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Global functional shifts in trees driven by alien naturalization and native extinction

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A list of authors and their affiliations appears at the end of the paper

Human activities are driving simultaneous native extinctions and alien naturalizations, reshaping global tree diversity with major implications for ecosystem structure and function. Here we analysed functional traits and environmental niches of 31,001 tree species worldwide, comparing naturalized, threatened and non-threatened species to assess current patterns and project future shifts under intensified extinction and naturalization. Future tree-rich ecosystems are projected to become increasingly dominated by fast-growing, high-resource-use species with acquisitive traits, while slow-growing, conservative species face greater extinction risk. Although group means along the main functional axes do not differ significantly, naturalized species occupy broader functional and environmental spaces and thrive in colder and more variable climates, whereas threatened species are more specialized to warm, stable and nutrient-rich environments, with non-threatened species intermediate. Projected naturalizations expand local functional diversity, but their acquisitive strategies could reduce long-term ecosystem stability, while extinctions cause pronounced contractions of functional and environmental trait space, especially in climatically variable regions. Overall, our findings reveal an accelerating global shift towards faster-growing tree communities, with likely consequences for carbon storage and biodiversity, underscoring the need to safeguard slow-growing species and limit the dominance of acquisitive trees.

Trees are fundamental components of terrestrial ecosystems, providing essential ecological, economic and social benefits. These benefits include regulating the climate by acting as carbon sinks[1–3] and serving as foundation species by providing habitat and food for diverse organisms[4–6]. However, intensified anthropogenic activities and environmental change over recent centuries have altered tree species distributions, leading to range contraction and elevating extinction risks for many threatened species[7–9]. At the same time, the introduction and spread of alien species (for example, naturalized species, a subset of alien species forming self-sustaining populations in their introduced ranges)[10,11] are further reshaping global tree diversity[12,13]. These dynamics can have cascading effects on ecosystem processes and stability[14,15], even though some alien trees may enhance certain ecosystem functions and provide benefits to humans[16,17]. Ultimately, such changes may influence the capacity of forests and woodlands to provide essential ecosystem services, potentially altering their long-term sustainability[9,18,19].

Although naturalized and threatened species follow contrasting ecological trajectories[20,21], they also share key similarities. Both are subject to distributional constraints that limit their fitness in novel and changing environments[20–22], and both are strongly influenced by human activities. Naturalized species often benefit from human-mediated dispersal and disturbance, enhancing their ability to establish and spread, while threatened species typically face range contractions and elevated extinction risks under similar pressures. Given these shared constraints but divergent outcomes, we hypothesize that naturalized and threatened tree species will occupy distinct functional and

e-mail: guowyhgy@gmail.com

environmental niches, reflecting differences in trait strategies and ecological tolerance[20,21,23]. Specifically, we expect that (1) naturalized species will occupy broader functional trait and environmental spaces characterized by acquisitive strategies (for example, fast growth and high resource use) and a relatively wide climatic tolerance[21,22], whereas (2) threatened species will be more functionally conservative (for example, slow growth and specialized traits)[21] and occur in narrower environmental niches (for example, warm, stable and resource-rich regions)[24,25].

The intensification of global change, including land-cover transformation, climate change and other anthropogenic pressures, may involve the introduction of many species to new areas[26,27], while simultaneously driving population declines and potential extinction within native ranges[28–30]. These dual processes of alien species expansion and native species loss contribute to the taxonomic homogenization of ecological floras[31–33]. However, the effects of these changes on the functional composition of the global tree flora and where these shifts are likely to occur remain unclear[34–36]. We predict that future assemblages will (1) become increasingly dominated by fast-growing, generalist species, particularly in climatically variable or colder environments; and (2) experience disproportionate losses of functional and environmental diversity due to extinctions in climatically stable regions, thereby narrowing the overall trait space. These projected changes are likely to compromise the resilience and functional integrity of forest ecosystems. Recognizing how alien expansions and native extinctions reshape functional composition is crucial for modelling invasion impacts and informing conservation priorities. In particular, identifying the combinations of environmental conditions and ecosystem states that favour alien species establishment, as well as those that exacerbate native species loss, will help guide the formulation of effective measures to protect ecosystems at risk[37–39].

Here we assess global differences in functional trait and environmental spaces between naturalized alien and threatened native tree species. We define threatened species according to the International Union for Conservation of Nature (IUCN) categories, and naturalized species as those establishing self-sustaining populations outside their native ranges after human introduction[11,40,41]. Specifically, we examined the functional traits and environmental trait spaces of three mutually exclusive species groups—naturalized, threatened and non-threatened—by analysing eight key leaf, wood and seed traits[42] (Supplementary Table 1) and 49 species-specific environmental parameters[43] (Supplementary Table 1) for tree species globally. Using principal component analysis (PCA) and multivariate kernel density estimations (trait probability density, TPD[44,45]), we quantified the functional and environmental spaces occupied by each group of species. Of the 31,001 (53.6% of known) tree species examined, 1,633 were classified as aliens naturalized somewhere in the world[10,11,46], while 9,529 species were identified as threatened, falling under the IUCN Red List Categories of critically endangered (CR), endangered (EN) and vulnerable (VU)[47] and supplemented by Bachman et al.[48]. The remaining 19,839 species were categorized as non-threatened (Supplementary Fig. 1).

We simulated future scenarios of species naturalization and extinction to evaluate the resulting shifts in the occupation of functional and environmental spaces. For the naturalization scenario, we identified potential candidates for future naturalization from the pool of currently non-threatened species ($n = 19{,}839$) by assessing their exposure to recent rates of changes in nine major anthropogenic drivers, including climate change, fire and cropland expansion[28], together with their economic uses by humans, a key global predictor of plant naturalization[49,50]. For each species, exposure values were extracted from global spatial layers describing the intensity of these pressures, and a composite similarity score was calculated by comparing each non-threatened species' exposure and use profile with that of already naturalized species. In reclassifying species as future naturalized species, we assumed that ongoing or accelerating global change may drive similar ecological responses. This scenario is exploratory and does not imply that all such species will inevitably become naturalized; rather it identifies those most likely to do so under continuing anthropogenic pressures. For the extinction scenario, we reclassified the remaining non-threatened species after the previous step and threatened species probabilistically according to IUCN-Red-List-category-specific extinction probabilities[35,44], thereby generating a range of plausible future assemblages. We applied both scenarios to the global tree dataset to project potential reorganizations of functional and environmental trait spaces. Scenario outcomes were quantified as differences in TPD distributions between current and future conditions. This enabled us to assess both the direction and magnitude of projected shifts in functional and environmental space occupancy, providing a foundation for anticipating species at risk of extinction or with high naturalization potential and for identifying geographic regions likely to experience future changes in species composition.

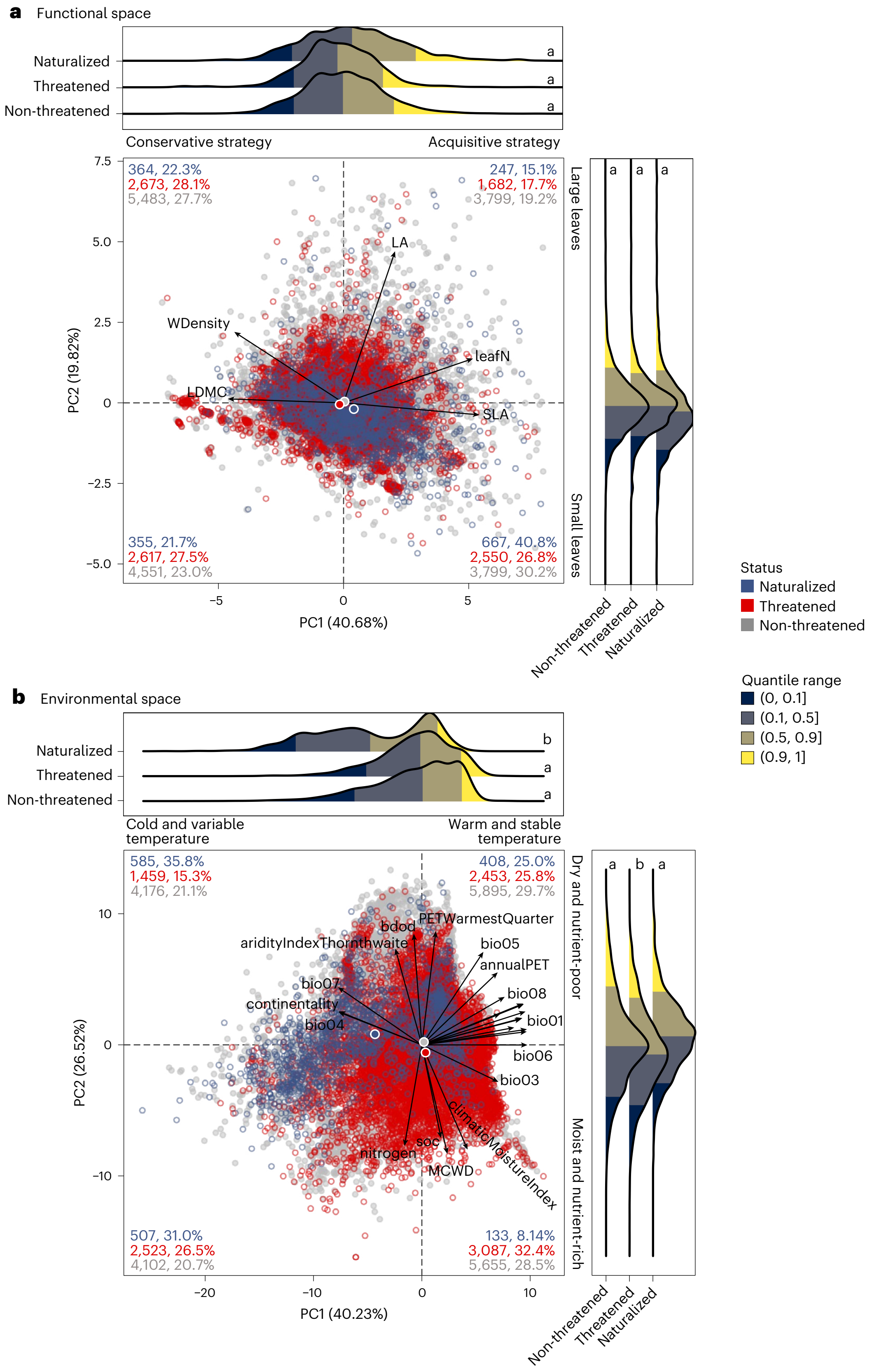
Results

Functional and environmental characteristics of tree species worldwide

The first two axes of the PCA for functional space explain 60.5% of the variance in traits (40.7% for PC1 and 19.8% for PC2; Fig. 1a and Supplementary Table 2). PC1 captures the plant economics spectrum[51–53], where positive scores indicate an acquisitive strategy (fast growth and high resource use rates) and negative scores indicate a conservative strategy (slow growth and resource conservation). PC2 reflects size-related traits, with higher scores corresponding to larger leaf sizes. This functional PCA aligns with the classic global spectra of plant form and function[52], and similar findings have been observed in other tree trait analyses[54]. Across the naturalized, threatened and non-threatened species groups, none of the means of the first two PCs showed a significant difference (Supplementary Table 4; phylogenetic-corrected analyses of variance (ANOVAs), $P > 0.05$), as species tend to cluster around the middle of the PCA space. However, naturalized species span a broader range along both axes than threatened and non-threatened species (Fig. 1a). Threatened species tend to exhibit a more conservative strategy, with

Fig. 1 | Functional and environmental spaces of tree species. a,**b**, Functional (**a**) and environmental (**b**) spaces of 31,001 tree species analysed in this study based on PCA of eight functional traits and 49 environmental variables (see Supplementary Table 1 for a description of each variable). The species were categorized as naturalized ($n = 1{,}633$), non-threatened ($n = 19{,}839$) and threatened ($n = 9{,}529$) (Supplementary Fig. 1), represented as blue, grey and red open points, respectively. The centroids of each species group are shown as closed points in the corresponding colours. The numbers and percentages in each corner represent the species count and its corresponding proportion relative to the total number of species in the respective group for that specific quadrant. The density plots along the first and second PCs illustrate the distributions of species PC scores for the three groups, with different letters indicating significant differences based on phylogenetically corrected ANOVAs ($P < 0.05$; Supplementary Table 4). In the functional space (**a**), the PC1 axis represents the leaf economic spectrum, while the PC2 axis represents the size spectrum (Supplementary Table 2). In the environmental space (**b**), PC1 represents a thermal gradient, with higher values indicating species adapted to warm and stable temperatures and lower values indicating species adapted to cold and variable temperatures; PC2 represents a gradient of water and nutrient availability, with higher values indicating species adapted to dry and nutrient-poor conditions and lower values indicating species adapted to moist and nutrient-rich conditions (Supplementary Table 3). For both **a** and **b**, only variables showing strong correlations (≥0.75) with each of the first two PC axes are shown. In **a**, SLA, specific leaf area; leafN, leaf nitrogen content; LA, leaf area; WDensity, woody density; LDMC, leaf dry matter content. In **b**, variables strongly correlated with the PC1 axis were randomly selected to facilitate visualization. The detailed descriptions of the abbreviations of environmental variables are provided in Supplementary Table 1.

55.6% positioned in the conservative (negative) half of the PC1 axis, whereas naturalized species, on average, show a more acquisitive strategy (55% in the positive half). In terms of size (PC2), all three groups tend to be characterized by small leaves, with 62.6%, 54.2% and 53.1% of naturalized, threatened and non-threatened species, respectively, falling into this category. Notably, 40.8% of naturalized species occupy the quadrant combining an acquisitive strategy with small leaf size—approximately 2.7 times more than those in the acquisitive large-leaf quadrant and 1.8 times more than in the conservative-strategy quadrats. In contrast, threatened and non-threatened species are more



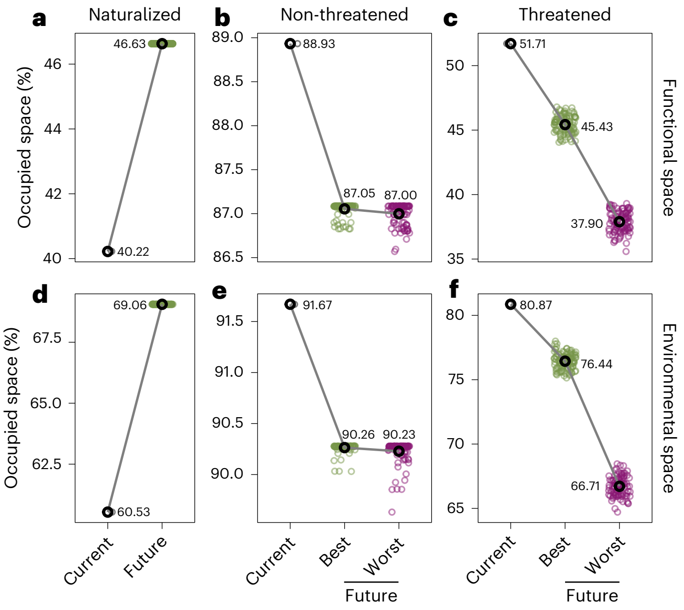


Fig. 2 | Shifts of the occupied functional and environmental PC spaces between current and future projection scenarios, represented as the occupied space in the 0.99 quantile distribution (representing the existing trait and environmental boundaries at the global scale) for each of the three tree groups. a–f, The ratio (in percentage) between the occupied space of each group and the spaces of total species is shown. For both the best-case and worst-case extinction scenarios, the points indicate the corresponding values of the 100 simulations, and the open black circles indicate the mean values of the simulations. The current value and the mean of the 100 simulations of future functional and environmental spaces for each species group are shown in Supplementary Fig. 2.

evenly distributed across the functional PCA space, although they also have fewer species in the acquisitive large-leaf quadrant, similar to naturalized species.

The first two axes of the PCA for environmental space explain 66.8% of the variance in environmental variables (40.2% for PC1 and 26.5% for PC2; Fig. 1b and Supplementary Table 3). PC1 primarily captures the thermal regime and its variability, with positive scores reflecting warm and stable climates (for example, higher annual mean temperature and minimum temperature of the coldest month) and negative scores reflecting colder, more fluctuating environments (for example, higher temperature annual range and temperature seasonality). PC2 represents precipitation patterns and soil quality, with positive scores indicating dry, nutrient-limited conditions and negative scores indicating moist, nutrient-rich environments. Naturalized species span a broader range along the environmental PC1 axis than the other two groups. They are more frequently found in colder and more variable climates in drier and nutrient-limited regions than threatened species, which are common in warmer, moister and nutrient-rich environments (Fig. 1b and Supplementary Table 4; $P < 0.05$). In contrast, non-threatened species display a more even distribution in the environmental space, with a slight preference (58.2%) for warmer and more stable environments.

Composition dynamics of tree functional and environmental spaces

We applied discriminant analysis of principal components (DAPC) to identify 771 of the 19,839 non-threatened species with responses similar to those of currently naturalized species, suggesting their potential future naturalization (Supplementary Table 6). The analysis explained 64% of the model variation, with species' responses to fire and cropland expansion and their economic uses by humans being the three most significant contributors (Supplementary Table 5). Meanwhile, we simulated two future extinction scenarios for the remaining non-threatened (that is, 19,068) and threatened species using an IUCN-category-based extinction probability method[35,44]. These scenarios represent best- and worst-case outcomes by applying lower or higher extinction risk probabilities for threatened (0.1 and 0.999, respectively) and non-threatened (0.0001 and 0.01, respectively) species. The simulations estimated that 2,986 species would go extinct under the best-case scenario and 6,028 species under the worst-case scenario. Consequently, the projected future species pool consists of 2,404 naturalized species, 3,576 or 6,568 threatened species and 18,993 or 19,043 non-threatened species under the worst-case and best-case extinction scenarios, respectively (Supplementary Fig. 1).

PCAs of functional traits and environmental variables under the projected naturalization and extinction scenarios revealed distinct shifts in trait space occupancy (Supplementary Fig. 2). For naturalized species, the proportion of occupied space in both functional and environmental PC spaces is projected to increase from 40.2% to 46.6% and from 60.5% to 69.1%, respectively (Fig. 2a,d). In contrast, the PC spaces occupied by threatened and non-threatened species are expected to shrink due to species extinctions (Fig. 2b,c,e,f). This reduction is particularly pronounced for threatened species, with both functional and environmental spaces predicted to contract by approximately 14% under the worst-case scenario (Fig. 2c,f). Non-threatened species showed a smaller (~1.5%) decrease in both PC spaces (Fig. 2b,e).

In addition to changes in PC space occupancy of each category, the projected future scenarios caused notable shifts in both functional and environmental spectra, as revealed by overlapping current and projected probability densities for all tree species. Both the worst-case projection scenario (Fig. 3) and the best-case scenario (Supplementary Fig. 3) showed broadly consistent patterns, despite some differences in PC space occupancy for threatened species group (Fig. 2). The shifts in functional spectra were asymmetrical, with greater reductions in the conservative portion of the PC1 axis (left) and a concomitant increase in the acquisitive half (Fig. 3a). Despite relatively stable dissimilarities and high shared proportions between the three species groups under current and future projected scenarios (Supplementary Fig. 4a–c,m–o), these changes suggest that the projected naturalized species cannot fully compensate for the functional losses caused by the projected extinctions, and vice versa. A similar pattern emerged in the environmental space, with marked increases in species associated with either warm, stable, moist and nutrient-rich conditions or dry, nutrient-poor regions, alongside reductions in the colder, more variable environments (Fig. 3b). An increase in the non-overlapping areas (Supplementary Fig. 4k) in the environmental space between current and future projected scenarios resulted in ~10% reductions in dissimilarities between the naturalized and non-threatened species groups as well as the naturalized and threatened species groups (Supplementary Fig. 4d,e). This indicates a substantial contraction of the environmental space due to the projected extinction of currently threatened and non-threatened species, and an extensive expansion of the environmental space occupied by projected naturalized species, with those contractions and expansions occurring predominantly in divergent environmental regions (Fig. 3b).

Discussion

Human activities are reshaping tree communities worldwide through the simultaneous extinction of native species and expansion of alien species, leading to significant shifts in functional trait and environmental spaces. Our results indicate that future tree-rich ecosystems (that is, ecosystems where trees play an ecologically prominent role—through either structural dominance or functional importance) could be increasingly dominated by species with acquisitive traits, characterized by rapid growth, short lifespans and rapid return of sequestered carbon to the atmosphere[55], while slow-growing, conservative species face

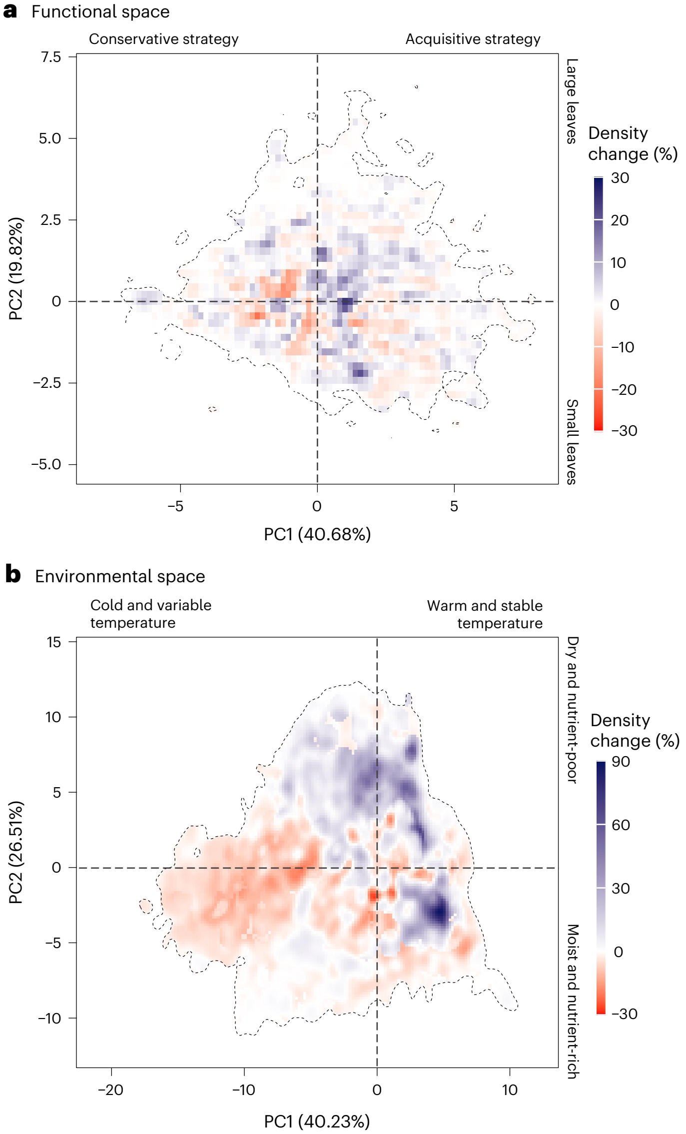


Fig. 3 | Shifts in functional and environmental spectra. a,**b**, Shifts in functional (**a**) and environmental spectra (**b**), expressed as changes in kernel density estimates (that is, TPDs), for tree species between the current state and the worst-case projected future scenario (that is, changes of species pools). Red tones indicate regions where TPD values decrease (that is, those traits or environmental preferences become less frequent in the future), while blue tones indicate areas where TPD values increase, indicating traits or environmental preferences that are expected to become more prevalent. The dashed contour lines represent the 0.99 quantile of the current functional and environmental space, delineating the existing boundaries of trait and environmental preferences at the global scale. Detailed explanations of each PC are provided in Fig. 1. The worst-case projected future scenario was simulated by applying different extinction probabilities to non-threatened and threatened species that were classified as data deficient (DD) and not evaluated (NE) by IUCN; that is, non-threatened species were assigned probabilities corresponding to near threatened (NT), and threatened species were assigned probabilities corresponding to CR.

heightened extinction risks. Naturalized species, typically generalists, exhibit a broader range of functional strategies, allowing them to thrive across diverse environmental conditions, particularly in colder and more variable climates (Supplementary Fig. 5a). In contrast, threatened tree species are primarily confined to warm, stable and nutrient-rich environments (Supplementary Fig. 5b), making them highly vulnerable to habitat disturbances and climatic fluctuations. Together with our future projections, this suggests that, as naturalized species continue to establish in new regions, they will drive an expansion of acquisitive trait dominance, yet this increase will not compensate for the functional and environmental losses caused by species extinctions. These findings highlight the complex shifts in tree biodiversity driven by human activities, emphasizing the urgent need for not only the mitigation of the dominance of acquisitive alien species but also the protection of functionally distinct, slow-growing native trees to maintain ecosystem processes and resilience.

Because of their contrasting fortunes, naturalized alien and threatened species are often assumed to be distinct[20–23]. However, despite clear differences in geographic ranges and human economic uses (Supplementary Fig. 6), our results revealed no significant differences in the average functional PCs between these groups. Despite being currently outnumbered by threatened and non-threatened species, naturalized alien tree species spanned a broader range of functional strategies, enabling them to survive in diverse environments. This is further reinforced by their economic utility, which facilitates human-assisted spread (that is, relatively high introduction effort in temperate regions)[50,56,57], and their broader environmental tolerances[58], leading to larger geographic distributions—especially in variable climates[21] and frequently disturbed habitats[49,59]. However, naturalized species are less frequently found in warm and stable climates with moist and nutrient-rich conditions, probably due to the strong biotic resistance of native species[60–62] and relatively low propagule pressure in these areas[11,57]. We also found a higher proportion of naturalized species adopting an acquisitive strategy, particularly among those with small leaves (40.8% of the total naturalized tree species). Consequently, the naturalization of tree species is shaped by a combination of high human affiliation, large environmental niches, high tolerance to diverse conditions, and fast economic traits and life cycles.

In contrast, both threatened and non-threatened tree species displayed very similar functional strategies, although threatened species exhibited a slightly narrower functional range and a tendency towards more conservative strategies. Threatened species also inhabit regions with less climate variability, particularly moist, nutrient-rich regions[21], such as eastern Madagascar and Central America (Supplementary Fig. 5b). These species, often endemic to tropical and subtropical regions (for example, tropical moist broadleaf forest[63]), face high competition for resources and thus adopt conservative traits[64,65], characterized by thick leaves, high wood density, slow growth and self-compatibility. Threatened tree species have narrower environmental niches, lower tolerance to environmental change and specialized habitat adaptation[28,42,66].

Under projected scenarios of naturalization and extinction, the functional and environmental spaces occupied by tree species showed notable shifts in both extent and intensity. Importantly, these shifts are asynchronous: the expansion of naturalized species does not fully compensate for the loss of functional and environmental space resulting from species extinctions. Future naturalized tree species are more likely to exhibit acquisitive strategies and have small leaves, whereas species at greater risk of extinction tend to possess more conservative traits and are concentrated in moist, nutrient-rich and climatically variable regions. Unlike present trends, future naturalized tree species may increasingly establish in warmer and relatively stable climates. This shift probably reflects broader environmental tolerances or intensified anthropogenic impacts, such as increased human-facilitated dispersal, habitat modifications and climate change[33,60,66,67]. While present-day naturalized species span colder and more variable environments (Fig. 1b), the projected environmental shifts (Fig. 3b) indicate that future tree assemblages will become increasingly dominated by species associated with warm and climatically stable regions. This transition reflects both the loss of cold-adapted threatened taxa and the continued expansion of generalist or warm-tolerant naturalized species. However, the potential loss of endemic species, particularly within tropical and subtropical biodiversity hotspots (Supplementary Figs. 7

and 8), remains a critical concern[7,8,42,66]. Although some losses from potential extinctions in trait space might be occupied by newly naturalized species, such replacements could further endanger native specialists in these regions[68]. An important caveat here is that our projections rely on currently naturalized species as proxies for future naturalizations. This assumes some continuity in the traits associated with naturalization success. However, the naturalization of trees is typically a slow, time-lagged process, and currently naturalized species may disproportionately represent fast-establishing, human-associated taxa[49,50]. In contrast, species with slower demographic strategies may still be in the lag phase of naturalization and thus underrepresented[41,69]. Nevertheless, given the inherently slow spread of such woody species, they are unlikely to substantially influence functional composition in the near future[70,71].

Our results indicate that future tree-rich ecosystems may become more dominated by functionally acquisitive species characterized by rapid growth, high resource uptake and short lifespans[52,53]. While the extent of these shifts is unknown, they could potentially enhance primary productivity and nutrient cycling efficiency in the short term but might also reduce ecosystem stability[53,72] and compromise long-term carbon storage, as fast-growing acquisitive species tend to have low resilience to stress and resource limitation[73,74]. The decline of conservative species, which are critical for maintaining ecosystem resilience and long-term services[66], highlights the importance of anticipating and mitigating the ecological consequences of trait-based shifts. Active management strategies, such as replanting locally extinct species, restoring functional megafauna[75–77] and controlling invasive species, can help buffer these impacts. By facilitating seed dispersal and establishment of conservative tree species and reducing the dominance of acquisitive alien species through targeted disturbances[78,79], such interventions can counteract the homogenizing influence of naturalizations. Ultimately, these efforts support ecosystem functions dependent on conservative traits[80], thereby enhancing biodiversity and promoting long-term ecosystem stability and resilience.

While our results show significant shifts in functional trait and environmental space due to projected tree species naturalization and extinction, they do not imply that all predicted events will necessarily occur. Both naturalization and extinction are driven by complex, occasional and often unpredictable processes[20–23], particularly given the relatively slow growth rates and long life cycles of tree species. Our binary classification of naturalization and extinction status may oversimplify nuanced ecological dynamics underlying these processes. Naturalization success can also be represented by metrics such as the area occupied or the number of regions colonized[49] while extinction risk may be better captured by measures of functional extinction[81]. Moreover, naturalization and extinction are not always mutually exclusive; for instance, *Pinus radiata* is narrowly distributed in its native range around the Californian coast but has naturalized extensively worldwide[82]. Despite these simplifications, our findings aim to illustrate potential future trends under a relatively conservative scenario for both naturalization and extinction (particularly given that the analysis includes only 53.6% of known tree species)[57] and assuming continued species exchange and ongoing changes in habitat conditions. In addition, our analysis is generally scale-free, as we did not incorporate spatial information. This is because the species-specific traits and environmental variables we used are based on mean values—representing theoretical optima—across a species' entire distribution range. While this approach overlooks intraspecific variation and local adaptation (particularly across native and introduced ranges for naturalized species), it remains widely applied in global-scale analyses where data availability is limited[52,83]. Consequently, our findings may differ from those of other studies[21] that show that naturalized alien species tend to be more acquisitive and occur in nutrient-rich sites. The scale-free nature of our analysis also prevents us from assessing the potential impacts of projected naturalization on native species, in particular threatened species that co-occur in the same ecosystems. Future studies at finer scales, complemented by experimental and standardized field-based approaches, and expanded global functional trait datasets are therefore needed to better understand the potential ecological consequences of tree species naturalization and extinction.

Our findings reveal that the concurrent processes of tree naturalization and species extinction are reshaping the global functional and environmental diversity of trees. Future tree-rich ecosystems are projected to be increasingly dominated by acquisitive species—characterized by rapid growth, high resource uptake and short lifespans—while slow-growing, conservative species face elevated extinction risks. This shift, accompanied by a tendency towards species associated with warmer and more stable climates (Fig. 3), may enhance short-term productivity and nutrient cycling but at the expense of long-term carbon storage and ecosystem stability. The projected expansion of naturalized species will not fully offset the loss of functionally and climatically distinct native trees, leading to an overall contraction of functional and environmental spaces. These trends highlight the urgency of proactive conservation and restoration strategies that both safeguard slow-growing, stress-tolerant species and curb the dominance of highly acquisitive alien species[79,80]. Maintaining broad functional and climatic diversity among tree species will be essential for sustaining ecosystem resilience and biodiversity in a rapidly changing world.

Methods

Data collection

We identified global tree species from previous published literature[42,84,85]. For these species, eight functional traits, including five leaf traits, one seed trait and two whole-plant traits (see Supplementary Table 1 for the details) were obtained from Guo et al. and Xu et al.[42,86]. These traits were initially extracted from major trait databases, including TRY (https://try-db.org/TryWeb/Home.php ref. 87), TOPIC[88–90] and BIEN (http://bien.nceas.ucsb.edu/bien/ refs. 91,92). Missing values were imputed using Bayesian hierarchical probabilistic matrix factorization (BHPMF), a robust and recommended gap-filling technique for functional trait studies[83,87,93]. Although functional trait data were available for only 11,659 species with at least one recorded trait, with measured values covering 6.67–26.1% of traits (Supplementary Table 1), the BHPMF imputation achieved a relatively low root mean squared error of 0.087, indicating robust performance and high imputation accuracy. This reliability is supported by the strong phylogenetic signals in all eight traits (Pagel's λ ranging from 0.602 to 0.954)[42,86]. We also extracted species' environmental requirements from the Tree Globally Observed Environmental Ranges (TreeGOER[43]) database. This database provides information on the environmental requirements on 38 bioclimatic, 8 soil and 3 topographic variables (see Supplementary Table 1 for the details) for 48,129 tree species. Although TreeGOER provides several summary metrics for each environmental variable (for example, mean, median, minimum and maximum), they are highly correlated. Therefore, only the mean values were used for further analysis to avoid redundancy. This study includes the 41,835 tree species that have data on both functional traits and environmental preferences for the following steps.

We aligned these tree species to the Global Naturalized Alien Flora database[10,46] to identify existing naturalized species, and 1,633 records were matched. We classified the conservation status of the remaining species according to the IUCN Red List[47] and the GlobalTreeSearch database[94]. Specifically, species classified as CR, EN or VU were considered threatened, while NT and least concern (LC) were considered non-threatened. For species classified as DD or NE, we updated their status following Bachman et al.[48], who used Bayesian additive regression trees to predict the extinction risk (threatened versus non-threatened) of angiosperms using multiple species characteristics (for example, range size, human footprint and climate). Accordingly, the 15,067 species classified as DD or NE were classified as non-threatened (6,383 species) or threatened (5,342 species).

We excluded species that have no informative IUCN conservation status and/or have low confidence (that is, predictions outside the 95% credible interval) of estimation in the predicted database. This process resulted in a total of 31,001 species being included in further analyses, with 1,633, 19,839 and 9,529 species classified as naturalized, non-threatened and threatened, respectively. The current distribution of naturalized tree species is broad but shows concentrations in northeastern and Central America, most of Europe and southeastern China. In contrast, threatened tree species are predominantly distributed in tropical regions, with notable hotspots in Madagascar and Central America (Supplementary Fig. 5).

Identifying species with potential for future naturalization or extinction

To identify potential naturalized species from non-threatened species, we applied DAPC using the adegenet package (v.2.1.10)[95] in R[96]. DAPC is a multivariate statistical method that combines PCA and discriminant analysis to identify clusters of related candidates[97]. The analysis used non-threatened and naturalized tree species' exposure to changes in major threats over a 20-year period (2000–2020) as input, including the percentage of each species' range burned, deforested, converted to cropland or urbanized, with tree cover decline per year as well as yearly changes in minimum and maximum temperature, precipitation and vapour pressure deficit within each species' extent[28]. We also included two key predictors of naturalization: species' human economic uses and native range size[49,50]. PCA was first performed on these collected metrics to reduce data dimensionality, and the resulting components were used as input for discriminant analysis to maximize differences between naturalized and non-threatened species while minimizing within-group variation. Three DAPC models were developed with stepwise inclusion of the change rates, human economic uses and native range size. The model incorporating change rates of major threats and human economic uses performed best, with 64% of the total variation explained. Non-threatened species identified as naturalized by DAPC were classified as potential naturalized species, resulting in 771 species being projected as naturalized.

To simulate future extinction, probabilities of extinction were assigned to both remaining non-threatened and threatened species according to their IUCN categories[35,44]: 0.0001 for LC, 0.01 for NT, 0.1 for VU, 0.667 for EN and 0.999 for CR. For the 15,067 species classified as non-threatened or threatened, two extinction scenarios were applied: (1) a best-case scenario, where non-threatened species were treated as LC and threatened species as VU; and (2) a worst-case scenario, where non-threatened species were treated as NT and threatened species as CR. For each scenario, the expected number of extinctions was calculated for each IUCN category, and species were randomly selected for extinction accordingly. This process was repeated 100 times to account for uncertainty in predicting which species might go extinct. Under the projected future scenario (Supplementary Fig. 7), naturalized species are more likely to originate from tropical areas, particularly parts of Africa and Malaysia (Supplementary Fig. 8a). This pattern may reflect the current underrepresentation of tropical regions as donors of naturalized species[11], the appeal of charismatic tropical species for introduction[49,50,98] and increasing global connectivity between tropical and non-tropical regions[99]. Potential extinction events are projected to occur primarily in regions that already host high numbers of threatened species (Supplementary Fig. 8b,c).

Data analysis

We performed several PCAs on the scaled functional traits and environmental spaces of all 30,983 species using the function PCA from the R package FactoMineR (v.2.11)[100]. The first two PC axes, together explaining over 60% of the total variation (Supplementary Tables 2 and 3), were used to construct two-dimensional functional and environmental spaces for global tree species, following the approach of Carmona et al.[44]. To assess whether the three species groups differ in functional traits and environmental spaces, we conducted phylogenetically corrected ANOVAs using the phylANOVA function from the R package phytools (v.2.3.0)[101] on the scores of the first two PCs, with a species-specific phylogeny of trees[42].

To analyse the occupied areas of the three species groups within the functional trait and environmental spaces under current and projected future scenarios, we estimated the probabilistic distribution of species across these spaces using multivariate kernel density estimations implemented in the R packages TPD (v.1.1.0)[45] and ks (v.1.14.3)[102,103]. Each functional and environmental space was divided into 40,000 cells (200 per dimension), and the TPD value was estimated for each cell. The TPD value of a cell reflects the relative density of species in that part of the space compared to the total number of species, representing areas where species share similar functional traits or environmental preferences. For future functional trait and environmental spaces of non-threatened and threatened species, the mean TPD value per cell was calculated across the 100 randomizations and used for visualization.

The area occupied by each species group, and by all species collectively, was quantified at the 99% quantile threshold within the functional and environmental spaces to minimize the influence of potential outliers. This estimation was conducted for both current scenarios and all randomizations of future scenarios. To assess changes between current and future conditions, we calculated the ratio of the area occupied by each species group to the total area. We also computed overlap-based dissimilarity and its decomposition (shared versus non-shared area) among each pair of the three species groups across scenarios, following the methodology described in Carmona et al.[44]. Furthermore, we quantified changes in the functional and environmental spectra under future scenarios by estimating the differences in occupied space of each species group. Specifically, for each group, we calculated the impact of simulated naturalization and extinction by subtracting, for each cell, the TPD value under future scenarios from the corresponding value under current conditions. Positive and negative values indicate increases and decreases in the relative density of species in each cell, respectively. For non-threatened and threatened species, these differences were averaged across all randomizations to generate mean changes for visualization.

Reporting summary

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

Data availability

The data that support the findings of this study are available via GitHub at https://github.com/kun-ecology/global_tree.fun-env.space and are mirrored on Zenodo at https://doi.org/10.5281/zenodo.17662284 (ref. 104). The trait data were obtained from ref. 42, and the environmental data were extracted from ref. 43.

Code availability

R scripts for reproducing the analyses and figures are available via GitHub at https://github.com/kun-ecology/global_tree.fun-env.space and are mirrored on Zenodo at https://doi.org/10.5281/zenodo.17662284 (ref. 104).

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Author contributions

W.-Y.G. conceived the project. J.M.S.-D., W.-Y.G., C.C.F.B., R.K. and all others collected the data. K.G. and W.-Y.G. analysed the data. W.-Y.G., K.G. and J.-C.S. interpreted the data and wrote the manuscript. All authors contributed data, discussed the results, revised the manuscript drafts, contributed to writing and approved the final manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to Wen-Yong Guo.

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Wen-Yong Guo[1,2,3] ✉, Josep M. Serra-Diaz[4], Kun Guo[5], Coline C. F. Boonman[6], Franziska Schrodt[7], Brian S. Maitner[8], Cory Merow[9], Cyrille Violle[10], Madhur Anand[11], Hans Henrik K. Bruun[12], Chaeho Byun[13], Jane A. Catford[14,15], Bruno E. L. Cerabolini[16], Eduardo Chacón-Madrigal[17,18], Daniela Ciccarelli[19], Anh Tuan Dang-Le[20,21,22], Arildo S. Dias[23], Aelton B. Giroldo[24], Alvaro G. Gutiérrez[25,26], Steven Jansen[27], Jens Kattge[28,29], Roeland Kindt[30], Tamir Klein[31], Koen Kramer[32,33], Christopher H. Lusk[34], Adam R. Martin[35], Sean T. Michaletz[36], Vanessa Minden[37], Akira S. Mori[38], Ülo Niinemets[39], Yusuke Onoda[40], Josep Peñuelas[41,42], Jan Pisek[43], Bjorn J. M. Robroek[44], Brandon Schamp[45], Nadejda A. Soudzilovskaia[46], Nelson Thiffault[47], Fons van der Plas[6], Brian J. Enquist[48,49] & Jens-Christian Svenning[50]

[1]Zhejiang Tiantong Forest Ecosystem National Observation and Research Station, Institute of Eco-Chongming & Research Center for Global Change and Ecological Forecasting, School of Ecological and Environmental Sciences, East China Normal University, Shanghai, P. R. China. [2]Zhejiang Zhoushan Island Ecosystem Observation and Research Station, Zhoushan, P. R. China. [3]State Key Laboratory of Estuarine and Coastal Research, East China Normal University, Shanghai, P. R. China. [4]Botanical Institute of Barcelona (CSIC-CMCNB), Barcelona, Spain. [5]Northeast Institute of Geography and Agroecology, Chinese Academy Sciences, Changchun, P. R. China. [6]Plant Ecology and Nature Conservation Group, Wageningen University, Wageningen, the Netherlands. [7]School of Geography, University of Nottingham, Nottingham, UK. [8]Department of Integrative Biology, University of South Florida, St. Petersburg, FL, USA. [9]Department of Ecology and Evolution and Eversource Energy Center, University of Connecticut, Storrs, CT, USA. [10]CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France. [11]School of Environmental Sciences, University of Guelph, Guelph, Ontario, Canada. [12]Department of Biology, University of Copenhagen, Copenhagen, Denmark. [13]Department of Biological Sciences, Gyeongkuk National University, Andong, Republic of Korea. [14]Department of Geography, King's College London, London, UK. [15]Fenner School of Environment & Society, Australian National University, Canberra, Australian Capital Territory, Australia. [16]Department of Biotechnology and Life Sciences, University of Insubria, Varese, Italy. [17]Herbario Luis Fournier Origgi, Centro de Investigación en Biodiversidad y Ecología Tropical, Universidad de Costa Rica, San José, Costa Rica. [18]Herbario Nacional, Departamento de Historia Natural, Museo Nacional de Costa Rica, San José, Costa Rica. [19]Department of Biology, University of Pisa, Pisa, Italy. [20]Department of Ecology—Evolutionary Biology, Faculty of Biology—Biotechnology, VNUHCM—University of Science, Ho Chi Minh City, Vietnam. [21]Vietnam National University, Ho Chi Minh City, Vietnam. [22]Center for Biodiversity Conservation and Endangered Species, Ho Chi Minh City, Vietnam. [23]FSC—International Center—Forest Stewardship Council, Bonn, Germany. [24]Embrapa Maranhão, Brazilian Agricultural Research Corporation (Embrapa), São Luís, Brazil. [25]Departamento de Ciencias Ambientales y Recursos Naturales Renovables, Facultad de Ciencias Agronómicas, Universidad de Chile, Santiago, Chile. [26]Instituto de Ecología y Biodiversidad, Santiago, Chile. [27]

Institute of Botany, Ulm University, Ulm, Germany. [28]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany. [29]Max Planck Institute for Biogeochemistry, Jena, Germany. [30]Trees and Forest Genetic Resources and Biodiversity, World Agroforestry, CIFOR-ICRAF, Nairobi, Kenya. [31]Department of Plant & Environmental Sciences, Weizmann Institute of Science, Rehovot, Israel. [32]Forest Ecology and Management Group, Wageningen University, Wageningen, the Netherlands. [33]Land Life Company, Amsterdam, the Netherlands. [34]Environmental Research Institute, University of Waikato, Hamilton, New Zealand. [35]Department of Physical and Environmental Sciences, University of Toronto Scarborough, Toronto, Ontario, Canada. [36]Department of Botany and Biodiversity Research Centre, University of British Columbia, Vancouver, British Columbia, Canada. [37]Department of Biology, Vrije Universiteit Brussel, Brussels, Belgium. [38]Research Center for Advanced Science and Technology, University of Tokyo, Tokyo, Japan. [39]Estonian University of Life Sciences, Tartu, Estonia. [40]Division of Forest and Biomaterials Science, Graduate School of Agriculture, Kyoto University, Kyoto, Japan. [41]CREAF, Barcelona, Spain. [42]CSIC, Global Ecology Unit CREAF-CSIC-UAB, Barcelona, Spain. [43]Tartu Observatory, University of Tartu, Tõravere, Estonia. [44]Department of Ecology, Radboud Institute for Biological and Environmental Sciences, Faculty of Science, Radboud University, Nijmegen, the Netherlands. [45]Department of Biology, Algoma University, Sault Ste. Marie, Ontario, Canada. [46]Centre for Environmental Sciences (CMK), Hasselt University, Hasselt, Belgium. [47]Canadian Forest Service, Natural Resources Canada, Quebec City, Quebec, Canada. [48]Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ, USA. [49]Santa Fe Institute, Santa Fe, NM, USA. [50]Center for Ecological Dynamics in a Novel Biosphere (ECONOVO), Department of Biology, Aarhus University, Aarhus, Denmark. ✉e-mail: guowyhgy@gmail.com

nature portfolio

Corresponding author(s): Wen-Yong Guo

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Reporting Summary

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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	All collected data was first processed in Microsoft Excel 365.
Data analysis	All data analyses were conducted in R v4.2.3. We used R package adegenet (version 2.1.11), FactoMineR (version 2.11), phytools (version 2.4-4), TPD (version 1.1.0), and ks (version 1.10.7).

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

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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

The data that supported the study are available on Github (https://github.com/kun-ecology/global_tree.fun-env.space/tree/main). Specifically, the trait data was obtained from [Guo, W. Y. et al. High exposure of global tree diversity to human pressure. Proc. Natl. Acad. Sci. U S A 119, e2026733119 (2022)]; and the

environmental data was extracted from [Kindt, R. TreeGOER: A database with globally observed environmental ranges for 48,129 tree species. Glob. Chang. Biol. 29, 6303–6318 (2023)].

Research involving human participants, their data, or biological material

Policy information about studies with human participants or human data. See also policy information about sex, gender (identity/presentation), and sexual orientation and race, ethnicity and racism.

Reporting on sex and gender	n.a.
Reporting on race, ethnicity, or other socially relevant groupings	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

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Life sciences study design

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

Sample size	*Describe how sample size was determined, detailing any statistical methods used to predetermine sample size OR if no sample-size calculation was performed, describe how sample sizes were chosen and provide a rationale for why these sample sizes are sufficient.*
Data exclusions	*Describe any data exclusions. If no data were excluded from the analyses, state so OR if data were excluded, describe the exclusions and the rationale behind them, indicating whether exclusion criteria were pre-established.*
Replication	*Describe the measures taken to verify the reproducibility of the experimental findings. If all attempts at replication were successful, confirm this OR if there are any findings that were not replicated or cannot be reproduced, note this and describe why.*
Randomization	*Describe how samples/organisms/participants were allocated into experimental groups. If allocation was not random, describe how covariates were controlled OR if this is not relevant to your study, explain why.*
Blinding	*Describe whether the investigators were blinded to group allocation during data collection and/or analysis. If blinding was not possible, describe why OR explain why blinding was not relevant to your study.*

Behavioural & social sciences study design

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

Study description	*Briefly describe the study type including whether data are quantitative, qualitative, or mixed-methods (e.g. qualitative cross-sectional, quantitative experimental, mixed-methods case study).*
Research sample	*State the research sample (e.g. Harvard university undergraduates, villagers in rural India) and provide relevant demographic information (e.g. age, sex) and indicate whether the sample is representative. Provide a rationale for the study sample chosen. For studies involving existing datasets, please describe the dataset and source.*
Sampling strategy	*Describe the sampling procedure (e.g. random, snowball, stratified, convenience). Describe the statistical methods that were used to predetermine sample size OR if no sample-size calculation was performed, describe how sample sizes were chosen and provide a rationale for why these sample sizes are sufficient. For qualitative data, please indicate whether data saturation was considered, and what criteria were used to decide that no further sampling was needed.*
Data collection	*Provide details about the data collection procedure, including the instruments or devices used to record the data (e.g. pen and paper, computer, eye tracker, video or audio equipment) whether anyone was present besides the participant(s) and the researcher, and whether the researcher was blind to experimental condition and/or the study hypothesis during data collection.*

Timing	*Indicate the start and stop dates of data collection. If there is a gap between collection periods, state the dates for each sample cohort.*
Data exclusions	*If no data were excluded from the analyses, state so OR if data were excluded, provide the exact number of exclusions and the rationale behind them, indicating whether exclusion criteria were pre-established.*
Non-participation	*State how many participants dropped out/declined participation and the reason(s) given OR provide response rate OR state that no participants dropped out/declined participation.*
Randomization	*If participants were not allocated into experimental groups, state so OR describe how participants were allocated to groups, and if allocation was not random, describe how covariates were controlled.*

Ecological, evolutionary & environmental sciences study design

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

Study description	By integrating functional traits and environmental characteristics across 31,001 tree species, we identify key differences among naturalized, threatened, and non-threatened species.
Research sample	Initial data collection was performed on all validated tree species following the GlobalTreeSearch v1.6, including taxonomic names and phylogeny, from existing and openly accessible databases. Due to the lack of data for specific species, some species were discarded from the analyses, leaving 31,001 species included in the study.
Sampling strategy	This is not an experimental study and we used all available data from the the multiple databases.
Data collection	The data was extracted by the authors, and the exact data sources are: Guo, W. Y. et al. High exposure of global tree diversity to human pressure. Proc. Natl. Acad. Sci. U S A 119, e2026733119 (2022); and Kindt, R. TreeGOER: A database with globally observed environmental ranges for 48,129 tree species. Glob. Chang. Biol. 29, 6303–6318 (2023).
Timing and spatial scale	The study is at a global scale and the temporal scale is not revelant.
Data exclusions	Only species with insufficient information (e.g., no IUCN category) were excluded.
Reproducibility	In the Methods section, we have provided a detailed description of each analysis, such as R packages and set-ups, to make sure our analyses are reproducible. In addition, the custom code and data used in the study are available in a GitHub repository (https://github.com/kun-ecology/global_tree.fun-env.space) and are mirrored on Zenodo (https://zenodo.org/records/17662284).
Randomization	As an global study, randomization is not applied here.
Blinding	Blinding was not relevant to our global study.

Did the study involve field work? ☐ Yes ☒ No

Field work, collection and transport

Field conditions	*Describe the study conditions for field work, providing relevant parameters (e.g. temperature, rainfall).*
Location	*State the location of the sampling or experiment, providing relevant parameters (e.g. latitude and longitude, elevation, water depth).*
Access & import/export	*Describe the efforts you have made to access habitats and to collect and import/export your samples in a responsible manner and in compliance with local, national and international laws, noting any permits that were obtained (give the name of the issuing authority, the date of issue, and any identifying information).*
Disturbance	*Describe any disturbance caused by the study and how it was minimized.*

Reporting for specific materials, systems and methods

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

Materials & experimental systems

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

Methods

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

Antibodies

Antibodies used	*Describe all antibodies used in the study; as applicable, provide supplier name, catalog number, clone name, and lot number.*
Validation	*Describe the validation of each primary antibody for the species and application, noting any validation statements on the manufacturer's website, relevant citations, antibody profiles in online databases, or data provided in the manuscript.*

Eukaryotic cell lines

Policy information about cell lines and Sex and Gender in Research

Cell line source(s)	*State the source of each cell line used and the sex of all primary cell lines and cells derived from human participants or vertebrate models.*
Authentication	*Describe the authentication procedures for each cell line used OR declare that none of the cell lines used were authenticated.*
Mycoplasma contamination	*Confirm that all cell lines tested negative for mycoplasma contamination OR describe the results of the testing for mycoplasma contamination OR declare that the cell lines were not tested for mycoplasma contamination.*
Commonly misidentified lines (See ICLAC register)	*Name any commonly misidentified cell lines used in the study and provide a rationale for their use.*

Palaeontology and Archaeology

Specimen provenance	*Provide provenance information for specimens and describe permits that were obtained for the work (including the name of the issuing authority, the date of issue, and any identifying information). Permits should encompass collection and, where applicable, export.*
Specimen deposition	*Indicate where the specimens have been deposited to permit free access by other researchers.*
Dating methods	*If new dates are provided, describe how they were obtained (e.g. collection, storage, sample pretreatment and measurement), where they were obtained (i.e. lab name), the calibration program and the protocol for quality assurance OR state that no new dates are provided.*

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Ethics oversight	*Identify the organization(s) that approved or provided guidance on the study protocol, OR state that no ethical approval or guidance was required and explain why not.*

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Animals and other research organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research, and Sex and Gender in Research

Laboratory animals	*For laboratory animals, report species, strain and age OR state that the study did not involve laboratory animals.*
Wild animals	*Provide details on animals observed in or captured in the field; report species and age where possible. Describe how animals were caught and transported and what happened to captive animals after the study (if killed, explain why and describe method; if released, say where and when) OR state that the study did not involve wild animals.*
Reporting on sex	*Indicate if findings apply to only one sex; describe whether sex was considered in study design, methods used for assigning sex. Provide data disaggregated for sex where this information has been collected in the source data as appropriate; provide overall*

	numbers in this Reporting Summary. Please state if this information has not been collected. Report sex-based analyses where performed, justify reasons for lack of sex-based analysis.
Field-collected samples	*For laboratory work with field-collected samples, describe all relevant parameters such as housing, maintenance, temperature, photoperiod and end-of-experiment protocol OR state that the study did not involve samples collected from the field.*
Ethics oversight	*Identify the organization(s) that approved or provided guidance on the study protocol, OR state that no ethical approval or guidance was required and explain why not.*

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Clinical data

Policy information about clinical studies

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Clinical trial registration	*Provide the trial registration number from ClinicalTrials.gov or an equivalent agency.*
Study protocol	*Note where the full trial protocol can be accessed OR if not available, explain why.*
Data collection	*Describe the settings and locales of data collection, noting the time periods of recruitment and data collection.*
Outcomes	*Describe how you pre-defined primary and secondary outcome measures and how you assessed these measures.*

Dual use research of concern

Policy information about dual use research of concern

Hazards

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

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

Experiments of concern

Does the work involve any of these experiments of concern:

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☐	☐	Confer resistance to therapeutically useful antibiotics or antiviral agents
☐	☐	Enhance the virulence of a pathogen or render a nonpathogen virulent
☐	☐	Increase transmissibility of a pathogen
☐	☐	Alter the host range of a pathogen
☐	☐	Enable evasion of diagnostic/detection modalities
☐	☐	Enable the weaponization of a biological agent or toxin
☐	☐	Any other potentially harmful combination of experiments and agents

Plants

Seed stocks	n.a.
Novel plant genotypes	n.a.
Authentication	n.a

ChIP-seq

Data deposition

☐ Confirm that both raw and final processed data have been deposited in a public database such as GEO.

☐ Confirm that you have deposited or provided access to graph files (e.g. BED files) for the called peaks.

Data access links *May remain private before publication.*	*For "Initial submission" or "Revised version" documents, provide reviewer access links. For your "Final submission" document, provide a link to the deposited data.*
Files in database submission	*Provide a list of all files available in the database submission.*
Genome browser session (e.g. UCSC)	*Provide a link to an anonymized genome browser session for "Initial submission" and "Revised version" documents only, to enable peer review. Write "no longer applicable" for "Final submission" documents.*

Methodology

Replicates	*Describe the experimental replicates, specifying number, type and replicate agreement.*
Sequencing depth	*Describe the sequencing depth for each experiment, providing the total number of reads, uniquely mapped reads, length of reads and whether they were paired- or single-end.*
Antibodies	*Describe the antibodies used for the ChIP-seq experiments; as applicable, provide supplier name, catalog number, clone name, and lot number.*
Peak calling parameters	*Specify the command line program and parameters used for read mapping and peak calling, including the ChIP, control and index files used.*
Data quality	*Describe the methods used to ensure data quality in full detail, including how many peaks are at FDR 5% and above 5-fold enrichment.*
Software	*Describe the software used to collect and analyze the ChIP-seq data. For custom code that has been deposited into a community repository, provide accession details.*

Flow Cytometry

Plots

Confirm that:

☐ The axis labels state the marker and fluorochrome used (e.g. CD4-FITC).

☐ The axis scales are clearly visible. Include numbers along axes only for bottom left plot of group (a 'group' is an analysis of identical markers).

☐ All plots are contour plots with outliers or pseudocolor plots.

☐ A numerical value for number of cells or percentage (with statistics) is provided.

Methodology

Sample preparation	*Describe the sample preparation, detailing the biological source of the cells and any tissue processing steps used.*
Instrument	*Identify the instrument used for data collection, specifying make and model number.*
Software	*Describe the software used to collect and analyze the flow cytometry data. For custom code that has been deposited into a community repository, provide accession details.*

Cell population abundance	*Describe the abundance of the relevant cell populations within post-sort fractions, providing details on the purity of the samples and how it was determined.*
Gating strategy	*Describe the gating strategy used for all relevant experiments, specifying the preliminary FSC/SSC gates of the starting cell population, indicating where boundaries between "positive" and "negative" staining cell populations are defined.*

☐ Tick this box to confirm that a figure exemplifying the gating strategy is provided in the Supplementary Information.

Magnetic resonance imaging

Experimental design

Design type	*Indicate task or resting state; event-related or block design.*
Design specifications	*Specify the number of blocks, trials or experimental units per session and/or subject, and specify the length of each trial or block (if trials are blocked) and interval between trials.*
Behavioral performance measures	*State number and/or type of variables recorded (e.g. correct button press, response time) and what statistics were used to establish that the subjects were performing the task as expected (e.g. mean, range, and/or standard deviation across subjects).*

Acquisition

Imaging type(s)	*Specify: functional, structural, diffusion, perfusion.*
Field strength	*Specify in Tesla*
Sequence & imaging parameters	*Specify the pulse sequence type (gradient echo, spin echo, etc.), imaging type (EPI, spiral, etc.), field of view, matrix size, slice thickness, orientation and TE/TR/flip angle.*
Area of acquisition	*State whether a whole brain scan was used OR define the area of acquisition, describing how the region was determined.*

Diffusion MRI ☐ Used ☐ Not used

Preprocessing

Preprocessing software	*Provide detail on software version and revision number and on specific parameters (model/functions, brain extraction, segmentation, smoothing kernel size, etc.).*
Normalization	*If data were normalized/standardized, describe the approach(es): specify linear or non-linear and define image types used for transformation OR indicate that data were not normalized and explain rationale for lack of normalization.*
Normalization template	*Describe the template used for normalization/transformation, specifying subject space or group standardized space (e.g. original Talairach, MNI305, ICBM152) OR indicate that the data were not normalized.*
Noise and artifact removal	*Describe your procedure(s) for artifact and structured noise removal, specifying motion parameters, tissue signals and physiological signals (heart rate, respiration).*
Volume censoring	*Define your software and/or method and criteria for volume censoring, and state the extent of such censoring.*

Statistical modeling & inference

Model type and settings	*Specify type (mass univariate, multivariate, RSA, predictive, etc.) and describe essential details of the model at the first and second levels (e.g. fixed, random or mixed effects; drift or auto-correlation).*
Effect(s) tested	*Define precise effect in terms of the task or stimulus conditions instead of psychological concepts and indicate whether ANOVA or factorial designs were used.*

Specify type of analysis: ☐ Whole brain ☐ ROI-based ☐ Both

Statistic type for inference (See Eklund et al. 2016)	*Specify voxel-wise or cluster-wise and report all relevant parameters for cluster-wise methods.*
Correction	*Describe the type of correction and how it is obtained for multiple comparisons (e.g. FWE, FDR, permutation or Monte Carlo).*

Models & analysis

n/a	Involved in the study
☐	☐ Functional and/or effective connectivity
☐	☐ Graph analysis
☐	☐ Multivariate modeling or predictive analysis

Functional and/or effective connectivity	*Report the measures of dependence used and the model details (e.g. Pearson correlation, partial correlation, mutual information).*
Graph analysis	*Report the dependent variable and connectivity measure, specifying weighted graph or binarized graph, subject- or group-level, and the global and/or node summaries used (e.g. clustering coefficient, efficiency, etc.).*
Multivariate modeling and predictive analysis	*Specify independent variables, features extraction and dimension reduction, model, training and evaluation metrics.*