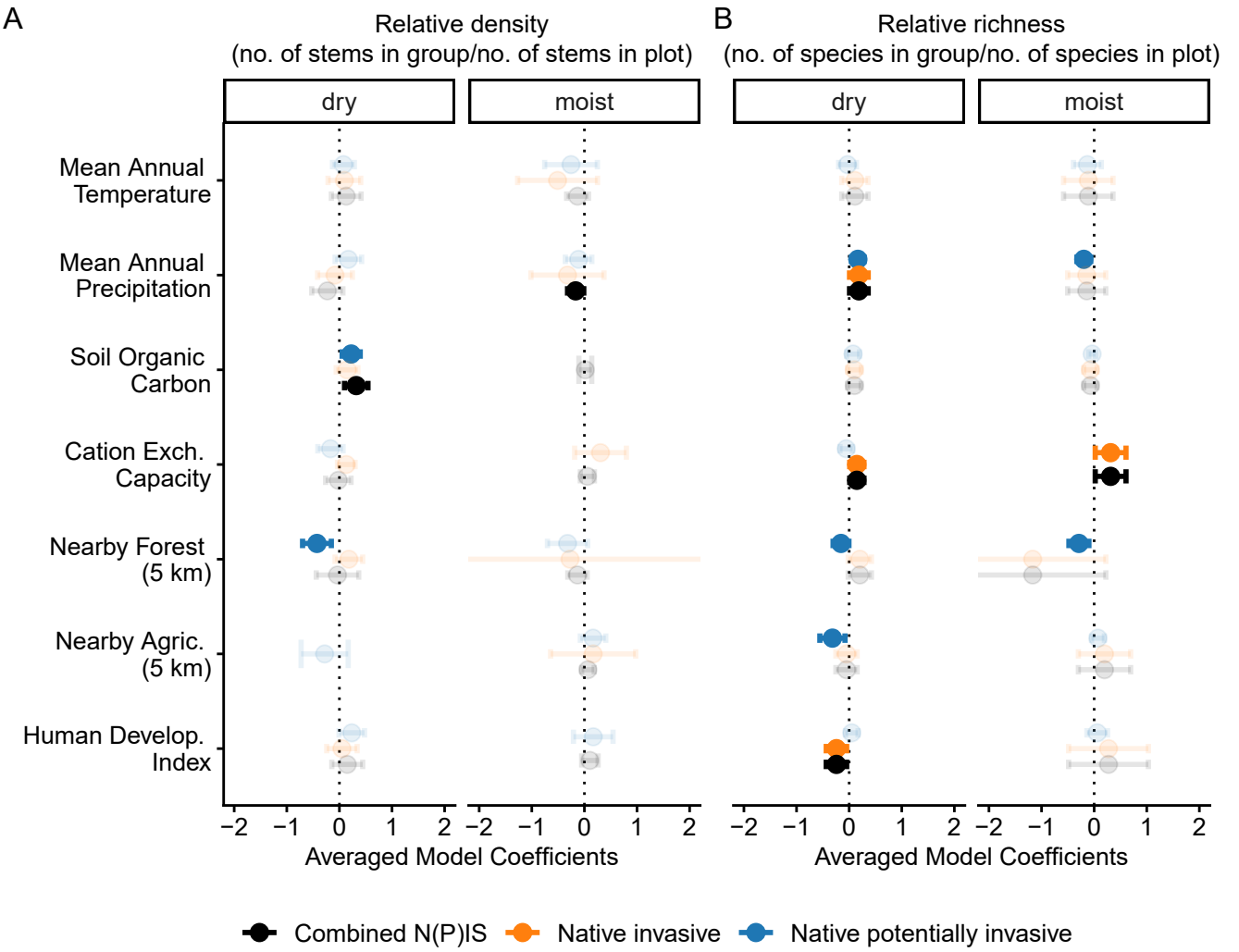


Extended Data Fig. 3 | Relative richness of native species. Modelled relationships of relative richness versus time since abandonment for native invasive species, native potentially invasive species, and the combined group (N(P)IS) in dry and moist forests. Dots represent observed values. Lines represent model predictions (conditional mean), and shaded areas indicate 95% confidence intervals. Colours indicate groups: native invasive (orange), native potentially invasive (blue), and combined N(P)IS (black). Models were fitted using the native-group dataset (n = 1,419; dry = 651, moist = 768).

https://doi.org/10.1038/s41477-026-02327-3



Extended Data Fig. 4 | Drivers of native species. Averaged standardized regression coefficients showing the effects of environmental and social drivers (temperature, precipitation, soil organic carbon, CEC, landscape cover, and HDI) on the relative stem density (a) and richness (b) of native (potentially) invasive species groups. Points represent model estimates, and horizontal lines indicate 95% confidence intervals. Colours indicate groups: combined N(P)IS (black), native invasive (orange), and native potentially invasive (blue). Panels show results for dry (left) and moist (right) forests. Models were fitted using the native-group dataset (n = 1,419; dry = 651, moist = 768).

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Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	The acquisition of spatial variables per plot was conducted using Google Earth Engine (https://eben.users.earthengine.app/view/plots2ndfor). The field data provided by the 2ndFor network were standardised: scientific names and species distribution were updated, and invasiveness classification was performed using the R (version 4.5.2 (2025-10-31 ucrt)) packages TNRS (version 0.3.6), and flora (version 0.3.4), as described and cited in the Methods. All statistical analyses were conducted in R (version 4.5.2 (2025-10-31 ucrt)). The analyses relied on established packages, including glmmTMB (version 1.1.13), DHARMa (version 0.4.7), randomForest (version 4.7-1.2) , and fitdistrplus (version 4.7-1.2). No custom algorithms were developed beyond the standard implementation of these packages.
Data analysis	Custom code used in this study is publicly available in a Zenodo repository (DOI: 10.5281/zenodo.19593673). Details on access and use are provided in the Code Availability statement. Moreover, all analyses were conducted using standard functions from publicly available R packages, as described in the Methods.

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Policy information about availability of data

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- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
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The forest inventory data supporting the findings of this study are available from the 2ndFor network (https://sites.google.com/view/2ndfor/home) upon reasonable request, subject to the network's data-sharing policy. Its use is subject to data ownership restrictions. Restrictions apply to the availability of the present paper data, which were used under license for the current study and so are not publicly available. Metadata regarding the chronosequences and plots used in this study are provided in Extended Data Table 2.
Publicly available datasets were analysed in this study. Taxonomic and invasiveness data are available from the World Checklist of Vascular Plants (https://powo.science.kew.org/), Flora do Brasil (https://floradobrasil.jbrj.gov.br/), the Global Naturalized Alien Flora (GLONAF, https://esajournals.onlinelibrary.wiley.com/doi/full/10.1002/ecy.2542#support-information-section) database, the IUCN SSC Invasive Species Specialist Group list (GISD, http://dx.doi.org/10.3391/mbi.2015.6.2.03) and the CABI Compendium (https://www.cabidigitallibrary.org/). Environmental data are available from CHELSA (https://www.chelsa-climate.org/datasets), SoilGrids (https://www.isric.org/explore/soilgrids), and the Copernicus Global Land Cover (https://land.copernicus.eu/). Socio-economic data (HDI) are available from the Dryad Digital Repository (https://doi.org/10.5061/dryad.dk1j0).

Research involving human participants, their data, or biological material

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Reporting on sex and gender	This information has not been collected.
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Ecological, evolutionary & environmental sciences study design

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Study description	We analysed non-native woody species in 1,561 secondary-forest plots from 58 chronosequences across 10 Neotropical countries. Plots (mostly 0.1 ha) represent a space-for-time chronosequence design covering 1 to >120 years since agricultural abandonment, in dry and moist forests. All woody individuals (DBH ≥5 or 10 cm) were inventoried and classified by origin and invasiveness. Response variables were relative stem density and relative species richness of non-native species. Explanatory factors were forest age, climate, soil properties, surrounding forest and agricultural cover, and Human Development Index. We analysed the data using zero-inflated generalized linear mixed models, with chronosequence as a random effect.
Research sample	We used data from 1561 forest plots and 58 chronosequences from ten Neotropical countries, DBH ≥5 or 10 cm. The plots combined contained 3,735 species, which were classified based on their distribution (native vs. non-native) and degree of invasiveness. The data is intended to represent the neotropical dry and moist forests. Data came from the 2ndFor network (https://sites.google.com/view/2ndfor/home?authuser=0)
Sampling strategy	We used the 2ndFor network database (https://sites.google.com/view/2ndfor/home) on secondary forests. We analysed 58 chronosequences from the tropical Americas and 1561 forest plots. A chronosequence approach provides a long-term perspective on succession (in our case, up to 100 years) by using a space-for-time substitution by comparing secondary forest plots that differ in age since agricultural abandonment. The chronosequence approach assumes that all plots have experienced similar starting conditions and follow the same successional trajectory, which is not necessarily the case. Therefore, during longer successional timeframes,

	within-chronosequence variation in successional trajectories is smaller than between-chronosequence variation. Hence, by using a large dataset across the Neotropics, we can detect such drivers of regional differences in recovery. Nearby mature forest plots are included as natural references for 60% of our chronosequences.
Data collection	Field data were collected by over 50 different research groups across the tropical Americas, all of them are authors in this paper. These combined datasets form the 2ndFor network database (https://sites.google.com/view/2ndfor/home), where information on each contributing group and the specific data collected is detailed. All data were collected using similar methodological approaches, primarily employing field plots distributed in chronosequences and complete floristic identification.
Timing and spatial scale	Data collection occurred synchronously (same year) within individual chronosequences but varied among different chronosequences (The full temporal range is 1994–2018, with peak collection (80% of the total) occurring between 2001 and 2011). This temporal variation is not a concern for our analysis, as the study utilizes the chronosequence approach to represent forest succession, rather than relying on repeated measurements. Spatially, the data comprises collections from 10 Neotropical countries, extending from Mexico to southern Brazil.
Data exclusions	No data were excluded from analysis. Seedlings, saplings, and non-woody plants were not sampled. Only woody individuals above the DBH threshold were sampled/analysed.
Reproducibility	Analyses conducted using documented R workflows (GLMMs with glmmTMB, variable selection, and diagnostics). Data sources and methods are fully described; raw plot data are available from the 2ndFor network upon request.
Randomization	Not relevant. This is an observational study using existing forest plots; no experimental allocation to treatments was performed. Sampling approaches varied among chronosequences and were not controlled in this study. Chronosequence was included as a random effect in the models to account for site-level differences.
Blinding	Not relevant. This is an observational study based on existing forest inventory data. Blinding of data collectors or analysts was not feasible or meaningful because no experimental treatments were applied and outcomes were derived from standardised field measurements and database-based species classification.

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	The data were collected across a wide range of Neotropical climates. The study sites span a mean annual precipitation of 850-6400 mm/year and a mean annual temperature of 14.8-27.7°C. Fieldwork was conducted in both seasonally dry forests and moist forests.
Location	The study encompasses 1,561 forest plots within 58 chronosequences distributed across ten countries: Puerto Rico, Mexico, Costa Rica, Panama, Venezuela, French Guiana, Colombia, Peru, Brazil, and Bolivia. The general locations of the chronosequences are shown in Figure 5 of the manuscript methods.
Access & import/export	Data were compiled from the 2ndFor network, which consists of numerous independent research groups. Each contributing group was responsible for obtaining the necessary local and national permits to access habitats and conduct research in compliance with their respective country's laws. No biological samples were imported or exported for the purpose of this synthesis study.
Disturbance	Any disturbance was limited to that caused by standard, low-impact forest inventory protocols. This typically includes establishing plot boundaries, taking tree measurements, sometimes collecting small branches for herbarium identification, and foot traffic, all of which have minimal and localized effects on the forest ecosystem.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☒	☐ Animals and other organisms
☒	☐ Clinical data
☒	☐ Dual use research of concern
☐	☒ Plants

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Dual use research of concern

Policy information about dual use research of concern

Hazards

Could the accidental, deliberate or reckless misuse of agents or technologies generated in the work, or the application of information presented in the manuscript, pose a threat to:

No	Yes	
☒	☐	Public health
☒	☐	National security
☒	☐	Crops and/or livestock
☒	☐	Ecosystems
☒	☐	Any other significant area

Experiments of concern

Does the work involve any of these experiments of concern:

No	Yes	
☒	☐	Demonstrate how to render a vaccine ineffective
☒	☐	Confer resistance to therapeutically useful antibiotics or antiviral agents
☒	☐	Enhance the virulence of a pathogen or render a nonpathogen virulent
☒	☐	Increase transmissibility of a pathogen
☒	☐	Alter the host range of a pathogen
☒	☐	Enable evasion of diagnostic/detection modalities
☒	☐	Enable the weaponization of a biological agent or toxin
☒	☐	Any other potentially harmful combination of experiments and agents

Plants

Seed stocks	No seed stocks or cultivated plant material were used. Data derive from field inventories of naturally regenerating forest vegetation.
Novel plant genotypes	No novel genotypes were generated or used.
Authentication	Not relevant. Species identification was based on field identification and taxonomic standardization using global plant databases.