



HAL
open science

Native diversity buffers against severity of non-native tree invasions

Camille S Delavaux, Thomas W Crowther, Constantin M Zohner, Niamh M Robmann, Thomas Lauber, Johan van den Hoogen, Sara Kuebbing, Jingjing Liang, Sergio De-Miguel, Gert-Jan Nabuurs, et al.

► **To cite this version:**

Camille S Delavaux, Thomas W Crowther, Constantin M Zohner, Niamh M Robmann, Thomas Lauber, et al.. Native diversity buffers against severity of non-native tree invasions. *Nature*, 2023, 10.1038/s41586-023-06440-7 . hal-04188507

HAL Id: hal-04188507

<https://hal.science/hal-04188507>

Submitted on 25 Aug 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Native diversity buffers against severity of non-native tree invasions


<https://doi.org/10.1038/s41586-023-06440-7>

Received: 2 November 2022

Accepted: 14 July 2023

Published online: 23 August 2023

Open access

 Check for updates

Determining the drivers of non-native plant invasions is critical for managing native ecosystems and limiting the spread of invasive species^{1,2}. Tree invasions in particular have been relatively overlooked, even though they have the potential to transform ecosystems and economies^{3,4}. Here, leveraging global tree databases^{5–7}, we explore how the phylogenetic and functional diversity of native tree communities, human pressure and the environment influence the establishment of non-native tree species and the subsequent invasion severity. We find that anthropogenic factors are key to predicting whether a location is invaded, but that invasion severity is underpinned by native diversity, with higher diversity predicting lower invasion severity. Temperature and precipitation emerge as strong predictors of invasion strategy, with non-native species invading successfully when they are similar to the native community in cold or dry extremes. Yet, despite the influence of these ecological forces in determining invasion strategy, we find evidence that these patterns can be obscured by human activity, with lower ecological signal in areas with higher proximity to shipping ports. Our global perspective of non-native tree invasion highlights that human drivers influence non-native tree presence, and that native phylogenetic and functional diversity have a critical role in the establishment and spread of subsequent invasions.

Plant invasions have multifaceted impacts on ecosystems and human wellbeing across the globe^{1–3,8}. It is expected that plant invasions will continue to increase in the coming decades owing to human-assisted introduction and naturalization of these species, with ever-growing impacts on biodiversity within native forest ecosystems^{1,9,10}. These invasions will undoubtedly also have considerable economic impacts in managed landscapes by disrupting timber production, agriculture and human livelihoods^{11–17}. In particular, non-native trees represent an important and increasing concern globally, as they are often actively planted far outside their native ranges for forestry, reforestation, residential, or ornamental purposes^{4,18}. Along with the passive spread of non-native species, the active propagation of trees by humans can often result in an increased potential to become problematic invaders^{4,19–21}. Given the prominent roles of trees in shaping the structure and functioning of ecosystems, such tree invasions have the capacity to alter plant composition, productivity, biodiversity and the services provided to humans^{1,4,22}. Previous research in invasion ecology has expanded our understanding of community-level properties that influence ecosystem susceptibility to invasion^{23–25}, as well as traits that make plant species more likely to become invasive^{26–30}. However, most work has been restricted to local and regional scales^{31,32}, with contrasting ecological mechanisms affecting invasion success in different regions. We thus lack a global unified theory of the human and ecological drivers of tree species invasions³³. Developing an integrated global understanding of ecological and anthropogenic forces that drive non-native tree invasions is critical to improve decision making in conservation and management.

Countless ecological mechanisms have been proposed to explain the susceptibility of different ecosystems to invasion by non-native species in different locations. Traditionally, more diverse or ecologically complex systems are thought to exhibit ‘biotic resistance’ to invasion^{23,34–39}.

This hypothesis is based on the assumption that greater diversity in the native community fills the available ecological niches and reduces available resources, limiting niche space to novel species. However, most work has focused on testing this hypothesis using species richness as an indicator of niche filling^{23,35}, which may not fully capture the proportion of niches that are filled in the native community. Instead, more informative metrics for niche filling may be phylogenetic or functional diversity. Phylogenetic diversity accounts for evolutionary similarity and represents a reasonable proxy for similarity between taxa, whereas functional diversity directly addresses the underlying mechanism of biotic resistance (that is, the breadth of ecological niches filled), but may be more difficult to measure. Conversely, there is also evidence for the opposite pattern in some ecosystems, whereby a more diverse community is indicative of a more favourable habitat, where a wide range of invasive species might survive. This ‘biotic acceptance’^{25,40,41} hypothesis leads to the expectation that highly diverse sites are optimal for many plant species and could promote invasion of non-native species. Nonetheless, we still lack a unified understanding of the relative importance of these two competing processes, and their variation across the globe, leading to ongoing calls to resolve this ‘invasion paradox’²⁵.

Invasion success is also likely to depend on the ecological strategy of the invading species relative to the recipient native community. One school of thought is that environmental constraints are the primary drivers of plant species distributions. Therefore, to be successful, invasive species ought to be similar to native species that are adapted for that region, especially in extreme environments⁴². Under this ‘environmental filtering hypothesis’^{43,44} (or ‘preadaptation hypothesis’), invasive species will be more successful if their traits mirror those of the native community⁴⁵. For example, to be successful in a harsh desert environment, non-native plants would need to be ecologically similar

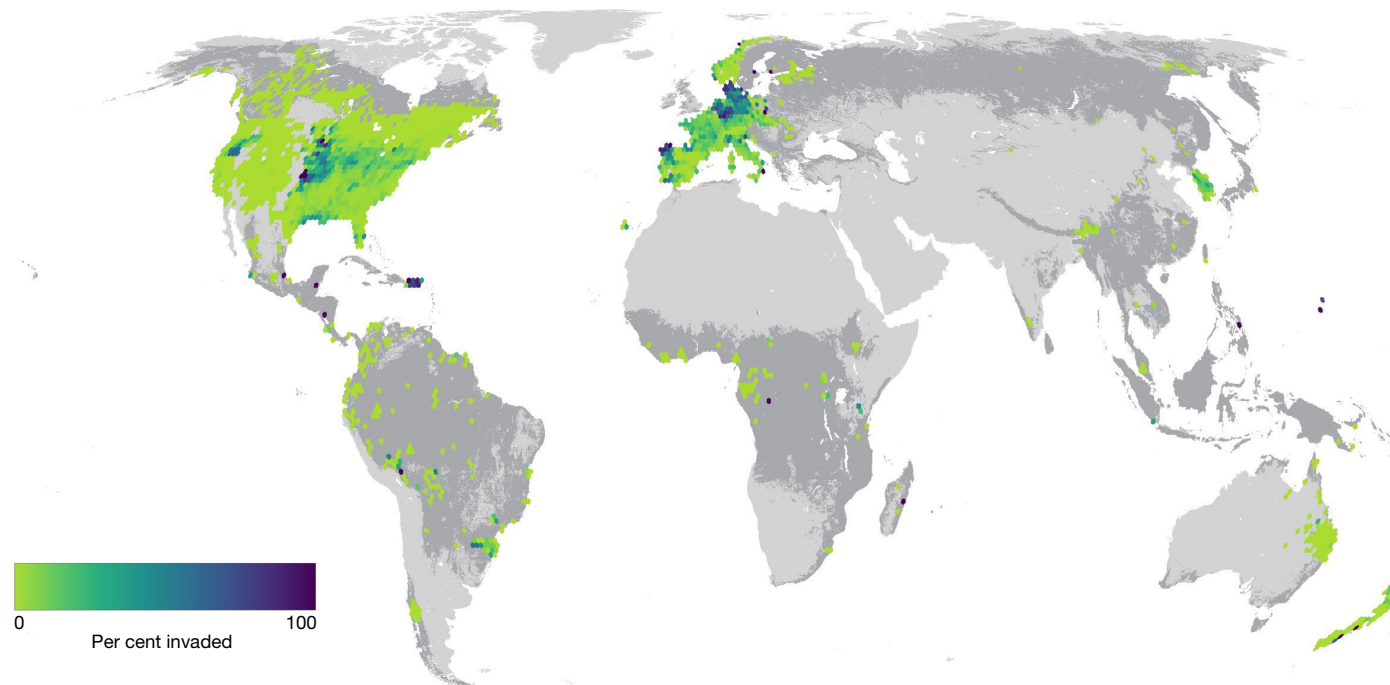


Fig. 1 | Distribution of the study data. Distribution of the full study dataset, coded for non-native severity ($n = 471,888$ plots). The map shows average per cent invasion across a 1-degree hexagonal grid, from non-invaded (0%) pixels

in green to completely invaded (100%) pixels in purple. Plots are considered invaded if there is any non-native tree present.

to native plants to survive, possessing traits that protect them against high heat and water loss. By contrast, the 'limiting similarity hypothesis' (also known as 'Darwin's naturalization hypothesis') postulates that invasive species need to be ecologically distinct from native species to avoid niche overlap^{46–49}. Here, invaders are thought to be more successful if they can fill unique niche spaces that are not already used by the native community, reducing competition and enabling their establishment. These two processes suggest contrasting mechanisms for how species invade: either species invade by being similar or dissimilar to the native community (Darwin's naturalization conundrum^{24,50}). It is possible that the relative importance of these opposing ecological mechanisms varies under different environmental conditions, with greater importance of environmental filtering in harsh conditions and greater niche differentiation in more moderate environments^{51,52}. Such regional variation in the relative importance of these mechanisms might help to explain the opposing responses observed across studies. However, until now, we lack a broad-scale analysis of these different invasion mechanisms that can help us to see past the idiosyncrasy of local-scale observations to identify unifying trends.

A key challenge hindering a global consensus of the ecological patterns and mechanisms underpinning plant invasion is that these processes are likely strongly influenced by anthropogenic activity, which may dampen the signal of ecological drivers. Humans drive contemporary plant invasions through highly efficient transport—both intentional and accidental—of non-native plants, with proximity to ports and airports being associated with increased invasion^{11,53,54}. A constant influx of non-native species may override a native community's ability to resist invasion⁵⁵ (biotic resistance) and obscure the impacts and importance of specific ecological drivers, such as native diversity, particularly at early stages of invasion. That is, with increased propagule pressure of non-natives species exerted by humans, the relative importance of ecological drivers may be reduced. Moreover, sites with high levels of non-native propagule pressure due to human activity are also likely to be heavily disturbed, compounding this anthropogenic influence. Accounting for human global change drivers may be particularly important when considering the role of invasion strategy, with the potential for

anthropogenic drivers and human propagule pressure to overwhelm the impact of ecological drivers. This could occur through an increase in the frequency and magnitude of introductions, which would be expected to increase stochastic variation and dampen ecological signals. So far, these hypotheses have been tested only at local and regional scales, with few studies integrating ecological and anthropogenic drivers of invasion at the global scale to disentangle the relative importance of human activity, environmental conditions and biological diversity³³.

Here, by combining global datasets of local-scale forest inventories, native status, environmental climate variables and anthropogenic drivers, we test for the relative importance of ecological and anthropogenic influence on non-native tree invasion. Using this large-scale approach, we search for a unifying perspective of the environmental and anthropogenic contexts driving non-native invasion and invasion severity, via both relative richness and abundance of non-natives, as well as invasion strategy. We consider three hypotheses: (H1) greater native diversity reduces non-native invasion²³; (H2) high levels of environmental filtering in extreme environmental conditions leads to similarity of non-natives with the surrounding natives, and moderate conditions are associated with greater levels of niche differentiation and dissimilarity²⁴; and (H3) human drivers, specifically proximity to ports and areas of high human population density, will mediate and potentially override these ecological relationships⁵⁶. We explore these hypotheses through the lens of different biodiversity metrics (phylogenetic diversity, functional diversity and species richness), providing a comprehensive view of the interactions between ecological processes and human influence on invasion. Addressing these hypotheses is important to highlight generalizations in the field for prevention and management of non-native tree invasions, which is key to mitigating the potential severe ecological and socio-economic toll of these invasions.

Using the Global Forest Biodiversity Initiative database⁷, we determined native tree status (native or non-native) according to the Global Naturalized Alien Flora⁶ and the KEW Plants of the World databases⁵. This dataset encompassed 471,888 plots, of which 4.9% of plots were invaded, or contained at least one non-native tree species (Fig. 1 and Supplementary Table 1a). Moreover, this dataset contained a larger

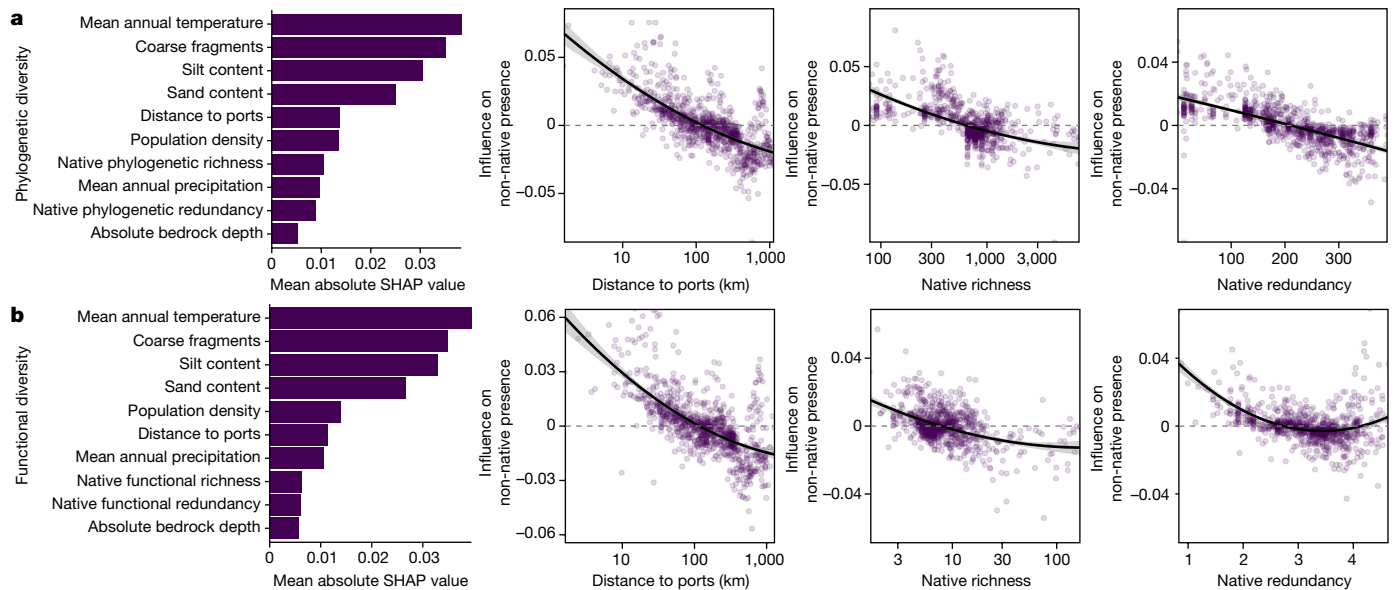


Fig. 2 | Anthropogenic drivers are more important than native diversity in determining invasion occurrence. **a, b**, Importance (Shapley additive explanations (SHAP) values) of all variables included in random forest models ordered from greatest to least important, alongside influence of distance to ports, native richness and native redundancy on non-native presence (whether a plot is invaded or not) for global models of phylogenetic (**a**) and functional

(**b**) diversity (phylogenetic diversity, $n = 17,640$ plots; functional diversity, $n = 17,271$ plots). All results shown are from random forest models. Note that y-axis ranges differ among panels, with the variable importance plots representing the corresponding magnitude. Error bands represent 95% confidence intervals.

proportion of invaded plots in tropical (15.2%) than in temperate systems (5.2%). Overall, 249 individual non-native tree species were identified, with the most frequent being *Robinia pseudoacacia*, *Pinus sylvestris*, *Maclura pomifera*, *Picea abies* and *Ailanthus altissima* labelled as non-native in 3,976, 2,603, 2,493, 2,468 and 1,597 plots, respectively (Supplementary Table 2). Regions with the greatest likelihood of being invaded include North America, Europe and East Asia (Extended Data Fig. 1), consistent with previous findings^{10,57} (but see ref. 58). To test for drivers of non-native tree invasion and invasion strategy, we used a down-sampled version of the dataset consisting of 17,738 forest plots, distributed across 14 biomes proportional to their global land cover.

We calculated three metrics of invasion: (1) presence of non-natives in the plot ('non-native presence'); (2) relative proportion of non-native species richness to total tree richness ('non-native richness'); and (3) relative proportion of non-native species basal area to total tree basal area ('non-native abundance'). The first metric (non-native presence) is simply a measure of the presence or absence of invasion, whereas the latter two metrics (relative abundance and richness) provide insight into the subsequent severity of the invasion.

To test how hypothesized human and environmental drivers affected the probability a forest plot was invaded or the invasion severity within invaded plots, we built generalized linear models (GLMs) and random forest models using either phylogenetic or functional diversity metrics (both as richness and redundancy) as predictor variables (Extended Data Fig. 3). For both functional and phylogenetic diversity, we used random forest models to determine variable importance and for visualization purposes, whereas GLMs were used to test for significance and directionality of relationships. Our models also included human drivers (distance to shipping ports (hereafter referred to as ports) and population density) and accounted for several additional soil chemical and climate variables. Next, to test whether non-native tree species invade by being similar or dissimilar to the native community (termed 'invasion strategy'), we again built models predicting non-native similarity from either native phylogenetic or functional diversity metrics, along with the same environmental and human impact variables. The non-native

invasion strategy was defined as the change in redundancy due to addition of non-native trees, with values below zero and values above zero indicating invasion via similarity and dissimilarity, respectively, to the native community.

Diversity limits invasion severity

We found that anthropogenic drivers were more important than local native tree diversity in determining non-native invasion (presence) globally (H3), whereas native diversity—both phylogenetic and functional—was most important in determining invasion severity (H1; Fig. 2 and Supplementary Tables 3 and 4; phylogenetic diversity random forest area under the curve (AUC) = 0.634, functional diversity random forest AUC = 0.631). These results indicate the importance of human-induced propagule pressure in initiating invasion of forests and of native biodiversity moderating the severity of the invasion. We found that forest plots closer to ports are more likely to be invaded (Supplementary Tables 3 and 4; linear model $P < 0.001$). Notably, these results are consistent whether we analyse all data together at the global level or separate data into either the temperate and tropical bioclimatic zones (Supplementary Tables 3 and 4). By contrast, we did not find that human population density was consistently related to non-native presence, with results being variable across diversity metrics and bioclimatic zones considered (Supplementary Tables 3 and 4). However, population density was always positively correlated with invasion probability; population density may be a weaker predictor as it only measures human presence, which is not necessarily related to propagule pressure.

Proximity to ports has long been known to influence invasion^{11,53,54}, with locations closer to a port being likely to experience greater propagule pressure. Moreover, proximity to ports may serve as a proxy for residence time, where plots closer to ports are more likely to have longer exposure to non-native propagule pressure, thus increasing the likelihood of invasion⁵⁶. Yet, at far enough distances, stochastic processes and historical land-use patterns may begin to weaken the role of ports (Fig. 3, distances greater than 500 km). For example, the third most frequent non-native tree in our dataset, *M. pomifera*, is widely naturalized throughout the

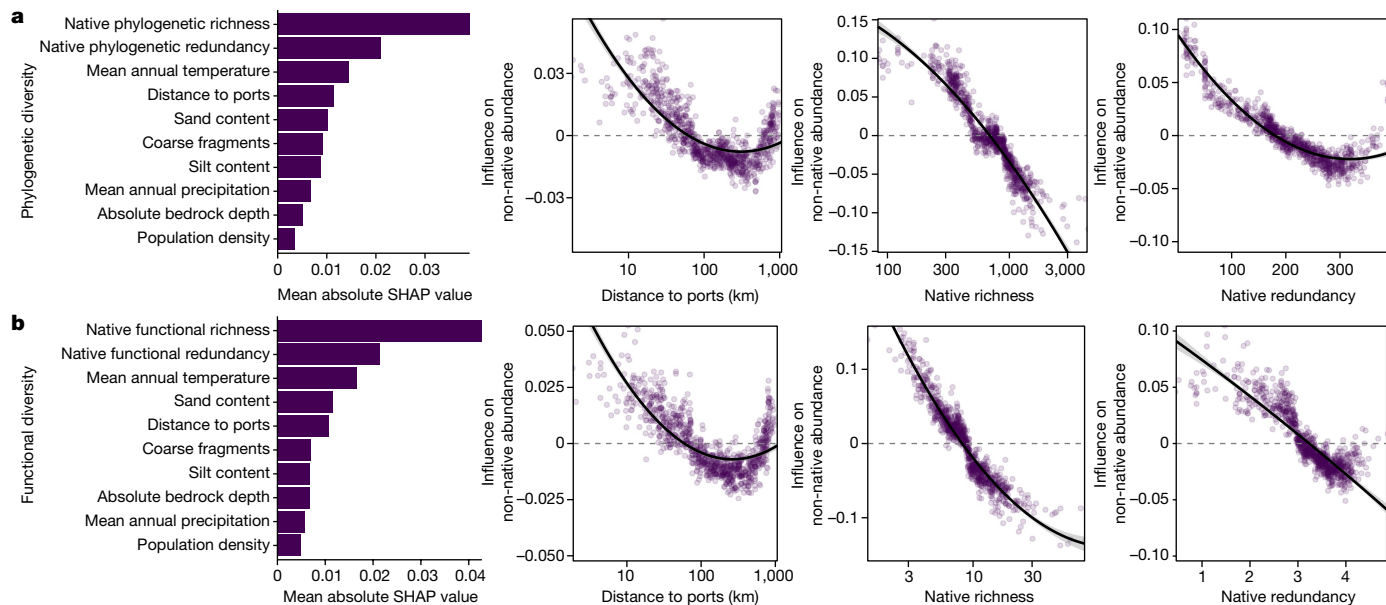


Fig. 3 | Native diversity is the most important driver of invasion severity. **a, b**, Importance (Shapley additive explanations (SHAP) values) of all variables included in random forest models ordered from greatest to least important, alongside influence of distance to ports, native richness and native redundancy on invasion severity for global models of phylogenetic (**a**) and functional (**b**) diversity (phylogenetic diversity, $n = 3,498$ plots; functional diversity, $n = 3,368$ plots). Plots are shown for the severity of invasion measured as

non-native species abundance (proportion of basal area with non-native plant species); plots for non-native species richness (proportion of non-native plant species) are shown in Extended Data Fig. 4. All results shown are from random forest models. Note that the y-axis ranges differ among panels, with the variable importance plots representing the corresponding magnitude. Error bands represent 95% confidence intervals.

interior of North America, where it has been used for various agricultural purposes dating back to the 1850s⁵⁹. Such results highlight the idiosyncratic use of trees across the globe, leading to unique invasion trends relative to herbaceous plants. Nevertheless, at more local scales, this strong signal of anthropogenic activity and associated propagule pressure relative to native diversity driving non-native presence is in agreement with previous work that considers invasion across stages⁵⁶ and recent assessments of regional and global tree invasion^{57,60}, and highlights the prominent role of humans in reshaping biological communities.

Although proximity to ports determined the probability a forest plot was invaded, native tree communities with higher phylogenetic and functional diversity exhibited lower invasion severity (Fig. 3, Extended Data Fig. 4 and Supplementary Tables 3 and 4; phylogenetic diversity random forest non-native richness $R^2 = 0.68$, phylogenetic diversity random forest non-native abundance $R^2 = 0.14$, functional diversity random forest non-native richness $R^2 = 0.69$ and functional diversity random forest non-native abundance $R^2 = 0.07$; GLM phylogenetic and functional diversity $P < 0.001$). Additionally, distance to ports was no longer significant in linear models predicting invasion severity (Supplementary Tables 3 and 4) for both phylogenetic ($P = 0.16$ and 0.28 for non-native richness and abundance, respectively) and functional diversity models ($P = 0.63$ and 0.86 for non-native richness and abundance, respectively), and showed reduced variable importance in the random forest models (Fig. 3 and Extended Data Fig. 4). When investigating these patterns using conventionally analysed species richness instead of phylogenetic or functional richness, we find similar qualitative results (Supplementary Table 5, random forest non-native richness $R^2 = 0.71$ and random forest non-native abundance $R^2 = 0.14$), suggesting that species diversity may be a useful proxy for projecting invasion severity in the absence of functional and phylogenetic information. Our results are consistent with the hypothesis of biotic resistance (H1), where increased native diversity reduces invasion success, which is probably driven by the native community utilizing more available niche spaces^{23,34–36,61}. These results are also consistent with work

investigating tree migration drivers that suggests that migration is slower into more diverse communities owing to greater resource use (fewer available niches) in these systems⁵⁷.

Overall, these results show that anthropogenic drivers, particularly distance to shipping centres (ports), are more important in determining which locations will experience non-native invasions compared with traditionally studied native diversity (H3). However, it is the intrinsic ecological drivers, including native tree community phylogenetic and functional diversity (richness and redundancy), that are more important in determining invasion severity (H1). Repeated human introduction of plant species has a more important role in the initial invasion process, but invasion severity is predominantly a result of native intrinsic diversity. Notably, both distance to ports and native diversity show patterns of saturation of effects, suggesting a threshold at which plots that are far enough from ports, or high enough in native diversity, will not benefit from further distance or diversity with regard to reduced invasion or invasion severity. Although our focus here is on the relative importance of human versus biotic drivers of introduction, we find that environmental variables—especially mean annual temperature—correlate strongly with patterns of non-native invasion, which may reflect resource availability²⁶, belowground microorganism composition³⁰ or potential climate compatibility between donor and recipient ranges⁶². Together, our results suggest that locations near human activity are more likely to experience non-native invasions in part due to increased propagule pressure, whereas those with lower diversity are more likely to experience more severe non-native invasions once non-natives are present. These results may suggest that managing forests to maintain high native tree diversity may be a good strategy to buffer communities against invasion, particularly for locations that are far from human activity.

Evidence for environmental filtering

When considering a range of climate, soil and anthropogenic variables, we find evidence for environmental filtering as a driver of invasion

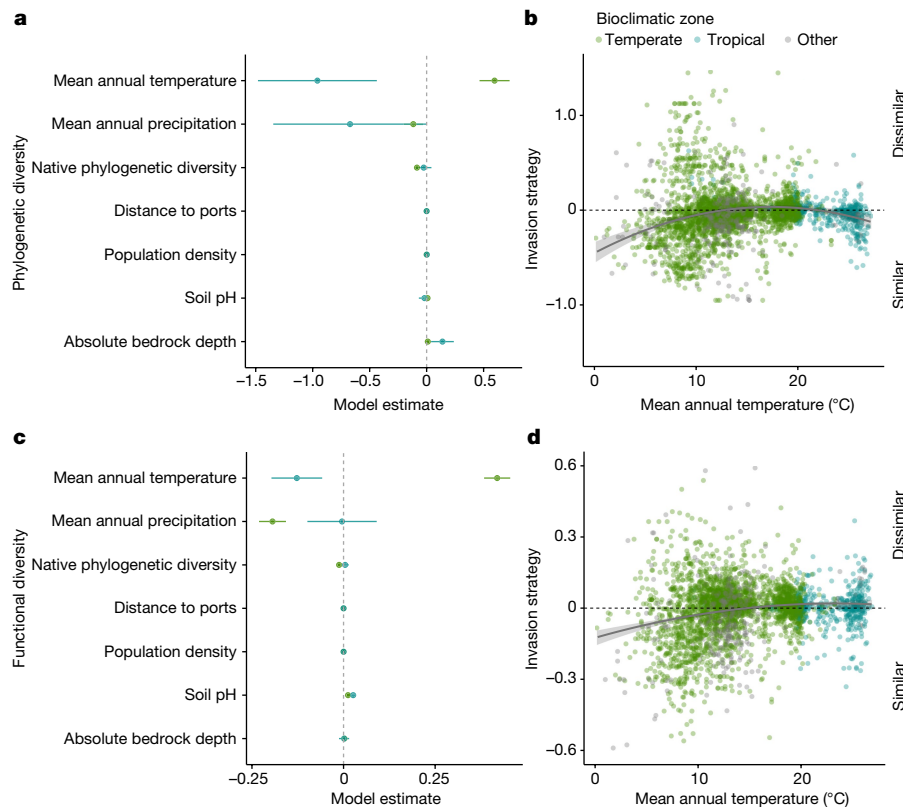


Fig. 4 | Environmental filtering at temperature extremes. a, c. Estimates of overlapping variables included in temperate and tropical GLM models (forest plot) for phylogenetic (a) and functional (c) diversity models (phylogenetic diversity, $n = 3,498$; functional diversity, $n = 3,368$). Values to the left of the zero line indicate negative model estimates, and those to the right indicate positive estimates. **b, d.** Relationship between mean annual temperature and invasion strategy for phylogenetic (b) and functional (d) diversity models, showing that

at extreme temperatures invasion occurs through similarity (Supplementary Table 7; phylogenetic diversity: $P_{(1)} = 9.69 \times 10^{-14}$, $P_{(2)} = 2.13 \times 10^{-11}$; functional diversity: $P_{(1)} < 2 \times 10^{-16}$, $P_{(2)} = 1.07 \times 10^{-4}$, where $P_{(1)}$ and $P_{(2)}$ represent each temperature and temperature squared P values, respectively). Note for functional diversity, this pattern only holds at low temperatures. Error bars and bands represent standard error.

strategy, in particular, with respect to mean annual temperature and precipitation. In all global models, temperature was important for predicting tree invasion strategy (Fig. 4, Extended Data Fig. 5 and Supplementary Table 6; phylogenetic diversity random forest $R^2 = 0.084$, functional diversity random forest $R^2 = 0.099$; H2), with our global analysis indicating that non-native trees were more similar to the native community in environments at cold and hot temperature extremes (Fig. 5 and Supplementary Table 6, $P < 0.001$). That is, in order to invade into a cold or hot environment, non-native plants are more successful if they share similar traits with native plants to survive in these harsher temperature conditions. By contrast, at locations with moderate temperatures, non-natives are neither more nor less similar to native communities, potentially because these less harsh environmental conditions allow a wider range of life strategies to coexist⁵¹. For functional diversity, invasion strategy at high temperatures is relatively neutral, with the line approaching a value of zero, suggesting that although phylogenetically similar, these communities show some level of functional divergence, highlighting the importance of including functional diversity in future studies. When separating the data into temperate and tropical systems, we found divergent temperature patterns (Supplementary Table 6; temperate $P < 0.001$, tropical $P = 0.01$). In temperate systems, non-native trees were more likely to be similar to the native tree community in colder environments relative to hot environments, in line with previous results in temperate North America⁶³. In tropical systems, we found the opposite pattern, with non-native trees being more likely to be similar to the native tree community in hotter tropical environments. At the lowest temperatures, non-natives invading through similarity were primarily gymnosperms (fir, spruce and pine species) invading into native

communities containing species in the same genus; by contrast, at the highest temperatures, non-natives invading through similarity were angiosperms, with a high prevalence of palms and legumes. Further, we detect a similar pattern of environmental filtering for mean annual precipitation when analysing phylogenetic and functional diversity with random forest models, where lower or higher precipitation is associated with non-native invasion through similarity (Extended Data Fig. 5). This suggests that the most likely invaders at low or high temperature or precipitation may be ecologically similar to the host communities, which could inform invasion risk checklists at ports.

Within the temperate bioclimatic zone, we found evidence that anthropogenic activity weakened the environmental filtering pattern for phylogenetic and functional diversity seen for temperature and precipitation, respectively (H3). In particular, proximity to ports modified the signal of environmental filtering due to temperature, weakening the influence of temperature on invasion strategy with respect to phylogenetic similarity (Fig. 5 and Supplementary Table 6; $P < 0.001$). Colder ecosystems show evidence of environmental filtering of invasion; however, increased proximity to ports reduces the prevalence of this strategy. We suggest that this may be due to increased introductions around shipping ports, which would increase stochastic variation and dampen ecological strategies. However, we did not detect a similar interaction governing the tropical bioclimatic zone, potentially owing to relatively lower human pressure, and particularly lower ship traffic⁶⁴, compared to temperate systems. Alternatively, this pattern may also reflect the fact that some temperate plots occur at greater distances to ports than tropical sites (95th percentile of 784 km versus 311 km for temperate and tropical, respectively), increasing statistical power for detecting this trend in

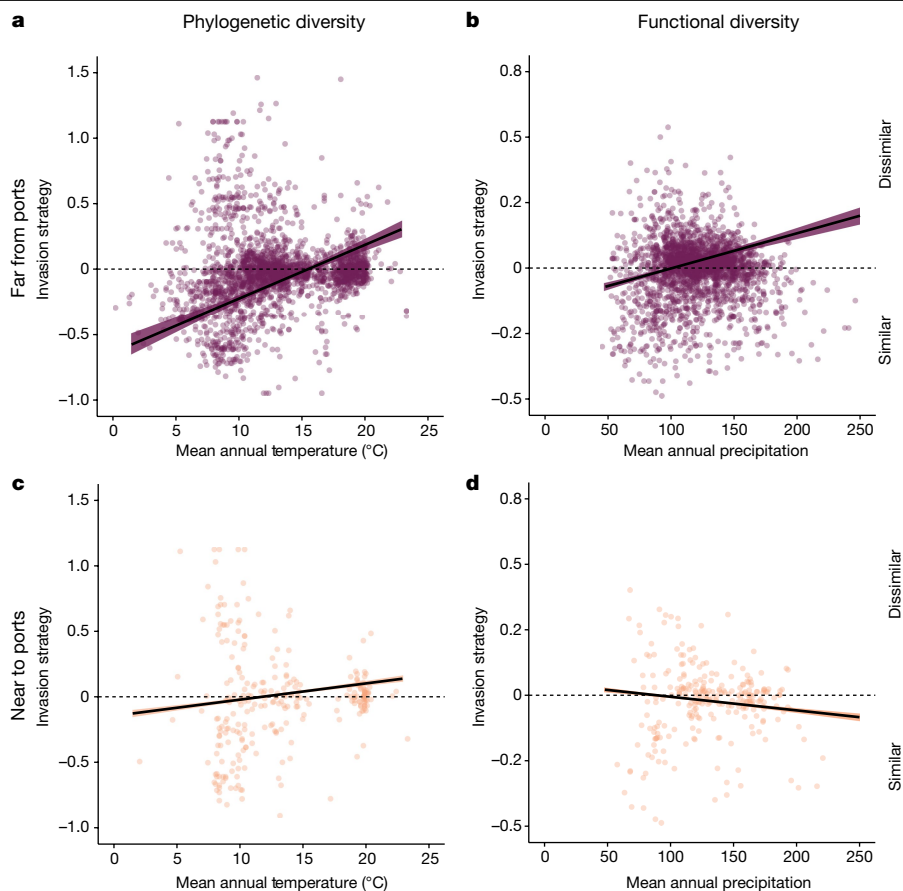


Fig. 5 | Proximity to ports weakens environmental filtering in the temperate bioclimate zone. **a,b**, In temperate plots far from ports, temperature is positively correlated with an invasion strategy of increasing dissimilarity for phylogenetic (**a**) and functional (**b**) diversity (phylogenetic diversity: $n = 2,710$ plots, $P = 6.37 \times 10^{-6}$; functional diversity: $n = 2,603$, $P < 2 \times 10^{-16}$). **c,d**, This

relationship between temperature and invasion strategy weakens for phylogenetic (**c**) and functional (**d**) diversity with proximity to ports (Supplementary Table 7; phylogenetic diversity: $P = 0.0001$; functional diversity: $P = 2.71 \times 10^{-13}$). Lines and points represent the lowest (**c,d**) and highest (**a,b**) 10% of data. Error bands represent standard error.

temperate regions. Furthermore, proximity to ports also marginally weakened the signal of environmental filtering due to precipitation for functional invasion strategy (Supplementary Table 6; $P = 0.07$). These results illustrate that human influence can override the ecological factors driving invasion, suggesting that at high enough propagule pressure, the phylogenetic and functional similarity of a non-native becomes less important in predicting its ability to invade a native community. Nevertheless, as our analyses are not causal, these results could also reflect correlations between port locations and invasion strategy. However, when we investigated the same effect with human population density, we did not see this weakening effect, demonstrating that distance to ports seems to be a particularly relevant mediator of these patterns. These results suggest that human activity may overwhelm ecological drivers of non-native invasion strategies and reduce the influence of ecological processes, making inclusion of human impacts critical for studying global invasion strategies.

Collectively, our work integrates biotic and anthropogenic factors across phylogenetic and functional diversity for both invasion presence and invasion severity of non-native tree species worldwide. Although non-native trees have been relatively overlooked relative to herbaceous plants, their large size, long lifespans and important history in forestry, food, reforestation and city landscaping exposes trees to unique ecological and anthropogenic factors that shape their worldwide distributions. Moreover, given that many tree invasions are in their infancy, with substantial ‘invasion debts’ of recent tree plantings³, understanding the ecological drivers promoting spread has the potential to provide real-time feedback for

the preventative management of invasive trees. However, there are important considerations when interpreting these findings, many of which could be addressed with increased data resolution and increased sampling within under-sampled geographic regions. First, our analysis is largely observational, whereas community composition would ideally be compared before and after invasion to better understand the causality of the trends observed here. We can gain some insight into this question by conducting a sensitivity analysis on the subset of invaded plots that were measured at multiple time points and that had no initial invasion. Doing so reveals that the reduction in native diversity due to invasion can potentially account for as much as 10.4% (mean of 6.7%) of the observed biotic resistance (Supplementary Table 9), but that the remainder of this effect is attributable to difference in native diversity (that is, biotic resistance) across plots. Additional long-term data on plots that are uninvaded and become invaded will be useful in further addressing the influence of invasion on native diversity. Second, many tree species in our analysis were only identified to genus level or were not present in the master plant phylogeny, which may lead to an underestimation of native diversity or invasive species richness in some plots, particularly in species-rich forests. Indeed, a key challenge in global analyses such as ours is the underrepresentation of certain ecosystems, for example, tropical ecosystems⁵⁸. This is addressed to some extent by our down-sampling approach, as well as our spatial cross-validation approach (Methods), but ongoing efforts to fund and develop open-access and fair⁶⁵ tropical forest inventory data are critical for gaining better insight into these ecologically and socially important ecosystems.

Many tree species are intentionally introduced for forestry or wood products and may be managed⁴, generating variation in the drivers underpinning invasion that are unique to trees. To minimize the influence of heavily managed forests, we included only plots with a minimum of three species and thus our dataset does not include monoculture forestry plantations. In addition, when restricting our analysis to the subset of global plots that occur in protected areas with minimal human footprint, our core results and inferences remain unchanged (Supplementary Table 7). Having additional high-quality data on the human role in invasion, including the type and time of management, and overall level in disturbance regime⁶⁶, would refine our results and better separate ecological versus human drivers. Future work should also focus on drivers of tree invasion and invasion strategies across scales^{25,63,67}, as patterns may differ at scales larger than the local plot level that we include here, which may be important for regional versus local management of non-native trees. Finally, emerging work shows that the consideration of native range size and change in environment and/or disturbance from donor to recipient community may be more helpful in understanding introduction and invasion success than simply quantifying these variables in the novel, recipient range^{62,66}. Therefore, including the change in environmental and human impact variables would also be a fruitful avenue for future research.

Together, these results provide important unifying insights into the global drivers of non-native tree invasions and the ecological strategies that might be most successful in different regions. The trends and ecological mechanisms identified here can provide tangible guidelines to support forest management of non-native tree invasions around the globe. However, because non-native trees are introduced purposefully for forestry or to support local livelihoods, which can lead to differences in forest management objectives and strategies⁴, it is critical that local stakeholders are included when making decisions about how to best manage these introductions^{68,69}. Ultimately, this emerging understanding of global tree invasions provides fundamental insights that are needed to understand how forest composition is being reshaped under global change, and for forest management practices to limit the spread and impacts of non-native tree invasions worldwide.

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at <https://doi.org/10.1038/s41586-023-06440-7>.

- Pyšek, P. et al. Scientists' warning on invasive alien species. *Biol. Rev.* **95**, 1511–1534 (2020).
- Pejchar, L. & Mooney, H. A. Invasive species, ecosystem services and human well-being. *Trends Ecol. Evol.* **24**, 497–504 (2009).
- Richardson, D. M., Hui, C., Nuñez, M. A. & Pauchard, A. Tree invasions: patterns, processes, challenges and opportunities. *Biol. Invasions* **16**, 473–481 (2014).
- Richardson, D. M. & Rejmánek, M. Trees and shrubs as invasive alien species—a global review. *Divers. Distrib.* **17**, 788–809 (2011).
- Plants of the World Online. *Royal Botanic Gardens Kew* <http://www.plantsoftheworldonline.org/> (2022).
- van Kleunen, M. et al. The Global Naturalized Alien Flora (GloNAF) database. *Ecology* **100**, e02542 (2019).
- Liang, J. et al. Positive biodiversity-productivity relationship predominant in global forests. *Science* **354**, aaf8957 (2016).
- Vitousek, P. M., D'Antonio, C. M., Loope, L. L., Rejmanek, M. & Westbrooks, R. Introduced species: a significant component of human-caused global change. *N. Z. J. Ecol.* **21**, 1–16 (1997).
- Butchart, S. H. et al. Global biodiversity: indicators of recent declines. *Science* **328**, 1164–1168 (2010).
- Early, R. et al. Global threats from invasive alien species in the twenty-first century and national response capacities. *Nat. Commun.* **7**, 12485 (2016).
- Lockwood, J. L., Hoopes, M. F. & Marchetti, M. P. *Invasion Ecology* 2nd edn (John Wiley & Sons, 2013).
- DiTomaso, J. M. Invasive weeds in rangelands: species, impacts, and management. *Weed Sci.* **48**, 255–265 (2000).
- Simberloff, D. We can eliminate invasions or live with them. Successful management projects. *Biol. Invasions* **11**, 149–157 (2008).
- Mack, R. N. et al. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol. Appl.* **10**, 689–710 (2000).
- Boyd, I. L., Freer-Smith, P. H., Gilligan, C. A. & Godfray, H. C. The consequence of tree pests and diseases for ecosystem services. *Science* **342**, 1235773 (2013).
- Vitousek, P. M., D'Antonio, C. M., Loope, L. L. & Westbrooks, R. Biological invasions as global environmental change. *Am. Sci.* **84**, 468–478 (1996).
- Diagne, C. et al. High and rising economic costs of biological invasions worldwide. *Nature* **592**, 571–576 (2021).
- Nunez, M. A. et al. Exotic mammals disperse exotic fungi that promote invasion by exotic trees. *PLoS ONE* **8**, e66832 (2013).
- Richardson, D. M. & Pyšek, P. Naturalization of introduced plants: ecological drivers of biogeographical patterns. *New Phytol.* **196**, 383–396 (2012).
- Richardson, D. M. & Pyšek, P. Plant invasions: merging the concepts of species invasiveness and community invasibility. *Prog. Phys. Geog.* **30**, 409–431 (2006).
- Seabloom, E. W. et al. Human impacts, plant invasion, and imperiled plant species in California. *Ecol. Appl.* **16**, 1338–1350 (2006).
- Dayton, P. K. in *Proc. Colloquium on Conservation Problems in Antarctica* (ed. Parker, B. C.) 81–96 (Allen Press, 1972).
- Beaury, E. M., Finn, J. T., Corbin, J. D., Barr, V. & Bradley, B. A. Biotic resistance to invasion is ubiquitous across ecosystems of the United States. *Ecol. Lett.* **23**, 476–482 (2020).
- Cadotte, M. W., Campbell, S. E., Li, S.-P., Sodhi, D. S. & Mandrak, N. E. Preadaptation and naturalization of nonnative species: Darwin's two fundamental insights into species invasion. *Annu. Rev. Plant Biol.* **69**, 661–684 (2018).
- Fridley, J. et al. The invasion paradox: reconciling pattern and process in species invasions. *Ecology* **88**, 3–17 (2007).
- Funk, J. L. The physiology of invasive plants in low-resource environments. *Conserv. Physiol.* **1**, cot026 (2013).
- Nuñez, M. A. & Dickie, I. A. Invasive belowground mutualists of woody plants. *Biol. Invasions* **16**, 645–661 (2014).
- van Kleunen, M., Weber, E. & Fischer, M. A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecol. Lett.* **13**, 235–245 (2010).
- Pyšek, P. & Richardson, D. M. in *Biological Invasions* (ed. Nentwig, W.) 97–125 (Springer, 2007).
- Dickie, I. A. et al. The emerging science of linked plant–fungal invasions. *New Phytol.* **215**, 1314–1332 (2017).
- Diez, J. M., Sullivan, J. J., Hulme, P. E., Edwards, G. & Duncan, R. P. Darwin's naturalization conundrum: dissecting taxonomic patterns of species invasions. *Ecol. Lett.* **11**, 674–681 (2008).
- Ma, C. et al. Different effects of invader–native phylogenetic relatedness on invasion success and impact: a meta-analysis of Darwin's naturalization hypothesis. *Proc. R. Soc. B* **283**, 20160663 (2016).
- Catford, J. A., Jansson, R. & Nilsson, C. Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Divers. Distrib.* **15**, 22–40 (2009).
- Levine, J. M. & D'Antonio, C. M. Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* **87**, 15–26 (1999).
- Tilman, D. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* **78**, 81–92 (1997).
- Fine, P. V. The invasibility of tropical forests by exotic plants. *J. Trop. Ecol.* **18**, 687–705 (2002).
- Elton, C. S. *The Ecology of Invasion by Animals and Plants* 1st edn (Methuen, 1958).
- Kennedy, T. A. et al. Biodiversity as a barrier to ecological invasion. *Nature* **417**, 636–638 (2002).
- Mungi, N. A., Qureshi, Q. & Jhala, Y. V. Role of species richness and human impacts in resisting invasive species in tropical forests. *J. Ecol.* **109**, 3308–3321 (2021).
- Stohlgren, T. J., Jarnevich, C., Chong, G. W. & Evangelista, P. H. Scale and plant invasions: a theory of biotic acceptance. *Preslia* **78**, 405–426 (2006).
- Zeiter, M. & Stampfli, A. Positive diversity–invasibility relationship in species-rich semi-natural grassland at the neighbourhood scale. *Ann. Bot.* **110**, 1385–1393 (2012).
- Zanne, A. E. et al. Functional biogeography of angiosperms: life at the extremes. *New Phytol.* **218**, 1697–1709 (2018).
- Kraft, N. J. et al. Community assembly, coexistence and the environmental filtering metaphor. *Funct. Ecol.* **29**, 592–599 (2015).
- Keddy, P. A. Assembly and response rules: two goals for predictive community ecology. *J. Veg. Sci.* **3**, 157–164 (1992).
- Gallien, L., Carboni, M. & Münckmüller, T. Identifying the signal of environmental filtering and competition in invasion patterns—a contest of approaches from community ecology. *Methods Ecol. Evol.* **5**, 1002–1011 (2014).
- Divišek, J. et al. Similarity of introduced plant species to native ones facilitates naturalization, but differences enhance invasion success. *Nat. Commun.* **9**, 4631 (2018).
- MacArthur, R. & Levins, R. The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.* **101**, 377–385 (1967).
- Park, D. S. & Potter, D. A test of Darwin's naturalization hypothesis in the thistle tribe shows that close relatives make bad neighbors. *Proc. Natl Acad. Sci. USA* **110**, 17915–17920 (2013).
- Schaefer, H., Hardy, O. J., Silva, L., Barraclough, T. G. & Savolainen, V. Testing Darwin's naturalization hypothesis in the Azores. *Ecol. Lett.* **14**, 389–396 (2011).
- Darwin, C. *On the Origin of Species by Means of Natural Selection, or Preservation of Favoured Races in the Struggle for Life* (John Murray, 1859).
- Hubbell, S. P. *The Unified Neutral Theory of Biodiversity and Biogeography* (Princeton Univ. Press, 2001).
- Pinto-Ledezma, J. N. et al. Testing Darwin's naturalization conundrum based on taxonomic, phylogenetic, and functional dimensions of vascular plants. *Ecol. Monogr.* **90**, e01420 (2020).
- Theoharides, K. A. & Dukes, J. S. Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. *New Phytol.* **176**, 256–273 (2007).

54. Hulme, P. E. Trade, transport and trouble: Managing invasive species pathways in an era of globalization. *J. Appl. Ecol.* **46**, 10–18 (2009).
55. Simberloff, D. & Von Holle, B. Positive interactions of nonindigenous species: invasion meltdown? *Biol. Invasions* **1**, 21–23 (1999).
56. Pyšek, P., Křivánek, M. & Jarošík, V. Planting intensity, residence time, and species traits determine invasion success of alien woody species. *Ecology* **90**, 2734–2744 (2009).
57. Rejmánek, M. Invasive trees and shrubs: where do they come from and what we should expect in the future? *Biol. Invasions* **16**, 483–498 (2014).
58. Chong, K. Y. et al. Are terrestrial biological invasions different in the tropics? *Annu. Rev. Ecol. Evol. Syst.* **52**, 291–314 (2021).
59. Smith, J. L. & Perino, J. V. Osage orange (*Maclura pomifera*): history and economic uses. *Econ. Bot.* **35**, 24–41 (1981).
60. Pyšek, P. et al. The global invasion success of Central European plants is related to distribution characteristics in their native range and species traits. *Divers. Distrib.* **15**, 891–903 (2009).
61. Svenning, J. C. et al. The influence of interspecific interactions on species range expansion rates. *Ecography* **37**, 1198–1209 (2014).
62. Amarasekare, P. & Simon, M. W. Latitudinal directionality in ectotherm invasion success. *Proc. R. Soc. B* **287**, 20191411 (2020).
63. Park, D. S., Feng, X., Maitner, B. S., Ernst, K. C. & Enquist, B. J. Darwin's naturalization conundrum can be explained by spatial scale. *Proc. Natl Acad. Sci. USA* **117**, 10904–10910 (2020).
64. Tournadre, J. Anthropogenic pressure on the open ocean: The growth of ship traffic revealed by altimeter data analysis. *Geophys. Res. Lett.* **41**, 7924–7932 (2014).
65. de Lima, R. A. F. et al. Making forest data fair and open. *Nat. Ecol. Evol.* **6**, 656–658 (2022).
66. Moles, A. T. et al. Invasions: the trail behind, the path ahead, and a test of a disturbing idea. *J. Ecol.* **100**, 116–127 (2012).
67. Peng, S., Kinlock, N. L., Gurevitch, J. & Peng, S. Correlation of native and exotic species richness: a global meta-analysis finds no invasion paradox across scales. *Ecology* **100**, e02552 (2019).
68. Dickie, I. A. et al. Conflicting values: ecosystem services and invasive tree management. *Biol. Invasions* **16**, 705–719 (2014).
69. Finnoff, D., Shogren, J. F., Leung, B. & Lodge, D. Take a risk: preferring prevention over control of biological invaders. *Ecol. Econ.* **62**, 216–222 (2007).

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.



Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

© The Author(s) 2023

Camille S. Delavaux^{1,2,3}, Thomas W. Crowther¹, Constantin M. Zohner¹, Niamh M. Robmann¹, Thomas Lauber¹, Johan van den Hoogen¹, Sara Kuebbing², Jingjing Liang³, Sergio de-Miguel^{4,5}, Gert-Jan Nabuurs⁶, Peter B. Reich^{7,8,9}, Meinrad Abegg¹⁰, Yves C. Adou Yao¹¹, Giorgio Alberti^{12,13}, Angelica M. Almeyda Zambrano¹⁴, Braulio Vilchez Alvarado¹⁵, Esteban Alvarez-Dávila¹⁶, Patricia Alvarez-Loayza¹⁷, Luciana F. Alves¹⁸, Christian Ammer¹⁹, Clara Antón-Fernández²⁰, Alejandro Araujo-Murakami²¹, Luzmila Arroyo²¹, Valerio Avitabile²², Gerardo A. Aymard^{23,24}, Timothy R. Baker²⁵, Radomir Batazy²⁶, Olaf Banki²⁷, Jorcely G. Barroso²⁸, Meredith L. Bastian^{29,30}, Jean-Francois Bastin³¹, Luca Biragazzi³², Philippe Birnbaum^{33,34,35}, Robert Bitariho³⁶, Pascal Boeckx³⁷, Frans Bongers³⁸, Olivier Bouriaud³⁹, Pedro H. S. Brancalion³⁹, Susanne Brandt⁴⁰, Roel Brienen²⁵, Eben N. Broadbent⁴¹, Helge Bruelheide^{42,43}, Filippo Bussotti⁴⁴, Roberto Cazzolla Gatti⁴⁵, Ricardo G. César³⁹, Goran Cesljar⁴⁶, Robin Chazdon^{47,48}, Han Y. H. Chen⁴⁹, Chelsea Chisholm¹, Hyunkook Cho⁵⁰, Emil Cienicala^{51,52}, Connie Clark⁵³, David Clark⁵⁴, Gabriel D. Colletta⁵⁵, David A. Coomes⁵⁶, Fernando Cornejo Valverde⁵⁷, José J. Corral-Rivas⁵⁸, Philip M. Crim^{59,60}, Jonathan R. Cumming⁵⁹, Selvadurai Dayanandan⁶¹, André L. de Gasper⁶², Mathieu Decuyper⁶³, Géraldine Derroire⁶⁴, Ben DeVries⁶⁵, Ilija Djordjevic⁶⁶, Jiri Dolezal^{67,68}, Aurélie Dourdain⁶⁴, Nestor Laurier Engone Obiang⁶⁹, Brian J. Enquist^{70,71}, Teresa J. Eyre⁷², Adandé Belarmain Fandohan⁷³, Tom M. Fayle^{74,75}, Ted R. Feldpausch⁷⁶, Leandro V. Ferreira⁷⁷, Markus Fischer⁷⁸, Christine Fletcher⁷⁹, Lorenzo Fizzerra⁸⁰, Javier G. P. Gamarra⁸¹, Damiano Gianelle⁸⁰, Henry B. Glack⁸², David J. Harris⁸³, Andrew Hector⁸⁴, Andreas Hemp⁸⁵, Geerten Hengeveld⁶, Bruno Héruit^{86,87}, John L. Herbohn^{88,89}, Martin Herold⁹⁰, Annika Hillers^{89,90}, Euridice N. Honorio Coronado⁹¹, Canghui^{92,93}, Thomas T. Ibanez⁹⁴, Iéda Amaral⁹⁵, Nobuo Imai⁹⁶, Andrzej M. Jagodziński^{97,98}, Bogdan Jaroszewicz⁹⁹, Vivian Kvist Johannsen¹⁰⁰, Carlos A. Joly¹⁰¹, Tommaso Jucker¹⁰², Ilbin Jung⁵⁰, Viktor Karminov¹⁰³, Kuswata Kartawinata¹⁰⁴, Elizabeth Kearsley¹⁰⁵, David Kenfack¹⁰⁶, Deborah K. Kennard¹⁰⁷, Sebastian Kepfer-Rojas¹⁰⁰, Gunnar Keppel¹⁰⁸, Mohammed Latif Khan¹⁰⁹, Timothy J. Killeen²¹, Hyun Seok Kim^{110,111,112,113}, Kanehiro Kitayama¹¹⁴, Michael Köhl¹¹⁵, Henn Korjus¹¹⁶, Florian Kraxner¹¹⁷, Diana Laarmann¹¹⁸, Mait Lang¹¹⁶, Simon L. Lewis¹¹⁹, Huicui Lu¹¹⁹, Natalia V. Lukina¹²⁰, Brian S. Maitner⁷⁰, Yadvinder Malhi¹²¹, Eric Marcon¹²², Beatriz Schwantes Marimon¹²³, Ben Hur Marimon-Junior¹²³, Andrew R. Marshall^{48,124,125}, Emanuel H. Martin¹²⁶, Olga Martynenko¹²⁷, Jorge A. Meave¹²⁷, Omar Melo-Cruz¹²⁸, Casimiro Mendoza¹²⁹, Cory Merow¹⁷, Abel Monteagudo Mendoza^{130,131}, Vanessa S. Moreno³⁹, Sharif A. Mukul^{48,132}, Philip Mundhenk¹³⁵, María Guadalupe Nava-Miranda^{133,134,135}, David Neill¹³⁶, Victor J. Neldner⁷², Radovan V. Nenovic⁸⁶, Michael R. Ngugi⁷², Pascal A. Niklaus¹³⁷,

Jacek Oleksyn⁹⁷, Petr Ontikov¹⁰³, Edgar Ortiz-Malavasi¹⁵, Yude Pan¹³⁸, Alain Paquette¹³⁹, Alexander Parada-Gutierrez²¹, Elena I. Parfenova¹⁴⁰, Minjee Park^{3,110}, Marc Parren¹⁴¹, Narayanaswamy Parthasarathy¹⁴², Pablo L. Peri¹⁴³, Sebastian Pfautsch¹⁴⁴, Oliver L. Phillips²⁵, Nicolas Picard¹⁴⁵, Maria Teresa T. F. Piedade¹⁴⁶, Daniel Piotto¹⁴⁷, Nigel C. A. Pitman¹⁰⁴, Irina Polo¹⁴⁸, Lourens Poorter⁶, Axel D. Poulsen⁸³, Hans Pretzsch¹⁴⁹, Freddy Ramirez Arevalo¹⁵⁰, Zorayda Restrepo-Correa¹⁵¹, Mirco Rodeghiero^{90,152}, Samir G. Rolim¹⁴⁷, Anand Roopsind¹⁵³, Francesco Rovero^{154,155}, Ervan Rutishauser¹⁵⁶, Purabi Saikia¹⁵⁷, Christian Salas-Eljatib^{158,159,160}, Philippe Saner¹⁶¹, Peter Schall¹¹⁹, Dmitry Schepaschenko^{177,140,162}, Michael Scherer-Lorenzen¹⁶³, Bernhard Schmid¹³⁷, Jochen Schöngert¹⁴⁶, Eric B. Searle¹³⁹, Vladimir Seben¹⁶⁴, Josep M. Serra-Diaz^{165,166}, Douglas Sheil^{167,168}, Anatoly Z. Shvidenko¹⁷⁷, Javier E. Silva-Espejo¹⁶⁹, Marcos Silveira¹⁷⁰, James Singh¹⁷¹, Plinio Sist⁸⁶, Ferry Slik¹⁷², Bonaventure Sonké¹⁷³, Alexandre F. Souza¹⁷⁴, Mircicki Stanislaw¹⁷⁵, Krzysztof J. Stępień²⁶, Jens-Christian Svenning^{166,176}, Miroslav Svoboda¹⁷⁷, Ben Swanepoel¹⁷⁸, Natalia Targhetta¹⁴⁶, Nadja Tchabakava¹⁴⁰, Hans ter Steege²¹⁷⁹, Raquel Thomas¹⁸⁰, Elena Tikhonova¹⁸⁰, Peter M. Umunay¹⁸¹, Vladimir A. Usoltsev¹⁸², Renato Valencia¹⁸³, Fernando Valladares¹⁸⁴, Fons van der Plas¹⁸⁵, Tran Van Do¹⁸⁶, Michael E. van Nuland¹⁸⁷, Rodolfo M. Vasquez¹³⁰, Hans Verbeke¹⁰⁵, Helder Viana^{188,189}, Alexander C. Vibrans^{62,190}, Simone Vieira¹⁹¹, Klaus von Gadow¹⁹², Hua-Feng Wang¹⁹³, James V. Watson¹⁹⁴, Gijbert D. A. Werne¹⁹⁵, Susan K. Wiser¹⁹⁶, Florian Wittmann¹⁹⁷, Hannsjoerg Woelt¹⁹⁸, Virginia Wortel¹⁹⁹, Roderik Zagat²⁰⁰, Tomasz Zawita-Niedzwiecki²⁰¹, Chunyu Zhang²⁰², Xiuhai Zhao²⁰², Mo Zhou³, Zhi-Xin Zhu¹⁹³, Irie C. Zo-Bi⁷² & Daniel S. Maynard^{1,203}

¹Institute of Integrative Biology, ETH Zurich (Swiss Federal Institute of Technology), Zurich, Switzerland. ²The Forest School at The Yale School of the Environment, Yale University, New Haven, CT, USA. ³Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN, USA. ⁴Department of Crop and Forest Sciences, University of Lleida, Lleida, Spain. ⁵Joint Research Unit CTFE-AGROTECNIO-CERCA, Solsona, Spain. ⁶Wageningen University and Research, Wageningen, The Netherlands. ⁷Department of Forest Resources, University of Minnesota, St Paul, MN, USA. ⁸Hawkesbury Institute for the Environment, Western Sydney University, Penrith, New South Wales, Australia. ⁹Institute for Global Change Biology, and School for Environment and Sustainability, University of Michigan, Ann Arbor, MI, USA. ¹⁰Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland. ¹¹UFR Biosciences, University Félix Houphouët-Boigny, Abidjan, Côte d'Ivoire. ¹²Department of Agricultural, Food, Environmental and Animal Sciences, University of Udine, Udine, Italy. ¹³Faculty of Science and Technology, Free University of Bolzano, Bolzano, Italy. ¹⁴Spatial Ecology and Conservation Laboratory, Department of Tourism, Recreation and Sport Management, University of Florida, Gainesville, FL, USA. ¹⁵Forestry School, Tecnológico de Costa Rica TEC, Cartago, Costa Rica. ¹⁶Fundacion ConVida, Universidad Nacional Abierta y a Distancia, UNAD, Medellín, Colombia. ¹⁷Field Museum of Natural History, Chicago, IL, USA. ¹⁸Center for Tropical Research, Institute of the Environment and Sustainability, UCLA, Los Angeles, CA, USA. ¹⁹Silviculture and Forest Ecology of the Temperate Zones, University of Göttingen, Göttingen, Germany. ²⁰Division of Forest and Forest Resources, Norwegian Institute of Bioeconomy Research (NIBIO), Ås, Norway. ²¹Museo de Historia Natural Noel Kempff Mercado, Santa Cruz, Bolivia. ²²European Commission, Joint Research Center, Ispra, Italy. ²³UNELLEZ-Guanare, Programa de Ciencias del Agrario y el Mar, Herbario Universitario (PORT), Portuguesa, Venezuela. ²⁴Compensation International S. A. Ci Progress-GreenLife, Bogotá, Colombia. ²⁵School of Geography, University of Leeds, Leeds, UK. ²⁶Department of Geomatics, Forest Research Institute, Raszyn, Poland. ²⁷Naturalis Biodiversity Center, Leiden, The Netherlands. ²⁸Centro Multidisciplinar, Universidade Federal do Acre, Rio Branco, Brazil. ²⁹Proceedings of the National Academy of Sciences, Washington, DC, USA. ³⁰Department of Evolutionary Anthropology, Duke University, Durham, NC, USA. ³¹TERRA Teach and Research Centre, Gembloux Agro Bio-Tech, University of Liege, Liege, Belgium. ³²United Nation Framework Convention on Climate Change, Bonn, Germany. ³³Institut Agronomique néo-Calédonien (IAC), Nouméa, New Caledonia. ³⁴AMAP, University of Montpellier, Montpellier, France. ³⁵CIRAD, CNRS, INRAE, IRD, Montpellier, France. ³⁶Institute of Tropical Forest Conservation, Mbarara University of Sciences and Technology, Mbarara, Uganda. ³⁷Isotope Bioscience Laboratory-ISOFYS, Ghent University, Ghent, Belgium. ³⁸Integrated Center for Research, Development and Innovation in Advanced Materials, Nanotechnologies, and Distributed Systems for Fabrication and Control (MANSID), Stefan cel Mare University of Suceava, Suceava, Romania. ³⁹Department of Forest Sciences, Luiz de Queiroz College of Agriculture, University of São Paulo, Piracicaba, Brazil. ⁴⁰Bavarian State Institute of Forestry, Freising, Germany. ⁴¹Spatial Ecology and Conservation Laboratory, School of Forest Resources and Conservation, University of Florida, Gainesville, FL, USA. ⁴²Institute of Biology, Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Halle-Wittenberg, Germany. ⁴³German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany. ⁴⁴Department of Agriculture, Food, Environment and Forest (DAGRI), University of Firenze, Florence, Italy. ⁴⁵Department of Biological, Geological, and Environmental Sciences, University of Bologna, Bologna, Italy. ⁴⁶Department of Spatial Regulation, GIS and Forest Policy, Institute of Forestry, Belgrade, Serbia. ⁴⁷Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT, USA. ⁴⁸Forest Research Institute, University of the Sunshine Coast, Sippy Downs, Queensland, Australia. ⁴⁹Faculty of Natural Resources Management, Lakehead University, Thunder Bay, Ontario, Canada. ⁵⁰Division of Forest Resources Information, Korea Forest Promotion Institute, Seoul, South Korea. ⁵¹IFER-Institute of Forest Ecosystem Research, Jilove u Prahy, Czech Republic. ⁵²Global Change Research Institute CAS, Brno, Czech Republic. ⁵³Nicholas School of the Environment, Duke University, Durham, NC, USA. ⁵⁴Department of Biology, University of Missouri-St Louis, St Louis, MO, USA. ⁵⁵Programa

de Pós-graduação em Biologia Vegetal, Instituto de Biologia, Universidade Estadual de Campinas, Campinas, Brazil. ⁵⁶Department of Plant Sciences and Conservation Research Institute, University of Cambridge, Cambridge, UK. ⁵⁷Andes to Amazon Biodiversity Program, Madre de Dios, Peru. ⁵⁸Facultad de Ciencias Forestales y Ambientales, Universidad Juárez del Estado de Durango, Durango, Mexico. ⁵⁹Department of Biology, West Virginia University, Morgantown, WV, USA. ⁶⁰Department of Physical and Biological Sciences, The College of Saint Rose, Albany, NY, USA. ⁶¹Biology Department, Centre for Structural and Functional Genomics, Concordia University, Montreal, Quebec, Canada. ⁶²Natural Science Department, Universidade Regional de Blumenau, Blumenau, Brazil. ⁶³World Agroforestry (ICRAF), Nairobi, Kenya. ⁶⁴Cirad, UMR EcoFoG (AgroParisTech, CNRS, INRAE), Université des Antilles, Université de la Guyane, Campus Agronomique, Kourou, France. ⁶⁵Department of Geographical Sciences, University of Maryland, College Park, MD, USA. ⁶⁶Institute of Forestry, Belgrade, Serbia. ⁶⁷Institute of Botany, The Czech Academy of Sciences, Třeboň, Czech Republic. ⁶⁸Department of Botany, Faculty of Science, University of South Bohemia, České Budějovice, Czech Republic. ⁶⁹RET, Herbar National du Gabon (CENAREST), Libreville, Gabon. ⁷⁰Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ, USA. ⁷¹The Santa Fe Institute, Santa Fe, NM, USA. ⁷²Queensland Herbarium, Department of Environment and Science, Toowoong, Queensland, Australia. ⁷³Ecole de Foresterie et Ingénierie du Bois, Université Nationale d'Agriculture, Kétou, Benin. ⁷⁴School of Biological and Behavioural Sciences, Queen Mary University of London, London, UK. ⁷⁵Biology Centre of the Czech Academy of Sciences, Institute of Entomology, Ceske Budejovice, Czech Republic. ⁷⁶Geography, College of Life and Environmental Sciences, University of Exeter, Exeter, UK. ⁷⁷Museu Paraense Emílio Goeldi. Coordenação de Ciências da Terra e Ecologia, Belém, Pará, Brazil. ⁷⁸Institute of Plant Sciences, University of Bern, Bern, Switzerland. ⁷⁹Forest Research Institute Malaysia, Kuala Lumpur, Malaysia. ⁸⁰Research and Innovation Center, Fondazione Edmund Mach, San Michele All'adige, Italy. ⁸¹Forestry Division, Food and Agriculture Organization of the United Nations, Rome, Italy. ⁸²Glick Designs LLC, Hadley, MA, USA. ⁸³Royal Botanic Garden Edinburgh, Edinburgh, UK. ⁸⁴Department of Plant Sciences, University of Oxford, Oxford, UK. ⁸⁵Department of Plant Systematics, University of Bayreuth, Bayreuth, Germany. ⁸⁶Cirad, UPR Forêts et Sociétés, University of Montpellier, Montpellier, France. ⁸⁷Department of Forestry and Environment, National Polytechnic Institute (INP-HB), Yamoussoukro, Côte d'Ivoire. ⁸⁸Tropical Forests and People Research Centre, University of the Sunshine Coast, Maroochydore, Queensland, Australia. ⁸⁹Centre for Conservation Science, The Royal Society for the Protection of Birds, Sandy, UK. ⁹⁰Wild Chimpanzee Foundation, Liberia Office, Monrovia, Liberia. ⁹¹Instituto de Investigaciones de la Amazonia Peruana, Iquitos, Peru. ⁹²Centre for Invasion Biology, Department of Mathematical Sciences, Stellenbosch University, Stellenbosch, South Africa. ⁹³Theoretical Ecology Unit, African Institute for Mathematical Sciences, Cape Town, South Africa. ⁹⁴Institut Agronomique néo-Calédonien (IAC), Equipe Sol & Végétation (SolVeg), Nouméa, New Caledonia. ⁹⁵National Institute of Amazonian Research, Manaus, Brazil. ⁹⁶Department of Forest Science, Tokyo University of Agriculture, Tokyo, Japan. ⁹⁷Institute of Dendrology, Polish Academy of Sciences, Kórnik, Poland. ⁹⁸Poznań University of Life Sciences, Department of Game Management and Forest Protection, Poznań, Poland. ⁹⁹Faculty of Biology, Białowieża Geobotanical Station, University of Warsaw, Białowieża, Poland. ¹⁰⁰Department of Geosciences and Natural Resource Management, University of Copenhagen, Copenhagen, Denmark. ¹⁰¹Department of Plant Biology, Institute of Biology, University of Campinas, UNICAMP, Campinas, Brazil. ¹⁰²School of Biological Sciences, University of Bristol, Bristol, UK. ¹⁰³Forestry Faculty, Bauman Moscow State Technical University, Mytishi, Russia. ¹⁰⁴Field Museum of Natural History, Chicago, IL, USA. ¹⁰⁵CAVELab-Computational and Applied Vegetation Ecology, Department of Environment, Ghent University, Ghent, Belgium. ¹⁰⁶CTFS-ForestGEO, Smithsonian Tropical Research Institute, Balboa, Panama. ¹⁰⁷Department of Physical and Environmental Sciences, Colorado Mesa University, Grand Junction, CO, USA. ¹⁰⁸UniSA STEM and Future Industries Institute, University of South Australia, Adelaide, South Australia, Australia. ¹⁰⁹Department of Botany, Dr Harisingh Gour Vishwavidyalaya (A Central University), Sagar, India. ¹¹⁰Department of Agriculture, Forestry and Bioresources, Seoul National University, Seoul, South Korea. ¹¹¹Interdisciplinary Program in Agricultural and Forest Meteorology, Seoul National University, Seoul, South Korea. ¹¹²National Center for Agro Meteorology, Seoul, South Korea. ¹¹³Research Institute for Agriculture and Life Sciences, Seoul National University, Seoul, South Korea. ¹¹⁴Graduate School of Agriculture, Kyoto University, Kyoto, Japan. ¹¹⁵Institute for World Forestry, University of Hamburg, Hamburg, Germany. ¹¹⁶Institute of Forestry and Engineering, Estonian University of Life Sciences, Tartu, Estonia. ¹¹⁷Biodiversity and Natural Resources Program, International Institute for Applied Systems Analysis (IIASA), Laxenburg, Austria. ¹¹⁸Department of Geography, University College London, London, UK. ¹¹⁹Faculty of Forestry, Qingdao Agricultural University, Qingdao, China. ¹²⁰Center for Forest Ecology and Productivity, Russian Academy of Sciences, Moscow, Russia. ¹²¹Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, UK. ¹²²AgroParisTech, UMR-AMAP, Cirad, CNRS, INRA, IRD, Université de Montpellier, Montpellier, France. ¹²³Departamento de Ciências Biológicas, Universidade do Estado de Mato Grosso, Nova Xavantina, Brazil. ¹²⁴Department of Environment and Geography, University of York, York, UK. ¹²⁵Flamingo Land, Malton, UK. ¹²⁶Department of Wildlife Management, College of African Wildlife Management, Mweka, Tanzania. ¹²⁷Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, Mexico City, Mexico. ¹²⁸Universidad del Tolima, Ibagué, Colombia. ¹²⁹Colegio de Profesionales Forestales de Cochabamba, Cochabamba, Bolivia. ¹³⁰Jardín Botánico de Missouri, Pasco, Peru. ¹³¹Universidad Nacional de San Antonio Abad del Cusco, Cusco, Peru. ¹³²Centre for Research on Land-use Sustainability, Dhaka, Bangladesh. ¹³³Laboratorio de geomática, Instituto de Silvicultura e Industria de la Madera, Universidad Juárez del Estado de Durango, Durango, Mexico. ¹³⁴Programa de doctorado en Ingeniería para el desarrollo rural y civil, Escuela de Doctorado Internacional de la Universidad de Santiago de Compostela, Santiago de Compostela, Spain. ¹³⁵Department of Environment and Development Studies, United International University, Dhaka, Bangladesh. ¹³⁶Universidad Estatal Amazónica, Puyo, Pastaza, Ecuador. ¹³⁷Department of Evolutionary Biology and Environmental Studies, University of Zürich, Zurich, Switzerland. ¹³⁸Climate, Fire, and Carbon Cycle Sciences, USDA Forest Service, Durham, NC, USA. ¹³⁹Centre for Forest Research, Université du Québec à Montréal, Montreal, Quebec, Canada. ¹⁴⁰V. N. Sukachev Institute of Forest, FRC KSC, Siberian Branch of the Russian Academy of Sciences, Krasnoyarsk, Russia. ¹⁴¹Forest Ecology and Forest Management Group, Wageningen University and Research, Wageningen, The Netherlands. ¹⁴²Department of Ecology and Environmental Sciences, Pondicherry University, Puducherry, India. ¹⁴³Instituto Nacional de Tecnología Agropecuaria (INTA), Universidad Nacional de la Patagonia Austral (UNPA), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Río Gallegos, Argentina. ¹⁴⁴School of Social Sciences (Urban Studies), Western Sydney University, Penrith, New South Wales, Australia. ¹⁴⁵Forestry Department, Food and Agriculture Organization of the United Nations, Rome, Italy. ¹⁴⁶Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil. ¹⁴⁷Laboratório de Dendrologia e Silvicultura Tropical, Centro de Formação em Ciências Agroflorestais, Universidade Federal do Sul da Bahia, Itabuna, Brazil. ¹⁴⁸Jardín Botánico de Medellín, Medellín, Colombia. ¹⁴⁹Chair for Forest Growth and Yield Science, TUM School for Life Sciences, Technical University of Munich, Munich, Germany. ¹⁵⁰Universidad Nacional de la Amazonia Peruana, Iquitos, Peru. ¹⁵¹Servicios Ecosistémicos y Cambio Climático (SECC), Fundación Con Vida & Corporación COL-TREE, Medellín, Colombia. ¹⁵²Centro Agricultura, Ambiente, University of Trento, San Michele All'adige, Italy. ¹⁵³Department of Biological Sciences, Boise State University, Boise, ID, USA. ¹⁵⁴Department of Biology, University of Florence, Florence, Italy. ¹⁵⁵Tropical Biodiversity, MUSE-Museo delle Scienze, Trento, Italy. ¹⁵⁶Info Flora, Geneva, Switzerland. ¹⁵⁷Department of Environmental Sciences, Central University of Jharkhand, Ranchi, Jharkhand, India. ¹⁵⁸Centro de Modelación y Monitoreo de Ecosistemas, Universidad Mayor, Santiago, Chile. ¹⁵⁹Vicerrectoría de Investigación y Postgrado, Universidad de La Frontera, Temuco, Chile. ¹⁶⁰Depto. de Silvicultura y Conservación de la Naturaleza, Universidad de Chile, Temuco, Chile. ¹⁶¹Datascientist.ch, Wallisellen, Switzerland. ¹⁶²Siberian Federal University, Krasnoyarsk Russian Federation, Krasnoyarsk, Russia. ¹⁶³Geobotany, Faculty of Biology, University of Freiburg, Freiburg im Breisgau, Germany. ¹⁶⁴National Forest Centre, Forest Research Institute Zvolen, Zvolen, Slovakia. ¹⁶⁵Université de Lorraine, AgroParisTech, INRAE, Silva, Nancy, France. ¹⁶⁶Center for Ecological Dynamics in a Novel Biosphere (ECONOVO) and Center for Biodiversity Dynamics in a Changing World (BIOCHANGE), Department of Biology, Aarhus University, Aarhus, Denmark. ¹⁶⁷Forest Ecology and Forest Management, Wageningen University and Research, Wageningen, The Netherlands. ¹⁶⁸Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Ås, Norway. ¹⁶⁹Departamento de Biología, Universidad de la Serena, La Serena, Chile. ¹⁷⁰Centro de Ciências Biológicas e da Natureza, Universidade Federal do Acre, Rio Branco, Acre, Brazil. ¹⁷¹Guyana Forestry Commission, Georgetown, France. ¹⁷²Environmental and Life Sciences, Faculty of Science, Universiti Brunei Darussalam, Bandar Seri Begawan, Brunei. ¹⁷³Plant Systematic and Ecology Laboratory, Department of Biology, Higher Teachers' Training College, University of Yaoundé I, Yaoundé, Cameroon. ¹⁷⁴Departamento de Ecologia, Universidade Federal do Rio Grande do Norte, Natal, Rio Grande do Norte, Brazil. ¹⁷⁵Warsaw University of Life Sciences, Warsaw, Poland. ¹⁷⁶Section for Ecoinformatics & Biodiversity, Department of Biology, Aarhus University, Aarhus, Denmark. ¹⁷⁷Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Prague, Czech Republic. ¹⁷⁸Wildlife Conservation Society, Vientiane, Laos. ¹⁷⁹Quantitative Biodiversity Dynamics, Betafaculty, Utrecht University, Utrecht, The Netherlands. ¹⁸⁰Iwokrama International Centre for Rainforest Conservation and Development (IIC), Georgetown, Guyana. ¹⁸¹School of Forestry and Environmental Studies, Yale University, New Haven, CT, USA. ¹⁸²Botanical Garden of Ural Branch of Russian Academy of Sciences, Ural State Forest Engineering University, Yekaterinburg, Russia. ¹⁸³Pontificia Universidad Católica del Ecuador, Quito, Ecuador. ¹⁸⁴LINCGlobal, Museo Nacional de Ciencias Naturales, CSIC, Madrid, Spain. ¹⁸⁵Plant Ecology and Nature Conservation Group, Wageningen University, Wageningen, The Netherlands. ¹⁸⁶Silviculture Research Institute, Vietnamese Academy of Forest Sciences, Hanoi, Vietnam. ¹⁸⁷Department of Biology, Stanford University, Stanford, CA, USA. ¹⁸⁸Centre for the Research and Technology of Agro-Environmental and Biological Sciences, CITAB, University of Trás-os-Montes and Alto Douro, UTAD, Viseu, Portugal. ¹⁸⁹Department of Ecology and Sustainable Agriculture, Agricultural High School, Polytechnic Institute of Viseu, Viseu, Portugal. ¹⁹⁰Department of Forest Engineering Universidade Regional de Blumenau, Blumenau, Brazil. ¹⁹¹Environmental Studies and Research Center, University of Campinas, UNICAMP, Campinas, Brazil. ¹⁹²Department of Forest and Wood Science, University of Stellenbosch, Stellenbosch, South Africa. ¹⁹³Key Laboratory of Tropical Biological Resources, Ministry of Education, School of Life and Pharmaceutical Sciences, Hainan University, Haikou, China. ¹⁹⁴Division of Forestry and Natural Resources, West Virginia University, Morgantown, WV, USA. ¹⁹⁵Department of Zoology, University of Oxford, Oxford, UK. ¹⁹⁶Manaaki Whenua-Landcare Research, Lincoln, New Zealand. ¹⁹⁷Department of Wetland Ecology, Institute for Geography and Geoecology, Karlsruhe Institute for Technology, Karlsruhe, Germany. ¹⁹⁸Independent Researcher, Bad Aussee, Austria. ¹⁹⁹Centre for Agricultural Research in Suriname (CELOS), Paramaribo, Suriname. ²⁰⁰Tropenbos International, Wageningen, The Netherlands. ²⁰¹Polish State Forests, Coordination Center for Environmental Projects, Warsaw, Poland. ²⁰²Research Center of Forest Management Engineering of State Forestry and Grassland Administration, Beijing Forestry University, Beijing, China. ²⁰³Department of Genetics, Evolution, and Environment, University College London, London, UK. ²⁰⁴e-mail: Camille.delavaux@usys.ethz.ch

Methods

Tree inventory and non-native status

For tree inventory data, we used the Global Forest Biodiversity Initiative (GFBI) database⁷, which contains tree-level abundance data for more than 1.2 million forest plots on all continents across the globe, containing more than 31 million unique georeferenced records of tree size and density dating from 1958. Each observation in the dataset consists of a unique tree ID, plot ID, plot coordinates, tree diameter at breast height (DBH), tree-per-hectare expansion factors, year of measurement, and binomial species names. In this study, we applied several filters to these data before analyses. First, where plots had multiple years of data, we kept only the most recent year of census data. We then subset the data to include only plots with at least three species as required for our phylogenetic metrics, excluding monoculture forest plantations from the study.

To assign native status to each tree species (native or non-native, representing naturalized and invasive), we established a consensus status between the Global Naturalized Alien Flora (GloNAF)⁶ and the KEW Plants of the World⁷⁰ databases. All databases were standardized to The Plant List taxonomy⁷¹. The GloNAF database contains detailed, georeferenced information on the naturalized status of more than 10,000 plant species in each of 1,029 regions across the globe representing countries or federal states; the KEW database outlines native ranges of vascular plant species for over 1.2 million plant species⁷⁰. The GFBI and GloNAF datasets were joined by matching each unique species by location in GFBI to a GloNAF region polygon and species status. Then, for each GFBI plot, we extracted the GloNAF region identifier using Google Earth Engine⁷². This process was then repeated for the KEW database. We then filtered out plots that included any species with disagreement between GloNAF and KEW databases (that is, conflicting native status), and only included trees with a minimum diameter of 5 cm and a minimum height of 1.3 m to allow for DBH measurements. All trees identified as 'non-native' were verified to be listed in the BGCI Tree List, which defines a tree as, "A woody plant with usually a single stem growing to a height of at least two metres, or if multi-stemmed, then at least one vertical stem five centimetres in diameter at breast height"⁷³. Note that this is an inclusive definition which includes monocots and tree ferns, as well as species that can occur both as tall single-stem and shrub-like multi-stem phenotypes.

To account for unequal representation of plots across biomes (Fig. 1), we used a reduced version of this database, down-sampled to a number of plots proportional to the land area covered by each of 14 biomes (Supplementary Table 1), while conserving as many tropical plots as possible. This ensured that we were not overrepresenting historically oversampled biomes, particularly in temperate regions. In addition, we preferentially retained invaded plots during this down-sampling to ensure adequate representation of invaded plots in the final dataset, with a maximum of half of the plots within a biome being invaded. This oversampling of invaded plots allowed for adequate representation of invaded and non-invaded plots in our analyses of non-native presence, and allowed sufficient data for our analyses of invasion severity, as these analyses only used data from plots that had non-native species invasions. Results were not qualitatively different if we did not preferentially retain invaded plots in our down-sampling (Extended Data Fig. 6 and Supplementary Table 8). Note also that the global mapping used the full dataset, with no subsampling. Prior to analyses, we also collapsed locations with multiple replicate plots and removed plots where phylogenetic or functional diversity could not be calculated for both native and full communities due to less than three species being present (see below).

Non-native invasion metrics

We split our invasion metrics into the two broad categories of 'non-native invasion' (presence) and 'invasion severity'. Specifically, using

our data, we were able to determine for each plot (1) whether any non-native tree species were present (non-native presence); (2) the proportion of tree species that were non-native relative to total tree species (invasion severity, assessed via non-native richness)²³; and (3) the proportion basal area of non-native tree species relative to total tree species basal area (invasion severity, assessed via non-native abundance). These metrics are congruent with recently proposed frameworks for measuring and reporting invasive plant species^{74,75}. The metric of relative introduced species richness may be hypothesized to lead to a bias in detection of biotic resistance, with greater biotic resistance falsely detected in diverse communities, as these communities will have a lower proportion of non-native trees due to the higher denominator (total site diversity). However, use of the binomial approach in our GLM modelling of this proportion, as opposed to direct proportion, overcomes this limitation, as it uses raw counts of proportion, effectively weighting observations by the total species number in the community²³.

Climatic and anthropogenic variables

For climatic and anthropogenic variables, we relied on the Global Environmental Composite^{76,77}. This global database contains spatially explicit geographic information system (GIS) layers of more than 260 unique environmental variables, encompassing climate, soil, land cover and land use, plant biomass, topography, human footprint, and disturbance^{78,79}. Climate variables were extracted from the CHELSA (climatology at high resolution for the earth's land surface areas) dataset⁷⁸, whereas soil variables were from the SoilGrids⁸⁰ dataset. In addition, we created distance measures by calculating the spherical distance to shipping ports⁸¹ and airports⁸². All layers were standardized to a 30 arcsec resolution (~1 km² at the equator), a resolution at which these variables have been shown to have an influence on plant biogeography and assembly patterns^{83,84}. We chose model variables to represent both climate and soil properties that exhibited low collinearity for each of three datasets: global (all 14 biomes from Supplementary Table 1), temperate (temperate broadleaf, coniferous, grassland biomes) and tropical (tropical moist broadleaf, deciduous broadleaf, coniferous, and grassland biomes). We chose to use distinct variables rather than transforming them into principal component analysis axes for increased interpretability of these variables and their effects. Because variables exhibiting collinearity varied between the three datasets, the resulting models include different variable combinations. For all models, we used mean annual temperature (MAT), mean annual precipitation (MAP), distance to shipping ports⁸¹ (hereafter 'ports') and human population density⁸⁵. For the global models, we used the following additional environmental variables: absolute depth to bedrock, coarse fragments, sand content and soil pH. For temperate models, we used absolute depth to bedrock, clay content, and soil pH as additional variables; for tropical models we used absolute depth to bedrock, soil organic content, and soil pH as additional variables. All soil variables used were determined at a depth of 0 cm, or the top layer of soil.

Diversity metrics

We analysed data using either phylogenetic or functional diversity; these two approaches were chosen to be as analogous as possible. Phylogenetic alpha diversity explains the genetic relatedness of species within a community and is often assumed to represent a proxy for functional similarity across species within a community assemblage. Yet, congruency between these two metrics remains under debate^{86,87} and their role in invasion patterns remains untested; therefore, we focused on two major axes of diversity, explaining richness and divergence in the community across both phylogenetic and functional space⁸⁸, capturing both evolutionary and ecological processes. For each native and entire tree community (native and non-native species), we calculated Faith's phylogenetic diversity (phylogenetic richness) and mean nearest taxon distance (MNTD, phylogenetic redundancy; Extended Data Fig. 2).

Entire tree community metrics were calculated on all species, whether they were matched to GloNAF and KEW or not; this included tree species which were identified to genus level. Faith's phylogenetic diversity was calculated as the sum of the branch lengths on the phylogenetic tree of the species in the community; MNTD was calculated as the average distance to the nearest neighbour across the community. These metrics were calculated based on tree placement of taxa in a recently published reference backbone tree for plants⁸⁹. Out of 13,345 starting taxa, a total of 12,325 were placed on the reference tree, with 4,960 placed at the species level and 7,365 placed at the genus level. We chose MNTD over other available metrics describing community divergence because we were interested in redundancy of the community, and this metric captures this best^{24,90}. To enable a more intuitive understanding of this metric, we transformed each community-level value of MNTD to the maximum MNTD across all communities minus calculated MNTD. This transformed the maximum value to zero and all smaller values transformed to increasingly larger numbers, with higher MNTD values indicating a greater native redundancy, similar to the expected increased redundancy with greater phylogenetic richness (Faith's phylogenetic diversity). To determine the non-native invasion strategy, or impact of non-natives on native MNTD, we calculated the difference between the native and non-native community relative to the native community alone. We used the following formula for non-native invasion strategy: (entire community MNTD – native community MNTD)/native community MNTD. When non-native invasion strategy was greater than zero, this indicated that the addition of the non-native species resulted in a more dissimilar community, whereas a non-native invasion strategy less than zero corresponded to the opposite.

For functional diversity, we calculated the analogous metrics using trait distance matrices instead of phylogenetic tree-based distances. We selected eight traits extracted from Maynard et al.⁸³ that represented the major clusters of functional trait diversity, thereby capturing the full spectrum of tree form and function while minimizing correlation between traits. Maynard et al.⁸³ used data from the TRY plant trait database to parametrize machine learning models to estimate the expression of 18 traits as a function of the local environment and/or phylogeny. The observed trait data underlying these models encompassed 491,001 unique observations across 13,189 species from 2,313 genera, with consistent representation across taxonomic orders. The resulting models were then used to generate trait estimates for 52,255 tree species, capturing approximately 80% of documented tree species⁹¹. Using this trait database, we were able to assign trait value to 81% of the tree species in GFBI reported to the species level. The eight traits we included in our metrics were chosen to include traits typically associated with plant invasion^{28,92} including those associated with dispersal, establishment, resource acquisition and competitive ability that represent the major trait clusters encompassing the full dimensionality of trait space from Maynard et al.⁸³ The eight traits included in our study were the following: wood density, root depth, leaf nitrogen, leaf phosphorus, leaf area, tree height, seed dry mass, and bark thickness. All traits were log-transformed and normalized to allow for statistically valid comparisons⁸³. To obtain functional diversity metrics analogous to those used for phylogenetic diversity, we used the dendrogram approach of Petchey and Gaston⁹³. Specifically, for every plot we calculated the species-by-species trait distance matrix encompassing all eight traits, and then used hierarchical clustering to create a functional dendrogram. This dendrogram was subsequently used to calculate 'functional richness' (analogous to Faith's phylogenetic diversity) and 'functional redundancy' (MNTD); we use this terminology for functional diversity to maintain naming of variables between phylogenetic and functional diversity analyses. Metrics were calculated in R using packages `ape`⁹⁴, `tidyverse`⁹⁵, `abdiv`⁹⁶, `doParallel`⁹⁷, `foreach`⁹⁸ and `pez`⁹⁹.

Because both functional and phylogenetic diversity metrics have unique limitations, we considered them both here so as to obtain a

more robust view of underlying patterns and processes. The benefit of phylogenetic diversity is that it does not rely on imputed data, and thus it provides more consistent results with lower uncertainty. However, phylogenetic diversity is only a loose proxy for functioning, depending on the degree to which the functional traits of interest are phylogenetically conserved. Thus, as a complement of this, we also use imputed trait values to estimate functional diversity, which should better capture underlying functional differences across species, but which is subject to higher uncertainty relative to phylogeny (or measured trait values), and may omit rare and potentially functionally unique species. Thus, by simultaneously considering both functional and phylogenetic diversity and showing that these metrics yield consistent global trends, our approach provides consistent evidence that these patterns are robust to the limitations of either approach taken individually.

Statistical analyses

We combined random forest¹⁰⁰ and GLM approaches to answer our focal questions. Specifically, we used random forest models to visualize patterns and determine variable importance, while GLMs were used to assess statistical significance and directionality of patterns. We first tested for environmental and anthropogenic drivers of non-native invasion, including non-native presence and invasion severity (non-native richness, non-native abundance). Our independent variables included either phylogenetic or functional metrics, climate and soil variables, and human impact variables. Next, we tested the impact of these variables on non-native invasion strategy (difference in MNTD due to non-natives). We focused on addressing specific hypotheses related to drivers of non-native invasion and invasion strategy. We acknowledge the importance of other variables, and therefore included them in our models, but do not interpret each variable.

Random forest models and GLMs used the same model designs. Models predicting non-native presence as well as invasion severity, for both non-native richness and abundance, included independent predictor variables of native diversity and native redundancy, as well as climate and human driver variables detailed in '*Climatic and anthropogenic variables*'. For comparison, we repeated these models with native tree species richness in place of both diversity variables (richness and redundancy), as species richness is commonly used in the invasion literature when testing for biotic resistance^{23,34,35}. Finally, we used an adapted version of the random forest models, removing diversity variables, to assess probability of locations with non-native trees globally and generate an associated map (Extended Data Fig. 1).

To account for spatial autocorrelation in the modelling step, we used residual autocovariates (RACs)^{101,102}. First, we used simple linear regression to determine the range of spatial autocorrelation for the models with continuous outcomes (invasion severity and invasion strategy). We then assessed residual spatial autocorrelation using correlelogram plots using the `ncf`¹⁰³ package in R, which showed that residual correlation was consistently negligible beyond 250 km, which was also applied to the models with binary outcomes (non-native presence). Using this buffer distance, we generated RAC values using the `autocov_dist()` function in the `spdep` package^{70,104}, which determines an inverse distance weighted residual value for each data point in the 250 km neighbourhood. RAC incorporates the spatial signature of the model residuals, relative to the model without any spatial autocorrelation correction, into a variable that is included in each model^{101,102}. The result is an inverse distance weighted residual value for each data point in the 250 km neighbourhood, which we used as continuous predictors in both the linear and random forest models.

Random forest models were used primarily to assess variable importance and influence. Specifically, we used Shapley additive explanations (SHAP) values to infer variable importance in the model outcome^{105,106}. SHAP values are a machine learning analogue of partial regression, quantifying the relative importance of each variable on the outcome, accounting for all other variables in the model. To estimate the SHAP

Article

values, random forest models were fit in R using the ranger package¹⁰⁷, using default hyperparameters (500 trees, observations sampled with replacement, number of variables per split equal to the square root of the number of predictors, a minimum of 5 observations per node). We then used the fastshap package¹⁰⁸ to estimate approximate SHAP values for each predictor, using $n = 100$ simulations. The overall variable importance was taken as the sum of the absolute value of the SHAP values, and the marginal effect of each variable was visualized by plotting the covariate versus the corresponding SHAP value for each observation.

To account for spatial autocorrelation in the accuracy assessment of random forest models, we implemented spatially-buffered leave-one-out cross-validation (LOO-CV) to obtain conservative lower-bound accuracy measures¹⁰⁹. To do this, we first randomly selected a focal observation as the test data, and then we omitted all observations within a 250 km buffer distance around this observation. The remaining data were used to train the model, and the resulting fit was used to predict outcome for the withheld focal observation. This was repeated 500 times for each model, each time selecting a new focal point and predicting its outcome using the 250 km spatially-buffered training set. The resulting accuracy measures were calculated on the set of 500 out-of-fit predictions. For continuous variables, we estimated accuracy using the cross-validated coefficient of determination relative to the one-to-one line (termed VE_{cv} ¹¹⁰), denoted simply R^2 here, and for binary outcomes we used area under the ROC curve (AUC), which quantifies the ability of the classifier to distinguish between classes, and serves as an assessment of model performance.

To create a global map of invasion probability and its local uncertainty, we used a repeated prediction approach in Google Earth Engine⁶⁰ (Extended Data Fig. 1a; AUC of spatial cross-validation = 0.84 ± 0.04 , mean F1 score of non-native presence = 0.36). This repeated prediction approach used the full dataset without any down-sampling. To our knowledge, no global maps on phylogenetic or functional diversity metrics exist, so we were unable to include these diversity metrics in the random forest model for mapping; therefore, these models include the same covariates as the other models except diversity metrics. We thought it reasonable to exclude diversity metrics in this analysis as distance to ports is the most important driver of invasion probability, while native diversity is less important. After aggregating samples within the 30-arcsec pixels, 368,030 data points remained for our repeated prediction approach. We first trained 50 random forest models on stratified bootstrapped samples with a total of 10,000 data points each, using biome as stratification category; this allowed us to repeatedly predict the probability of non-native presence for each terrestrial pixel on Earth. The resulting 50 predictions were used to create per-pixel mean and coefficient of variation maps of the probability of non-native presence, with probabilities calibrated using Platt scaling^{111,112}. These two maps allow us to investigate the patterns of invasion and the regions of uncertainty in the predictions. Next, the extrapolation extent was estimated as a per-pixel percentage of predictor variables, and interactions of predictor variables, outside of the training range, in univariate and multivariate space, respectively (Extended Data Fig. 1b)⁶⁰. In addition, to account for gaps in predictor space, we estimated the Area of Applicability¹¹³, used to mark regions of extrapolation in this map. All maps are restricted to regions with a minimum of 10% forest cover¹¹⁴.

GLM models were used to estimate statistical parameters and conduct statistical tests. All GLM models included the same variables as those in the random forest models. In the models predicting non-native presence, we used a binomial distribution and logit link. For non-native abundance, we used a beta regression approach to predict the proportion of non-native basal area, as a method of modelling proportions between 0 and 1. We could not use a binomial GLM analogous to that used for non-native abundance because basal area measurements were not whole numbers and we wanted to retain all information in the data. Finally, to account for spatial autocorrelation and non-independently

distributed residuals, we employed the inclusion of RACs as described above. These models were repeated separately for temperate and tropical bioclimatic zones, but results were qualitatively similar to the global model, so we report only global results here. All GLM results can be found in Supplementary Tables 3–5. GLMs were run in R (v. 4.2.2)¹¹⁵ using lme4¹¹⁶, lmerTest¹¹⁷, and betareg¹¹⁸, while visualizations for these models used ggplot2¹¹⁹; tidyverse⁹⁵ was used throughout as well.

Because invasion of non-native species may alter the native diversity of the site into which they invade, we conducted a sensitivity test using plots where we had data across two time points to incorporate this effect. We first took all plots for which we had two time points, where the first time point represented a fully native community (that is, no presence of non-natives; $n = 8,221$ plots). We then modelled the per cent change of species richness in each plot from this uninvaded first time point to a later time point. Our predictor variables included final invasion status (non-natives present or not) to determine the impact of invasion on per cent change of species richness, along with all climate, soil, and anthropogenic impact variables we included in other global models. We extracted the coefficient of final invasion status (along with upper and lower confidence ranges), which quantifies the per cent change in richness due to invasion, and we used this to update the native species richness of the full global dataset. We then used these coefficients to estimate the pre-invasion native diversity for each plot in the global dataset by adding the corresponding species change resulting from invasion. Finally, we reran our global analysis with this updated pre-invasion native diversity. The relative contribution of native species loss to biotic resistance was calculated by comparing the relative change in the richness coefficient for each of the updated models relative to the original model (Supplementary Table 9).

Non-native invasion strategy was predicted using the difference in redundancy (MNTD) in the tree community due to invasion. We included the same variables as in the previous set of models, except native redundancy, as this is integrated in our response variable and therefore would exhibit high collinearity. In GLM models, we tested for the interaction between MAP and MAT to detect potential non-additive environmental filtering effects of these two dominant climate variables. In addition, we tested for the interaction between each MAP and MAT with distance to ports, to examine whether this important anthropogenic driver modified main ecological relationships. Final reported models are those resulting from a process of first creating a full model with all interactions, and subsequently removing nonsignificant interactions. All GLM results for invasion strategy can be found in Supplementary Table 7.

Reporting summary

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

Data availability

Data used in this study can be found in cited references for the Global Naturalized Alien Flora (GloNAF) database⁶ (non-native status), the KEW Plants of the World database⁵ (native ranges) and the Global Environmental Composite^{63,77} (environmental data layers). Plant trait data were extracted from Maynard et al.⁷⁸. Data from the Global Forest Biodiversity Initiative (GFBI) database⁵⁷ are not available due to data privacy and sharing restrictions, but can be obtained upon request via Science-I (<https://science-i.org/>) or GFBI (gfbinitiative.org) and an approval from data contributors.

Code availability

All code used to complete analyses for the manuscript is available at the following link: <https://github.com/thomaslauber/Global-Tree-Invasion>. Data analyses were conducted and were visualizations generated

in R (v. 4.2.2), Python (v. 3.9.7), Google Earth Engine (earthengine-api 0.1.306), QGIS-LTR (v. 3.16.7) and the ETH Zurich Euler cluster.

70. Bivand, R. & Piras, G. Comparing implementations of estimation methods for spatial econometrics. *J. Stat. Softw.* **63**, 1–36 (2015).
71. Kalwij, J. M. Review of 'The Plant List, a working list of all plant species'. *J. Veg. Sci.* **23**, 998–1002 (2012).
72. Gorelick, N. et al. Google Earth Engine: planetary-scale geospatial analysis for everyone. *Remote Sens. Environ.* **202**, 18–27 (2017).
73. Beech, E., Rivers, M., Oldfield, S. & Smith, P. P. GlobalTreeSearch: the first complete global database of tree species and country distributions. *J. Sustain. For.* **36**, 454–489 (2017).
74. Catford, J. A., Veski, P. A., Richardson, D. M. & Pyšek, P. Quantifying levels of biological invasion: towards the objective classification of invaded and invulnerable ecosystems. *Glob. Change Biol.* **18**, 44–62 (2012).
75. Guo, Q. et al. A unified approach for quantifying invasibility and degree of invasion. *Ecology* **96**, 2613–2621 (2015).
76. Van Den Hoogen, J. et al. Soil nematode abundance and functional group composition at a global scale. *Nature* **572**, 194–198 (2019).
77. Bastin, J.-F. et al. The global tree restoration potential. *Science* **365**, 76–79 (2019).
78. Karger, D. N. et al. Climatologies at high resolution for the earth's land surface areas. *Sci. Data* **4**, 170122 (2017).
79. Stewart, S. et al. Climate extreme variables generated using monthly time-series data improve predicted distributions of plant species. *Ecography* **44**, 626–639 (2021).
80. Hengl, T. et al. SoilGrids250m: Global gridded soil information based on machine learning. *PLoS ONE* **12**, e0169748 (2017).
81. Global Ports. *All Layers and Tables (GLOBAL/GlobalPorts)* <https://gis.wfp.org/arcgis/rest/services/GLOBAL/GlobalPorts/MapServer/layers> (2021).
82. Global Airports. *The World Bank Data Catalog* <https://datacatalog.worldbank.org/search/dataset/O038117> (2021).
83. Maynard, D. S. et al. Global relationships in tree functional traits. *Nat. Commun.* **13**, 3185 (2022).
84. Joswig, J. S. et al. Climatic and soil factors explain the two-dimensional spectrum of global plant trait variation. *Nat. Ecol. Evol.* **6**, 36–50 (2022).
85. Florczyk, A. J. et al. *GHS Data Package 2019: Public Release GHS P2019* (European Commission, Joint Research Centre, 2019).
86. Owen, N. R., Gumbs, R., Gray, C. L. & Faith, D. P. Global conservation of phylogenetic diversity captures more than just functional diversity. *Nat. Commun.* **10**, 859 (2019).
87. Mazel, F. et al. Prioritizing phylogenetic diversity captures functional diversity unreliably. *Nat. Commun.* **9**, 2888 (2018).
88. Tucker, C. M. et al. A guide to phylogenetic metrics for conservation, community ecology and macroecology. *Biol. Rev.* **92**, 698–715 (2017).
89. Jin, Y. & Qian, H. V. PhyloMaker: an R package that can generate very large phylogenies for vascular plants. *Ecography* **42**, 1353–1359 (2019).
90. Strauss, S. Y., Webb, C. O. & Salamin, N. Exotic taxa less related to native species are more invasive. *Proc. Natl Acad. Sci. USA* **103**, 5841–5845 (2006).
91. Cazzolla Gatti, R. et al. The number of tree species on Earth. *Proc. Natl Acad. Sci. USA* **119**, e2115329119 (2022).
92. Pyšek, P. & Richardson, D. M. in *Biological Invasions* (ed. Nentwig, W.) 97–125 (Springer, 2008).
93. Petchey, O. L. & Gaston, K. J. Functional diversity (FD), species richness and community composition. *Ecol. Lett.* **5**, 402–411 (2002).
94. Paradis, E. & Schliep, K. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* **35**, 526–528 (2019).
95. Wickham, H. et al. Welcome to the Tidyverse. *J. Open Source Softw.* **4**, 1686 (2019).
96. Bittinger, K. Abdiv: Alpha and beta diversity measures. R package version 0.2.0 <https://cran.r-project.org/web/packages/abdiv/index.html> (2020).
97. Calaway, R., Analytics, R., Weston, S., Tenenbaum, D. & Calaway, M. doParallel: Foreach parallel adaptor for the 'parallel' package. R package version 1.0.17 <https://cran.r-project.org/web/packages/doParallel/index.html> (2015).
98. Microsoft & Weston, S. foreach: Provides foreach looping construct. R package version 1.5.1. <https://CRAN.R-project.org/package=foreach> (2020).
99. Pearse, W. D. et al. Pez: phylogenetics for the environmental sciences. *Bioinformatics* **31**, 2888–2890 (2015).
100. Breiman, L. Bagging predictors. *Mach. Learn.* **24**, 123–140 (1996).
101. Crase, B., Liedloff, A. C. & Wintle, B. A. A new method for dealing with residual spatial autocorrelation in species distribution models. *Ecography* **35**, 879–888 (2012).
102. Portier, J., Gauthier, S., Robitaille, A. & Bergeron, Y. Accounting for spatial autocorrelation improves the estimation of climate, physical environment and vegetation's effects on boreal forest's burn rates. *Landsc. Ecol.* **33**, 19–34 (2018).
103. Bjornstad, O. N. ncf: Spatial covariance functions. R package version 1.3-2 <https://cran.r-project.org/web/packages/ncf/index.html> (2022).
104. Bivand, R. S., Pebesma, E. J., Gómez-Rubio, V. & Pebesma, E. J. *Applied spatial data analysis with R* (Springer, 2008).
105. Lundberg, S. M. et al. From local explanations to global understanding with explainable AI for trees. *Nat. Mach. Intell.* **2**, 56–67 (2020).
106. Lundberg, S. M. & Lee, S.-I. in *Advances in Neural Information Processing Systems 30* (eds Guyon, I. et al.) (NIPS, 2017).
107. Wright, M. N., Wager, S. & Probst, P. Ranger: A fast implementation of random forests. R package version 0.12 (2020).
108. Greenwell, B. fastshap: Fast approximate Shapley values. R package version 0.0.7 <https://github.com/bggreenwell/fastshap> (2020).
109. Roberts, D. R. et al. Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. *Ecography* **40**, 913–929 (2017).
110. Li, J. Assessing the accuracy of predictive models for numerical data: not r nor r^2 , why not? Then what? *PLoS ONE* **12**, e0183250 (2017).
111. Platt, J. in *Advances in Large Margin Classifiers*, Vol. 10 (eds Smola, A. J. et al.) 61–74 (MIT Press, 1999).
112. Niculescu-Mizil, A. & Caruana, R. in *Proc. 22nd International Conference on Machine Learning* 625–632 (Association for Computing Machinery, 2005).
113. Meyer, H. & Pebesma, E. Predicting into unknown space? Estimating the area of applicability of spatial prediction models. *Methods Ecol. Evol.* **12**, 1620–1633 (2021).
114. FAO. *Global Forest Resources Assessment 2020: Main Report* (Food and Agriculture Organization of the United Nations, 2020).
115. R Core Team. R: A Language and Environment for Statistical Computing. <http://www.R-project.org/> (R Foundation for Statistical Computing, 2019).
116. Bates, D., Maechler, M., Bolker, B. & Walker, S. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* <https://doi.org/10.18637/jss.v067.i01> (2015).
117. Kunzetsova, A., Brockhoff, P. & Christensen, R. lmerTest package: tests in linear mixed effect models. *J. Stat. Softw.* <https://doi.org/10.18637/jss.v082.i13> (2017).
118. Zeileis, A. et al. betareg: Beta regression. R package version 3.1-4 <https://cran.r-project.org/web/packages/betareg/index.html> (2021).
119. Wickham, H., Chang, W. & Wickham, M. H. ggplot2: Create elegant data visualisations using the grammar of graphics. R package version 2 <https://search.r-project.org/CRAN/refmans/ggplot2/html/ggplot2-package.html> (2016).

Acknowledgements The authors acknowledge the Bernina Foundation and DOB Ecology for financial support. C.S.D. thanks the Swiss National Science Foundation (Postdoctoral Fellowship #TMPFP3_209925). C.S.D. also acknowledges funding from the Marc R. Benioff Revocable Trust, which, in collaboration with the World Economic Forum, also made this work possible. D.S.M. thanks the Swiss National Science Foundation (Ambizione Grant #PZ00P3_193612). The authors thank L. Mo for assistance in compiling the author list and G. Smith for early discussions about invasion severity. J.C.S. considers this work a contribution to Center for Ecological Dynamics in a Novel Biosphere (ECONOVO), funded by Danish National Research Foundation (grant DNRF173) and his VILLUM Investigator project 'Biodiversity Dynamics in a Changing World', funded by VILLUM FONDEN (grant 16549). P. Schall thanks the Deutsche Forschungsgemeinschaft (DFG) Priority Program 1374 Biodiversity Exploratories. G.A. thanks the French National Forest Inventory and the Italian Forest Inventory; G.A. was supported by the Italian National Recovery Plan through the National Biodiversity Future Center. Financial support from Monafor network in Mexico was funded by the National Forestry Commission (CONAFOR), Council of Science and Technology of the State of Durango (COCYTED), the Natural Environment Research Council, UK (NERC; NE/T011084/1), and local support of Ejidos and Comunidades.

Author contributions C.S.D., T.W.C., D.S.M. and C.M.Z. contributed the conceptualization of the project. C.S.D. and D.S.M. contributed methodology, investigation and project administration. All authors contributed to data collection and/or curation. C.S.D., D.S.M., N.M.R. and T.L. contributed visualization. T.W.C., D.S.M. and C.S.D. obtained funding and provided supervision. Writing was led by C.S.D. and D.S.M., with review and editing contributed by all other co-authors.

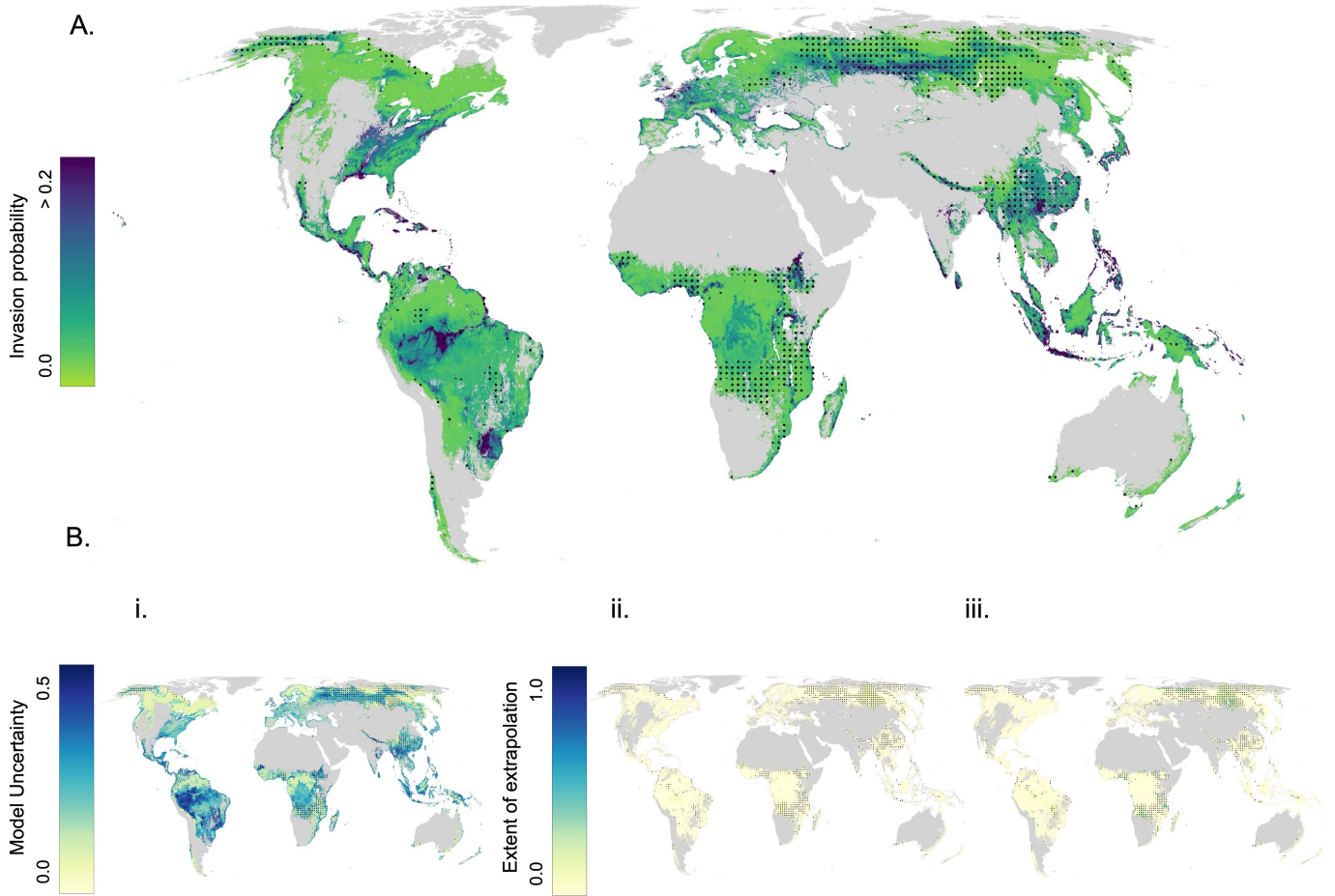
Funding Open access funding provided by Swiss Federal Institute of Technology Zurich.

Competing interests The authors declare no competing interests.

Additional information
Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s41586-023-06440-7>.

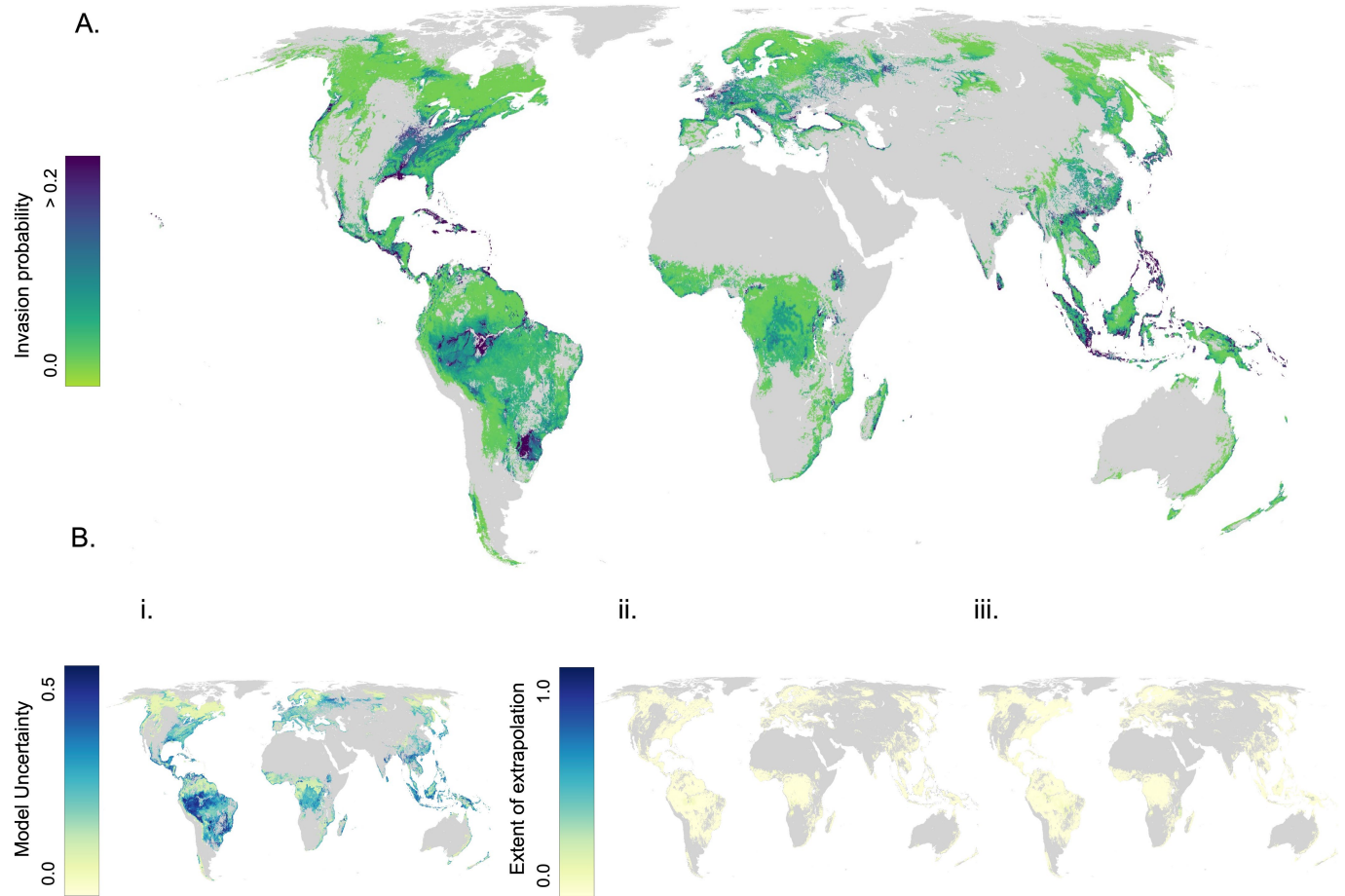
Correspondence and requests for materials should be addressed to Camille S. Delavaux.
Peer review information Nature thanks Blas Benito, Kevin Potter, Marcel Rejmánek and the other, anonymous, reviewer(s) for their contribution to the peer review of this work.

Reprints and permissions information is available at <http://www.nature.com/reprints>.



Extended Data Fig. 1 | Map of non-native invasion probability. Map showing probability of non-native tree presence based on the probability output of the random forest classifier (A, total $n = 368,030$ plots, n per iteration = 10,000 plots) alongside maps showing uncertainty in predictions (B) including

local uncertainty of invasion probability via bootstrapped coefficient of variation (i) and extent of extrapolation as percentage of bands outside univariate (ii) and multivariate (ii) training range. Regions outside the Area of Applicability are indicated with dots.



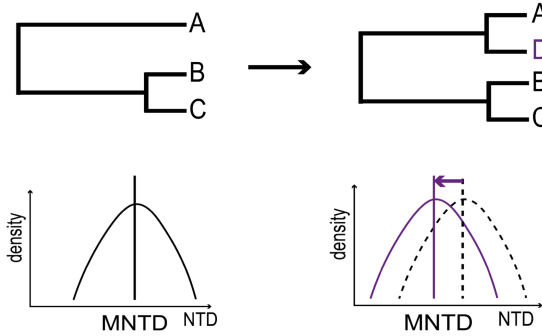
Extended Data Fig. 2 | Map of non-native invasion probability inside the area of applicability. Map showing probability of non-native tree presence based on the probability output of the random forest classifier (A, total $n = 368,030$ plots, n per iteration = 10,000 plots) alongside maps showing

uncertainty in predictions (B) including local uncertainty of invasion probability via bootstrapped coefficient of variation (i) and extent of extrapolation as percentage of bands outside univariate (ii) and multivariate (iii) training range. Regions outside the Area of Applicability are masked.

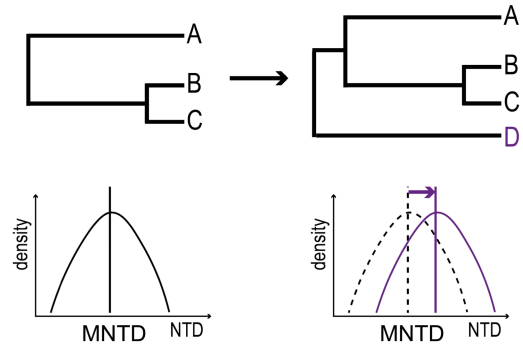
A.

$$MNTD = \frac{\sum_{i=1}^N \min (\sum_{j=1}^{N(j \neq i)} d_{ij})}{N}$$

B.

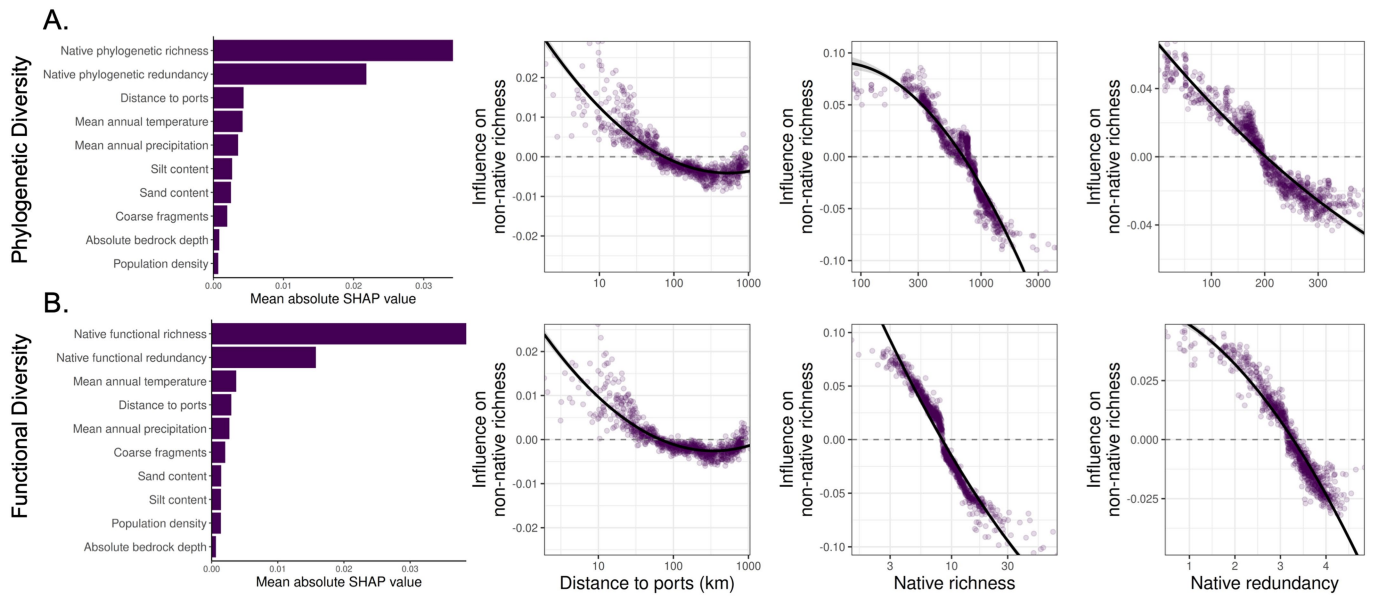


C.



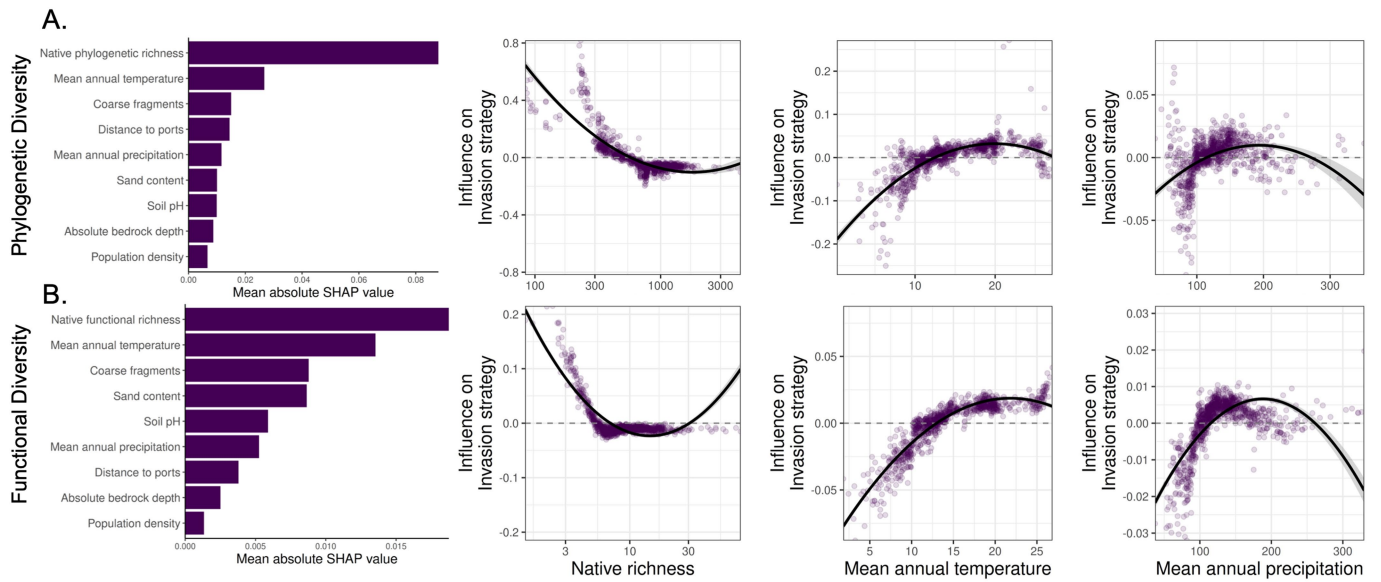
Extended Data Fig. 3 | Mean nearest taxon distance (MNTD). Mean nearest taxon distance is the average distance to nearest neighbor by branch length on the tree, which represents redundancy in the community (A). For each species i , the sum of all shortest distances d to each other taxa j is calculated; these values are then averaged across the total species in the tree (N). If invasion occurs via

non-natives being similar to the native community, this would lead to the expectation that MNTD decreases, increasing redundancy (B). Conversely, if non-native invasion occurs via non-natives being dissimilar to the native community, this would lead to the expectation that MNTD increases, reducing redundancy (C). Taxon D represents a non-native addition to the community.



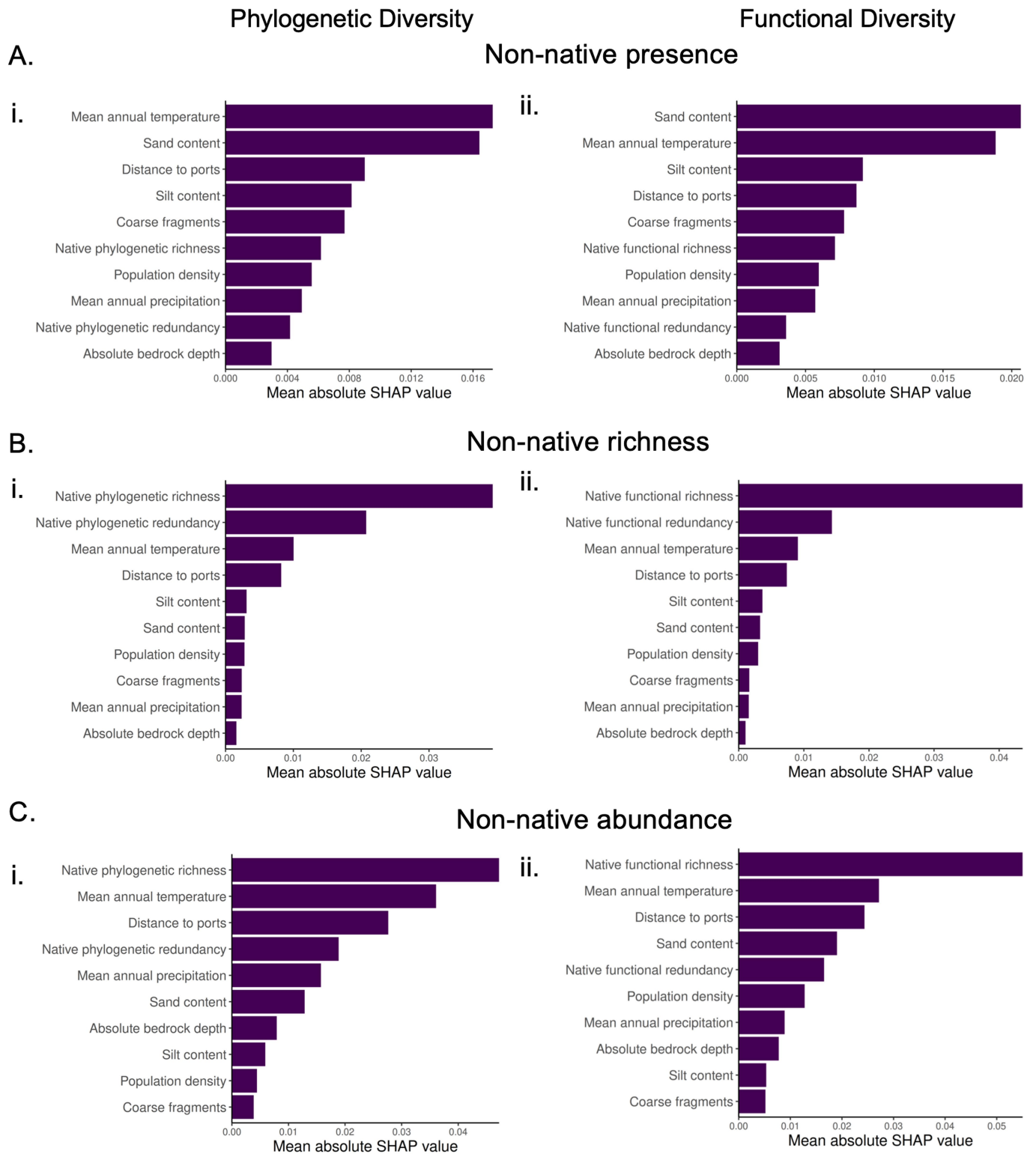
Extended Data Fig. 4 | Native diversity mediates degree of non-native invasion. Variable importance (SHAP values) of all variables included in random forest models, ordered from greatest to least importance alongside the influence of distance to ports, native richness and native redundancy on invasion severity (proportion of non-native plant species) for (A) phylogenetic

diversity and (B) functional diversity global models (phylogenetic $n = 3,498$ plots; functional $n = 3,368$ plots). All results shown are from random forest models. Note that y-axis ranges differ among panels, with the variable importance plots representing the corresponding magnitude.



Extended Data Fig. 5 | Variable importance for non-native invasion strategy. Variable importance (SHAP values) of all variables included in random forest models, ordered from greatest to least importance alongside influence of native richness, mean annual temperature and mean annual precipitation on invasion strategy for (A) phylogenetic diversity and (B) functional diversity

global models (phylogenetic $n = 3,498$ plots; functional $n = 3,368$ plots). All results shown are from random forest models. Note that y-axis ranges differ among panels, with the variable importance plots representing the corresponding magnitude. Error bands represent 95% confidence intervals.



Extended Data Fig. 6 | Variable importance for analyses using data down-sampled without preferentially retaining invaded plots. Variable importance (SHAP values) for all variables included in random forest models, ordered from greatest to least importance for (A) non-native presence, (B) richness, and (C) abundance, each for (i) phylogenetic diversity and (ii) functional diversity global models (presence: phylogenetic $n = 18,898$;

functional $n = 18,611$, richness: phylogenetic $n = 840$ plots; functional $n = 823$ plots, abundance: phylogenetic $n = 840$ plots; functional $n = 823$ plots). All results shown are from random forest models with down-sampled data, but without preferentially retaining invaded plots. Error bands represent 95% confidence intervals.

Reporting Summary

Nature Portfolio wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Portfolio policies, see our [Editorial Policies](#) and the [Editorial Policy Checklist](#).

Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a | Confirmed

- The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement
- A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
- The statistical test(s) used AND whether they are one- or two-sided
Only common tests should be described solely by name; describe more complex techniques in the Methods section.
- A description of all covariates tested
- A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
- A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
- For null hypothesis testing, the test statistic (e.g. F , t , r) with confidence intervals, effect sizes, degrees of freedom and P value noted
Give P values as exact values whenever suitable.
- For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
- For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
- Estimates of effect sizes (e.g. Cohen's d , Pearson's r), indicating how they were calculated

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

Data analysis

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio [guidelines for submitting code & software](#) for further information.

Data

Policy information about [availability of data](#)

All manuscripts must include a [data availability statement](#). This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our [policy](#)

Data used in this study can be found in cited references for the Global Naturalized Alien Flora (GloNAF) database⁶ (non-native status), the KEW Plants of the World database⁵ (native ranges), and the Global Environmental Composite^{65,82} (environmental data layers). Plant trait data were extracted from Maynard et al.⁸³ Data from Global Forest Biodiversity Initiative (GFBI) database⁵⁹ are not available due to data privacy and sharing restrictions, but can be obtained upon request via Science-I (<https://science-i.org/>) or GFBI (<https://www.gfbiinitiative.org/>) and an approval from data contributors.

Human research participants

Policy information about [studies involving human research participants and Sex and Gender in Research](#).

Reporting on sex and gender	N/A
Population characteristics	N/A
Recruitment	N/A
Ethics oversight	N/A

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

- Life sciences Behavioural & social sciences Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	We combined random forest and generalized linear model (GLM) approaches to answer our focal questions. Specifically, we used random forest models to visualize patterns and determine variable importance, while GLMs were used to assess statistical significance and directionality of patterns. We first tested for environmental and anthropogenic drivers of non-native invasion, including non-native presence and invasion severity (non-native richness, non-native abundance). Our independent variables included either phylogenetic or functional metrics, climate and soil variables, and human impact variables. Next, we tested the impact of these variables on non-native invasion strategy (difference in MNTD due to non-natives). We focused on addressing specific hypotheses related to drivers of non-native invasion and invasion strategy. We acknowledge the importance of other variables, and therefore included them in our models, but do not interpret each variable.
Research sample	The Global Forest Biodiversity Initiative (GFBI) database, which contains tree-level abundance data for more than 1.2 million forest plots on all continents across the globe, containing more than 31 million unique georeferenced records of tree size and density dating from 1958. Each observation in the dataset consists of a unique tree ID, plot ID, plot coordinates, tree diameter at breast height (DBH), tree-per-hectare expansion factors, year of measurement, and binomial species names.
Sampling strategy	To account for unequal representation of plots across biomes (Figure 1), we used a reduced version of this database, down-sampled to a number of plots proportional to the land area covered by each of 14 biomes (Table S1), while conserving as many tropical plots as possible. This ensured that we were not overrepresenting historically oversampled biomes (down-sampling), particularly in temperate regions. In addition, we preferentially retained invaded plots, or up-sampled to invasion within our down-sampling proportional to biome cover, to ensure that no more than half of the plots within a biome were invaded. This oversampling of invaded plots allowed for adequate representation of invaded and non-invaded plots in our analyses on non-native presence, and allowed sufficient data for our analyses of invasion severity, as these analyses only used data from plots that had non-native species invasions.
Data collection	Data collection varies across all datasets. Please refer to references for each dataset for more details.
Timing and spatial scale	Data timing and spatial scale varies across all datasets. Please refer to references for each dataset for more details.

Data exclusions	We applied several filters to this data before analyses. First, where plots had multiple years of data, we kept only the most recent year of census data. We then subset the data to include only plots with at least three species as required for our phylogenetic metrics, excluding monoculture forest plantations from the study.
Reproducibility	This study uses experimental data so was not possible to reproduce.
Randomization	Please see "Sampling strategy" for a detailed explanation of random subsampling.
Blinding	Blinding was not possible during data analysis.

Did the study involve field work? Yes No

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
<input checked="" type="checkbox"/>	<input type="checkbox"/> Antibodies
<input checked="" type="checkbox"/>	<input type="checkbox"/> Eukaryotic cell lines
<input checked="" type="checkbox"/>	<input type="checkbox"/> Palaeontology and archaeology
<input checked="" type="checkbox"/>	<input type="checkbox"/> Animals and other organisms
<input checked="" type="checkbox"/>	<input type="checkbox"/> Clinical data
<input checked="" type="checkbox"/>	<input type="checkbox"/> Dual use research of concern

Methods

n/a	Involved in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> ChIP-seq
<input checked="" type="checkbox"/>	<input type="checkbox"/> Flow cytometry
<input checked="" type="checkbox"/>	<input type="checkbox"/> MRI-based neuroimaging