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RESEARCH ARTICLE

Dominance and rarity in tree communities across the globe: Patterns, predictors and threats

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Abstract

Aim: Ecological and anthropogenic factors shift the abundances of dominant and rare tree species within local forest communities, thus affecting species composition and ecosystem functioning. To inform forest and conservation management it is important

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to understand the drivers of dominance and rarity in local tree communities. We answer the following research questions: (1) What are the patterns of dominance and rarity in tree communities? (2) Which ecological and anthropogenic factors predict these patterns? And (3) what is the extinction risk of locally dominant and rare tree species?

Location: Global.

Time period: 1990–2017.

Major taxa studied: Trees.

Methods: We used 1.2 million forest plots and quantified local tree dominance as the relative plot basal area of the single most dominant species and local rarity as the percentage of species that contribute together to the least 10% of plot basal area. We mapped global community dominance and rarity using machine learning models and evaluated the ecological and anthropogenic predictors with linear models. Extinction risk, for example threatened status, of geographically widespread dominant and rare species was evaluated.

Results: Community dominance and rarity show contrasting latitudinal trends, with boreal forests having high levels of dominance and tropical forests having high levels of rarity. Increasing annual precipitation reduces community dominance, probably because precipitation is related to an increase in tree density and richness. Additionally, stand age is positively related to community dominance, due to stem diameter increase of the most dominant species. Surprisingly, we find that locally dominant and rare species, which are geographically widespread in our data, have an equally high rate of elevated extinction due to declining populations through large-scale land degradation.

Main conclusions: By linking patterns and predictors of community dominance and rarity to extinction risk, our results suggest that also widespread species should be considered in large-scale management and conservation practices.

KEYWORDS

community, dominance, environmental predictors, forests, macroecology, rarity, species abundance, species population threats

1 | INTRODUCTION

Tree communities typically contain a few dominant and relatively many rare tree species, both of which contribute to ecosystem functioning, resilience and services (Dee et al., 2019; McGill et al., 2007). Communities are defined as 'a group of interacting species populations occurring together in space' (Roughgarden & Diamond, 1986; Stroud et al., 2015) and it is therefore important to analyse what drives local dominance and rarity, and hence, species composition. Here, dominance and rarity refer to the relative abundance of dominant and rare species in the community (Hillebrand et al., 2008). Dominant tree species make up most of the community biomass and contribute therefore most to ecosystem services, whereas rare tree species increase functional diversity and therefore ecosystem multifunctionality (Fauset et al., 2015; Grime, 1998; Mouillot et al., 2013). Habitat conversion and degradation shift the abundances of dominant and rare species within communities and may lead to species loss, with potentially strong impacts on ecosystem functioning and biodiversity (Bowler et al., 2017; Butchart et al., 2010; Doncaster et al., 2016; Fei et al., 2017; Xu et al., 2014). Quantifying broad-scale dominance and rarity patterns at a tree community level and identifying the predictors of extinction risk of locally dominant and rare tree species are therefore critical for management and conservation (Chapin et al., 2000; Enquist et al., 2019; Wilsey et al., 2009).

Patterns in community dominance and rarity are shaped by interacting biotic and abiotic factors operating at various scales. First, global patterns in the relative abundance of species generally follow the latitudinal gradient in diversity (Liang et al., 2022; Scheiner & Rey-Benayas, 1994; Ulrich et al., 2016). In general, species-rich forests have many rare species, whereas less speciose forests tend to have relatively few species that are more evenly distributed (Bazzaz, 1975; Hordijk et al., 2023). By definition, only a few

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species can dominate a community, although the absolute dominance might differ between forest types (Pitman et al., 2001; Ter Steege et al., 2013); forests can either be dominated by one single species or multiple species (Hart et al., 1989; Hobi et al., 2015). Second, abiotic factors shape community dynamics by filtering out species that cannot survive in a given environment, which subsequently can increase the abundance of well adapted species (Arnillas & Cadotte, 2019; Avolio et al., 2019; Venn et al., 2011). Once a species is established, its abundance will be determined by its suitability to the abiotic environment, and by interactions with the biotic environment, such as competition and facilitation (Goldberg, 1990; Lynn et al., 2019; Meier et al., 2010). Across environmental gradients, the suitability of species to the local environment shifts, leading to differences in community composition (Cornwell & Ackerly, 2009). Third, dominant and rare species can also directly affect each other's abundance through interactions, whereby dominant species compete for resources and ultimately exclude rare species from the community when they reach a high abundance (Markham, 2015; Zhang et al., 2015). Besides the biotic and abiotic factors shaping tree communities, also (historical) forest management and preference for certain tree species affects tree community composition (Albert et al., 2023; Li et al., 2023; Paillet et al., 2010).

Rabinowitz identified seven forms of rarity (Rabinowitz et al., 1986). Species can be rare because they occupy a narrow geographical range, have locally low population densities, have specialized habitat requirements, or combinations of these (adding up to seven). Here we focus on species that have low local population densities. Rare species are inherently more susceptible to human disturbance than dominant species as small stochastic fluctuations in population density can drive them to local extinction (Goodman, 1987; Matthies et al., 2004; Menges, 1991). When severe enough, human activity can drive species to extinction through habitat conversion, habitat fragmentation, or the introduction of invasive species (Newbold et al., 2015; Richardson & Rejmánek, 2011). However, dominant species can also decline rapidly in abundance, particularly due to overexploitation, accidentally introduced fungal pathogens, pests, diseases or severe droughts that can decimate species across their distribution range (Gaston & Fuller, 2008; Hartmann et al., 2022). Whereas the drivers of elevated extinction risk for rare species with a narrow distribution range are well established, an assessment of the patterns and predictors of extinction risk for locally dominant and rare species with a wider geographical distribution is lacking (Gaston, 2010; Wan et al., 2017).

In this study, we use 1.2 million forest plots distributed across the globe and relate local tree dominance and rarity to ecological predictors (i.e. climate and soil characteristics) and anthropogenic predictors (i.e. population density and human development). Specifically, we answer the following research questions: (1) What are the patterns of dominance and rarity in tree communities? (2) Which ecological and anthropogenic factors predict these patterns? And (3) are locally rare species more likely to be threatened with extinction compared to dominant species within ecological communities? The species we captured in this study are generally widespread tree species that differ in their local abundances. We hypothesize that (i) at low latitudes community rarity is highest and dominance is lowest, as with an increase in species richness, the number of rare species increases and the single most dominant species becomes less dominant (Magurran & Henderson, 2003; Ulrich et al., 2016), (ii) community dominance increases in environments with higher resource limitations, as it increases competition, and human disturbance, as it selects for early successional species (Huston, 1979; Keddy, 2023; Morris, 2010; Rozendaal et al., 2019), and (iii) dominant species have a lower extinction risk under anthropogenic pressure on forests than rare species due to their higher population density (Vincent et al., 2020).

2 | METHODS

2.1 | Dataset

To assess tree community dominance and rarity in forest communities worldwide, we used the database of the Global Forest Biodiversity Initiative (GFBI database, 2021). Our analysis also includes the data of Condit et al. (2019a, 2019b). The plots include all trees with stem diameter at breast height (DBH) ≥ 5 cm. The plots in the GFBI database contain information on tree species composition and DBH of every individual tree, along with the latitudinal and longitudinal coordinates of the forest plots (Figure 1a).

The entire GFBI database consists of approximately 1.2 million plots. However, since the number of dominant and rare species can vary with spatial scale (Weiher & Keddy, 1999; Wilson et al., 1999; Zhang et al., 2012), we excluded plots that were smaller than the first quantile (0.02 ha) and larger than 1.6 ha. This resulted in the exclusion of 8.3% of the database, and resulted in a mean plot size of 0.06 ha. Within the filtered database, the correlations between plot size and community dominance or rarity explained very little variation as indicated by the low r and r^2 values (Pearson's $r = -0.16$, $r^2 = 0.03$, $N = 670{,}527$, $p < 0.001$ and Pearson's $r = 0.20$, $r^2 = 0.04$, $N = 670{,}527$, $p < 0.01$, respectively), the apparent significance being driven by the large number of observational data. Additionally, plots measured before 1990 were filtered out, as these plots may not represent current forest composition and do not match with the climatic data we used. This resulted in filtering out 21% of the database, and the average measurement year being 2006. The filtered GFBI dataset consisted of 858,315 forest plots (including plots in for example savannas), of which 668,812 are in the six forest biomes (boreal forest, temperate conifer forest, temperate broadleaf forest, tropical conifer forest, tropical dry forest, tropical moist forest) (Dinerstein et al., 2017). Species names in the GFBI dataset were standardized using The Plant List, at least up to genus level (The Plant List, 2013). Of the 10,141 species names, around 10% could not be matched using The Plant List, including around 20% of the genera, therefore subsequently the Global Biodiversity Information Facility (GBIF) backbone was sourced to standardize these species names as well to accepted species names (GBIF Secretariat, 2020).

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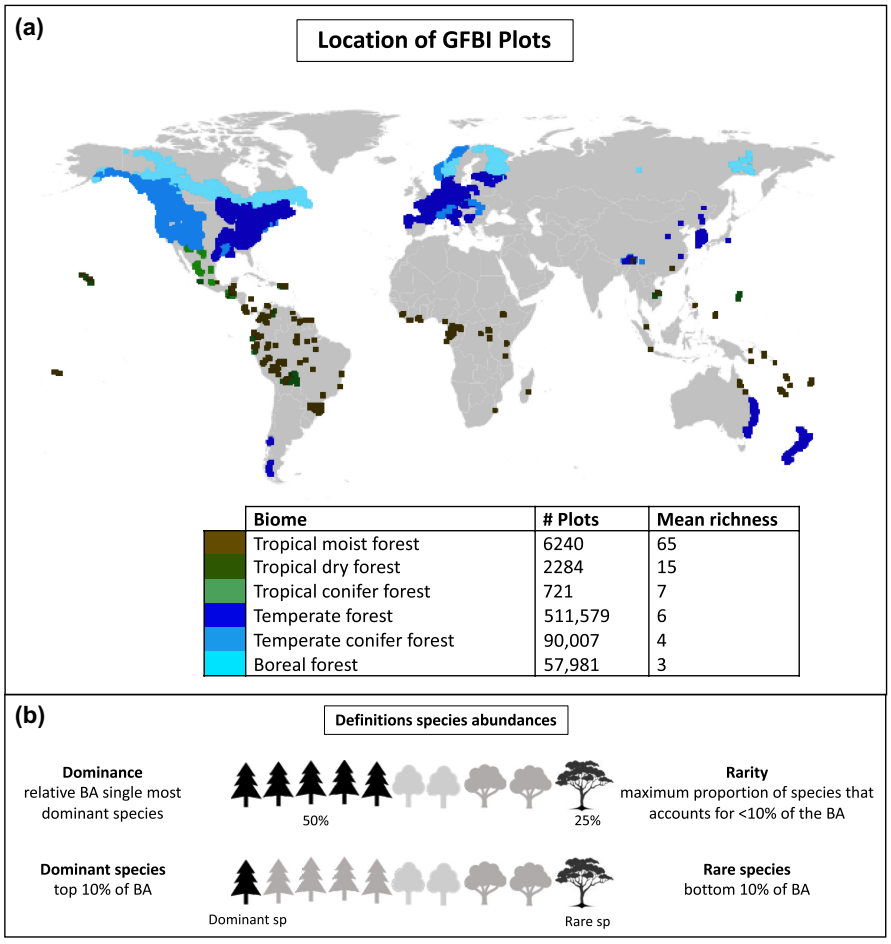

FIGURE 1 (a) Location of the Global Forest Biodiversity Initiative database plots used in this study (GFBI database), coloured by biome ($n = 668{,}812$). In the table, the number of plots and mean species richness per plot is indicated per forest biome (Dinerstein et al., 2017). (b) A graphical illustration of the definitions of dominance, rarity and dominant and rare species. Dominance is defined as the relative basal area (BA) of the single most dominant species, while rarity is defined as the maximum proportion of species that accounts for the least 10% of the basal area. In this graph, rarity equals 25%. Dominant and rare species are defined as the species which make up respectively the top and bottom 10% of basal area in a plot.

2.2 | Calculating community dominance and rarity

There are many definitions of dominant and rare species at different spatial levels and suitable for different communities (e.g. Avolio et al., 2019; Rabinowitz et al., 1986). This study assesses dominance and rarity at the community level. A community is defined as "a group of interacting species populations occurring together in space" (Roughgarden & Diamond, 1986; Stroud et al., 2015). Hence, we quantified dominance and rarity at the plot level, as this is the spatial scale at which tree species interact directly with each other, and therefore where the outcome of both abiotic and biotic interactions affecting species abundances are most directly reflected (Roughgarden & Diamond, 1986; Stroud et al., 2015). Classification of tree community dominance and rarity is based on basal area (m^2) of each species per hectare, calculated from the tree-level DBH measurements (in cm) for each inventory plot (Figure 1b). The total basal area (BA) per species is calculated as $BA_j\ (m^2/ha) = \sum_{i=1}^{n} \pi * (d_{i-n}/200)^2$. Where BA_j stands for the total basal area per species, and d_i for the DBH of the individual(s) of that species. Basal area integrates both the number of tree stems and the stem size, is commonly used to compute competition (Biging & Dobbertin, 1992; Contreras et al., 2011; Kunstler et al., 2016), and is correlated with the ecosystem functions of aboveground biomass and carbon sequestration (Balderas Torres & Lovett, 2013; Rao et al., 2015; Slik et al., 2010), but also with leaf area index and therefore photosynthetic capacity and respiration (Bartelink, 1997; Buckley et al., 1999; Fang et al., 2019; Jonckheere et al., 2005). In this analysis, we quantify community dominance as the percentage of basal area occupied by the single most dominant species in a given plot (cf. Friedman & Reich, 2005; Koike, 2001; Majumdar et al., 2014; Riemann et al., 2018; Zilliox & Gosselin, 2014). Values closer to 100% indicates therefore that the most dominant species contributes relatively more to plot basal area. Because we expressed the dominance metric as a percentage we quantified rarity also as a percentage, for sake of symmetry. Rarity was defined as the percentage of the total species in a plot that had the smallest basal area and accounted together for <10% of the accumulated plot basal area (Bracken & Low, 2012; Gaston, 1994; Magurran, 2004; Molina, 2013) (Figure 1b). Although in both cases dominance and rarity is expressed as a percentage to account for large biome differences in plot basal area and richness, for dominance the percentage refers to the plot basal area, and for rarity to the percentage of species making up the least 10% of the basal area (Figure 1b). We chose 10% as a threshold because this clearly distinguishes dominant from rare species, it allows to compare plots with different numbers of species, and it allows to include a representative number of plots for all biomes (which would not be the case with a species richness threshold) (Bracken & Low, 2012). This means that not every plot contains rare species, as the least dominant species might comprise >10% of the basal area of the plot. The measure of rarity can include multiple species, as long as the least 10% of the basal area threshold

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is not reached. If a species does not occur in a given plot, it is not categorized as dominant or rare species in that plot. Community dominance and rarity were calculated for each plot in the GFBI database, providing single point values that together describe the spatial variation in dominance and rarity for forests globally. The effect of plot size on richness, dominance and rarity is visualized in Figure S1.

2.3 | Mapping community dominance and rarity globally

To map community dominance and rarity across all forested biomes (including savannas), we used the approach described in van den Hoogen et al., (2019, 2021). We extracted information available at global scale that is reported to influence plant dominance, including 10 climatic variables (Kraft et al., 2015; Venn et al., 2011): mean annual temperature, temperature seasonality, isothermality, maximum temperature of the warmest month, minimum temperature of coldest month, annual temperature range, mean annual precipitation, precipitation seasonality, precipitation of the driest month, precipitation of the wettest month (Karger et al., 2017), 7 soil variables (Hillebrand et al., 2007; Stevens et al., 2004): cation exchange capacity, sand content, clay content, silt content, organic carbon, pH, saturated water content (Batjes et al., 2017; Ribeiro et al., 2018), 9 biomass and greenness variables (Bradford, 2011): tree density (Crowther et al., 2015), above ground biomass, growing stock volume (Santoro et al., 2018), annual net primary productivity (Running et al., 2011), NDVI, EVI (Didan, 2015), LAI (Myneni et al., 2015), EVI dissimilarity, Shannon index of greenness (Tuanmu & Jetz, 2015), 2 landscape characteristics: slope and elevation (Amatulli et al., 2018), 2 stand age variables: percentage secondary forests (forests younger than 150 years) and mean age of the secondary forest (Poulter et al., 2019), and 2 human disturbance variables: population density (Center for International Earth Science Information Network—CIESIN—Columbia University, 2016) and human development (Tuanmu & Jetz, 2014) (See Table 1 for details of the variables).

To assure that all predictor variables had the same spatial resolution, we extracted all these variables from global maps at a 30 arc second resolution (Poulter et al., 2019; Richardson & Rejmánek, 2011; Urbieta et al., 2008) (see Table 1 for full list of covariates). Using these covariates as independent variables, we predicted tree community dominance and rarity using random forest models, with 100 decision trees, a minimum of three variables per split, and a bag fraction (the proportion of training data to be used in the next tree, which by default is 0.5) of 0.632. To overcome computational limitations inherent in dealing with millions of observations and have a similar sample number per biome, we performed a stratified bootstrapping mapping procedure, where 1000 plots were sampled with replacement per biome (or the maximum number of plots for biomes with <1000 unique plots) and used to train the models. We repeated this bootstrapping approach 500 times for both community dominance and rarity. For every pixel we then calculated a mean and standard deviation across the 500 model-based predictions. The final maps have a resolution of 30 arcseconds and were projected in WGS84 (EPSG:4326) coordinate system, and only forested areas were visualized in the maps (FAO, 2001; Hansen et al., 2013). The modelling and mapping procedure was performed with Google Earth Engine (Gorelick et al., 2017).

We tested the predictive accuracy of our models using a spatial leave-one-out cross-validation (van den Hoogen et al., 2021). In this test, a random forest model is trained on all data except for points that fall within a predefined buffer zone from a test point. This procedure is repeated for every data point across ten randomly sampled stratified bootstrapped training sets per biome and across a range of buffer zone radii (1 km, 5 km, 10 km, 25 km, 50 km, 100 km) (Table 2). Tukey's test indicated that the mean r^2 of the random forest model for buffer zone radii was significantly different (Tukey's test, $p < 0.05$) indicating that they showed spatial autocorrelation, at 1 km, but did not show spatial autocorrelation at spatial scales of 5 km and beyond (Tukey's test, $p > 0.1$ in all cases). Thus, no spatial autocorrelation was detected for dominance and rarity values sampled further apart than 5 km.

To further analyse confidence in the final maps, we visualized the predicted versus observed values (Figure S2) and evaluated the coefficient of variation for the community dominance and rarity map by dividing the standard deviation across the 500 model-based predictions by the mean value per pixel (Figure 2). Additionally, we evaluated the percentage of data interpolation and extrapolation for the global community dominance and rarity maps (Figure S3), as a general limitation of our approach is the limited capacity of random forest models to predict outside the range of the training data (Hengl et al., 2018). To visualize the areas of extrapolation, we assessed whether predicted pixel values of dominance and rarity are within the range of the training data (van den Hoogen et al., 2021). In general, 92% to 97% of the predicted values of dominance and rarity in the global forest pixels were predicted within the range of the training data, which is the measured tree community data (Figure S3).

2.4 | Analysing predictors of community dominance and rarity

In global datasets, tropical biomes are usually under-represented, and the GFBI database used in this present study is no exception (McGill, 2003; Meyer et al., 2016). To address the problem of under sampled tropical regions, we performed the analyses with a subset of the dataset where the proportion of plots within a biome was approximately representative of that biome's forest cover across the globe. We therefore selected 14,282 plots, composed of at least 1000 plots from each of the six Ecoregions2017©[Resolve] forest biomes, and proportional to the forested area within that biome (Dinerstein et al., 2017). These proportions were calculated in Google Earth Engine by overlaying the biomes with a global map of existing forest cover (Hansen et al., 2013), where areas with more than 10% canopy cover for vegetation taller than 5 m were defined as forests (FAO, 2001).

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TABLE 1 The variables used to create the global map of dominance and rarity.

Variable category	Variable	Reference
Climate	**Mean annual temperature**	Karger et al. (2017)
	Temperature seasonality	
	Isothermality	
	Maximum temperature of the warmest month	
	Minimum temperature of coldest month	
	Annual temperature range	
	Mean annual precipitation	
	Precipitation seasonality	
	Precipitation of the driest month	
	Precipitation of the wettest month	
Soil (at 15 cm depth)	Cation exchange capacity	Batjes et al. (2017), Ribeiro et al. (2018)
	Sand content	
	Clay content	
	Silt content	
	Organic carbon	
	pH	
	Saturated water content	
Biomass and greenness	**Tree density**	Crowther et al. (2015)
	Above ground biomass	Santoro et al. (2018)
	Growing stock volume	
	Annual Net Primary Productivity	Running et al. (2011)
	NDVI	Didan (2015)
	LAI	Myneni et al. (2015)
	EVI	Didan (2015)
	EVI dissimilarity	Tuanmu and Jetz (2015)
	Shannon index of greenness	
Landscape	Slope	Amatulli et al. (2018)
	Elevation	
Stand age	**Secondary forest percentage**	Poulter et al. (2019)
	Age secondary forest	
Human impact	**Population density**	Center for International Earth Science Information Network—CIESIN—Columbia University (2016)
	Human development	Tuanmu and Jetz (2014)

Note: In the machine learning models to produce the maps the Nadir reflectance bands 1 to 7 are included as well (Schaaf & Wang, 2015). The variables in bold were included in the random forest models to evaluate the importance of climate, soil and human impact on dominance and rarity.

The relationship between community dominance, community rarity and species richness within the six forest biomes was evaluated with a Pearson correlation. Species richness was calculated as the number of species in the plot, and log (Ln) transformed in the correlation to ensure normality. Plots without rare species (i.e. if the least abundant species accounted for >10% of the basal area), were excluded when evaluating the relationship between dominance and rarity (58% of the plots). Also, monodominant plots were excluded when evaluating the relationship between dominance and rarity as they introduced a mathematical artefact, forcing the regression line to change from a positive to negative slope (Figure S4a,b).

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To evaluate how dominance and rarity were predicted by ecological and anthropogenic factors, we included the variables having the largest effect per variable category on dominance and rarity based on the random forest model to map the global distribution. We selected for climate mean and seasonality in temperature and precipitation (Karger et al., 2017), for soil variables soil pH and sand content at 15 cm depth (Batjes et al., 2017; Ribeiro et al., 2018), for topography elevation (Amatulli et al., 2018), for forest attributes tree density, stand age, for the landscape the percentage forest classified as secondary forest (Poulter et al., 2019), and for human impact population density and human development (Tuanmu & Jetz, 2015; University, 2016) (Table 1). To quantify the relative importance of the effect of these variables on community dominance and rarity, we used random forest models. Biome, latitude, longitude, plot size and species richness were included in the models as well, to correct respectively for the effect of different biomes, geographical locations, plot sizes and the number of species within the forest plot on dominance and rarity. Both dominance (Pearson's $r = -0.82$, $N = 670{,}527$, $p < 0.001$) and rarity are related to species richness (Pearson's $r = 0.60$, $N = 670{,}527$, $p < 0.001$). To ensure that the patterns we find can be assigned to the effect of dominance or rarity and not to richness, we corrected for the confounding effect of species richness by including species richness as a predictor variable in the models. See Table S2 for an overview of the variable importance values for all variables predicting dominance and rarity.

TABLE 2 The r^2 of the dominance and rarity maps across a range of buffer zone radii.

	Dominance		Rarity	
Radius (km)	Mean r^2	Standard deviation r^2	Mean r^2	Standard deviation r^2
1	0.448	0.025	0.416	0.036
5	0.353	0.020	0.299	0.040
10	0.355	0.020	0.298	0.043
25	0.361	0.021	0.287	0.041
50	0.348	0.030	0.259	0.037
100	0.335	0.025	0.222	0.035

2.5 | Identifying conservation status and range dominant and rare species

Here, we define dominant species as the species which make up the top 10% of plot level basal area, and rare species as the species which make up the bottom 10% of plot level basal area (Figure 1b). To assess if the definition of dominant and rare species affects the results, we also analyse the data when dominant and rare species are defined based on respectively the highest and lowest 10% of the number of stems in the plot and when dominance is defined as the single most dominant species (Figures S5–S7). Additionally, we show for species that are neither defined as dominant nor rare (the 'locally common' species), their distribution characteristics (Figures S5–S7). It is possible for a species to be locally dominant and locally rare within different plots within a biome because of a chance effect in

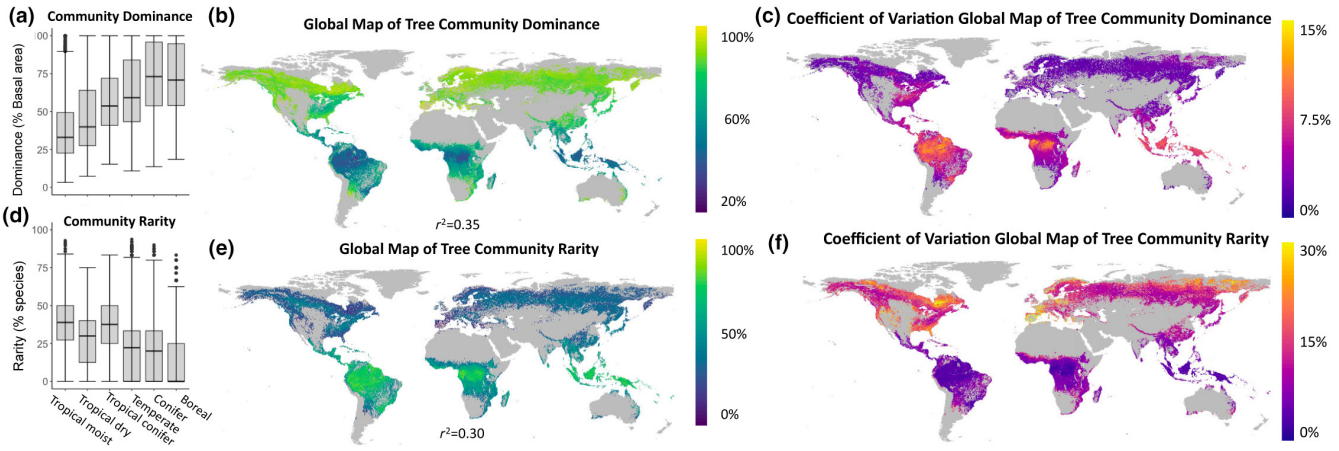

FIGURE 2 Global tree community dominance and rarity. (a) Community dominance is the percentage basal area of the most dominant species in the forest plot. The boxplot visualizes the measured data in the six forest biomes. (b) The map of predicted community dominance in global forests, with the spatially corrected r^2 indicated. (c) Coefficient of variation for the community dominance maps. The coefficient of variation is the standard deviation divided by the mean, and is expressed in percentages. The coefficient of variation indicates the variation in the different model outcomes, the higher the coefficient of variation the larger the distances between the values of the different models and the less accurate the mean value. (d) Community rarity is defined as the percentage of rare species, which are defined as the proportion of species contributing to the least 10% basal area. The boxplot visualizes the measured data in the six forest biomes. (e) The map of predicted community rarity in global forests, with the spatially corrected r^2 indicated. (f) Coefficient of variation for the community rarity maps. The map of tree community dominance was less variable, with a maximum coefficient of variation of 15%, whereas the map of tree rarity had a maximum coefficient of variation of 30%. The predicted dominance values exhibited particularly high variation in species rich areas, whereas in Spain, France, Northern Canada and Russia, the rarity predictions are more variable.

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relatively small plots, or because of within biome differences in environmental conditions. The species were therefore categorized as locally dominant or rare only if their local abundance was consistent (i.e. in at least in 95% of the plot occurrences they were either dominant or rare). We use this strict categorization of dominant and rare species as we want to limit our analyses to species that have consistent abundances within the community. In total, consistently 3% of the species have been categorized as dominant, 29% as common and 68% as rare at biome level.

According to the definition of the IUCN, a species has an elevated extinction risk (i.e. threatened) if it: (i) is restricted in geographical range, (ii) has a low number of individuals, or (iii) exhibits rapid declines in population density over time (IUCN Standards and Petitions Committee, 2019). Therefore, we evaluated the conservation status (e.g. not threatened or threatened), extent of occurrence (EOO, which is a measure for the range where the species occurs) and endemism of locally dominant, common, and rare species with data generated for the first report of the Global Tree Assessment from Botanic Gardens Conservation International (BGCI, 2021a). Additionally, the population trend over three generations of locally dominant, common, and rare species was evaluated with data from IUCN Red list (IUCN, 2021b). The Global Tree Assessment database provides the most comprehensive overview of extinction risks of tree species, covering 84% of the global number of tree species. However, we are aware of the constraints of the databases used, such as the impact of spatial scale on rarity and extinction risk (Hartley & Kunin, 2003). The GFBI and Global Tree Assessment data (BGCI, 2021a) were matched using the species names. In the GFBI database 371 dominant and 7815 rare species were classified as either "not threatened", "possibly threatened" or "threatened" (BGCI, 2021a). Of the dominant species, the conservation status of 1.2% were not evaluated and 3.5% were evaluated but data is too uncertain and therefore considered data deficient. For the rare species, 4.9% was not evaluated, and 3.6% was data deficient. With a Fisher's exact test, which is used to test associations between categorical variables, we identified if there is a difference in conservation status between dominant and rare species. To identify if the conservation status (i.e. "not threatened", "possibly threatened" or "threatened") of dominant and rare species differs between biomes, we performed a Poisson regression, as this is count data, with biome, species category (dominant or rare species), and their interaction as predictors.

To evaluate the spatial range where the locally dominant and rare species occur, the extent of occurrence (EOO) was calculated for the threatened dominant and rare species. The latitude and longitude of the species distribution was extracted using the GBIF database, and distribution was refined to native countries only using GlobalTreeSearch (BGCI, 2021b; GBIF Backbone Taxonomy, 2020). EOO was calculated as the minimum convex hull in km^2 where the species can occur, however there can be areas within the EOO where the species is absent. The methodology for EOO follows the IUCN mapping standards (IUCN, 2021a). For each forest biome, the mean difference between EOO of in total 315 dominant and 5923 rare species was tested with a t-test. As our locally common and rare species are based on inventory plots, rather than on sampling all unique habitats, this may result in a selection of more widespread species. To check if this affects the results, we also compared the EOO of tree species in the GFBI dataset to the average EOO of tree species per forest biome (IUCN, 2021b). A one-sample t-test was performed to analyse if the EOO of the species included in GFBI within a specific forest biome differs between the average EOO of that forest biome. We also assessed if the number of species considered by IUCN Red List to have a high extinction risk was higher for locally rare species, endemic species and species with smaller distribution range (EOO) (Figure S8). We defined endemism based on whether a species was restricted to a single country (endemic) or not (non-endemic) (BGCI, 2021a). Extinction risk information was available for all dominant and 89.1% of the rare species (BGCI, 2021a). The difference in endemism between the two groups was evaluated with a Fisher's exact test.

Additionally, we used data from the IUCN Red List to evaluate for locally dominant and rare species the population trend (e.g. decreasing or increasing) and the type of threats (e.g. logging leading to mortality, ecosystem conversion or ecosystem degradation) (IUCN, 2021b; IUCN Standards and Petitions Committee, 2019). The IUCN Red List could provide population trend or threat information on of 81% of the dominant and 48% of the rare species. To identify if there is a difference between population trend or type of threats to the population between threatened dominant and rare species, a Fisher's exact test was performed. Data management and statistical analyses in this study were performed in R, version 3.6.1 (R Core Team, 2019). The data to simulate the main graphs, and the code used to perform the statistical analyses can be found at Github, following this link: tinyurl.com/376m4pra.

3 | RESULTS

3.1 | Global and regional patterns of community dominance and rarity

The contribution of dominant and rare species to local community structure shows a clear opposing latitudinal pattern at the global scale (Figure 2). These patterns are consistent across different spatial scales (i.e. it was analysed with grid sizes varying from 0.01 to 1000 km^2) (Figure S9). Community dominance increases gradually with latitude, where the single most dominant species comprises on average 35% of local basal area near the equator to 70% in boreal forest (Figure 2a,c). In contrast, the proportion of species that are rare (those compromising the bottom 10% of basal area) ranges from an average of 40% in tropical forest to nearly 0% in boreal forest. These results closely mirror global patterns in species richness: community rarity is positively related to species richness (Pearson's $r = 0.60$, $N = 670{,}527$, $p < 0.001$), whereas dominance is negatively related to species richness (Pearson's $r = -0.82$, $N = 670{,}527$, $p < 0.001$) (Figure 3).

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At the biome scale, within the tropical forest biome a positive relationship between rarity and species richness (tropical moist forest: Pearson's $r=0.52$, $N=6263$, $p<0.001$), whereas the temperate and boreal forest biomes show a negative relationship (boreal forest: Pearson's $r=-0.54$, $N=58{,}522$, $p<0.001$). While at the global scale there is a negative relationship between dominance and rarity, at the forest biome scale, species-poor communities tend to exhibit a stronger positive relationship between community dominance and rarity (boreal forest: Pearson's $r=0.75$, $N=20{,}648$, $p<0.001$) (Figure 3). These results suggest that two mechanisms structure these patterns at different scales: (1) at the global scale, the inverse correlation between community dominance and rarity is predicted by turnover in richness across ecosystems, and (2) at regional scales, with less variation in species richness, an increase in the abundance of the dominant species necessarily decreases the abundance of the remaining species, thereby promoting rarity.

3.2 | Predictors of community dominance and rarity

When exploring the predictors underpinning community dominance and rarity with a random forest model ($N=14{,}282$), biome differences explained ≈2% of the variation, whereas richness explained 23% of dominance and 12% of rarity. Regarding the abiotic environment, climate was the most important predictor (≈31%), followed by soil characteristics (≈20%) (Figure 4a). Specifically, annual precipitation decreases community dominance (≈8%), and soil sand content is an equally strong predictor for both community dominance and rarity (≈9%). Dominance increases with soil sand (pseudo $r^2=0.08$), whereas the relationship between soil sand content and rarity is not well predicted by a generalized linear model (pseudo $r^2=0.001$). Interestingly, community dominance and rarity are equally predicted by human impact (≈15%) and stand age (≈14%). Community dominance showed a gradual increase with stand age (generalized linear model, pseudo $r^2=0.28$), whereas community rarity shows a very slight decrease (generalized linear model, pseudo $r^2=0.06$) (Figure 4b).

3.3 | Conservation status of dominant and rare species

BGCI categories the extinction risk of species in three broad categories; threatened, possibly threatened, or at risk (BGCI, 2021a). Both locally dominant and rare species have a similar percentage of species that are either 'threatened with extinction' (11% and 16%, respectively) or 'possibly threatened with extinction' (5% and 7%, respectively) (Figure 5a). There is no significant difference between the number of locally at-risk dominant and rare species, neither globally (Fisher's exact test, $p=0.89$) nor between biomes (Poisson regression, z-value$=0.971$, $\beta=0.10$, $p=0.33$). Of the species threatened with extinction, dominant and rare species show a similar population decline of 95% and 75%, respectively (Fisher's exact test, $p=0.17$) (Figure 5b), and a similar percentage (36% and 41%, respectively) are identified as endemic (Fisher's exact test, $p=0.61$) (Figure 5c). Dominant species have a larger distribution range (EOO) than rare species (t-test, $p=0.04$) (Figure 5d). These trends are consistently found when different definitions of locally dominant and rare species are used. (Figures S5–S7). Ecosystem degradation is the most important threat for both dominant and rare species, followed by mortality for dominant species and ecosystem conversion for rare species (Table S2).

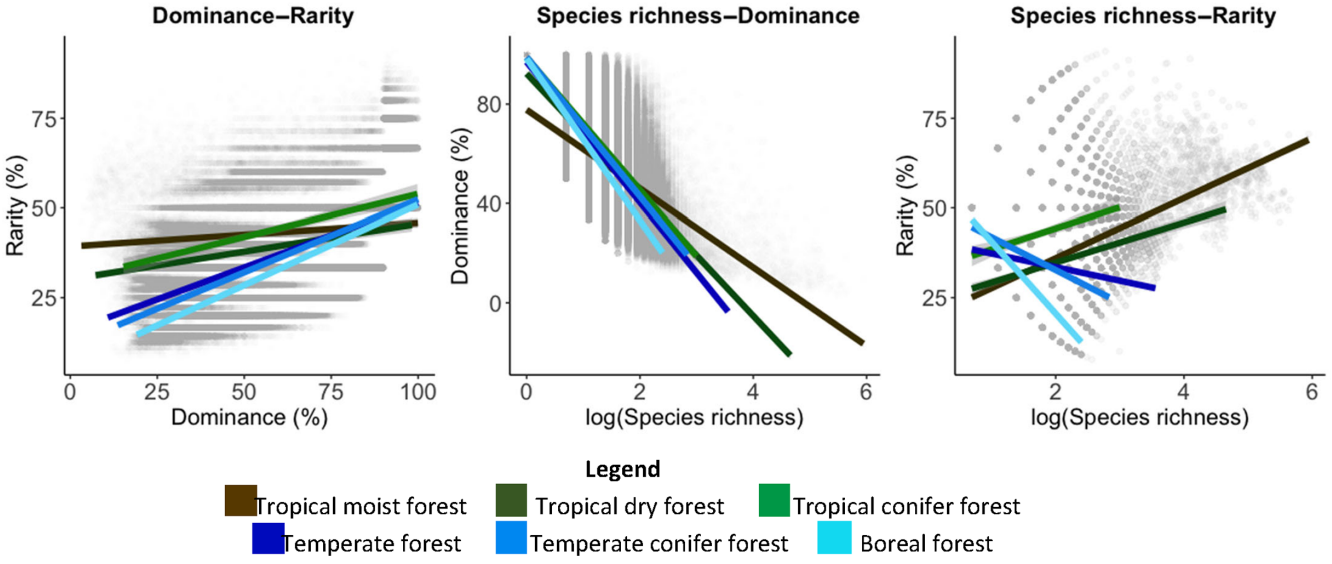

FIGURE 3 The relationship between dominance, rarity and species richness in forests globally ($N=670{,}527$). For the relationship between rarity and dominance, and rarity and species richness, only the plots that included rare species were considered ($N=X$). In Figure S4, the relationships between rarity and dominance, and rarity and species richness were visualized for all plots, including monodominant plots.

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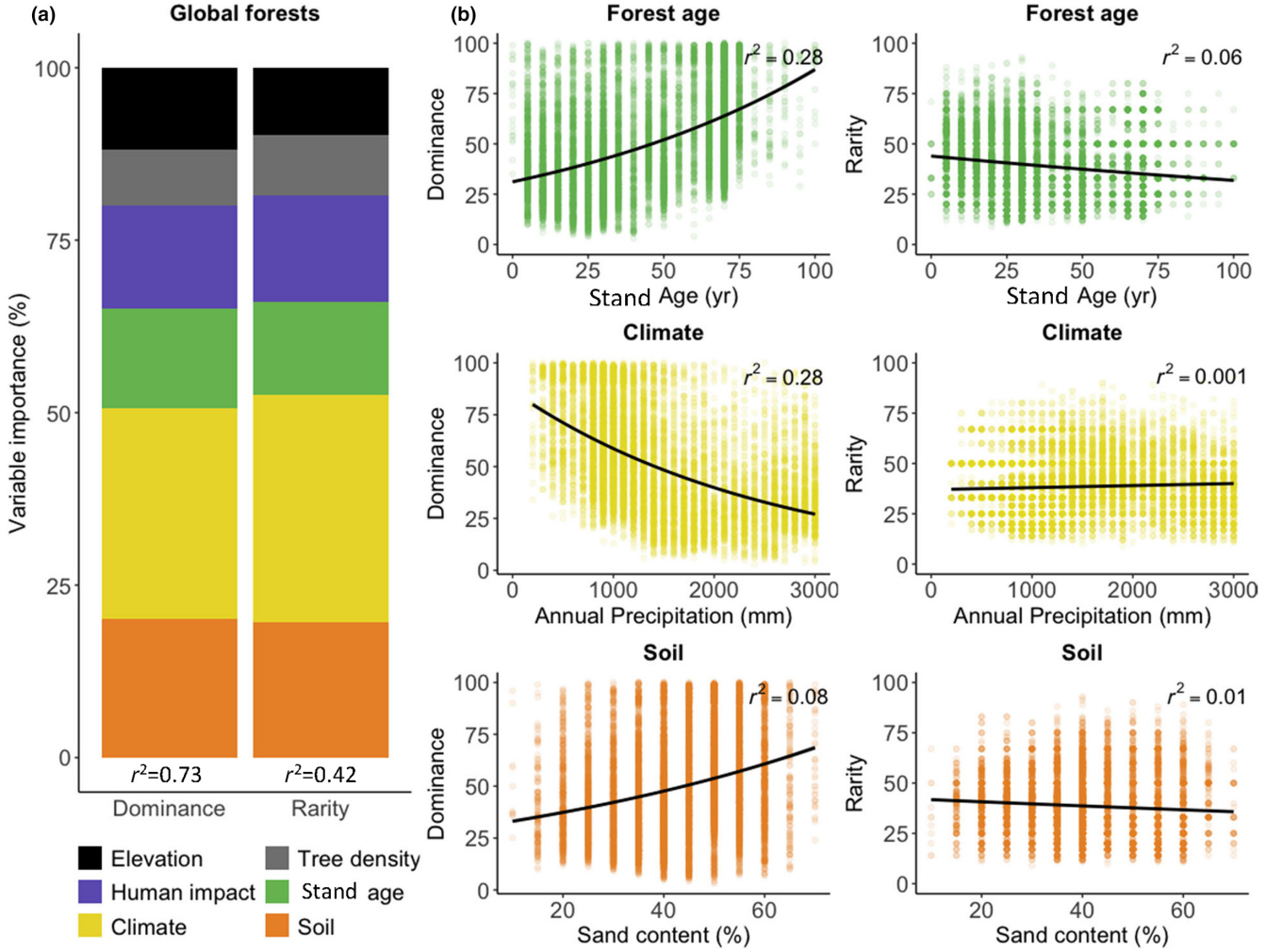

FIGURE 4 (a) Relative variable importance of soil characteristics (soil pH and soil sand content), climate (annual mean and seasonality of precipitation and temperature), stand age (percentage secondary forest, stand age) and human impact (human development and population density) on tree community dominance and rarity. Variable importance is calculated with a random forest model, incorporating species richness (variable importance 23% for dominance and 12% for rarity), plot size (variable importance 4% for dominance and rarity), biomes (variable importance 2% for dominance and rarity), latitude (variable importance 4.8% for dominance and 8.6% for rarity) and longitude (variable importance 6% for dominance and 5.4% for rarity), which are not shown in the bar graph. The r^2 of the random forest models are indicated under the bar graph. (b) The relationship between community dominance, rarity and the best fitting climatic, soil, and stand age variables to a gaussian generalized linear model. The data density is visualized with the colour saturation. The pseudo r^2 of the generalized linear models are indicated in the graphs.

4 | DISCUSSION

In this study, we evaluated patterns and population status of locally dominant and rare species across forests globally. Specifically, we analysed (1) global patterns, (2) abiotic and anthropogenic predictors and (3) extinction risk and population decline of locally dominant and rare tree species. We found clear latitudinal trends, which are predicted by species richness both across and within biomes (Figure 2–4). Across biomes, community dominance decreased with annual precipitation (Figure 4b) and increased with stand age (Figure 4b). Dominant and rare species show similar levels of extinction risk, with ecosystem degradation and land use conversion being the most important causes (Figure 5a). Taken together, these results suggest that species relative abundances are clearly related to species richness and affected by human impact, and that locally dominant and rare species are equally threatened.

4.1 | Global and regional patterns of community dominance and rarity

At the global scale, higher number of tree species correlates with a decrease in the abundance of the locally most dominant species and a slight increase in the proportion of locally rare species (Figure 2), which is consistent with previous studies (Bock et al., 2007; Enquist et al., 2019; Sabatini et al., 2022; Soininen et al., 2012; Stirling & Wilsey, 2001). However, at the biome scale, the relationship between community dominance and rarity is

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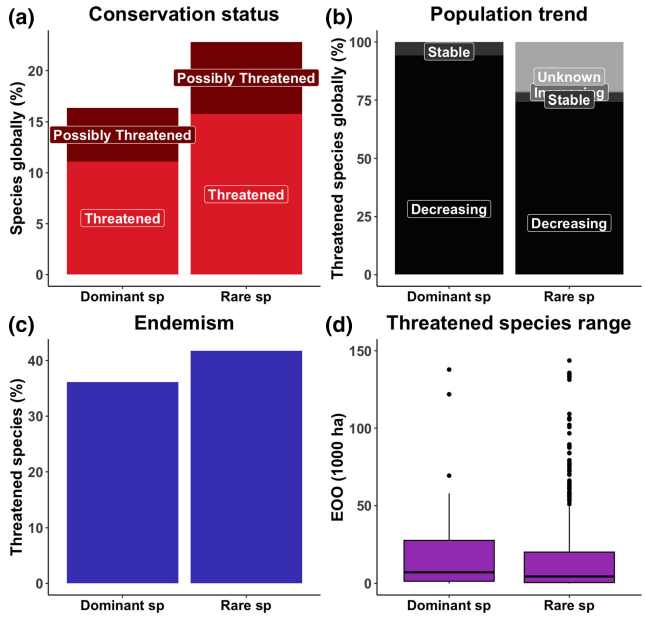

FIGURE 5 (a) The percentage of locally dominant and rare species identified as "threatened", or "possibly threatened" according to the Global Tree Assessment (BGCI, 2021a). (b) The population trend of threatened dominant and rare species. Threatened species are defined as "vulnerable", "endangered" or "critically endangered" according to the IUCN Red List assessment. (c) The percentage of endemic threatened dominant and rare species according to the Global Tree Assessment (BGCI, 2021a). (d) The extent of occurrence (EOO) for threatened dominant and rare species according to the Global Tree Assessment (BGCI, 2021a). The difference between the EOO of dominant and rare species is evaluated with a *t*-test ($p = 0.04$).

generally positive, apart from very species rich biomes (i.e. tropical forest) where there is no significant relationship (Figure 3). Based on the definition of dominance and rarity, a stronger and consistent relationship between rarity and richness would be expected as richness is included in the calculation of rarity. However, the relationship between dominance and richness is stronger and consistent (Figure 3). These results suggest fundamentally different processes structuring global versus biome level patterns of species abundance, which is also known as Simpson's paradox (Scheiner et al., 2000; Simpson, 1951). At the global scale, patterns of community dominance and rarity are predicted by species richness, whereas at a regional scale there is more direct competition between dominant and rare species for space and resources (Markham, 2015). However, this local pattern breaks down for moist tropical forests, suggesting that other mechanisms play a role in speciose forests (Svenning et al., 2004; Volkov et al., 2003).

At biome level, local dominance declines with species richness (Figure 3), which indicates that with a higher number of species in the community, the most dominant species have a relatively smaller basal area. A higher species richness indicates higher interspecific competition, which can indeed affect tree diameter and architecture (Forrester et al., 2017; van de Peer et al., 2017). Interestingly, the relationship between richness and rarity is positive for the tropical forests, but negative for the temperate and boreal forests (Figure 3). It is widely accepted that a higher species richness leads to a higher number of rare species, and that in an ecological community most of the species are, by definition, rare (Preston, 1962). Species richness is indeed positively correlated with rarity (Pearson's $r = 0.60$, $N = 670{,}527$, $p < 0.001$), which might indicate that in less species-rich forests an additional species will be present in relatively high abundance. This would mean that species have a more equal abundance in a forest containing fewer species, which is supported by the most common species-abundance distribution models and a global analysis on the relationship between richness and relative abundance of species (Hordijk et al., 2023; Ulrich et al., 2010).

4.2 | Predictors of community dominance and rarity

When evaluating the effect of abiotic, biotic and anthropogenic predictors on local community dominance and rarity, the random forest model explained community dominance better ($r^2 = 0.73$) than rarity ($r^2 = 0.42$). Therefore, the relationships between the most important abiotic, biotic and anthropogenic predictors were stronger with dominance compared to rarity. Overall, rarity is best explained by richness, which might be caused by the way rarity is calculated, whereas dominance increases with stand age and soil sand content, and decreases with annual precipitation. With an increase in stand age, trees increase in diameter after the initial phase where trees mainly invest in height growth (Ryan & Yoder, 1997). Our results suggest that the basal area of the most dominant species increases with stand age, indicating that species' basal area might differentiate more during succession due to competition. Soil sand content also increases community dominance, which might be a result of fewer tree species able to establish and dominate on less fertile soils with a lower water holding capacity (Avolio et al., 2019; Ehbrecht et al., 2021; Laurance et al., 2010). Additionally, we found that precipitation is negatively related to dominance, a possible explanation is that under more benign and productive conditions, more species are able to persist, which increases richness and reduces absolute dominance.

4.3 | Conservation status of dominant and rare species

The IUCN Red list regards a species to have an elevated extinction risk (i.e. threatened) if it: (i) is restricted in geographical range, (ii) has a low number of individuals, or (iii) exhibits rapid declines in population density over time (IUCN Standards and Petitions Committee, 2019). We indeed found that endemic species and species with narrow distribution ranges have a higher risk of extinction than widespread species (Figure S8) (consistent with e.g. Chichorro et al. (2019), Cardillo et al. (2005) and Purvis et al. (2000)). However,

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we also show that species that are locally dominant or rare in the community have a similar level of extinction risk (11% and 16% of the species, respectively), endemism and range (Figure 5a). In general, the range of tree species in our dataset is larger or equal to the average range of tree species per biome ($p < 0.001$), which indicates that the species we are evaluating are relatively widespread (Gaston et al., 1997). Indeed, species can be geographically widespread, but regionally and locally rare (Rabinowitz et al., 1986). A surprisingly large proportion of locally dominant and rare species show a decline in population size (respectively 95% and 75%) (de Lima et al., 2024). This might be explained by the main threat, which is ecosystem degradation, as this has probably an equally high impact on dominant and rare species within the same community (Curtis et al., 2018; Newbold et al., 2015). Additionally, in the boreal and temperate conifer forests, where species are widespread and thought to have a high population density, the threatened status of widespread dominant and rare species shows a rapid decline in population size due to disease outbreaks and invasive species (e.g. Dutch elm disease, emerald ash borer, invasive pests) (Table S1). In this context, our results point to declining population densities across species ranges as the primary cause of elevated extinction risk for these widespread species (Boonman et al., 2024; Gaston & Fuller, 2007, 2008).

The main challenges when working with global forest inventory data and extinction risk assessments are unbalanced sampling with biomes over-represented and other biomes under-sampled and the lack of species population assessments to evaluate extinction risk, which can be particularly limited in tropical regions. To reduce this sampling bias, we analysed a weighted subset of the data for our global analyses of predictors of community dominance and rarity. Moreover, especially in the tropical forest biomes there is relatively a lower percentage of assessed locally dominant and rare species, compared to the temperate and boreal forests. Therefore, the percentage of at-risk species could differ between biomes if a higher percentage of the species in the most speciose forest biomes were assessed. Additionally, it became apparent that our dataset is biased towards species with larger ranges (although rare species can have larger distribution ranges as well, see Zizka et al., 2018). Therefore, an effort can be made to include in the future also datasets within GFBI with a focus on species with a smaller range, especially in the tropics. Another challenge when working with global forest inventory data without a standardized protocol are the different management histories of the plots and the different plot sizes within the dataset. We filtered very small and large plots out of the data but are aware that a larger plot size in the same region could lead to a higher richness, lower dominance and higher rarity. The differences in plot sizes, however, are more pronounced between biomes versus within biomes, and the more species rich biomes have generally a larger plot size (Figure S1).

Typically, the focus of plant conservation studies are on dispersal-limited species and localized endemics with naturally low geographical range distributions, usually in more species rich regions (e.g. Corlett, 2016; Myers et al., 2000; With & King, 1999). However, we find that geographically widespread species also have high levels of extinction risk, a conclusion which has not previously been reported at this global scale to our knowledge. Widespread and dominant species are key for ecosystem functioning, such as carbon sequestration to mitigate climate change, and their decline is therefore a major concern (Gaston & Fuller, 2007; Grime, 1998). Furthermore, we show that the primary predictors of population decline and elevated extinction risk for both rare and dominant species are land degradation, land conversion for farming and agro-industry, and species mortality mainly due to logging (Table S1), consistent with global studies (Curtis et al., 2018; DeFries et al., 2010; Foley et al., 2005). Together, our results bring a new perspective on biodiversity loss, highlighting the importance of implementing conservation and restoration actions to bend the curve of biodiversity loss (Cazzolla Gatti et al., 2022; Leclère et al., 2020) and reverse the trajectory of species decline and elevated extinction risk for geographically widespread species (Thakur et al., 2018). Together, our findings and previous works emphasize the need to develop more holistic, ecosystem scale, biodiversity conservation efforts that explicitly include the protection of widespread species, which are not traditionally a high priority of conservation and restoration actions. However, these results capture broad-scale macro-ecological patterns at the biome and global scale, contingent on the specific dataset we use. To responsibly manage local forest ecosystems and tree species, it is important to consider the local environmental and social context (Swanson et al., 2021).

5 | CONCLUSIONS

The attention of conservation biologists has focused primarily on species with narrow range distributions (endemics and dispersal-limited species), as these species that have a higher intrinsic risk of extinction. In this study, we focus on global and biome level patterns in community dominance and rarity, and show that across ecosystems, annual precipitation is a strong predictor of the variation in dominance and rarity, with lower dominance in regions characterized by high precipitation levels. Within forest communities, stand age and successional dynamics influence patterns of community dominance, indicating the effect of habitat disturbance on species abundances. We show that relatively widespread tree species which are locally dominant or rare are equally threatened by anthropogenic pressures, with land degradation being the largest threat. Although forests are continuously changing over time and space, there is a clear footprint of human activity on the abundance of both dominant and rare species. Our results therefore suggest that conservation efforts should focus not only on the geographically limited species but also incorporate the more widespread but locally rare or dominant species that are also critical for functioning of forest ecosystems.

AUTHOR CONTRIBUTIONS

Iris Hordijk, Tom W. Crowther and Daniel S. Maynard conceived of the study. Iris Hordijk extracted and analysed the data, and Thomas Lauber and Devin Routh assisted in the map making process. Iris

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Hordijk drafted the manuscript with assistance from Daniel S. Maynard, Lalasia Bialic-Murphy and Tom W. Crowther. Members of the GFBI consortium (all authors not mentioned previously) provided data for the analysis. All authors assisted with revisions and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Tree community dominance values are available in the ETH research collection: https://www.research-collection.ethz.ch/handle/20.500.11850/682380

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REFERENCES

Albert, J. S., Carnaval, A. C., Flantua, S. G. A., Lohmann, L. G., Ribas, C. C., Riff, D., Carrillo, J. D., Fan, Y., Figueiredo, J. J. P., Guayasamin, J. M., Hoorn, C., de Melo, G. H., Nascimento, N., Quesada, C. A., Ulloa Ulloa, C., Val, P., Arieira, J., Encalada, A. C., & Nobre, C. A. (2023). Human impacts outpace natural processes in the Amazon. *Science*, *379*(6630), eabo5003.

Amatulli, G., Domisch, S., Tuanmu, M.-N., Parmentier, B., Ranipeta, A., Malczyk, J., & Jetz, W. (2018). A suite of global, cross-scale topographic variables for environmental and biodiversity modeling. *Scientific Data*, *5*, 180040.

Arnillas, C. A., & Cadotte, M. W. (2019). Experimental dominant plant removal results in contrasting assembly for dominant and non-dominant plants. *Ecology Letters*, *22*(8), 1233–1242.

Avolio, M. L., Forrestel, E. J., Chang, C. C., La Pierre, K. J., Burghardt, K. T., & Smith, M. D. (2019). Demystifying dominant species. *New Phytologist*, *223*(3), 1106–1126.

Balderas Torres, A., & Lovett, J. C. (2013). Using basal area to estimate aboveground carbon stocks in forests: La primavera biosphere's reserve, Mexico. *Forestry*, *86*(2), 267–281.

Bartelink, H. (1997). Allometric relationships for biomass and leaf area of beech (*Fagus sylvatica* L). *Annales des Sciences Forestières*, *54*(1), 39–50.

Batjes, N., Ribeiro, E., van Oostrum, A., Leenaars, J., Hengl, T., & Mendes de Jesus, J. (2017). WoSIS—Providing standardised soil profile data for the world. *Earth System Science Data*, *9*, 1–14.

Bazzaz, F. A. (1975). Plant species diversity in old-field successional ecosystems in Southern Illinois. *Ecology*, *56*(2), 485–488.

BGCI. (2021a). *State of the world's trees*. BGCI.

BGCI. (2021b). *GlobalTreeSearch Database*. https://tools.bgci.org/global_tree_search.php

Biging, G. S., & Dobbertin, M. (1992). A comparison of distance-dependent competition measures for height and basal area growth of individual conifer trees. *Forest Science*, *38*(3), 695–720.

Bock, C. E., Jones, Z. F., & Bock, J. H. (2007). Relationships between species richness, evenness, and abundance in a Southwestern Savanna. *Ecology*, *88*(5), 1322–1327.

Boonman, C. C., Serra-Diaz, J. M., Hoeks, S., Guo, W. Y., Enquist, B. J., Maitner, B., Malhi, Y., Merow, C., Buitenwerf, R., & Svenning, J. C. (2024). More than 17,000 tree species are at risk from rapid global change. *Nature Communications*, *15*(1), 166.

Bowler, D. E., Hof, C., Haase, P., Kröncke, I., Schweiger, O., Adrian, R., Baert, L., Bauer, H.-G., Blick, T., Brooker, R. W., Dekoninck, W.,

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Domisch, S., Eckmann, R., Hendrickx, F., Hickler, T., Klotz, S., Kraberg, A., Kühn, I., Matesanz, S., … Böhning-Gaese, K. (2017). Cross-realm assessment of climate change impacts on species' abundance trends. *Nature Ecology & Evolution*, *1*(3), 0067.

Bracken, M. E. S., & Low, N. H. N. (2012). Realistic losses of rare species disproportionately impact higher trophic levels. *Ecology Letters*, *15*(5), 461–467.

Bradford, J. B. (2011). Divergence in forest-type response to climate and weather: Evidence for regional links between forest-type evenness and net primary productivity. *Ecosystems*, *14*(6), 975–986.

Buckley, D. S., Isebrands, J. G., & Sharik, T. L. (1999). Practical field methods of estimating canopy cover, PAR, and LAI in Michigan oak and pine stands. *Northern Journal of Applied Forestry*, *16*(1), 25–32.

Butchart, S. H. M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J. P. W., Almond, R. E. A., Baillie, J. E. M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K. E., Carr, G. M., Chanson, J., Chenery, A. M., Csirke, J., Davidson, N. C., Dentener, F., Foster, M., Galli, A., … Watson, R. (2010). Global biodiversity: Indicators of recent declines. *Science (New York, N.Y.)*, *328*(5982), 1164–1168.

Cardillo, M., Mace, G. M., Jones, K. E., Bielby, J., Bininda-Emonds, O. R., Sechrest, W., Orme, C. D. L., & Purvis, A. (2005). Multiple causes of high extinction risk in large mammal species. *Science*, *309*(5738), 1239–1241.

Cazzolla Gatti, R., Reich, P. B., Gamarra, J. G., Crowther, T., Hui, C., Morera, A., Bastin, J.-F., de-Miguel, S., Nabuurs, G.-J., Svenning, J.-C., Serra-Diaz, J. M., Merow, C., Enquist, B., Kamenetsky, M., Lee, J., Zhu, J., Fang, J., Jacobs, D. F., Pijanowski, B., … Liang, J. (2022). The number of tree species on Earth. *Proceedings of the National Academy of Sciences*, *119*(6), e2115329119.

Center for International Earth Science Information Network—CIESIN—Columbia University. (2016). *Gridded population of the world, version 4 (GPWv4): Population density adjusted to Match 2015 revision of UN WPP country totals*. NASA Socioeconomic Data and Applications Center (SEDAC).

Chapin, F. S., Sala, O. E., Burke, I. C., Grime, J. P., Hooper, D. U., Lauenroth, W. K., Lombard, A., Mooney, H. A., Mosier, A. R., Naeem, S., Pacala, S. W., Roy, J., Steffen, W. L., & Tilman, D. (2000). Ecosystem consequences of changing biodiversity. *Nature*, *405*, 234–242.

Chichorro, F., Juslén, A., & Cardoso, P. (2019). A review of the relation between species traits and extinction risk. *Biological Conservation*, *237*, 220–229.

Condit R., Perez, R., Aguilar, S., Lao, S., Foster, R., & Hubbell, S. P. (2019a). BCI 50-ha plot taxonomy, 2019 version. *Dryad*. https://doi.org/10.15146/R3FH61

Condit R., Perez, R., Aguilar, S., Lao, S., Foster, R., & Hubbell, S. P. (2019b). Complete data from the Barro Colorado 50-ha plot: 423617 trees, 35 years, 2019 version. *Dryad*. https://doi.org/10.15146/5xcp-0d46

Contreras, M. A., Affleck, D., & Chung, W. (2011). Evaluating tree competition indices as predictors of basal area increment in western Montana forests. *Forest Ecology and Management*, *262*(11), 1939–1949.

Corlett, R. T. (2016). Plant diversity in a changing world: Status, trends, and conservation needs. *Plant Diversity*, *38*(1), 10–16.

Cornwell, W. K., & Ackerly, D. D. (2009). Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs*, *79*(1), 109–126.

Crowther, T. W., Glick, H. B., Covey, K. R., Bettigole, C., Maynard, D. S., Thomas, S. M., Smith, J. R., Hintler, G., Duguid, M. C., Amatulli, G., Tuanmu, M.-N., Jetz, W., Salas, C., Stam, C., Piotto, D., Tavani, R., Green, S., Bruce, G., Williams, S. J., … Bradford, M. A. (2015). Mapping tree density at a global scale. *Nature*, *525*(7568), 201–205.

Curtis, P. G., Slay, C. M., Harris, N. L., Tyukavina, A., & Hansen, M. C. (2018). Classifying drivers of global forest loss. *Science (New York, N.Y.)*, *361*(6407), 1108–1111.

de Lima, R. A., Dauby, G., de Gasper, A. L., Fernandez, E. P., Vibrans, A. C., Oliveira, A. A. D., Prado, P. I., Souza, V. C., de Siqueira, M. F., & Ter Steege, H. (2024). Comprehensive conservation assessments reveal high extinction risks across Atlantic Forest trees. *Science*, *383*(6679), 219–225.

Dee, L. E., Cowles, J., Isbell, F., Pau, S., Gaines, S. D., & Reich, P. B. (2019). When do ecosystem services depend on rare species? *Trends in Ecology & Evolution*, *34*(8), 746–758.

DeFries, R. S., Rudel, T., Uriarte, M., & Hansen, M. (2010). Deforestation driven by urban population growth and agricultural trade in the twenty-first century. *Nature Geoscience*, *3*(3), 178–181.

Didan, K. (2015). *MYD13Q1 MODIS/Aqua Vegetation Indices 16-Day L3 Global 250m SIN Grid V006*. NASA EOSDIS Land Processes DAAC.

Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N. D., Wikramanayake, E., Hahn, N., Palminteri, S., Hedao, P., Noss, R., Hansen, M., Locke, H., Ellis, E. C., Jones, B., Barber, C. V., Hayes, R., Kormos, C., Martin, V., Crist, E., … Saleem, M. (2017). An ecoregion-based approach to protecting half the terrestrial realm. *Bioscience*, *67*(6), 534–545.

Doncaster, C. P., Alonso Chávez, V., Viguier, C., Wang, R., Zhang, E., Dong, X., Dearing, J. A., Langdon, P. G., & Dyke, J. G. (2016). Early warning of critical transitions in biodiversity from compositional disorder. *Ecology*, *97*(11), 3079–3090.

Ehbrecht, M., Seidel, D., Annighöfer, P., Kreft, H., Köhler, M., Zemp, D. C., Puettmann, K., Nilus, R., Babweteera, F., Willim, K., Stiers, M., Soto, D., Boehmer, H. J., Fisichelli, N., Burnett, M., Juday, G., Stephens, S. L., & Ammer, C. (2021). Global patterns and climatic controls of forest structural complexity. *Nature Communications*, *12*(1), 519.

Enquist, B. J., Feng, X., Boyle, B., Maitner, B., Newman, E. A., Jørgensen, P. M., Roehrdanz, P. R., Thiers, B. M., Burger, J. R., Corlett, R. T., Couvreur, T. L. P., Dauby, G., Donoghue, J. C., Foden, W., Lovett, J. C., Marquet, P. A., Merow, C., Midgley, G., Morueta-Holme, N., … McGill, B. J. (2019). The commonness of rarity: Global and future distribution of rarity across land plants. *Science Advances*, *5*(11), eaaz0414.

Fang, H., Baret, F., Plummer, S., & Schaepman-Strub, G. (2019). An overview of global leaf area index (LAI): Methods, products, validation, and applications. *Reviews of Geophysics*, *57*(3), 739–799.

FAO. (2001). *Global forest resources assessment 2000*. FAO Forestry Paper No. 140. UN Food and Agriculture Organization.

Fauset, S., Johnson, M. O., Gloor, M., Baker, T. R., Monteagudo, M. A., Brienen, R. J. W., Feldpausch, T. R., Lopez-Gonzalez, G., Malhi, Y., Ter Steege, H., Pitman, N. C. A., Baraloto, C., Engel, J., Pétronelli, P., Andrade, A., Camargo, J. L. C., Laurance, S. G. W., Laurance, W. F., Chave, J., … Phillips, O. L. (2015). Hyperdominance in Amazonian forest carbon cycling. *Nature Communications*, *6*, 1–9.

Fei, S., Desprez, J. M., Potter, K. M., Jo, I., Knott, J. A., & Oswalt, C. M. (2017). Divergence of species responses to climate change. *Science Advances*, *3*(5), e1603055.

Foley, J. A., Defries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., Chapin, F. S., Coe, M. T., Daily, G. C., Gibbs, H. K., Helkowski, J. H., Holloway, T., Howard, E. A., Kucharik, C. J., Monfreda, C., Patz, J. A., Prentice, I. C., Ramankutty, N., & Snyder, P. K. (2005). Global consequences of land use. *Science (New York, N.Y.)*, *309*(5734), 570–574.

Forrester, D. I., Benneter, A., Bouriaud, O., & Bauhus, J. (2017). Diversity and competition influence tree allometric relationships–developing functions for mixed-species forests. *Journal of Ecology*, *105*(3), 761–774.

Friedman, S. K., & Reich, P. B. (2005). Regional legacies of logging: Departure from presettlement forest conditions in Northern Minnesota. *Ecological Applications*, *15*(2), 726–744.

Gaston, K. J. (1994). *Rarity* (Vol. *13*). Chapman & Hall.

Gaston, K. J. (2010). Valuing common species. *Science (New York, N.Y.)*, *327*(5962), 154–155.

Gaston, K. J., Blackburn, T. M., & Lawton, J. H. (1997). Interspecific abundance-range size relationships: An appraisal of mechanisms. *Journal of Animal Ecology*, *66*, 579–601.

Gaston, K. J., & Fuller, R. A. (2007). Biodiversity and extinction: Losing the common and the widespread. *Progress in Physical Geography*, *31*(2), 213–225.

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Gaston, K. J., & Fuller, R. A. (2008). Commonness, population depletion and conservation biology. *Trends in Ecology & Evolution*, *23*(1), 14–19.

GBIF Secretariat. (2020). GBIF Backbone Taxonomy. Checklist dataset. https://doi.org/10.15468/39omei accessed via GBIF.org on 2020-06-08.

GFBI database. (2021). Global forest biodiversity initiative. http://www.gfbinitiative.org Please be aware that the map on the GFBI website may not include all the plots we incorporated in this study due to updates in the database.

Goldberg, D. E. (1990). Components of resource competition in plant communities. In J. B. Grace & D. Tilman (Eds.), *Perspectives on plant competition* (pp. 27–49). Academic Press.

Goodman, D. (1987). The demography of chance extinction. In M. E. Soulé (Ed.), *Viable populations for conservation* (pp. 11–34). Cambridge University Press.

Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., & Moore, R. (2017). Google Earth Engine: Planetary-scale geospatial analysis for everyone. *Remote Sensing of Environment*, *202*, 18–27.

Grime, J. P. (1998). Benefits of plant diversity to ecosystems: Immediate, filter and founder effects. *Journal of Ecology*, *86*, 902–910.

Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., Thau, D., Stehman, S. V., Goetz, S. J., Loveland, T. R., Kommareddy, A., Egorov, A., Chini, L., Justice, C. O., & Townshend, J. R. G. (2013). High-resolution global maps of 21st-century forest cover change. *Science*, *342*(6160), 850–853.

Hart, T. B., Hart, J. A., & Murphy, P. G. (1989). Monodominant and species-rich forests of the humid tropics: Causes for their co-occurrence. *The American Naturalist*, *133*(5), 613–633.

Hartley, S., & Kunin, W. E. (2003). Scale dependency of rarity, extinction risk, and conservation priority. *Conservation Biology*, *17*(6), 1559–1570.

Hartmann, H., Bastos, A., Das, A. J., Esquivel-Muelbert, A., Hammond, W. M., Martínez-Vilalta, J., McDowell, N. G., Powers, J. S., Pugh, T. A., Ruthrof, K. X., & Allen, C. D. (2022). Climate change risks to global forest health: Emergence of unexpected events of elevated tree mortality worldwide. *Annual Review of Plant Biology*, *73*, 673–702.

Hengl, T., Nussbaum, M., Wright, M. N., Heuvelink, G. B., & Gräler, B. (2018). Random forest as a generic framework for predictive modeling of spatial and spatio-temporal variables. *PeerJ*, *6*, e5518.

Hillebrand, H., Bennett, D. M., & Cadotte, M. W. (2008). Consequences of dominance: A review of evenness effects on local and regional ecosystem processes. *Ecology*, *89*(6), 1510–1520.

Hillebrand, H., Gruner, D. S., Borer, E. T., Bracken, M. E. S., Cleland, E. E., Elser, J. J., Harpole, W. S., Ngai, J. T., Seabloom, E. W., Shurin, J. B., & Smith, J. E. (2007). Consumer versus resource control of producer diversity depends on ecosystem type and producer community structure. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(26), 10904–10909.

Hobi, M. L., Commarmot, B., & Bugmann, H. (2015). Pattern and process in the largest primeval beech forest of Europe (Ukrainian Carpathians). *Journal of Vegetation Science*, *26*(2), 323–336.

Hordijk, I., Maynard, D. S., Hart, S. P., Lidong, M., Ter Steege, H., Liang, J., de-Miguel, S., Nabuurs, G. J., Reich, P. B., Abegg, M., & Adou Yao, C. Y. (2023). Evenness mediates the global relationship between forest productivity and richness. *Journal of Ecology*, *111*(6), 1308–1326.

Huston, M. (1979). A general hypothesis of species diversity. *The American Naturalist*, *113*(1), 81–101.

IUCN. (2021a). *Mapping standards and data quality for the IUCN red list spatial data version 1.19*. IUCN SSC Red List Technical Working Group.

IUCN. (2021b). The IUCN Red List of Threatened Species. Version 2021-1. https://www.iucnredlist.org

IUCN Standards and Petitions Committee. (2019). Guidelines for Using the IUCN Red List Categories and Criteria. Version 14. Prepared by the Standards and Petitions Committee.

Jonckheere, I., Muys, B., & Coppin, P. (2005). Allometry and evaluation of in situ optical LAI determination in scots pine: A case study in Belgium. *Tree Physiology*, *25*(6), 723–732.

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, *4*, 170122.

Keddy, P. A. (2023). Competition. In *Causal factors for wetland management and restoration: A concise guide* (pp. 73–80). Springer International Publishing.

Koike, F. (2001). Plant traits as predictors of woody species dominance in climax forest communities. *Journal of Vegetation Science*, *12*(3), 327–336.

Kraft, N. J. B., Adler, P. B., Godoy, O., James, E. C., Fuller, S., & Levine, J. M. (2015). Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology*, *29*, 592–599.

Kunstler, G., Falster, D., Coomes, D. A., Hui, F., Kooyman, R. M., Laughlin, D. C., Poorter, L., Vanderwel, M., Vieilledent, G., Joseph Wright, S., Aiba, M., Baraloto, C., Caspersen, J., Cornelissen, J. H. C., Gourlet-Fleury, S., Hanewinkel, M., Herault, B., Kattge, J., Kurokawa, H., … Westoby, M. (2016). Plant functional traits have globally consistent effects on competition. *Nature*, *529*(7585), 204–207.

Laurance, S. G., Laurance, W. F., Andrade, A., Fearnside, P. M., Harms, K. E., Vicentini, A., & Luizão, R. C. (2010). Influence of soils and topography on Amazonian tree diversity: A landscape-scale study. *Journal of Vegetation Science*, *21*(1), 96–106.

Leclère, D., Obersteiner, M., Barrett, M., Butchart, S. H., Chaudhary, A., De Palma, A., … Young, L. (2020). Bending the curve of terrestrial biodiversity needs an integrated strategy. *Nature*, *585*(7826), 551–556.

Li, W., Guo, W. Y., Pasgaard, M., Niu, Z., Wang, L., Chen, F., … Svenning, J. C. (2023). Human fingerprint on structural density of forests globally. *Nature Sustainability*, *6*(4), 368–379.

Liang, J., Gamarra, J. G., Picard, N., Zhou, M., Pijanowski, B., Jacobs, D. F., Reich, P. B., Crowther, T. W., Nabuurs, G.-J., de-Miguel, S., Fang, J., Woodall, C. W., Svenning, J.-C., Jucker, T., Bastin, J.-F., Wiser, S. K., Slik, F., Hérault, B., Alberti, G., … Marcon, E. (2022). Co-limitation towards lower latitudes shapes global forest diversity gradients. *Nature Ecology & Evolution*, *6*(10), 1423–1437.

Lynn, J. S., Kazenel, M. R., Kivlin, S. N., & Rudgers, J. A. (2019). Context-dependent biotic interactions control plant abundance across altitudinal environmental gradients. *Ecography*, *42*(9), 1600–1612.

Magurran, A. E. (2004). *Measuring biological diversity*. Blackwell Science Ltd.

Magurran, A. E., & Henderson, P. A. (2003). Explaining the excess of rare species in natural species abundance distributions. *Nature*, *422*(6933), 714–716.

Majumdar, K., Shankar, U., & Datta, B. K. (2014). Trends in tree diversity and stand structure during restoration: A case study in fragmented moist deciduous forest ecosystems of Northeast India. *Journal of Ecosystems*, *2014*, 1–10.

Markham, J. (2015). Rare species occupy uncommon niches. *Scientific Reports*, *4*(1), 6012.

Matthies, D., Bräuer, I., Maibom, W., & Tscharntke, T. (2004). Population size and the risk of local extinction: Empirical evidence from rare plants. *Oikos*, *105*(3), 481–488.

McGill, B. J., Etienne, R. S., Gray, J. S., Alonso, D., Anderson, M. J., Benecha, H. K., Dornelas, M., Enquist, B. J., Green, J. L., He, F., & Hurlbert, A. H. (2007). Species abundance distributions: Moving beyond single prediction theories to integration within an ecological framework. *Ecology Letters*, *10*, 995–1015.

McGill, B. J. (2003). Does mother nature really prefer rare species or are log-left-skewed SADs a sampling artefact? *Ecology Letters*, *6*(8), 766–773.

Meier, E. S., Kienast, F., Pearman, P. B., Svenning, J. C., Thuiller, W., Araújo, M. B., Guisan, A., & Zimmermann, N. E. (2010). Biotic and

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abiotic variables show little redundancy in explaining tree species distributions. *Ecography*, *33*(6), 1038–1048.

Menges, E. S. (1991). The application of minimum viable population theory to plants. *Genetics and Conservation of Rare Plants*, *45*, 158–164.

Meyer, C., Weigelt, P., & Kreft, H. (2016). Multidimensional biases, gaps and uncertainties in global plant occurrence information. *Ecology Letters*, *19*(8), 992–1006.

Molina, N. (2013). *Conservation of rare or little-known species: Biological, social, and economic considerations*. Island Press.

Morris, R. J. (2010). Anthropogenic impacts on tropical forest biodiversity: A network structure and ecosystem functioning perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1558), 3709–3718.

Mouillot, D., Bellwood, D. R., Baraloto, C., Chave, J., & Galzin, R. (2013). Rare species support vulnerable functions in high-diversity ecosystems. *PLoS Biology*, *11*(5), 1001569. https://doi.org/10.1371/journal.pbio.1001569

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, *403*(6772), 853–858. https://doi.org/10.1038/35002501

Myneni, R., Knyazikhin, Y., & Park, T. (2015). *MCD15A3H MODIS/Terra+Aqua Leaf Area Index/FPAR 4-day L4 Global 500m SIN Grid V006*. NASA EOSDIS Land Processes DAAC.

Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Lysenko, I., Senior, R. A., Börger, L., Bennett, D. J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria-Londoño, S., Edgar, M. J., Feldman, A., Garon, M., Harrison, M. L. K., Alhusseini, T., … Purvis, A. (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, *520*(7545), 45–50.

Paillet, Y., Bergès, L., Hjältén, J., Ódor, P., Avon, C., Bernhardt-Römermann, M., … Virtanen, R. (2010). Biodiversity differences between managed and unmanaged forests: Meta-analysis of species richness in Europe. *Conservation Biology*, *24*(1), 101–112.

Pitman, N. C., Terborgh, J. W., Silman, M. R., Núñez, V., Neill, D. A., Cerón, C. E., Palacios, W. A., & Aulestia, M. (2001). Dominance and distribution of tree species in upper Amazonian terra firme forests. *Ecology*, *82*(October 2000), 2101–2117.

Poulter, B., Aragão, L., Andela, N., Bellassen, V., Ciais, P., Kato, T., Lin, X., Nachin, B., Luyssaert, S., Pederson, N., Peylin, P., Piao, S., Pugh, T., Saatchi, S., Schepaschenko, D., Schelhaas, M., & Shivdenko, A. (2019). *The global forest age dataset and its uncertainties (GFADv1.1)*. NASA National Aeronautics and Space Administration, PANGAEA.

Preston, F. W. (1962). The canonical distribution of commonness and rarity: Part I. *Ecology*, *43*(2), 185–215.

Purvis, A., Gittleman, J. L., Cowlishaw, G., & Mace, G. M. (2000). Predicting extinction risk in declining species. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *267*(1456), 1947–1952.

R Core Team. (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.r-project.org/

Rabinowitz, D., Cairns, S., & Dillion, T. (1986). Seven forms of rarity and their frequency in the flora of the British Isles. In M. E. Soule (Ed.), *Conservation biology: The science of scarcity and diversity* (pp. 182–204). Sinauer Associates.

Rao, V. S., Ravi, B., & Rao, P. (2015). Carbon sequestration potential of tropical deciduous forests of Nallamalais, India. *Pelagia Research Library Asian Journal of Plant Science and Research*, *5*(3), 24–33.

Ribeiro, E., Batjes, N., & Van Oostrum, A. (2018). World Soil Information Service (WoSIS)—Towards the standardization and harmonization of world soil data. Procedures Manual 2018. ISRIC report 2018/01, ISRIC—World Soil Information.

Richardson, D. M., & Rejmánek, M. (2011). Trees and shrubs as invasive alien species - a global review. *Diversity and Distributions*, *17*(5), 788–809.

Riemann, R., Wilson, B. T., Lister, A. J., Cook, O., & Crane-Murdoch, S. (2018). Tree species distribution in the United States part 1. *Journal of Maps*, *14*(2), 561–566.

Roughgarden, J., & Diamond, J. (1986). Overview: The role of species interactions in community ecology. In J. Diamond & T. J. Case (Eds.), *Community ecology* (pp. 333–343). Harper & Row Publishers.

Rozendaal, D. M. A., Bongers, F., Aide, T. M., Alvarez-Dávila, E., Ascarrunz, N., Balvanera, P., Becknell, J. M., Bentos, T. V., Brancalion, P. H. S., Cabral, G. A. L., Calvo-Rodriguez, S., Chave, J., César, R. G., Chazdon, R. L., Condit, R., Dallinga, J. S., De Almeida-Cortez, J. S., De Jong, B., De Oliveira, A., … Poorter, L. (2019). Biodiversity recovery of Neotropical secondary forests. *Science. Advances*, *5*(3), eaau3114.

Running, S., Mu, Q., & Zhao, M. (2011). *MOD17A3 MODIS/Terra Net Primary Production Yearly L4 Global 1km SIN Grid V055 [Data set]*. NASA EOSDIS Land Processes DAAC.

Ryan, M. G., & Yoder, B. J. (1997). Hydraulic limits to tree height and tree growth. *Bioscience*, *47*(4), 235–242.

Sabatini, F. M., Jiménez-Alfaro, B., Jandt, U., Chytrý, M., Field, R., Kessler, M., Lenoir, J., Schrodt, F., Wiser, S. K., Arfin Khan, M. A. S., Attorre, F., Cayuela, L., De Sanctis, M., Dengler, J., Haider, S., Hatim, M. Z., Indreica, A., Jansen, F., Pauchard, A., … Bruelheide, H. (2022). Global patterns of vascular plant alpha diversity. *Nature Communications*, *13*(1), 4683.

Santoro, M., Cartus, O., Mermoz, S., Bouvet, A., Le Toan, T., Carvalhais, N., Rozendaal, D., Herold, M., Avitabile, V., Quegan, S., Carreiras, J., Rauste, Y., Balzter, H., Schmullius, C., & Seifert, F. M. (2018). A detailed portrait of the forest aboveground biomass pool for the year 2010 obtained from multiple remote sensing observations. *Geophysical Research Abstracts*, *20*(1), 18932.

Schaaf, C., & Wang, Z. (2015). *MCD43A4 MODIS/Terra+Aqua BRDF/Albedo Nadir BRDF Adjusted Ref Daily L3 Global—500 m V006 [Data set]*. NASA EOSDIS Land Processes DAAC.

Scheiner, S. M., Cox, S. B., & Willig, M. R. (2000). Species richness, species–area curves and Simpson's paradox. *Evolutionary Ecology Research*, *2*(6), 791–802.

Scheiner, S. M., & Rey-Benayas, J. M. (1994). Global patterns of plant diversity. *Evolutionary Ecology*, *8*, 331–347.

Simpson, E. H. (1951). The interpretation of interaction in contingency tables. *Journal of the Royal Statistical Society: Series B (Methodological)*, *13*(2), 238–241.

Slik, J. W. F., Aiba, S., Brearley, F. Q., Cannon, C. H., Forshed, O., Kitayama, K., Nagamasu, H., Nilus, R., Payne, J., Paoli, G., Poulsen, A. D., Raes, N., Sheil, D., Sidiyasa, K., Suzuki, E., & van Valkenburg, J. L. C. H. (2010). Environmental correlates of tree biomass, basal area, wood specific gravity and stem density gradients in Borneo's tropical forests. *Global Ecology and Biogeography*, *19*(1), 50–60.

Soininen, J., Passy, S., & Hillebrand, H. (2012). The relationship between species richness and evenness: A meta-analysis of studies across aquatic ecosystems. *Oecologia*, *169*, 803–809.

Stevens, C. J., Dise, N. B., Mountford, J. O., Gowing, D. J., Hautier, Y., Hector, A., Harpole, W. S., O'Halloran, L. R., Grace, J. B., Anderson, T. M., Bakker, J. D., Biederman, L. A., Brown, C. S., Buckley, Y. M., Calabrese, L. B., Chu, C. J., Cleland, E. E., Collins, S. L., Cottingham, K. L., … Yang, L. H. (2004). Impact of nitrogen deposition on the species richness of grasslands. *Science*, *303*(5665), 1876–1879.

Stirling, G., & Wilsey, B. (2001). Empirical relationships between species richness, evenness, and proportional diversity. *The American Naturalist*, *158*(3), 286–299.

Stroud, J. T., Bush, M. R., Ladd, M. C., Nowicki, R. J., Shantz, A. A., & Sweatman, J. (2015). Is a community still a community? Reviewing definitions of key terms in community ecology. *Ecology and Evolution*, *5*(21), 4757–4765.

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Svenning, J.-C., Kinner, D. A., Stallard, R. F., Engelbrecht, B. M. J., & Wright, S. J. (2004). Ecological determinism in plant community structure across a tropical forest landscape. *Ecology*, *85*(9), 2526–2538.

Swanson, H. A., Svenning, J. C., Saxena, A., Muscarella, R., Franklin, J., Garbelotto, M., Mathews, A. S., Saito, O., Schnitzler, A. E., Serra-Diaz, J. M., & Tsing, A. L. (2021). History as grounds for interdisciplinarity: Promoting sustainable woodlands via an integrative ecological and socio-cultural perspective. *One Earth*, *4*(2), 226–237.

Ter Steege, H., Pitman, N. C. A., Sabatier, D., Baraloto, C., Salomão, R. P., Guevara, J. E., Phillips, O. L., Castilho, C. V., Magnusson, W. E., Molino, J. F., Monteagudo, A., Vargas, P. N., Montero, J. C., Feldpausch, T. R., Coronado, E. N. H., Killeen, T. J., Mostacedo, B., Vasquez, R., Assis, R. L., … Silman, M. R. (2013). Hyperdominance in the Amazonian tree flora. *Science*, *342*(6156), 1243092-1–1243092-9.

Thakur, M., Schättin, E. W., & McShea, W. J. (2018). Globally common, locally rare: Revisiting disregarded genetic diversity for conservation planning of widespread species. *Biodiversity and Conservation*, *27*(11), 3031–3035.

The Plant List. (2013). The Plant List (2013). Version 1.1. www.theplantlist.org/

Tuanmu, M.-N., & Jetz, W. (2014). A global 1-km consensus land-cover product for biodiversity and ecosystem modelling. *Global Ecology and Biogeography*, *23*(9), 1031–1045.

Tuanmu, M.-N., & Jetz, W. (2015). A global, remote sensing-based characterization of terrestrial habitat heterogeneity for biodiversity and ecosystem modelling. *Global Ecology and Biogeography*, *24*(11), 1329–1339.

Ulrich, W., Kusumoto, B., Shiono, T., & Kubota, Y. (2016). Climatic and geographic correlates of global forest tree species-abundance distributions and community evenness. *Journal of Vegetation Science*, *27*(2), 295–305.

Ulrich, W., Ollik, M., & Ugland, K. I. (2010). A meta-analysis of species–abundance distributions. *Oikos*, *119*(7), 1149–1155.

University, C. for I. E. S. I. N.-C.-C. (2016). *Gridded population of the world, version 4 (GPWv4): Population density adjusted to match 2015 revision UN WPP country totals*. NASA Socioeconomic Data and Applications Center (SEDAC).

Urbieta, I. R., Zavala, M. A., & Marañón, T. (2008). Human and non-human determinants of forest composition in southern Spain: Evidence of shifts towards cork oak dominance as a result of management over the past century. *Journal of Biogeography*, *35*(9), 1688–1700.

van de Peer, T., Verheyen, K., Kint, V., Van Cleemput, E., & Muys, B. (2017). Plasticity of tree architecture through interspecific and intraspecific competition in a young experimental plantation. *Forest Ecology and Management*, *385*, 1–9.

van den Hoogen, J., Geisen, S., Routh, D., Ferris, H., Traunspurger, W., Wardle, D. A., de Goede, R. G. M., Adams, B. J., Ahmad, W., Andriuzzi, W. S., Bardgett, R. D., Bonkowski, M., Campos-Herrera, R., Cares, J. E., Caruso, T., de Brito Caixeta, L., Chen, X., Costa, S. R., Creamer, R., … Crowther, T. W. (2019). Soil nematode abundance and functional group composition at a global scale. *Nature*, *572*(7768), 194–198.

van den Hoogen, J., Robmann, N., Routh, D., Lauber, T., van Tiel, N., Danylo, O., & Crowther, T. W. (2021). A geospatial mapping pipeline for ecologists. BioRxiv, 2021.07.07.451145.

Venn, S. E., Green, K., Pickering, C. M., & Morgan, J. W. (2011). Using plant functional traits to explain community composition across a strong environmental filter in Australian alpine snowpatches. *Plant Ecology*, *212*(9), 1491–1499.

Vincent, H., Bornand, C. N., Kempel, A., & Fischer, M. (2020). Rare species perform worse than widespread species under changed climate. *Biological Conservation*, *246*, 108586.

Volkov, I., Banavar, J. R., Hubbell, S. P., & Maritan, A. (2003). Neutral theory and relative species abundance. *Nature*, *424*(13), 1035–1037.

Wan, J.-Z., Wang, C.-J., & Yu, F.-H. (2017). Spatial conservation prioritization for dominant tree species of Chinese forest communities under climate change. *Climatic Change*, *144*(2), 303–316.

Weiher, E., & Keddy, P. A. (1999). Relative abundance and evenness patterns along diversity and biomass gradients. *Oikos*, *87*(2), 355–361.

Wilsey, B. J., Teaschner, T. B., Daneshgar, P. P., Isbell, F. I., & Polley, H. W. (2009). Biodiversity maintenance mechanisms differ between native and novel exotic-dominated communities. *Ecology Letters*, *12*(5), 432–442.

Wilson, J. B., Steel, J. B., King, W. M., & Gitay, H. (1999). The effect of spatial scale on evenness. *Journal of Vegetation Science*, *10*(4), 463–468.

With, K. A., & King, A. W. (1999). Extinction thresholds for species in fractal landscapes. *Conservation Biology*, *13*(2), 314–326.

Xu, Z., Shimizu, H., Ito, S., Yagasaki, Y., Zou, C., Zhou, G., & Zheng, Y. (2014). Effects of elevated CO2, warming and precipitation change on plant growth, photosynthesis and peroxidation in dominant species from North China grassland. *Planta*, *239*(2), 421–435.

Zhang, H., John, R., Peng, Z., Yuan, J., Chu, C., Du, G., & Zhou, S. (2012). The relationship between species richness and evenness in plant communities along a successional gradient: A study from sub-alpine meadows of the Eastern Qinghai-Tibetan Plateau, China. *PLoS ONE*, *7*(11), e49024.

Zhang, J., Huang, S., & He, F. (2015). Half-century evidence from western Canada shows forest dynamics are primarily driven by competition followed by climate. *Proceedings of the National Academy of Sciences*, *112*(13), 4009–4014.

Zilliox, C., & Gosselin, F. (2014). Tree species diversity and abundance as indicators of understory diversity in French mountain forests: Variations of the relationship in geographical and ecological space. *Forest Ecology and Management*, *321*, 105–116.

Zizka, A., Steege, H. T., Pessoa, M. D. C. R., & Antonelli, A. (2018). Finding needles in the haystack: Where to look for rare species in the American tropics. *Ecography*, *41*(2), 321–330.

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The leading author of this manuscript is especially interested in (1) how environmental filtering, the surrounding landscape and land use history affect tree species presence, (2) how traits and the local biotic and abiotic environment affect tree species abundances, and (3) how abundances of tree species contribute to ecosystem functioning.

SUPPORTING INFORMATION

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