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RESEARCH ARTICLE

Evenness mediates the global relationship between forest productivity and richness

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Mait Lang[108] | Simon Lewis[25,110] | Huicui Lu[111] | Natalia Lukina[112] | Brian Maitner[65] | Yadvinder Malhi[113] | Eric Marcon[114] | Beatriz Schwantes Marimon[115] | Ben Hur Marimon-Junior[115] | Andrew Robert Marshall[45,116,117] | Emanuel Martin[118] | Olga Martynenko[96] | Jorge A. Meave[119] | Omar Melo-Cruz[120] | Casimiro Mendoza[121] | Cory Merow[44] | Miscicki Stanislaw[122] | Abel Monteagudo Mendoza[123,124] | Vanessa Moreno[36] | Sharif A. Mukul[45,125] | Philip Mundhenk[107] | Maria G. Nava-Miranda[126] | David Neill[127] | Victor Neldner[128] | Radovan Nevenic[62] | Michael Ngugi[66] | Pascal A. Niklaus[129] | Jacek Oleksyn[90] | Petr Ontikov[96] | Edgar Ortiz-Malavasi[16] | Yude Pan[130] | Alain Paquette[131] | Alexander Parada-Gutierrez[22] | Elena Parfenova[132] | Minjee Park[5,102] | Marc Parren[133] | Narayanaswamy Parthasarathy[134] | Pablo L. Peri[135] | Sebastian Pfautsch[136] | Oliver L. Phillips[25] | Nicolas Picard[137] | Maria Teresa Piedade[138] | Daniel Piotto[139] | Nigel C. A. Pitman[18] | Irina Polo[140] | Lourens Poorter[8] | Axel Dalberg Poulsen[77] | John R. Poulsen[49] | Hans Pretzsch[141] | Freddy Ramirez Arevalo[142] | Zorayda Restrepo-Correa[143] | Mirco Rodeghiero[74,144] | Samir Rolim[139] | Anand Roopsind[145] | Francesco Rovero[146,147] | Ervan Rutishauser[148] | Purabi Saikia[149] | Christian Salas-Eljatib[150,151,152] | Peter Schall[20] | Dmitry Schepaschenko[109] | Michael Scherer-Lorenzen[153] | Bernhard Schmid[154] | Jochen Schöngart[138] | Eric B. Searle[131] | Vladimír Šebeň[155] | Josep M. Serra-Diaz[156,157] | Douglas Sheil[8,158] | Anatoly Shvidenko[109] | Javier Silva-Espejo[159] | Marcos Silveira[160] | James Singh[161] | Plinio Sist[80] | Ferry Slik[162] | Bonaventure Sonké[163] | Alexandre F. Souza[164] | Krzysztof Stereńczak[25] | Jens-Christian Svenning[156,165] | Miroslav Svoboda[166] | Ben Swanepoel[167] | Natalia Targhetta[137] | Nadja Tchebakova[131] | Raquel Thomas[168] | Elena Tikhonova[111] | Peter Umunay[75] | Vladimir Usoltsev[169] | Renato Valencia[170] | Fernando Valladares[171] | Fons van der Plas[172] | Do Van Tran[173] | Michael E. Van Nuland[174] | Rodolfo Vasquez Martinez[122] | Hans Verbeeck[96] | Helder Viana[175,176] | Alexander C. Vibrans[57,177] | Simone Vieira[178] | Klaus von Gadow[179] | Hua-Feng Wang[180] | James Watson[181] | Gijsbert D. A. Werner[182] | Susan K. Wiser[183] | Florian Wittmann[184] | Verginia Wortel[185] | Roderick Zagt[186] | Tomasz Zawila-Niedzwiecki[187] | Chunyu Zhang[188] | Xiuhai Zhao[188] | Mo Zhou[4] | Zhi-Xin Zhu[180] | Irie Casimir Zo-Bi[80] | Thomas W. Crowther[1]

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Abstract

1. Biodiversity is an important component of natural ecosystems, with higher species richness often correlating with an increase in ecosystem productivity. Yet, this relationship varies substantially across environments, typically becoming less pronounced at high levels of species richness. However, species richness alone cannot reflect all important properties of a community, including community evenness, which may mediate the relationship between biodiversity and productivity. If the evenness of a community correlates negatively with richness across forests globally, then a

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greater number of species may not always increase overall diversity and productivity of the system. Theoretical work and local empirical studies have shown that the effect of evenness on ecosystem functioning may be especially strong at high richness levels, yet the consistency of this remains untested at a global scale.

2. Here, we used a dataset of forests from across the globe, which includes composition, biomass accumulation and net primary productivity, to explore whether productivity correlates with community evenness and richness in a way that evenness appears to buffer the effect of richness. Specifically, we evaluated whether low levels of evenness in speciose communities correlate with the attenuation of the richness–productivity relationship.

3. We found that tree species richness and evenness are negatively correlated across forests globally, with highly speciose forests typically comprising a few dominant and many rare species. Furthermore, we found that the correlation between diversity and productivity changes with evenness: at low richness, uneven communities are more productive, while at high richness, even communities are more productive.

4. *Synthesis*. Collectively, these results demonstrate that evenness is an integral component of the relationship between biodiversity and productivity, and that the attenuating effect of richness on forest productivity might be partly explained by low evenness in speciose communities. Productivity generally increases with species richness, until reduced evenness limits the overall increases in community diversity. Our research suggests that evenness is a fundamental component of biodiversity–ecosystem function relationships, and is of critical importance for guiding conservation and sustainable ecosystem management decisions.

KEYWORDS
diversity, ecosystem function and services, evenness, forests, global, productivity, species richness

1 | INTRODUCTION

In this era of diminishing biodiversity, understanding how changes in plant biodiversity will impact the functioning of ecosystems is critical (Ceballos et al., 2015; Isbell et al., 2017). Many studies show that the productivity of ecosystems typically increases with a greater number of species (Balvanera et al., 2006; Cardinale et al., 2007; Grace et al., 2016; Hooper et al., 2005). However, this positive relationship between productivity and diversity generally saturates and decays at high levels of species richness (Brun et al., 2019; Fei et al., 2018; Fraser et al., 2015; Liang et al., 2016; Schmid, 2002). Despite the consistency of this pattern across forests globally (Liang et al., 2016), we still lack a comprehensive understanding of the ecological relationships driving this attenuating effect of richness, which limits our capacity to relate diversity with productivity across the globe (Cardinale et al., 2012; Fraser et al., 2015).

The species redundancy hypothesis has been proposed to explain the saturating shape of the relationship between richness and ecosystem productivity (Cardinale et al., 2011; Loreau & Hector, 2001). This theory posits that, as the number of species in a region increases, functional redundancy increases and the proportional impact of any single species on ecosystem functioning declines (Cardinale et al., 2011; Gitay et al., 1996). However, another possible explanation for the diminishing effect of diversity on productivity is that species richness only captures one aspect of community structure, and does not reflect the true 'diversity' of a community (Caswell, 1976; Stirling & Wilsey, 2001) (Figure 1). By reflecting the homogeneity of species abundances within the community, evenness serves as the other central component of diversity (Jost, 2010; Peet, 1974; Tuomisto, 2012). The relationship between community productivity and evenness might differ from the relationship between productivity and richness.

Broad-scale analyses suggest that speciose communities tend to be dominated by a few species, with a long tail of rare species (i.e. are highly uneven) (ter Steege et al., 2013). If such a negative relationship between richness and evenness holds across forests globally, then (i) speciose communities might tend to be dominated by a small number of species that have a disproportionate influence on ecosystem functioning, and (ii) the increasing richness of speciose communities might come at the expense of evenness. This trade-off might ultimately limit both functional diversity and ecosystem productivity.

Of course, a negative relationship between richness and evenness would only be relevant if both components of diversity influence the productivity of the community. Experimental studies provide clear evidence that community evenness has a direct effect on productivity (Kirwan et al., 2007; Sonkoly et al., 2019; Yan et al., 2021). Furthermore, if uneven communities tend to be dominated by one or a few species, the mass-ratio hypothesis suggests that increasing the number of rare species should have a relatively minimal impact on productivity (Grime, 1998; Lembrechts et al., 2018; Loreau, 1998). In contrast, in highly even communities, introducing a new species that is relatively abundant could substantially alter overall community productivity, for example through niche complementarity (see Figure 1) (Lembrechts et al., 2018; Nijs & Roy, 2000; Niklaus et al., 2017). Still, it remains unclear whether these effects of evenness mediate the effects of richness on productivity within complex natural communities and across biomes, because we do not know whether (i) the apparent negative relationship between richness and evenness is consistent across forests globally (Soininen et al., 2012; Zhang, John, et al., 2012) and (ii) there is an interactive effect of evenness and richness on productivity across a range of environmental conditions. Disentangling these relationships between richness, evenness and productivity is critical for understanding the mechanisms governing the diversity–productivity relationship across broad spatial scales (Figure 1).

Here, we used approximately 1 million forest inventory plots (sourced from the Global Forest Biodiversity Initiative database) to explore whether community evenness affects the relationship between richness and productivity across global forests. If evenness restricts the positive effect of richness on ecosystem productivity, then two things must hold: (i) richness trades off with evenness across forests globally, such that speciose communities tend to be dominated by a few species and (ii) there is an interactive effect of both richness and evenness on the productivity of forest ecosystems. Specifically, we tested the hypothesis that (i) high species richness generally comes at the expense of evenness, as the greater number of species within

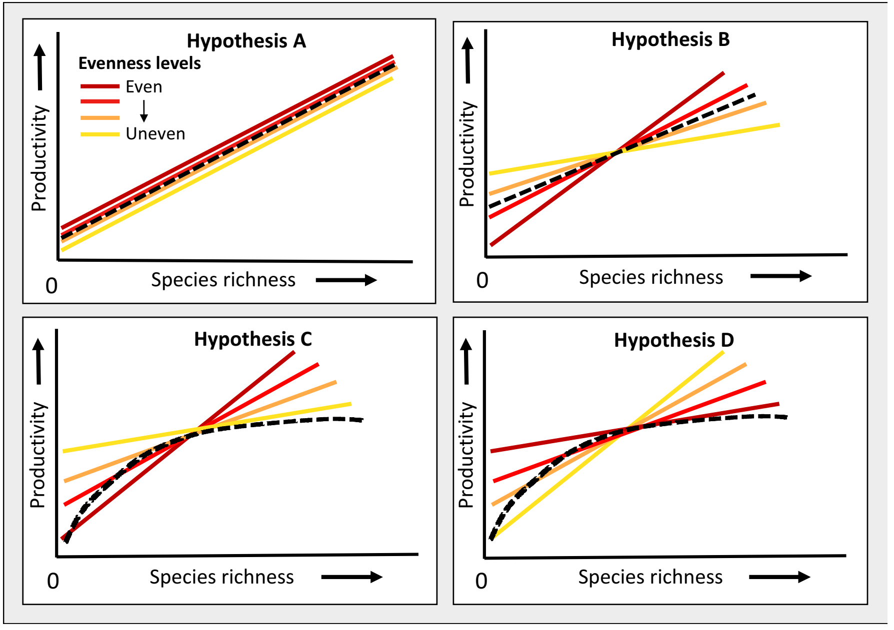

FIGURE 1 Four hypotheses describing how evenness interacts with the relationship between richness and productivity. The four levels of evenness are indicated with different colours from low evenness (yellow) to high evenness (red), and lower colour intensity indicates a lower data density. The dashed black line indicates the average relationship across the system. In all hypotheses, it is assumed that species richness has a positive effect on productivity (Balvanera et al., 2006; Cardinale et al., 2007; Hooper et al., 2005). If community evenness interacts with the effect of species richness on productivity, then (1) the effect of species richness on productivity depends on the evenness of the community, and (2) richness is correlated with evenness across the system (either positively or negatively). If there is no interaction between richness and evenness (Hypothesis A) or if there is no correlation between evenness and richness (Hypothesis B) (Ma, 2005), then the average effect (dashed line) of richness on productivity will neither attenuate nor increase at high richness levels. In such instances, the observed decrease in productivity at high richness levels is more likely a by-product of other ecological processes (e.g. functional redundancy). If, however, there is a significant interaction between richness and evenness, such that uneven communities have lower productivity at high richness (Hypothesis C), then a negative correlation between richness and evenness (Cook & Graham, 1996; Hanlin et al., 2000; Symonds & Johnson, 2008) would lead to an attenuation in productivity at high richness level: the marginal trend (dashed line) first tracks the high evenness isocline at low richness levels but then bends down towards the low evenness isoclines at high richness. Conversely, if uneven communities exhibit higher productivity at high richness levels (Hypothesis D), then a positive correlation between richness and evenness (Cotgreave & Harvey, 1994; Manier & Hobbs, 2006; Tramer, 1969) would explain this reduction in productivity: the marginal trend first tracks the low evenness isocline at low richness levels but then bends down towards the high evenness isoclines at high richness.

a community corresponds to a greater proportion of locally rare species, and (ii) that richness positively correlates with productivity in highly even, species-poor communities, but at the highest levels of species richness this positive relationship will break down due to an intrinsic reduction in evenness (Figure 1, Hyp. C).

2 | MATERIALS AND METHODS

To evaluate the relationship between evenness and richness, we incorporated all 1,011,027 forest inventory plots from the Global Forest Biodiversity Initiative (GFBI database, 2021, including data from Condit et al., 2019a, 2019b). Forest plot size ranged from 0.0008 to 2.0 ha. Because evenness and richness inherently vary with scale (Gleason, 1922; Wilson et al., 1999), plot sizes smaller than 0.02 and larger than 1.5 ha were excluded to ensure comparable results. Indeed, the effect of plot size on richness is especially strong when plots are smaller than 0.02 ha ($r=0.39$, $r^2=0.15$, $p<0.001$) or larger than 1.5 ha ($r=-0.84$, $r^2=0.71$, $p<0.001$). Elimination of these two plot size groups resulted in a filtered dataset with weak correlations between plot size and richness ($r=0.13$, $r^2=0.02$, $p<0.001$), and plot size and evenness ($r=-0.09$, $r^2=0.008$, $p<0.001$). Although there is a range in plot sizes, 75% of the plots have a size between 0.02 and 0.06 ha. Quality controls of tree density estimations were conducted, and we removed plots with tree densities that fell outside the median ± 2.5 times the median absolute deviation, a moderately conservative threshold, within each biome (0.8% of total plots) (Leys et al., 2013). Additionally, we removed plots with unlikely biomass accumulation and productivity values (for details, see Section 2.2). The final dataset (Figure 2) comprised 896,276 forest plots, containing information on tree species richness and abundance. Of these, 367,565 plots contained diameter at breast height (DBH) information of individual trees which allowed us to estimate biomass. For both datasets, the plots were measured once between 1980 and 2017, with 2002 as the mean measurement year. The mean age of the forest where the plots are established is 52 years, with a standard deviation of 15 years (estimated with the global forest age map; Poulter et al., 2019).

Richness and evenness were calculated for each plot, enabling us to evaluate the nature of the relationship between these two components of diversity at biome and global scales. To examine the effect of evenness and richness on biomass accumulation and

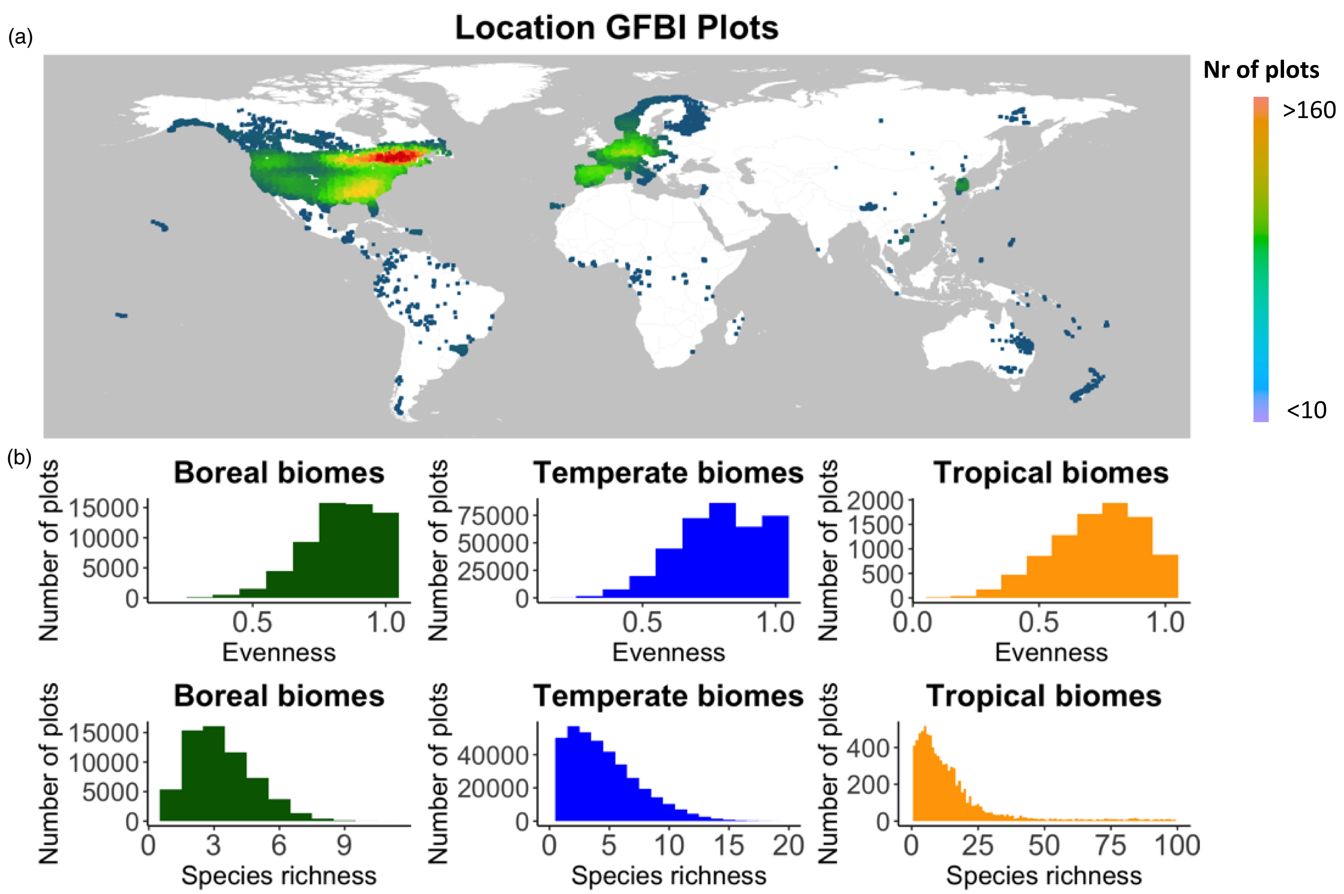

FIGURE 2 (a) Location of the Global Forest Biodiversity Initiative (GFBI) plots used in this study, where the density of forest plots is indicated from low density (blue) to high density (red). (b) The distribution of evenness and richness in the boreal, temperate and tropical biomes. An evenness value of one resembles either a monospecific stand or an even abundance of species. The tail of richness values of the tropical biomes extends to 380 species (not shown in the graph). The majority of our dataset is composed of secondary forests (mean age is 52 years), and especially the monospecific and relatively species-poor stands were affected by human activity in some degree.

productivity, we fit linear models that simultaneously accounted for evenness and richness while controlling for a wide range of environmental variables, including temperature, precipitation and soil characteristics.

We estimated forest productivity using two complementary approaches. First, we used biomass estimates, calculated using regional allometric equations that included information about DBH and species information from each individual tree, and divided this information by forest age (Poulter et al., 2019) to approximate stand-level biomass accumulation over time. Second, we estimated net primary productivity (NPP) for each plot using MODIS satellite data (Running et al., 2011), thus providing both ground-sourced and remotely sensed estimates of productivity. Satellite-derived NPP estimates largely agreed with ground measured temporal data for the plots where this information was available ($r=0.65$, $p<0.001$), see Section 2.3 for more details.

2.1 | Examining the relationship between species richness and evenness

Richness was defined as the total number of tree species per forest plot. We estimated Hill's evenness at the same plot level using the following equation:

$$\text{Evenness} = \exp(H)/S, \tag{1}$$

where H is Shannon's entropy, S is the species richness and $\exp(H)$ can be figuratively interpreted as an approximation of the number of relatively abundant species (Hill, 1973; Jost, 2010). Therefore, Hill's evenness can roughly be seen as the proportion of species that dominate the community in terms of abundance. Evenness values range from close to zero, when the community is dominated by only a few species, to one, where all species in the community have the same number of individuals.

There are many evenness indices available in the ecological literature (Tuomisto, 2012), and some commonly used indices are mathematically restricted by richness (including Pielou's *J*), reflect particularly dominance in the community (e.g. Simpson's evenness) or express evenness as the ratio between diversity and richness (including Hill's evenness). We also included the standardized Hill's evenness index in our supplementary analyses, as Hill's evenness reports an evenness of one in monospecific sites, which is avoided when using standardized Hill's evenness. As we explored the relationship between richness and evenness, each commonly used and distinct evenness index evaluated (standardized Hill's evenness, Pielou's *J*, Simpson's evenness, Evar, PIE, Eq) revealed similar overall trends (Figure S2) (Tuomisto, 2012). Given this overall consistency across different indices, including standardized Hill's evenness, we focus on the well-known Hill's evenness for the majority of our analyses because (i) it reflects evenness according to the current understanding of evenness as the ratio between diversity and richness (Tuomisto, 2012) and therefore (ii) consists of the mathematically robust components of Shannon's entropy and richness (Hill, 1973).

In addition to analysing the relationship between evenness and richness at a global scale and for the major forest biomes (boreal, temperate and tropical biomes), for every World Wildlife Fund (WWF) biome we selected a number of plots that is proportional to the forested area within that biome (Table S2; Olson et al., 2001). By taking this subset of the data, we reduced the sampling bias by assuring that the results are more representative for either the forests globally or the boreal, temperate or tropical biomes. Regarding the global dataset, the majority of the plots fall within the temperate broadleaf and mixed forest biome and a smaller proportion of the data represents the tropical moist forest, but with subsetting the data we create a more representative global dataset. The same procedure is followed when subsetting biomes to represent the boreal, temperate and tropical biomes. The proportions of forested area for every biome were calculated in Google Earth Engine by overlaying the WWF biomes with a global map of existing forest cover (Hansen et al., 2013). Areas with more than 10% canopy closure for vegetation taller than 5 m were defined as forests (FAO, 2000). To avoid heteroscedasticity due to the skewed nature of the species richness distribution, richness was log transformed, and the relationship was evaluated with a Pearson correlation (see Figure 3). To show that the relationship between evenness and richness is neither a mathematical artefact of the Hill's index nor dependent on the evenness index used, we visualized the results of a null model (Figure S1) and the relationship for commonly used evenness indices (Figure S2). The null model was created by evaluating the relationship between evenness and richness of 10.000 random data subsets, formed by drawing species according to a multinomial distribution from the dataset (see Figure S1 for a more detailed explanation). Additionally, to evaluate the effect of monospecific stands on the relationship between evenness and richness in forests globally, we compared the correlation coefficients of the relationship with and without monospecific stands.

2.2 | Biomass estimation

To estimate the above-ground biomass of each tree in extratropical biomes, we used 430 species-specific DBH-based allometric equations obtained from the GlobAllomeTree database to estimate the above-ground biomass of each tree (Henry et al., 2013). These allometric equations use a common logarithmic equation for estimating above-ground biomass from DBH measures (Jenkins et al., 2003):

$$\text{Biomass} = e^{\left(\beta_0+\beta_1\times\ln^{\text{DBH}}\right)}, \tag{2}$$

where biomass is the total above-ground biomass (kg dry weight), DBH is the measured diameter at breast height (cm), ln is the logarithm to the base e (2.718), and ß0 and ß1 are free parameters governing the effect of DBH on above-ground biomass. Following Jenkins et al. (2003), we applied back calculation to generate a pseudo dataset for biomass

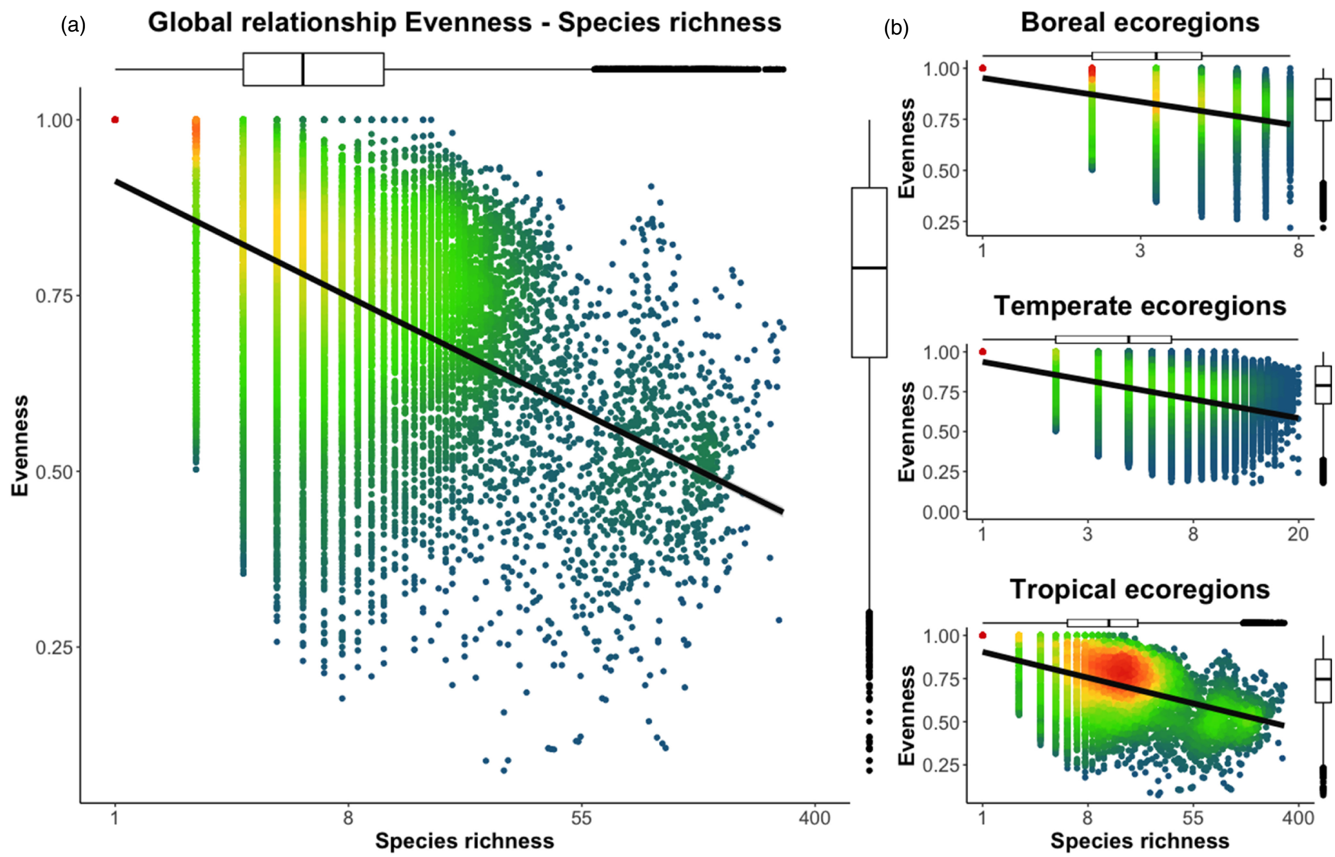

FIGURE 3 The relationship between evenness and logged species richness, where the data density is indicated from low density (blue) to high density (red). The Pearson correlation is highly significant for all relationships, we therefore describe the adjusted r^2 as a measure of effect size. (a) The global relationship between evenness and richness ($N=20,272$, $r=-0.52$, $r^2=0.28$). (b) The relationship between evenness and richness for the boreal ($N=61,712$, $r=-0.42$, $r^2=0.18$), temperate ($N=374,142$, $r=-0.53$, $r^2=0.28$), and tropical ($N=9570$, $r=-0.48$, $r^2=0.23$) biomes.

changes along DBH gradients based on each of the 430 allometric equations. To generate the pseudo data, we applied the following rules: (1) for a DBH between 5 and 25 cm, each centimetre was assigned a corresponding pseudo biomass value; (2) for a DBH between 25 and 100 cm, every 5 cm were assigned a corresponding value, (3) for a DBH between 100 and 300 cm (maximum DBH), every 10 cm were assigned a corresponding value. Consequently, we trained biome-specific allometric equations for each biome (varying in the β_0 and β_1 parameter estimates) based on the pseudo-DBH and biomass dataset (Olson et al., 2001) (Table S1; Figure S3).

Biomass estimations for the tropical biomes followed the allometric equations for pantropical regions from Chave et al. (2014), which are available through the R package 'BIOMASS' (Réjou-Méchain et al., 2017). These equations require information on wood density, and we compiled species-specific wood density estimates from the Global Wood Density Database (Chave et al., 2009) and the BAAD database (Falster et al., 2015). To match the binomial species names between the GFBI and the wood density databases, we standardized species binomials using the Taxonomic Name Resolution Service platform (Boyle et al., 2013).

After computing the above-ground biomass for all 24 million individuals in our dataset, plot-level biomass values were obtained by summing up the biomass of all individuals in the respective plot. Biomass densities (t/ha) of each plot were obtained by dividing the total above-ground biomass (t) by the plot size (ha).

2.3 | Biomass accumulation rates and productivity data

We selected approximately 95% of the data by excluding plots that had biomass values greater than two times the standard deviation above and below the mean plot-level biomass per biome to filter potential outliers in biomass values due to errors in measurement or data management. Additionally, we excluded plots with biomass values higher than 1 million kg/ha, as these values were likely overestimating biomass due to the presence of a large tree in the plot (Bastin et al., 2018; Chave et al., 2004; Slik et al., 2013). This filtering procedure resulted in 367,565 plots that were used in the final analyses (see Table S2 for an overview of the number of plots for the biomass and productivity analyses). All biomass values were divided by estimated forest age (Poulter et al., 2019), to control for differences in forest developmental stage that cause striking differences in forest biomass accumulation (Peichl & Arain, 2006; Poorter et al., 2016).

As such, final biomass estimates reflect the mean annual biomass accumulation over time.

Biomass accumulation over time is not a precise indicator of forest productivity, as it cannot account for all of the ecological dynamics and disturbances that occurred during forest development, but it is a useful proxy for overall cumulative growth at the ecosystem level. However, to attempt to account for the annual variation in forest productivity, we used productivity estimates from an independent satellite-derived product. Specifically, we estimated NPP for every plot location from MODIS satellite images, using Google Earth Engine (Gorelick et al., 2017; Running et al., 2011) to supplement the forest biomass analysis. NPP is calculated as absorbed fraction of photosynthetically active radiation, which is a combination of leaf area index and fraction of photosynthetically active radiation, while taking temperature and water stress into account as well (Running et al., 2011). We calculated the mean productivity between 2000 (first year of NPP data availability) and 2009 (third quartile of forest age in our data), to obtain a robust NPP value and coincide the average NPP measurement year with the median forest age in our dataset. In the temperate biomes—the only region where sufficient DBH information was available across multiple years in the GFBI database—the ground-measured temporal changes in biomass were fairly well correlated with the satellite-derived productivity data ($r=0.65$, $p<0.001$). The lack of forest plots measured multiple times in the boreal and tropical biomes, precluded the estimation of the accuracy of the NPP data from these regions. We conducted all analyses across both mean annual biomass accumulation and NPP to explore the unifying trends that emerge across both approaches.

2.4 | Evaluating the effect of evenness and richness on biomass accumulation and productivity

We used linear models to assess the effect of evenness, richness and their interaction, on NPP and biomass accumulation. The data met the linear model assumptions and evaluation of the model fit (Q–Q plots, distribution of residuals) suggested that linear models were applicable. To account for the fact that biomass accumulation does not necessarily vary linearly with time or successional state, we included time as a covariate in the model of biomass accumulation rate, which is equivalent to allowing the relationship between stand-level biomass and time to be quadratic (Poulter et al., 2019). Additionally, we controlled for the potentially confounding effects of climatic drivers and other environmental influences (Ali et al., 2019), including mean annual temperature, isothermality, annual precipitation, variation in seasonal precipitation (Hijmans et al., 2005), and soil carbon, sand content and pH in the upper 15 cm of the soil as covariates, each extracted from global maps at a 30-arc second resolution (Batjes et al., 2017; Ribeiro et al., 2018). These climate variables capture both the mean and variation in temperature and rainfall, while the edaphic variables include the most important soil drivers of biomass and productivity (Ali et al., 2019). Human impact was also considered in the linear models by including estimates of the percentage of human development, calculated as the percentage urban areas and managed vegetation per square kilometre (Tuanmu & Jetz, 2014), and population density as the number of people per square kilometre (Center for International Earth Science Information Network—CIESIN—Columbia University, 2016). The density of trees was included as an independent variable in the analyses, as this can affect both evenness (Wilson et al., 1999) and richness values (Lomolino, 2000). Additionally, 'biome' was included as a factor in the global model, and we accounted for plot size in all models (Poulter et al., 2019). To explore the possible effect of plot size, we analysed the relationship between evenness and richness and the effect of both on the two measures of productivity for small, medium and large plot sizes for the dataset globally (Figure S5). Additionally, we performed a sensitivity analysis on species richness, evenness and their interaction to plot size when predicting NPP or biomass accumulation rates in the global dataset (Figure S6A) and on biome level (Figure S6B–D).

Collinearity between variables in our model was evaluated using variance inflation factors (VIF). Although evenness and richness were negatively correlated, on average, there was substantial variation in this trend (Figure 3), such that the VIF values between evenness and richness were less than 3.0 in all models, and both were therefore included in every model (Becker et al., 2015). The model was implemented at the global scale, in which every biome was proportionally represented according to the extent of forested area within that biome (as described above), and at the biome level. At the biome level, the boreal, temperate and tropical biomes were represented by their largest forested ecosystems, respectively, the boreal forest, temperate broadleaf and mixed forest, and tropical moist forest. To visualize how richness and evenness interacted to affect productivity, we plotted the relationship between richness and productivity at four different levels of evenness (<0.4, 0.4–0.6, 0.6–0.8, and 0.8–1). The lowest evenness level <0.4 was chosen as this represents the lower end of the evenness values in the dataset, while including sufficient observations in this category. The subsequent categories were defined as an increase of 20% in the evenness values. For each evenness level, productivity was predicted with every model covariate (e.g. climate, soil, human impact) set at its median value. Thus, each predicted productivity is marginal to the aggregate trend at the global scale and for each biome. To examine whether the relationship between richness, evenness and productivity varied with evenness index, we evaluated the global trend for six commonly used evenness indices (Figure S7). We used a bootstrapping approach to incorporate uncertainty in the biomass calculations and satellite-derived NPP (Figure S8).

To quantify the relative importance of evenness, richness, their interaction, environmental variables and human impact, we used the scaled calc.relimp function in R (Grömping, 2006). This function evaluates the contribution of each independent variable to the variation explained, by averaging the contribution of each independent variable to the r^2 in terms of its sum of squares across all possible fitting sequences. The statistical analyses were performed in R version 3.5.1 (R Core Team, 2018). The code used to perform the statistical analyses can be found at Github, following this link: tinyurl.com/3vvf52v9.

3 | RESULTS

There was a consistent, negative correlation between evenness and richness at the global scale, which was apparent across all forest biomes (Figure 3a–d), scales (Figure S4) and plot sizes (Figure S5). This negative correlation was also found using several other commonly used evenness indices, including the normalized Hill's evenness index, Simpson's evenness, E_{var} index and PIE (Figure S2), suggesting that the relationship is robust to the evenness index used. Moreover, the magnitude of the negative correlation was more negative than expected at random, suggesting that the relationship between evenness and richness is not a mathematical artefact of the evenness metrics used (Figure S1). Instead, it demonstrates that highly speciose, highly even forest communities are less rare in nature than would be expected by chance (Figure S1), suggesting that biotic processes may play a role in shaping the relationship between richness and evenness. Additionally, excluding monospecific stands did not change the sign of the correlation, although the relationship was stronger when monospecific stands were included as they force the correlation through one ($r = -0.08$ for forests globally, $r = -0.07$ excluding monospecific stands). Within forests, species-poor communities tend to have a relatively uniform distribution of abundances, while among speciose communities, having more species is associated with increasingly uneven abundance distributions caused by a few dominant and many rare species (Figure 3a–d). Temperate and boreal biomes exhibited a saturating relationship, with evenness never extending below $E = 0.75$, on average, even at the highest richness levels.

However, after accounting for underlying environmental variation, we identified a significant positive relationship between richness and both biomass accumulation and productivity ($0.06 < ß < 0.48$, $p < 0.01$), supporting a recent global analysis (Liang et al., 2016) (but see also (Sheil & Bongers, 2020)). However, the relationship varied among regions, as temperate forests exhibited a marginally negative relationship between richness and productivity ($ß = -0.09$, $p < 0.05$) (Figure 4). Given the observed negative relationship between richness and evenness, increasing evenness was generally associated with lower biomass accumulation. However, this pattern was not observed in tropical forests ($ß = 0.04$, $p < 0.01$), where there was a positive relationship between evenness and productivity ($0.004 < ß < 0.014$, $p < 0.01$) (Figure 4).

In combination, both the evenness and richness of forest communities were more strongly related to plot-level biomass accumulation than to productivity (25% vs. 19% of variance explained in the global model) (Figure 4). Among boreal forests, which are species poor, richness was more strongly related to both biomass accumulation and productivity than was evenness (variance explained by $richness_{Biomass} = 10.1$, $evenness_{Biomass} = 6.8$ and $richness_{NPP} = 14.8$, $evenness_{NPP} = 0.4$) (Figure 5b,f). In contrast, among moist tropical forests, which are species rich, productivity was similarly related to either richness or evenness (variance explained by $richness_{NPP} = 1.8$, $evenness_{NPP} = 1.6$) (Figure 5d,h).

Experimentally increasing species richness increases biomass accumulation (Balvanera et al., 2006; Cardinale et al., 2007; Grace et al., 2016; Hooper et al., 2005), but observational data suggest that the effect becomes weaker or even reverses at high species richness (Brun et al., 2019; Fei et al., 2018; Fraser et al., 2015; Liang et al., 2016; Schmid, 2002). We hypothesized that if increasing community evenness causes productivity to decline, then the attenuating effect of richness on productivity could be explained by a negative correlation between species richness and community evenness (Figure 1). To explore if productivity data from the world's forests might be explained by such a hypothesis, we modelled the data with a regression featuring the hypothesized interaction between richness and evenness (Figure 5). The proposed interaction between richness and evenness is statistically significant in every model ($p < 0.05$), although the strength of the interaction varies. The strongest interactive effect was observed on biomass accumulation in the moist tropical forest, which are highly speciose ($ß = 0.14$) (Figure 5d). A weaker interaction was observed in temperate and boreal forests ($ß = 0.03$ and $ß = -0.06$, respectively), which contained fewer species (Figure 5b,c). In the tropics, biomass accumulation is predicted to vary by 2.5-fold between high- and low-evenness communities (6000 vs. 15,000 kg/ha year^{-1} at maximum richness) (Figure 5c), whereas this range is much lower in the temperate (4700–5000 kg/ha year^{-1} at maximum richness) (Figure 5c) and boreal systems (850–1150 kg/ha year^{-1} at maximum richness) (Figure 5b). Moreover, we find the same trend for productivity (Figure 5f–h), across different evenness indices (Figure S7), plot sizes (Figure S5) and when incorporating uncertainty of the biomass and productivity values (Figure S8). Additionally, the sensitivity analyses show that there is no consistent effect or no effect of plot size on the relationship of evenness, richness and their interaction on both measures of productivity (Figure S6).

4 | DISCUSSION

Among forests across the globe, the positive correlation between species richness and ecosystem productivity appears to attenuate in the most speciose communities (Liang et al., 2016). Our analysis examines whether the evenness of plant communities might contribute to this attenuation. We observed a consistent negative correlation between richness and evenness across forests, globally (Figure 3), whereby highly specious communities exhibited relatively low levels of evenness. We also detected interactive effects of the correlation of richness and evenness with ecosystem productivity, which lends support to the hypothesis that evenness might mediate the impacts of richness on

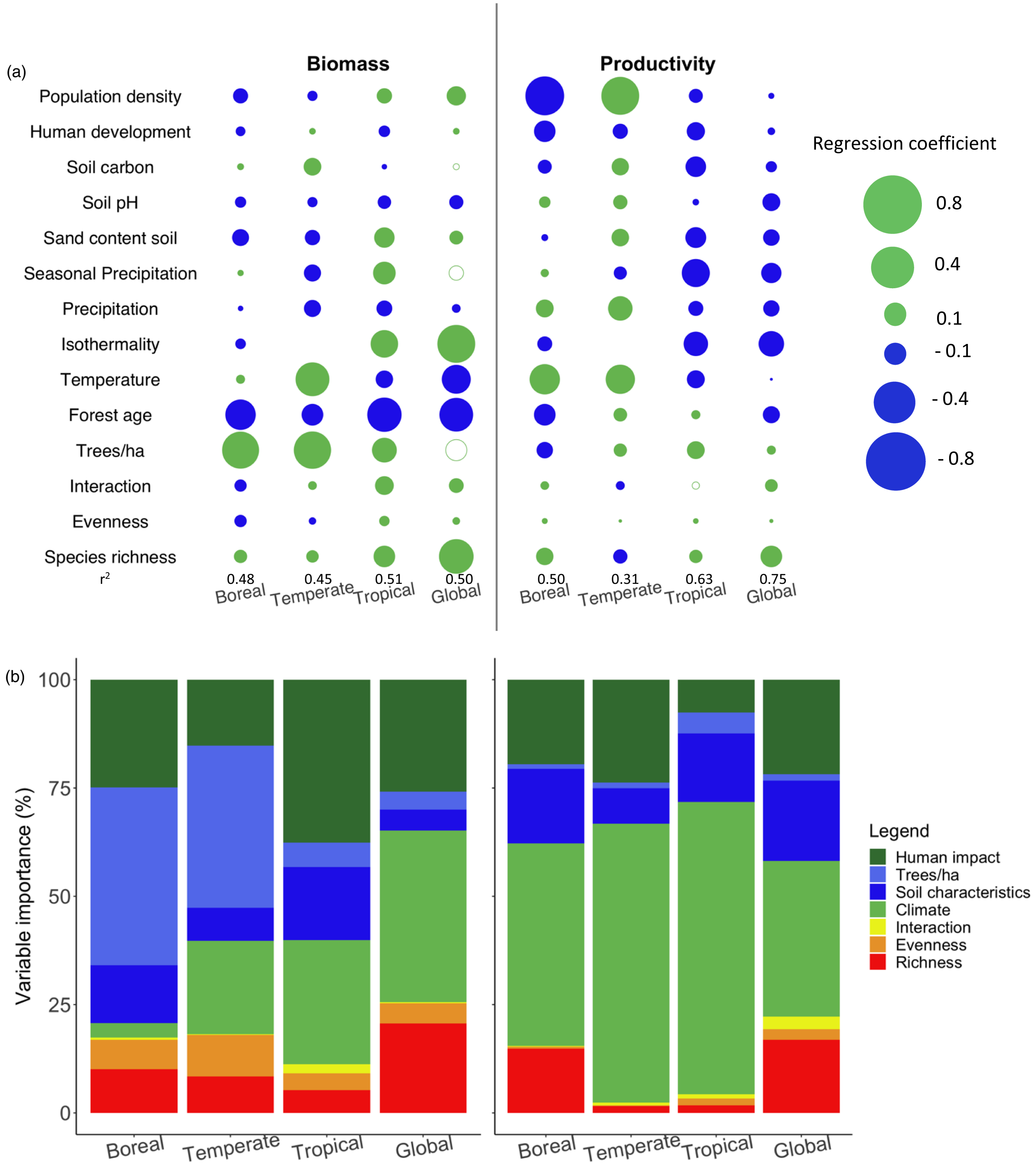

FIGURE 4 (a) Positive (green) and negative (blue) regression coefficients, and (b) variable importance of evenness, richness, the interaction of evenness and richness and climate, soil and human impact variables on biomass and productivity. Only the results for the boreal, temperate, tropical moist forest and all the biomes globally are visualized, and variables causing multicollinearity are taken out (see Section 2). The open circles in (a) indicate non-significant coefficients, while the filled circles indicate significant coefficients. The adjusted r^2 values of the linear models are displayed in (a).

forest productivity. In short, when the number of species is relatively low, species richness correlates positively with productivity. However, in the most speciose communities, the long tail of rare species makes them highly uneven, which may limit the impact of diversity on productivity. As such, in these highly uneven communities, a greater number of species does not necessarily correlate with greater productivity.

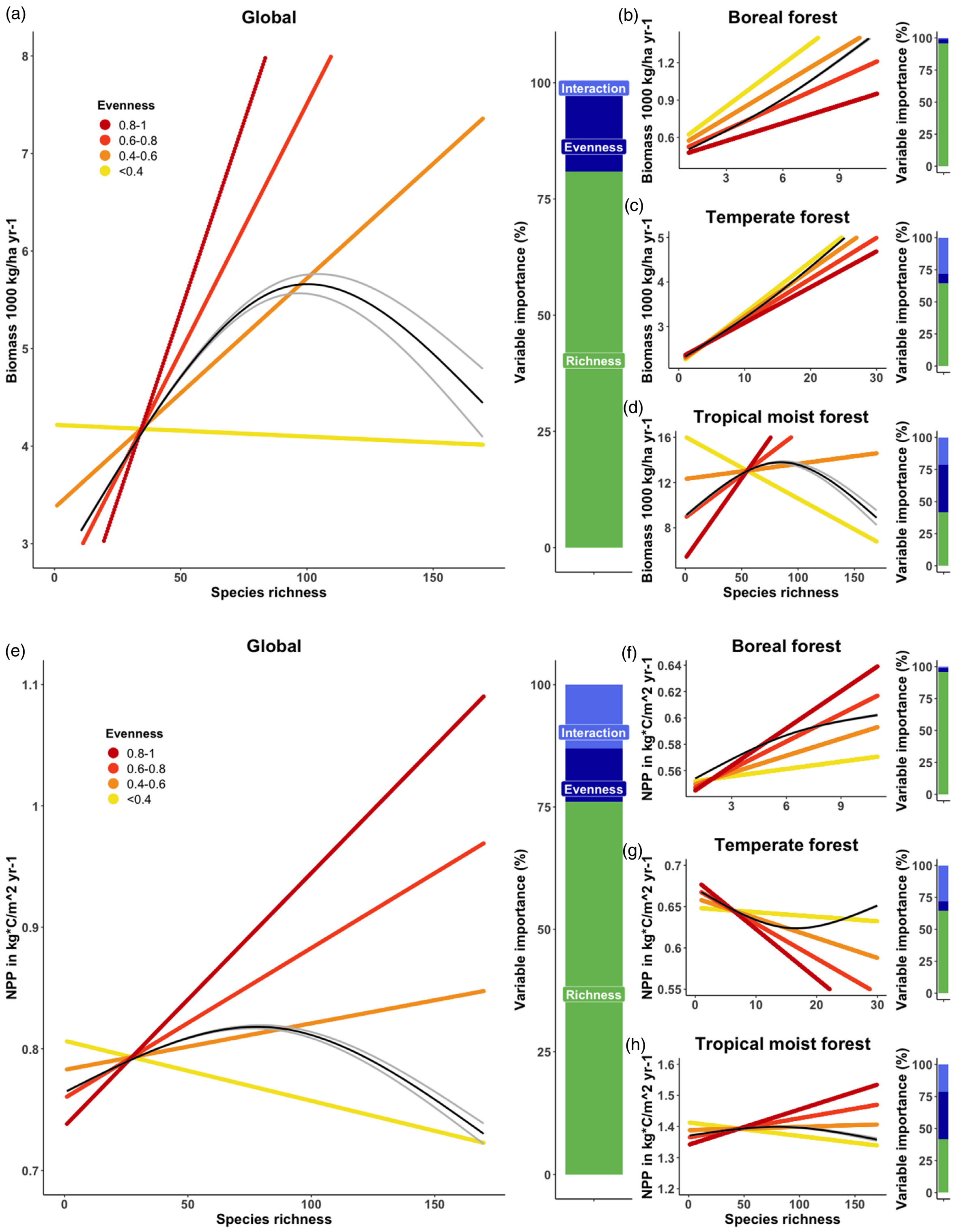

FIGURE 5 The hypothesized effect of different levels of evenness on the relationship between species richness and mean annual biomass accumulation (a–d) or productivity (h–e). The graphs visualize predicted values based on the results of a linear model, with the covariates held constant (see methods), and as a cut-off point the third quantile of the biomass and NPP values to avoid overfitting. The data are projected on the graph (black line), and the 95% upper and lower confidence intervals are visualized in grey. At the right side of every graph the scaled variable importance, according to a linear model including covariates, of richness (green), evenness (dark blue), and the interaction between richness and evenness (light blue) is visualized. In the graphs at the left side, the global effect is visualized, while at the right side the data are split among boreal, temperate and moist tropical forests. The uncertainty of the biomass calculations and estimated productivity are visualized in Figure S7.

Our results suggest that, when there are more species present, they are more likely to have an uneven distribution. However, this relationship between richness and evenness was significantly more negative for our observational data than would be expected under null-model predictions (Figure S1), highlighting this pattern is at least partially a by-product of ecological and evolutionary processes. The observed negative relationship between evenness and richness observed across forests globally (Figure 3) may potentially arise if species-rich ecosystems contain relatively fewer dominant, but more rare species than species-poor systems. We focus on the Hill's evenness index because it is largely uncorrelated with richness (Hill, 1973), to ensure that the observed negative correlation between richness and evenness is not merely a mathematical artefact of the evenness index used (Figure S1). Nevertheless, our results are robust to a range of common evenness indices (Figures S2 and S7), demonstrating the generality of this relationship and of the resulting global trends. The drivers of this trend are likely to include a range of ecological coexistence mechanisms. A possible explanation for this negative correlation could be that in cold boreal forests, there are only a few species present, and intraspecific competition is expected to be higher than the interspecific competition (Aguiar et al., 2001). However, in warm, moist environments, such as moist tropical forests, there are many species present. Higher species richness is likely to give rise to substantial interspecific competition, as well as scope for additional ecological mechanisms such as the Janzen Connell effect to influence the abundance of species (Connell, 1971; Janzen, 1970). As species have different competitive abilities and strategies, high levels of asymmetric competition allow relatively few species to become dominant, with the majority of the species being either abundant or rare (McGill et al., 2007).

The strength of the negative correlation between evenness and productivity varies between biomes (Figure 5) (Sonkoly et al., 2019; Zhang, Chen, & Reich, 2012), which may be indicative of a greater effect of niche partitioning in more speciose and even forests. In biomes with few species, increasing the richness of species tends to enhance resource partitioning and productivity (Figure 5b,c) (Isbell et al., 2009; van Ruijven & Berendse, 2005). In contrast, in biomes with many species, evenness of those species is relatively low as there are many rare species, and so increasing the evenness might increase ecosystem productivity (Kirwan et al., 2007; Zhang, John, et al., 2012; Zhang, Chen, & Reich, 2012) (Figure 5d,h). Interestingly, a different trend was observed for productivity in temperate forests, where at high evenness productivity peaks at low richness, and at low evenness productivity peaks at high richness (Figure 5c). This could possibly be explained by the overarching importance of environmental drivers for productivity in this biome, with the combined effects of richness and evenness explaining only 2% of the total explained variance (Figure 4b). Conversely, this biome contains the greatest proportion of forest plots with high human activity (Figure 4b), such that this trend may reflect different management practices across biomes.

Our results suggest that it may not only be the redundancy of the species that drives the attenuating effect of the relationship between richness and ecosystem productivity (see Cardinale et al., 2011), but also the low abundances (and corresponding minimal contribution to productivity) of the rare species that flattens the relationship between richness and productivity at high richness levels. Our hypothesis predicts that, within speciose communities, adding new species at extremely low abundances will have little impact on the overall productivity, relative to the effect on productivity of adding new species to less speciose communities. We stress that this finding does not discount the importance of rare species, which contribute significantly to productivity through positive complementarity effects in many ecological communities (Loreau & Hector, 2001; Sonkoly et al., 2019). Indeed, rare species contribute to ecosystem multifunctionality, which can have very important indirect effects on productivity (e.g. being critical for pollination) (Dee et al., 2019; Lyons et al., 2005), or sustain productivity over the long term when they become more abundant with (environmental) change (Loreau & Hector, 2001; Loreau et al., 2003; Yachi & Loreau, 1999). However, our analysis supports the idea that—in line with the mass-ratio hypothesis—rare species tend to contribute less to productivity than do dominant species. If this hypothesis were correct, then a higher relative abundance of rarer species (i.e. increasing evenness) would increase the biodiversity and productivity within the system.

The two measures of productivity used here—biomass accumulation and satellite-derived NPP—each have their unique drawbacks and challenges (Sheil & Bongers, 2020), such as relying on coarse estimates of forest age, being susceptible to mismatches between plot size and satellite resolution, and uncertainty in the calculations. For the temperate region, satellite-derived NPP and productivity calculated from multiple times measured ground-sourced data were well correlated ($r=0.65$); however, we could not estimate the accuracy for the other biomes due to limited data. Despite the uncertainty in the biomass and productivity calculations, the main results were robust when considering the uncertainty within these two estimates of productivity individually (Figure S8). We chose to consider these metrics in tandem specifically to minimize the data limitations of each, and ensure that our results are qualitatively robust to the choice of productivity metric. Additionally, in our dataset, we have considerable variability in plot sizes, which can affect both species richness and evenness values, and subsequently the importance of niche and neutral processes (Gleason, 1922; Viana & Chase, 2019; Wilson et al., 1999). Yet, sensitivity analyses show that the differences in plot size do not change the main results (Figure S5), with no consistent biases across plot sizes (Figure S6). However, we do detect considerable noise across the range of plot sizes, partially due to unbalanced sample sizes in relation to plot size in between biomes.

Although our work establishes baseline empirical trends, it is important to highlight that these results rely on correlative trends using observational data from a compilation of different databases and sources. Future experimental research will be needed to test the hypotheses we have presented and to explore direct causal relationships among evenness, richness and productivity.

Long-term experimental studies with various plot sizes and successional stages will be critical for disentangling the relative importance of the different processes underpinning diversity and function. By being able to manipulate species richness, evenness and functional redundancy, while also obtaining direct temporal measurements of productivity, experimental studies will be critical for identifying mechanistic drivers that are difficult to assess from broad-scale observational and statistical approaches (Paquette et al., 2018). Nevertheless, our analysis is consistent with the findings from a wide range of biodiversity–ecosystem function experiments, observational and modelling studies, highlighting that the positive effect of species richness on forest productivity declined in the most speciose communities (Cardinale et al., 2007; Hooper et al., 2005). In addition, by exploring how these trends vary across biomes, this analysis can help to provide the context for the highly variable relationships between richness and productivity across the globe.

5 | CONCLUSIONS

An ever-growing body of evidence suggests that, across forests globally, plant species richness correlates with ecosystem productivity of plant communities (Liang et al., 2016; Luo et al., 2019). Our results support previous studies, showing that richness correlates positively with ecosystem productivity, particularly in communities with few species. However, as the number of species increases, the relationship between richness and productivity attenuates. We observed that, as species richness increases, the evenness of those communities tends to decline, which may potentially limit the influence of richness on ecosystem productivity in the most speciose communities. Because communities with many species tend to be dominated by relatively few species, the evenness of those communities tends to be relatively low. This negative correlation between richness and evenness may partially contribute to the attenuating effect of species richness on ecosystem productivity observed in highly diverse communities (Liang et al., 2016). In addition, this apparent trade-off between richness and evenness may explain some of the idiosyncrasies observed in previous biodiversity–productivity analyses, as the slope of the richness–productivity relationship will vary considerably across time and space due to the confounding effect of evenness. These trends have direct implications for ecosystem management practices by showing where community productivity is most dependent on richness or evenness. Ultimately, the interacting effects of richness and evenness help shape our understanding of the biodiversity–productivity relationship, identifying core relationships that link community structure to the functioning of forest ecosystems worldwide.

AUTHOR CONTRIBUTIONS

Iris Hordijk, Tom W. Crowther, Daniel S. Maynard and Simon P. Hart conceived of the study. Iris Hordijk extracted and analysed the data, and drafted the manuscript with assistance from Dan Maynard and Tom Crowther. Biomass calculation was carried out by Lidong Mo. 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.

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DATA AVAILABILITY STATEMENT

The plot-level evenness data are stored in the Research Data Repository of the Research Collection of ETH Zürich http://doi.org/10.3929/ethz-b-000597256. The GFBI database is 3rd party data, and is publicly available upon request at https://gfbinitiative.net/data/.

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SUPPORTING INFORMATION

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

Figure S1: The relationship between evenness and richness is more negative, than a null model comprised of 10,000 random subsets of the global GFBI data.

Figure S2: The global relationship between evenness and logged species richness for several commonly used evenness indices ($N = 20{,}272$) (Tuomisto, 2012).

Figure S3: DBH-based allometric models of tree biomass for non-tropical biomes based on the approach presented in Jenkins et al. (2003).

Figure S4: The Pearson correlation coefficient of the relationship between Hill's evenness and the log of species richness for the boreal, temperate and tropical biomes.

Figure S5: Visualising the differences between small, medium and large plot sizes on (A) the relationship between Hill's evenness and richness, (B) the interaction between evenness, richness and Modis NPP at four different levels of evenness, and (C) the interaction between evenness, richness and biomass accumulation at four different levels of evenness.

Figure S6: Analysis of the sensitivity to plot size of a hypothetical relationship among species richness, evenness and their interaction when predicting NPP or biomass accumulation rates (A) in the global dataset and (B–D) on biome level.

Figure S7: The hypothesized effect of different levels of evenness for the global relationship between species richness and Modis NPP.

Figure S8: The global relationship between evenness, richness and (A) biomass accumulation, or (C) Modis derived NPP, with uncertainty incorporated.

Table S1: Allometric equations used for each of the non-tropical biomes, following Jenkins et al. (2003).

Table S2: Overview of the WWF biomes.

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