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RESEARCH ARTICLE

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

Iris Hordijk[1,2] | Lalasia Bialic-Murphy[1] | Thomas Lauber[1] | Devin Routh[3,4] | Lourens Poorter[2] | Malin C. Rivers[5] | Hans ter Steege[6,7] | Jingjing Liang[8] | Peter B. Reich[9,10] | Sergio de-Miguel[11,12] | Gert-Jan Nabuurs[2] | Javier G. P. Gamarra[13] | Han Y. H. Chen[14] | Mo Zhou[8] | Susan K. Wiser[15] | Hans Pretzsch[16] | Alain Paquette[17] | Nicolas Picard[18] | Bruno Hérault[19,20] | Jean-Francois Bastin[21] | Giorgio Alberti[22,23] | Meinrad Abegg[24] | Yves C. Adou Yao[25] | Angelica M. Almeyda Zambrano[26] | Braulio V. Alvarado[27] | Esteban Alvarez-Davila[28] | Patricia Alvarez-Loayza[29] | Luciana F. Alves[30] | Christian Ammer[31] | Clara Antón-Fernández[32] | Alejandro Araujo-Murakami[33] | Luzmila Arroyo[33] | Valerio Avitabile[34] | Gerardo A. Aymard Corredor[35,36] | Timothy Baker[37] | Olaf Banki[6] | Jorcely Barroso[38] | Meredith L. Bastian[39,40] | Luca Birigazzi[41] | Philippe Birnbaum[42] | Robert Bitariho[43] | Pascal Boeckx[44] | Frans Bongers[2] | Olivier Bouriaud[45] | Pedro H. S. Brancalion[46] | Susanne Brandl[47] | Roel Brienen[37] | Eben N. Broadbent[48] | Helge Bruelheide[49,50] | Filippo Bussotti[51] | Roberto Cazzolla Gatti[52] | Ricardo G. Cesar[46] | Goran Cesljar[53] | Robin Chazdon[54,55] | Chelsea Chisholm[1] | Emil Cienciala[56,57] | Connie J. Clark[58] | David B. Clar[59] | Gabriel Colletta[60] | David Coomes[61] | Fernando Cornejo Valverde[62] | Jose J. Corral-Rivas[63] | Philip Crim[64,65] | Jonathan Cumming[65] | Selvadurai Dayanandan[66] | André L. de Gasper[67] | Mathieu Decuyper[2,68] | Géraldine Derroire[69] | Ben DeVries[70] | Ilija Djordjevic[71] | Amaral Iêda[72] | Aurélie Dourdain[69] | Jiri Dolezal[73,74] | Nestor Laurier Engone Obiang[75] | Brian Enquist[76,77] | Teresa Eyre[78] | Adandé Belarmain Fandohan[79] | Tom M. Fayle[80,81,82] | Leandro V. Ferreira[83] | Ted R. Feldpausch[84] | Leena Finér[85] | Markus Fischer[86] | Christine Fletcher[87] | Lorenzo Frizzera[88] | Damiano Gianelle[88] | Henry B. Glick[89] | David Harris[90] | Andrew Hector[91] | Andreas Hemp[92] | Geerten Hengeveld[2] | John Herbohn[55] | Annika Hillers[93,94] | Eurídice N. Honorio Coronado[95] | Cang Hui[96,97] | Hyunkook Cho[98] | Thomas Ibanez[42] | Ilbin Jung[98] | Nobuo Imai[99] | Andrzej M. Jagodzinski[100,101] | Bogdan Jaroszewicz[102] | Vivian Johannsen[103] | Carlos A. Joly[104] | Tommaso Jucker[105] | Viktor Karminov[106] | Kuswata Kartawinata[29] |

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Elizabeth Kearsley[107] | David Kenfack[108] | Deborah Kennard[109] | Sebastian Kepfer-Rojas[103] | Gunnar Keppel[110] | Mohammed Latif Khan[111] | Timothy Killeen[33] | Hyun Seok Kim[112,113,114,115] | Kanehiro Kitayama[116] | Michael Köhl[117] | Henn Korjus[118] | Florian Kraxner[119] | Diana Laarmann[118] | Mait Lang[118] | Simon Lewis[37,120] | Huicui Lu[121] | Natalia Lukina[122] | Brian Maitner[76] | Yadvinder Malhi[123] | Eric Marcon[124] | Beatriz Schwantes Marimon[125] | Ben Hur Marimon-Junior[125] | Andrew Robert Marshall[55,126,127] | Emanuel Martin[128] | Olga Martynenko[106] | Jorge A. Meave[129] | Omar Melo-Cruz[130] | Casimiro Mendoza[131] | Cory Merow[54] | Stanislaw Miscicki[132] | Abel Monteagudo Mendoza[133,134] | Vanessa Moreno[46] | Sharif A. Mukul[55,135] | Philip Mundhenk[117] | Maria G. Nava-Miranda[136,137] | David Neill[138] | Victor Neldner[78] | Radovan Nevenic[71] | Michael Ngugi[78] | Pascal A. Niklaus[139] | Jacek Oleksyn[99] | Petr Ontikov[106] | Edgar Ortiz-Malavasi[27] | Yude Pan[140] | Alexander Parada-Gutierrez[33] | Elena Parfenova[141] | Minjee Park[8,112] | Marc Parren[142] | Narayanaswamy Parthasarathy[143] | Pablo L. Peri[144] | Sebastian Pfautsch[145] | Oliver L. Phillips[37] | Maria Teresa Piedade[146] | Daniel Piotto[147] | Nigel C. A. Pitman[29] | Irina Polo[148] | Axel Dalberg Poulsen[90] | John R. Poulsen[58] | Freddy Ramirez Arevalo[149] | Zorayda Restrepo-Correa[150] | Mirco Rodeghiero[151] | Samir Rolim[147] | Anand Roopsind[152] | Francesco Rovero[153,154] | Ervan Rutishauser[155] | Purabi Saikia[156] | Christian Salas-Eljatib[157,158,159] | Peter Schall[31] | Dmitry Schepaschenko[119] | Michael Scherer-Lorenzen[160] | Bernhard Schmid[17] | Jochen Schöngart[146] | Eric B. Searle[17] | Vladimír Seben[161] | Josep M. Serra-Diaz[162,163] | Douglas Sheil[2,164] | Anatoly Shvidenko[119] | Javier Silva-Espejo[165] | Marcos Silveira[166] | James Singh[167] | Plinio Sist[19] | Ferry Slik[168] | Bonaventure Sonké[169] | Alexandre F. Souza[170] | Krzysztof Stereńczak[171] | Jens-Christian Svenning[163,172] | Miroslav Svoboda[173] | Ben Swanepoel[174] | Natalia Targhetta[146] | Nadja Tchebakova[141] | Raquel Thomas[175] | Elena Tikhonova[123] | Peter Umunay[89] | Vladimir Usoltsev[176] | Renato Valencia[177] | Fernando Valladares[178] | Fons van der Plas[179] | Tran Van Do[180] | Michael E. Van Nuland[181] | Rodolfo Vasquez Martinez[132] | Hans Verbeeck[107] | Helder Viana[182,183] | Alexander C. Vibrans[57,184] | Simone Vieira[185] | Klaus von Gadow[186] | Hua-Feng Wang[187] | James Watson[188] | Gijsbert D. A. Werner[189] | Florian Wittmann[190] | Verginia Wortel[191] | Roderick Zagt[192] | Tomasz Zawila-Niedzwiecki[193] | Chunyu Zhang[194] | Xiuhai Zhao[194] | Zhi-Xin Zhu[187] | Irie Casimir Zo-Bi[20] | Daniel S. Maynard[1,195] | Thomas W. Crowther[1]

Correspondence
Iris Hordijk, Institute of Integrative Biology, ETH Zurich (Swiss Federal Institute of Technology), Universitätsstrasse 16, Zurich 8092, Switzerland.
Email: irishordijk@hotmail.com

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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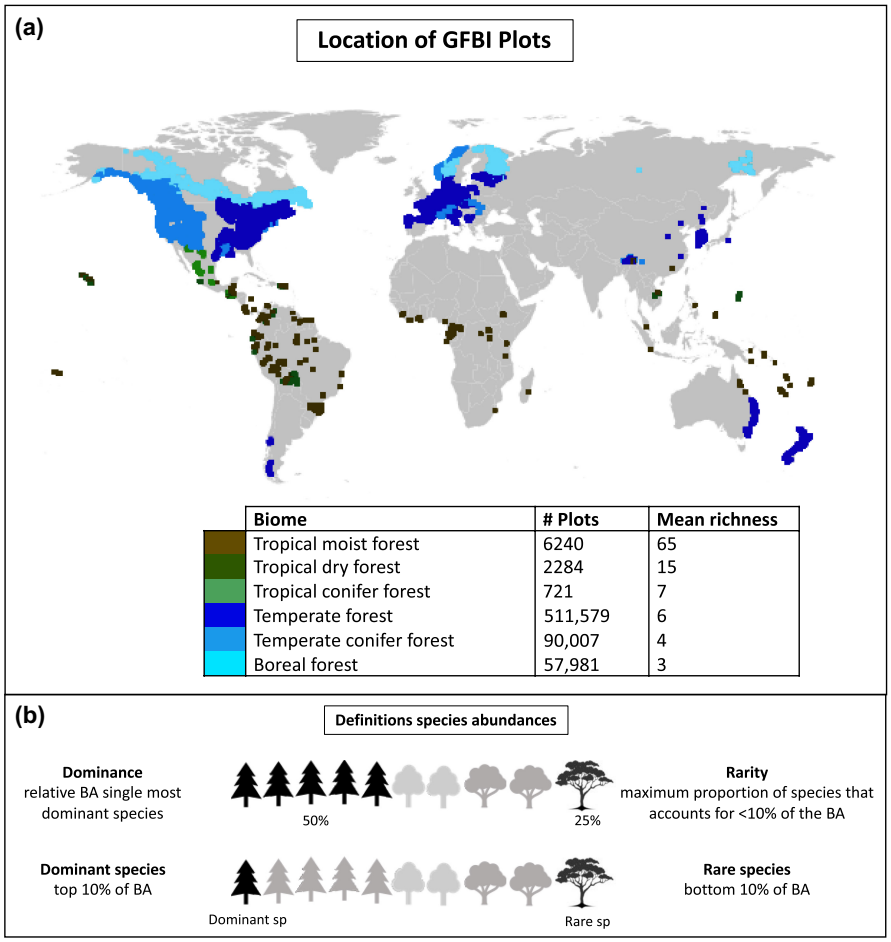

Biome	# Plots	Mean richness
Tropical moist forest	6240	65
Tropical dry forest	2284	15
Tropical conifer forest	721	7
Temperate forest	511,579	6
Temperate conifer forest	90,007	4
Boreal forest	57,981	3

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

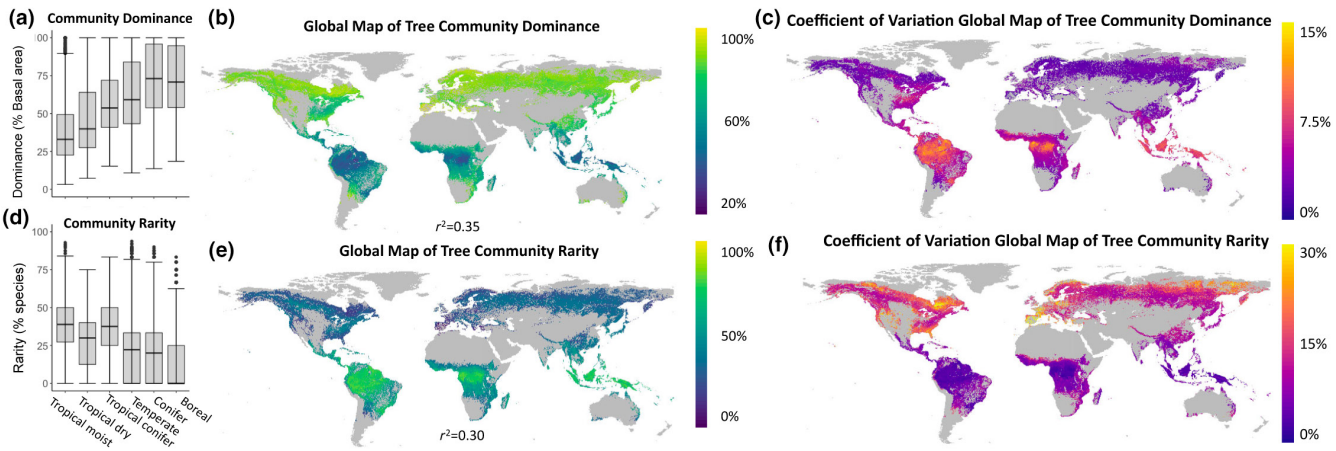

FIGURE 2 Global tree community dominance and rarity. (a) Community dominance is the percentage basal area of the most dominant species in the forest plot. The boxplot visualizes the measured data in the six forest biomes. (b) The map of predicted community dominance in global forests, with the spatially 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).

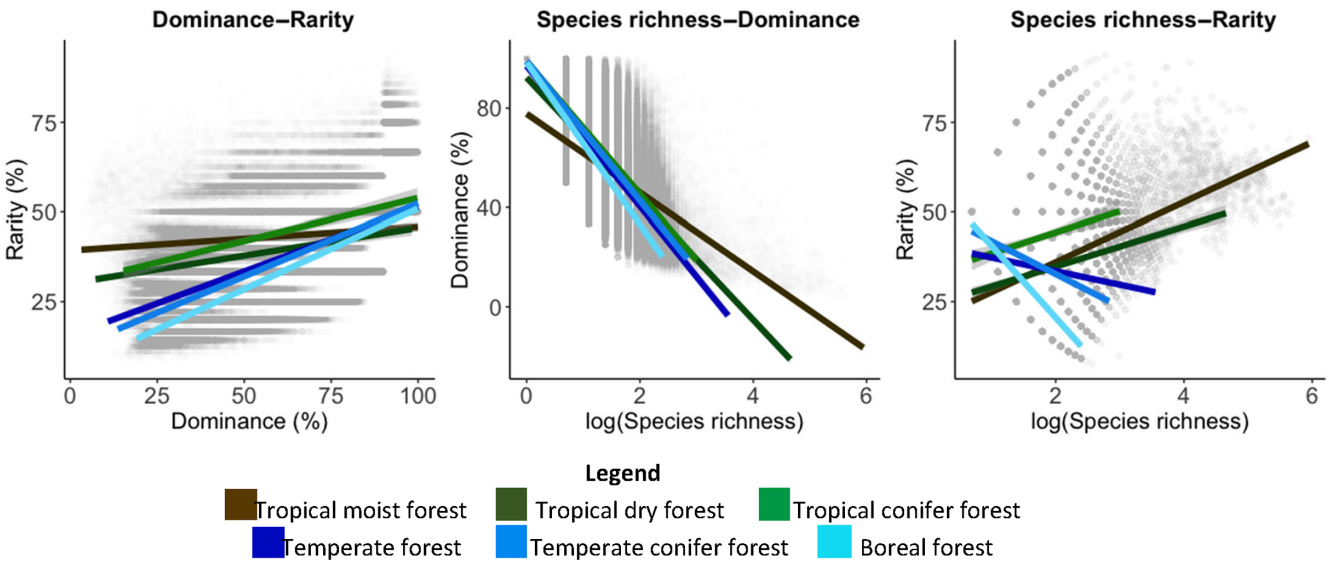

FIGURE 3 The relationship between dominance, rarity and species richness in forests globally ($N=670{,}527$). For the relationship between rarity and dominance, and rarity and species richness, only the plots that included rare species were considered ($N=X$). In Figure S4, the relationships between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

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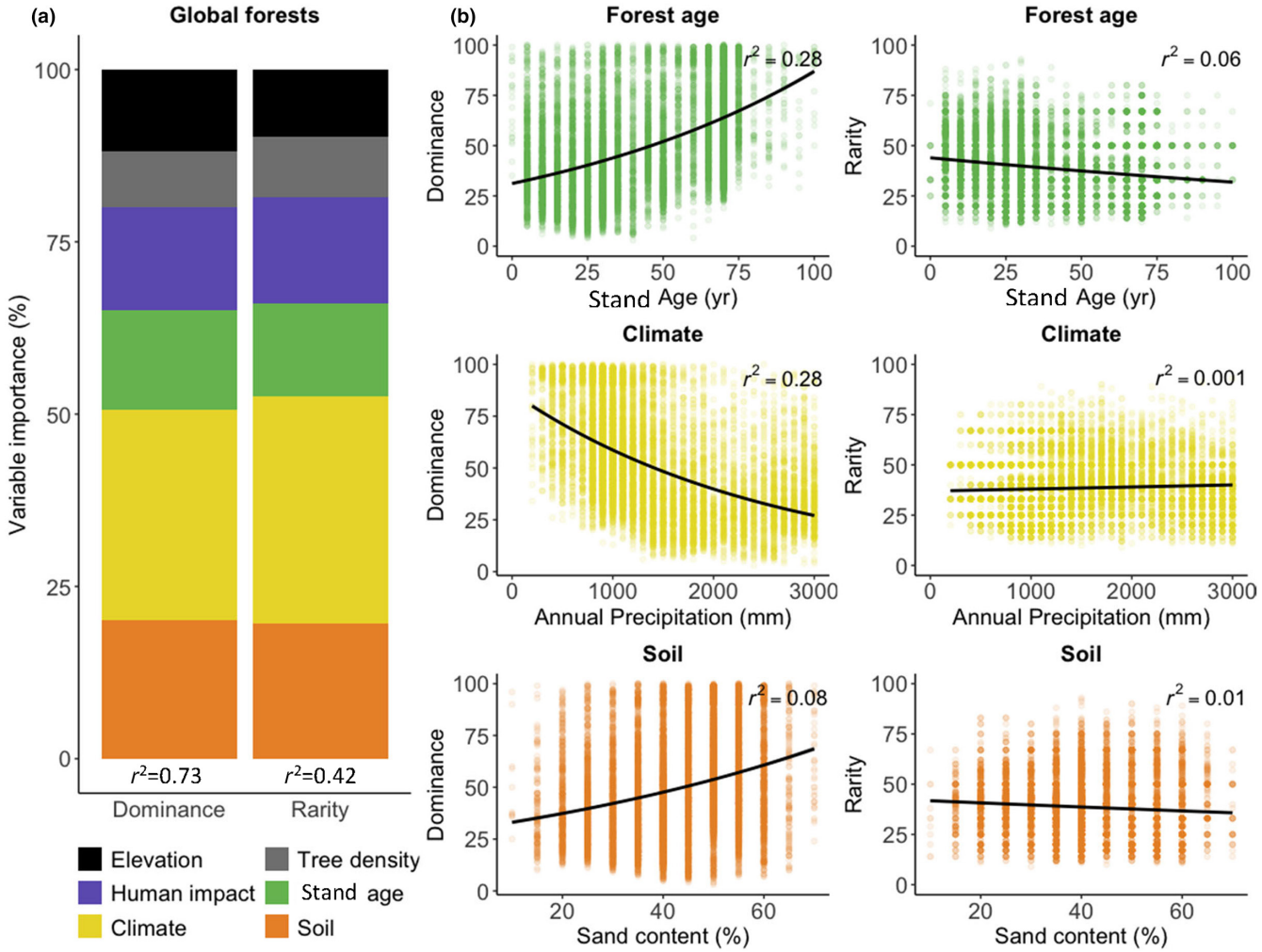

FIGURE 4 (a) Relative variable importance of soil characteristics (soil pH and soil sand content), climate (annual mean and seasonality of precipitation and temperature), stand age (percentage secondary forest, stand age) and human impact (human development and population density) on tree community dominance 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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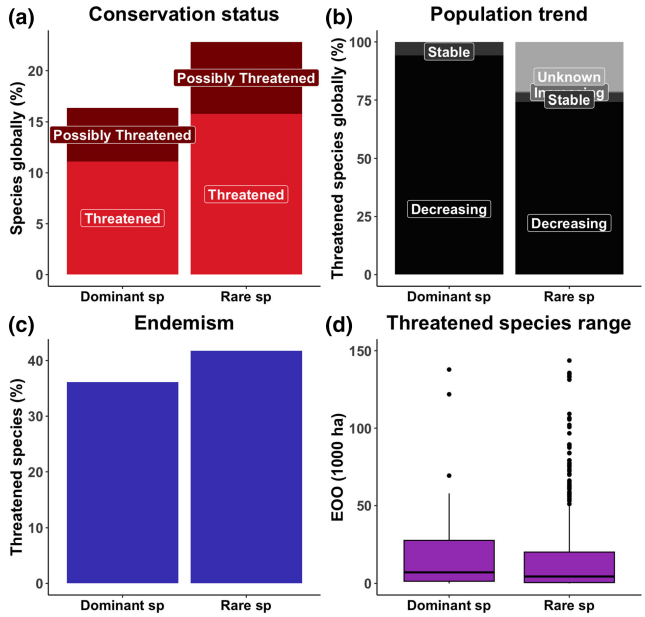

FIGURE 5 (a) The percentage of locally dominant and rare species identified as "threatened", or "possibly threatened" according to the Global Tree Assessment (BGCI, 2021a). (b) The population trend of threatened dominant and rare species. Threatened species are defined as "vulnerable", "endangered" or "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.

AFFILIATIONS

[1]Institute of Integrative Biology, ETH Zurich (Swiss Federal Institute of Technology), Zurich, Switzerland
[2]Wageningen University and Research, Wageningen, The Netherlands
[3]Department of Geography, University of Zürich, Zürich, Switzerland
[4]Department of Science IT, University of Zürich, Zürich, Switzerland
[5]Botanic Gardens Conservation International, Richmond, UK
[6]Naturalis Biodiversity Centre, Leiden, The Netherlands
[7]Quantitative Biodiversity Dynamics, Department of Biology, Utrecht University, Utrecht, The Netherlands
[8]Department of Forestry and Natural Resources, Purdue University, West Lafayette, Indiana, USA
[9]Department of Forest Resources, University of Minnesota, St Paul, Minnesota, USA
[10]Hawkesbury Institute for the Environment, Western Sydney University, Penrith, New South Wales, Australia
[11]Department of Agricultural and Forest Sciences and Engineering, University of Lleida, Lleida, Spain
[12]Joint Research Unit CTFC – AGROTECNIO – CERCA, Solsona, Spain
[13]Forestry Division, Food and Agriculture Organization of the United Nations, Rome, Italy
[14]Faculty of Natural Resources Management, Lakehead University, Thunder Bay, Ontario, Canada
[15]Manaaki Whenua–Landcare Research, Lincoln, New Zealand
[16]Chair for Forest Growth and Yield Science, TUM School for Life Sciences, Technical University of Munich, Munich, Germany
[17]Centre for Forest Research, Université du Québec à Montréal, Montréal, Quebec, Canada
[18]GIP ECOFOR, Paris, France
[19]Cirad, UPR Forêts et Sociétés, University of Montpellier, Montpellier, France
[20]Department of Forestry and Environment, National Polytechnic Institute (INP-HB), Yamoussoukro, Côte d'Ivoire
[21]Gembloux Agro Bio-Tech, University of Liege, Liege, Belgium
[22]Faculty of Science and Technology, Free University of Bolzano, Bolzano, Italy
[23]Department of Agricultural, Food, Environmental and Animal Sciences, University of Udine, Udine, Italy
[24]Swiss Federal Institute for Forest, Snow and Landscape Research, WSL, Birmensdorf, Switzerland
[25]UFR Biosciences, University Félix Houphouët-Boigny, Abidjan, Côte d'Ivoire
[26]Spatial Ecology and Conservation Laboratory, Center for Latin American Studies, University of Florida, Gainesville, Florida, USA
[27]Forestry School, Tecnológico de Costa Rica TEC, Cartago, Costa Rica
[28]Fundacion ConVida, Universidad Nacional Abierta y a Distancia, UNAD, Medellin, Colombia
[29]Field Museum of Natural History, Chicago, Illinois, USA
[30]Center for Tropical Research, Institute of the Environment and Sustainability, UCLA, Los Angeles, California, USA
[31]Silviculture and Forest Ecology of the Temperate Zones, University of Göttingen, Göttingen, Germany
[32]Division of Forest and Forest Resources, Norwegian Institute of Bioeconomy Research (NIBIO), Ås, Norway
[33]Museo de Historia natural Noel kempff Mercado, Santa Cruz, Bolivia
[34]European Commission, Joint Research Centre, Ispra, Italy
[35]UNELLEZ-Guanare, Programa de Ciencias del Agro y el Mar, Herbario Universitario (PORT), Portuguesa, Venezuela
[36]Compensation International S. A. Ci Progress-GreenLife, Bogotá D.C., Colombia
[37]School of Geography, University of Leeds, Leeds, UK
[38]Centro Multidisciplinar, Universidade Federal do Acre, Rio Branco, Brazil
[39]Proceedings of the National Academy of Sciences, Washington, District of Columbia, USA
[40]Department of Evolutionary Anthropology, Duke University, Durham, North Carolina, USA
[41]United Nation Framework Convention on Climate Change, Bonn, Germany
[42]Cirad, UMR-AMAP, CNRS, INRA, IRD, Université de Montpellier, Montpellier, France
[43]Institute of Tropical Forest Conservation, Mbarara University of Sciences and Technology, Mbarara, Uganda
[44]Isotope Bioscience Laboratory – ISOFYS, Ghent University, Ghent, Belgium
[45]Integrated Center for Research, Development and Innovation in Advanced Materials, Nanotechnologies, and Distributed Systems for Fabrication and Control (MANSiD), Stefan cel Mare University of Suceava, Suceava, Romania
[46]Department of Forest Sciences, Luiz de Queiroz College of Agriculture, University of São Paulo, Piracicaba, Brazil
[47]Bavarian State Institute of Forestry, Freising, Germany
[48]Spatial Ecology and Conservation Laboratory, School of Forest, Fisheries, and Geomatics Sciences, University of Florida, Gainesville, Florida, USA
[49]Institute of Biology, Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Halle-Wittenberg, Germany
[50]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany
[51]Department of Agriculture, Food, Environment and Forest (DAGRI), University of Firenze, Florence, Italy
[52]Biological Institute, Tomsk State University, Tomsk, Russia
[53]Department of Spatial Regulation, GIS and Forest Policy, Institute of Forestry, Belgrade, Serbia
[54]Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut, USA
[55]Tropical Forests and People Research Centre, University of the Sunshine Coast, Maroochydore, Queensland, Australia
[56]IFER – Institute of Forest Ecosystem Research, Jilove u Prahy, Czech Republic
[57]Global Change Research Institute CAS, Brno, Czech Republic
[58]Nicholas School of the Environment, Duke University, Durham, North Carolina, USA
[59]Department of Biology, University of Missouri-St Louis, St Louis, Missouri, USA
[60]Programa de Pós-graduação em Biologia Vegetal, Instituto de Biologia, Universidade Estadual de Campinas, Campinas, Brazil
[61]Department of Plant Sciences and Conservation Research Institute, University of Cambridge, Cambridge, UK
[62]Andes to Amazon Biodiversity Program, Madre de Dios, Peru
[63]Facultad de Ciencias Forestales, Universidad Juárez del Estado de Durango, Durango, Mexico
[64]Department of Physical and Biological Sciences, The College of Saint Rose, Albany, New York, USA
[65]Department of Biology, West Virginia University, Morgantown, West Virginia, USA
[66]Biology Department, Centre for Structural and Functional Genomics, Concordia University, Montreal, Quebec, Canada
[67]Natural Science Department, Universidade Regional de Blumenau, Blumenau, Brazil
[68]World Agroforestry (ICRAF), Nairobi, Kenya
[69]Cirad, UMR EcoFoG (AgroParistech, CNRS, INRAE, Université des Antilles, Université de la Guyane), Campus Agronomique, Kourou, French Guiana
[70]Department of Geographical Sciences, University of Maryland, College Park, Maryland, USA
[71]Institute of Forestry, Belgrade, Serbia
[72]National Institute of Amazonian Research, Manaus, Brazil
[73]Institute of Botany, The Czech Academy of Sciences, Průhonice, Czech Republic
[74]Department of Botany, Faculty of Science, University of South Bohemia, České Budějovice, Czech Republic
[75]IRET, Herbier National du Gabon (CENAREST), Libreville, Gabon
[76]Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona, USA

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[77]The Santa Fe Institute, Santa Fe, New Mexico, USA
[78]Department of Environment and Science, Queensland Herbarium, Toowong, Queensland, Australia
[79]Ecole de Foresterie et Ingénierie du Bois, Université Nationale d'Agriculture, Ketou, Benin
[80]School of Biological and Behavioural Sciences, Queen Mary University of London, London, UK
[81]Institute of Entomology, Biology Centre of the Czech Academy of Sciences, Ceske Budejovice, Czech Republic
[82]Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Kota Kinabalu, Malaysia
[83]Museu Paraense Emílio Goeldi. Coordenação de Ciências da Terra e Ecologia, Belém, Brazil
[84]Geography, College of Life and Environmental Sciences, University of Exeter, Exeter, UK
[85]Natural Resources Institute Finland (Luke), Joensuu, Finland
[86]Institute of Plant Sciences, University of Bern, Bern, Switzerland
[87]Forest Research Institute Malaysia, Kuala Lumpur, Malaysia
[88]Department of Sustainable Agro-Ecosystems and Bioresources, Research and Innovation Center, Fondazione Edmund Mach, San Michele all'Adige, Italy
[89]School of Forestry and Environmental Studies, Yale University, New Haven, Connecticut, USA
[90]Royal Botanic Garden Edinburgh, Edinburgh, UK
[91]Department of Plant Sciences, University of Oxford, Oxford, UK
[92]Department of Plant Systematics, University of Bayreuth, Bayreuth, Germany
[93]Centre for Conservation Science, The Royal Society for the Protection of Birds, Sandy, UK
[94]Wild Chimpanzee Foundation, Liberia Office, Monrovia, Liberia
[95]Instituto de Investigaciones de la Amazonía Peruana, Iquitos, Peru
[96]Centre for Invasion Biology, Department of Mathematical Sciences, Stellenbosch University, Stellenbosch, South Africa
[97]Theoretical Ecology Unit, African Institute for Mathematical Sciences, Cape Town, South Africa
[98]Division of Forest Resources Information, Korea Forest Promotion Institute, Seoul, South Korea
[99]Department of Forest Science, Tokyo University of Agriculture, Tokyo, Japan
[100]Institute of Dendrology, Polish Academy of Sciences, Kórnik, Poland
[101]Department of Game Management and Forest Protection, Poznań University of Life Sciences, Poznań, Poland
[102]Faculty of Biology, Białowieża Geobotanical Station, University of Warsaw, Białowieża, Poland
[103]Department of Geosciences and Natural Resource Management, University of Copenhagen, Copenhagen, Denmark
[104]Department of Plant Biology, Institute of Biology, University of Campinas, UNICAMP, Campinas, Brazil
[105]School of Biological Sciences, University of Bristol, Bristol, UK
[106]Forestry Faculty, Bauman Moscow State Technical University, Mytischi, Russia
[107]CAVElab-Computational and Applied Vegetation Ecology, Department of Environment, Ghent University, Ghent, Belgium
[108]CTFS-ForestGEO, Smithsonian Tropical Research Institute, Balboa, Panama
[109]Department of Physical and Environmental Sciences, Colorado Mesa University, Grand Junction, Colorado, USA
[110]UniSA STEM and Future Industries Institute, University of South Australia, Adelaide, South Australia, Australia
[111]Department of Botany, Dr Harisingh Gour Vishwavidyalaya (A Central University), Sagar, India
[112]Department of Agriculture, Forestry and Bioresources, Seoul National University, Seoul, South Korea
[113]Interdisciplinary Program in Agricultural and Forest Meteorology, Seoul National University, Seoul, South Korea
[114]National Center for Agro Meteorology, Seoul, South Korea
[115]Research Institute for Agriculture and Life Sciences, Seoul National University, Seoul, South Korea
[116]Graduate School of Agriculture, Kyoto University, Kyoto, Japan
[117]Institute for World Forestry, University of Hamburg, Hamburg, Germany
[118]Institute of Forestry and Rural Engineering, Estonian University of Life Sciences, Tartu, Estonia
[119]International Institute for Applied Systems Analysis, Laxenburg, Austria
[120]Department of Geography, University College London, London, UK
[121]Faculty of Forestry, Qingdao Agricultural University, Qingdao, China
[122]Center for Forest Ecology and Productivity, Russian Academy of Sciences, Moscow, Russia
[123]School of Geography, University of Oxford, Oxford, UK
[124]UMR EcoFoG, AgroParisTech, Kourou, France
[125]Programa de Pós-graduação em Ecologia e Conservação, Universidade do Estado de Mato Grosso, Nova Xavantina, Brazil
[126]Flamingo Land Ltd, Kirby Misperton, UK
[127]Department of Environment & Geography, University of York, York, UK
[128]Department of Wildlife Management, College of African Wildlife Management, Mweka, Tanzania
[129]Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, Mexico City, Mexico
[130]Universidad del Tolima, Ibagué, Colombia
[131]Colegio de Profesionales Forestales de Cochabamba, Cochabamba, Bolivia
[132]Department of Forest Management, Dendrometry and Forest Economics, Warsaw University of Life Sciences, Warsaw, Poland
[133]Jardín Botánico de Missouri, Oxapampa, Peru
[134]Universidad Nacional de San Antonio Abad del Cusco, Cusco, Peru
[135]Department of Environment and Development Studies, United International University, Dhaka, Bangladesh
[136]Laboratorio de geomática, Instituto de Silvicultura e Industria de la Madera, Universidad Juárez del Estado de Durango, Durango, Mexico
[137]Programa de doctorado en Ingeniería para el desarrollo rural y civil, Escuela de Doctorado Internacional de la Universidad de Santiago de Compostela (EDIUS), Santiago de Compostela, Spain
[138]Universidad Estatal Amazónica, Puyo, Ecuador
[139]Department of Evolutionary Biology and Environmental Studies, University of Zürich, Zürich, Switzerland
[140]Climate, Fire, and Carbon Cycle Sciences, USDA Forest Service, Durham, North Carolina, USA
[141]V. N. Sukachev Institute of Forest, FRC KSC, Siberian Branch of the Russian Academy of Sciences, Krasnoyarsk, Russia
[142]Forest Ecology and Forest Management Group, Wageningen University & Research, Wageningen, The Netherlands
[143]Department of Ecology and Environmental Sciences, Pondicherry University, Puducherry, India
[144]Instituto Nacional de Tecnología Agropecuaria (INTA), Universidad Nacional de la Patagonia Austral (UNPA), Consejo Nacional de Investigaciones Científicas y Tecnicas (CONICET), Rio Gallegos, Argentina
[145]School of Social Sciences (Urban Studies), Western Sydney University, Penrith, New South Wales, Australia
[146]Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil
[147]Laboratório de Dendrologia e Silvicultura Tropical, Centro de Formação Em Ciências Agroflorestais, Universidade Federal do Sul da Bahia, Itabuna, Brazil
[148]Jardín Botánico de Medellín, Medellín, Colombia
[149]Universidad Nacional de la Amazonía Peruana, Iquitos, Peru
[150]Servicios Ecosistémicos y Cambio Climático (SECC), Fundación con Vida & Corporación COL-TREE, Medellín, Colombia
[151]Centro Agricoltura, Alimenti, Ambiente, University of Trento, San Michele all'Adige, Italy
[152]Department of Biological Sciences, Boise State University, Boise, Idaho, USA
[153]Department of Biology, University of Florence, Florence, Italy
[154]Tropical Biodiversity, MUSE – Museo delle Scienze, Trento, Italy
[155]Info Flora, Geneva, Switzerland
[156]Department of Environmental Sciences, Central University of Jharkhand, Ranchi, India

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[157]Centro de Modelación y Monitoreo de Ecosistemas, Universidad Mayor, Santiago, Chile
[158]Vicerrectoría de Investigación y Postgrado, Universidad de La Frontera, Temuco, Chile
[159]Departamento de Silvicultura y Conservación de la Naturaleza, Universidad de Chile, Santiago, Chile
[160]Faculty of Biology, Geobotany, University of Freiburg, Freiburg im Breisgau, Germany
[161]National Forest Centre, Forest Research Institute Zvolen, Zvolen, Slovakia
[162]Université de Lorraine, AgroParisTech, Inra, Silva, Nancy, France
[163]Department of Biology, Center for Ecological Dynamics in a Novel Biosphere (ECONOVO) & Center for Biodiversity Dynamics in a Changing World (BIOCHANGE), Aarhus University, Aarhus, Denmark
[164]Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Ås, Norway
[165]Departamento de Biología, Universidad de la Serena, La Serena, Chile
[166]Centro de Ciências Biológicas e da Natureza, Universidade Federal do Acre, Rio Branco, Brazil
[167]Guyana Forestry Commission, Georgetown, French Guiana
[168]Environmental and Life Sciences, Faculty of Science, Universiti Brunei Darussalam, Bandar Seri Begawan, Brunei Darussalam
[169]Plant Systematic and Ecology Laboratory, Department of Biology, Higher Teachers' Training College, University of Yaoundé I, Yaoundé, Cameroon
[170]Departamento de Ecologia, Universidade Federal do Rio Grande do Norte, Natal, Brazil
[171]Department of Geomatics, Forest Research Institute, Raszyn, Poland
[172]Section for Ecoinformatics & Biodiversity, Department of Biology, Aarhus University, Aarhus, Denmark
[173]Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Prague, Czech Republic
[174]Wildlife Conservation Society, Vientiane, Laos
[175]Iwokrama International Centre for Rainforest Conservation and Development (IIC), Georgetown, French Guiana
[176]Botanical Garden of Ural Branch of Russian Academy of Sciences, Ural State Forest Engineering University, Ekaterinburg, Russia
[177]Pontificia Universidad Católica del Ecuador, Quito, Ecuador
[178]LINCGlobal, Museo Nacional de Ciencias Naturales, CSIC, Madrid, Spain
[179]Plant Ecology and Nature Conservation Group, Wageningen University, Wageningen, The Netherlands
[180]Silviculture Research Institute, Vietnamese Academy of Forest Sciences, Hanoi, Vietnam
[181]Department of Biology, Stanford University, Stanford, California, USA
[182]Centre for the Research and Technology of Agro-Environmental and Biological Sciences, CITAB, University of Trás-os-Montes and Alto Douro, UTAD, Vila Real, Portugal
[183]Department of Ecology and Sustainable Agriculture, Agricultural High School of Polytechnic Institute of Viseu, Portugal
[184]Department of Forest Engineering, Universidade Regional de Blumenau, Blumenau, Brazil
[185]Environmental Studies and Research Center, University of Campinas, UNICAMP, Campinas, Brazil
[186]Department of Forest and Wood Science, University of Stellenbosch, Stellenbosch, South Africa
[187]Key Laboratory of Tropical Biological Resources, Ministry of Education, School of Life and Pharmaceutical Sciences, Hainan University, Haikou, China
[188]Division of Forestry and Natural Resources, West Virginia University, Morgantown, West Virginia, USA
[189]Department of Zoology, University of Oxford, Oxford, UK
[190]Department of Wetland Ecology, Institute for Geography and Geoecology, Karlsruhe Institute for Technology, Karlsruhe, Germany
[191]Centre for Agricultural Research in Suriname (CELOS), Paramaribo, Suriname
[192]Tropenbos International, Wageningen, The Netherlands
[193]Polish State Forests, Coordination Center for Environmental Projects, Warsaw, Poland
[194]Research Center of Forest Management Engineering of State Forestry and Grassland Administration, Beijing Forestry University, Beijing, China
[195]Department of Genetics, Evolution and Environment, University College London, London, UK

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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

ORCID

Iris Hordijk https://orcid.org/0000-0002-6302-6254
Lourens Poorter https://orcid.org/0000-0003-1391-4875
Jingjing Liang https://orcid.org/0000-0001-9439-9320
Sergio de-Miguel https://orcid.org/0000-0002-9738-0657
Han Y. H. Chen https://orcid.org/0000-0001-9477-5541
Bruno Hérault https://orcid.org/0000-0002-6950-7286
Jean-Francois Bastin https://orcid.org/0000-0003-2602-7247
Christian Ammer https://orcid.org/0000-0002-4235-0135
Helge Bruelheide https://orcid.org/0000-0003-3135-0356
Géraldine Derroire https://orcid.org/0000-0001-7239-2881
Jiri Dolezal https://orcid.org/0000-0002-5829-4051
Brian Enquist https://orcid.org/0000-0002-6124-7096
Leena Finér https://orcid.org/0000-0001-7623-9374
Andreas Hemp https://orcid.org/0000-0002-5369-2122
Cang Hui https://orcid.org/0000-0002-3660-8160
Andrzej M. Jagodzinski https://orcid.org/0000-0001-6899-0985
Elizabeth Kearsley https://orcid.org/0000-0003-0046-3606
Cory Merow https://orcid.org/0000-0003-0561-053X
John R. Poulsen https://orcid.org/0000-0002-1532-9808
Francesco Rovero https://orcid.org/0000-0001-6688-1494
Ferry Slik https://orcid.org/0000-0003-3988-7019
Krzysztof Stereńczak https://orcid.org/0000-0002-9556-0144
Tran Van Do https://orcid.org/0000-0001-9059-5842
Chunyu Zhang https://orcid.org/0000-0003-3091-5060
Xiuhai Zhao https://orcid.org/0000-0003-0879-4063

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BIOSKETCH

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

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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