Wind dispersed tree species have greater maximum height

Running title Emergent tree species are more likely wind dispersed

Abstract

Aim Here we test the hypothesis that wind dispersal is more common among emergent tree species as being tall ensures effective seed dispersal.

Location Americas, Africa and the Asia-Pacific.

Time period Between 1970-2020.

Major taxa studied Gymnosperms and Angiosperms (excluding Monocots and Cactaceae).

Methods We use a dataset of tree inventories from 2821 plots across three biogeographic regions (Americas, Africa and Asia-Pacific), including dry and wet forests, to determine the maximum height and dispersal strategy of 5314 tree species. A web search was used to determine whether species were wind dispersed. We explored differences in tree species maximum height between biogeographic regions and determined the relationship between tree species maximum height and wind dispersal using logistic regression. Finally, we tested whether emergent tree species, i.e., species with at least one individual taller than the 95% height percentile in one or more plots for each region-forest type combination, were disproportionally wind dispersed.

Results Our dataset provides maximum height values for 5314 tree species, 2,914 of which had no record of this trait in existing global databases. We found that, on average, tree species in the Americas have lower maximum heights compared to Africa and the Asia Pacific. The probability of wind dispersal increased significantly with tree species maximum height and was significantly more common in emergent than non-emergent tree species in dry and wet forests in all three biogeographic regions.

Main conclusion Wind dispersal is more prevalent in tall, emergent tree species across three biogeographic regions and may thus be an important factor in the evolution of tree species maximum height. By providing the most comprehensive dataset of the tree species maximum height and wind dispersal strategies across most of the (sub-)tropics, this study also paves the way for advancing our understanding of the eco-evolutionary drivers of tree size.

Keywords

Emergent trees, Evolution, Functional traits, Seed dispersal, Tree species maximum height, Wind dispersal.

Introduction

Tree species maximum height should be closely linked to competition for light; a fundamental resource for tree growth, survival and reproduction. If light were the predominant selection pressure on trees in closed canopy forests, one would expect to find little variation in tree species maximum height as smaller species should be shaded out and eventually disappear from the community (Scheffer & van Nes, 2006; D'Andrea, Riolo & Ostling, 2019; D'Andrea et al. 2020), while emergent tree species would be exposed to wind, lightning and elevated levels of evaporation, thus also limiting their abundance (Larjavaara 2014; Margrove et al. 2015; Olson et al. 2018; Jackson et al. 2021). However, maximum heights of co-existing tree species vary considerably, reflecting a range of life history strategies (Kohyama 1993; Kohyama, Suzuki, Partomihardjo, Yamada & Kubo, 2003; Rüger et al. 2020; Souza 2021), with some species seemingly completing their entire life cycle in the forest understorey while others tower above their neighbours as 2mergent (Banin et al. 2012; Iida et al. 2014). Thus, selective pressures on maximum tree height in addition to light must account for this variation.

In this study we explore the hypothesis that emergent tree species – those capable of growing taller than the surrounding canopy – are more likely to be wind dispersed than non-emergent species. For dispersal to be effective, seeds must generally be carried away from the parent tree to avoid negative distance- and density-dependence, and to colonize favorable sites for regeneration (Comita et al. 2014). Thus, it should be advantageous for wind-dispersed species to be tall because wind speeds increase logarithmically with height above the canopy (Smith et al. 2015, 2016; Santana, Dias-Junior, Vale, Tota & Fitzjarrald, 2017). Release of wind dispersed fruits and seeds at elevated heights increases the probability of long-distance dispersal, which can facilitate successful establishment (Nathan et al. 2002; Heydel, Cunze, Bernhardt-Romermann & Tackenberg, 2014; Wu et al. 2023). Therefore, wind-dispersed tree species likely have an evolutionary advantage by being emergent, which may offset the increased mortality risks that result from their size (Larjavaara 2014; Margrove et al. 2015; Olson et al. 2018;

Jackson et al. 2021). However, the relationship between emergence and wind dispersal has not been examined for a large group of species at a global scale.

Here we test this relationship using a dataset of tree surveys with height measurements that covers most of the (sub-)tropics and some temperate forests in the Americas, Africa and Asia-Pacific, thus encompassing a wide variety of tree species in three more or less independent biogeographic regions (Slik et al. 2015; Gatti et al. 2022). We also provide an appendix containing maximum heights for more than 5,000 tree species to promote further study on the ecology and evolution of tree species maximum height.

Material and Methods

Tree height data

We used tree inventory data (diameter at breast height ≥ 10 cm, excluding monocots and Cactaceae) from 2821 individual old-growth forest plots varying in size from 0.003 to 18 ha, which covered 246 one-degree latitude/longitude grid cells across the Americas, Africa and Asia Pacific (Fig. 1; Appendix 1). Species' taxonomy was updated using the Taxonomic Name Resolution Service (https://tnrs.biendata.org/). We used the Plants of the World Online database (https://powo.science.kew.org/) to resolve any remaining taxonomic issues.

The dataset contained heights for a total of 7,913 tree species. To ensure an adequate sample of each species, we only considered those with a minimum of 10 reported height values, which reduced the number of species for analysis to 5,314 (Appendix 2). To reduce measurement errors and outliers, we used the upper 10-percentile height value as a proxy for the maximum height of each species (Appendix 2). We compared these values with tree height data available in the two largest global plant trait databases: TRY (Kattge et al. 2020) and BIEN (Maitner et al. 2018). These two databases contained 2,400 of the species found in our dataset, of which 926 had lower and 1,474 had higher maximum height than the 90-percentile height value (Appendix 2). Our dataset thus provided maximum height values for an additional 2,914 tree species with no record of this trait in either TRY or BIEN. For consistency, all analyses were done using our 90-percentile height values as a proxy for maximum height. Maximum height values reported in TRY and BIEN are shown in Appendix 2.

Wind dispersal syndrome data

We considered species that have fruits or seeds with wings, hairs or other structures that aid flight, as well as minute (< 1 mm) seeds released from dehiscent dry fruits as being wind dispersed. To determine the fruit or seed types for each species included in our dataset, we used the search string [species name + fruit] in Google images. If no images were found, we scanned through the first 20 hits that provided textual information on the species to see if there were species descriptions that included fruit or dispersal type. If that did not resolve the issue, we used the search string [genus name + fruit] to determine the dispersal type at the genus level, and assigned that to the species because dispersal type is a phylogenetically conserved trait that is generally shared among congenerics (Chazdon, Careaga, Webb & Vargas, 2003). In cases where the fruit type was a dehiscent dry fruit (e.g., pods, follicles, capsules), we repeated the same search method using the search string [species name + seed], and so on. In this way we classified all species in a binary format as either wind dispersed or not (Appendix 2).

Comparisons of species maximum tree height among biogeographic regions

We used a Kruskal-Wallis test followed by Dunn's post-hoc test to determine if there were any differences in species maximum tree heights between the three main biogeographic regions (Africa, Americas and Asia-Pacific). Since the Americas contain more dry forests than Africa and the Asia-Pacific region (Miles et al. 2009), and dry forests tend to have smaller trees, we repeated this analysis including only the 10% tallest tree species in each biogeographic region. To map patterns in tree species maximum height across sample locations, we used the tree species lists of each location in combination with the species' 90-percentile maximum height values to determine the median maximum height value for each location in our dataset.

Tree species maximum height and wind dispersal

We applied generalized linear models with binomial (Bernoulli) distribution and the logit function to conduct logistic regressions of wind dispersal (binary variable) as a function of maximum tree height (continuous variable) for trees with a maximum height > 15 m. Because dry forests differ in physiognomic structure from wet forests, especially with regard to canopy cover and tree sizes, analysing them together might bias results, especially when study regions differ in amount of dry versus wet forests. We therefore analysed these two forest types separately in each biogeographic region. Using climatic information from WorldClim version 2.0 (Fick & Hijmans, 2017), we defined dry and wet sites as those with mean annual precipitation lower or higher than 1,800 mm, respectively (Fig. 1).

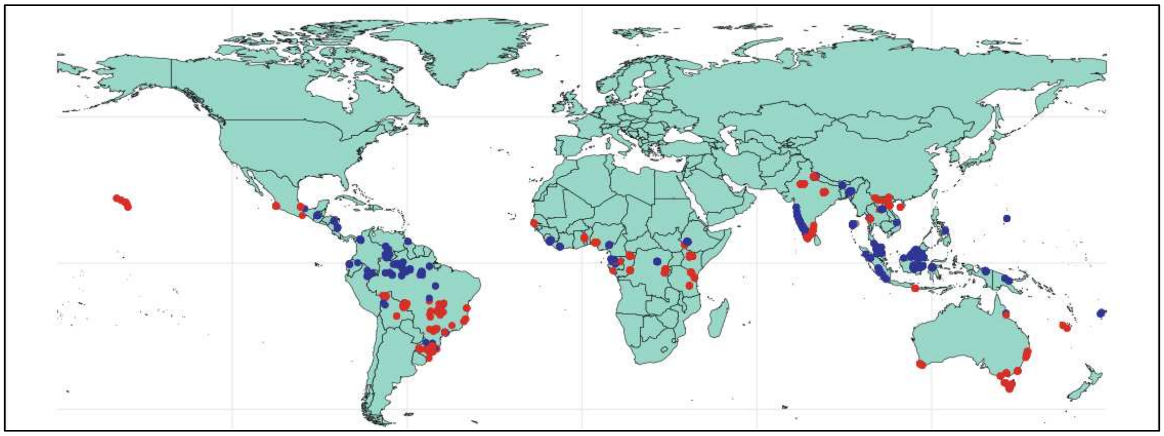

Figure 1. Location of the 246 one-degree latitude/longitude grid cells comprising 2821 forest plots with tree height data used in this study. Sites were classified as wet (annual rainfall ≥ 1800 mm, blue dots) and dry (< 1800 mm, red dots) forests.

Emergent tree species and wind dispersal

We defined emergent species as those with at least one individual taller than the 95% height percentile in one or more sample plots for each region-forest type combination (Appendix 3). Pearson's Chi-squared tests with Yates' continuity correction were used to test whether emergent species had higher proportions of wind dispersal than non-emergent species in wet and dry forests for each biogeographic region.

All statistical analyses were performed with PAST (paleontological statistics software package for education and data analysis) v4.06b (Hammer, Harper & Ryan, 2001) and R 4.3.1.

Results

Maximum tree height differences among biogeographic regions

Tree species maximum height was highest in the Asia-Pacific region (median = 23.9 m) when all species were included in the analysis, followed by Africa (median = 22.0 m) and the Americas (median = 18.0 m) (Kruskal-Wallis test $H = 377.8$, $n = 5290$, $p < 0.0001$) (Fig. 2). According to Dunn's posthoc test the three biogeographic regions differed significantly from one another in median maximum tree height with Bonferroni corrected $p < 0.0018$ for the least significant comparison. In the comparison of the 10% tallest species in each region, species maximum height was highest in Africa (median = 40.6 m), followed by the Asia-Pacific (median = 38.7 m) and the Americas (median = 30.0 m) (Kruskal-Wallis test $H = 272.0$, n = 529, p < 0.0001) (Fig. 3). The three biogeographic regions were again significantly different from one another in median maximum height of the 10% tallest species with Bonferroni corrected p = 0.0165 for the least significant comparison.

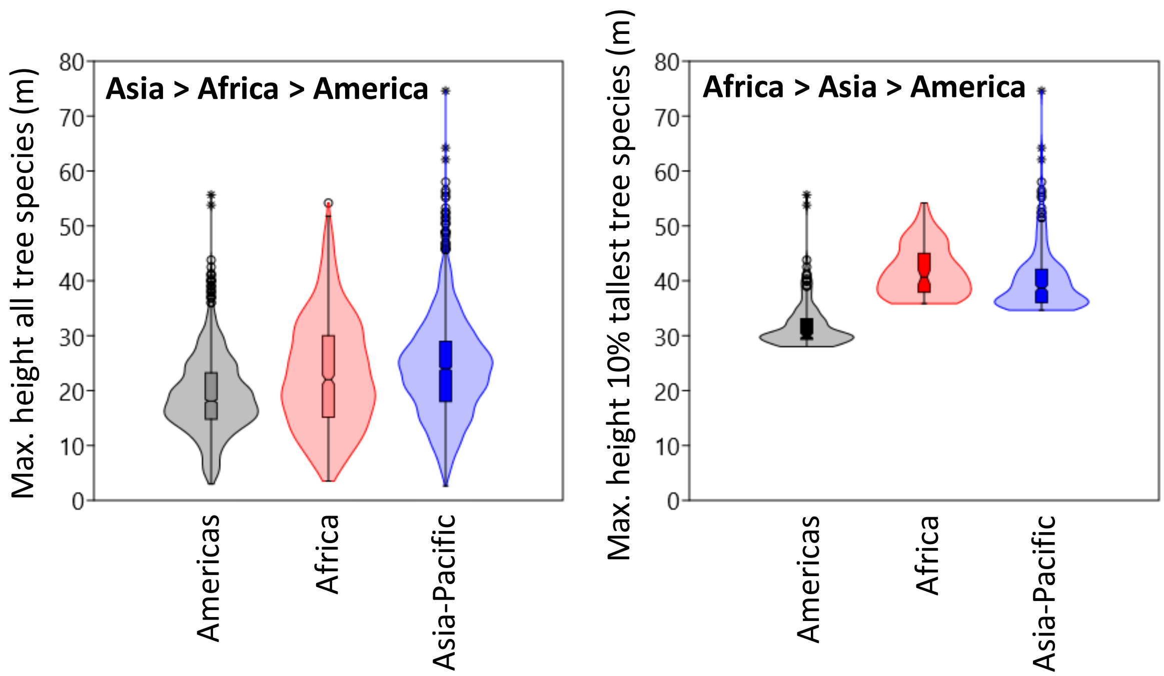

Figure 2. Distribution of species maximum heights across the three biogeographical regions for all tree species (left) and the 10% tallest tree species (right). The middle line represents the median and the lower and upper boxes represent the first and third quartiles, respectively. Number of tree species included in the analysis: Africa 769; Americas 1879, Asia-Pacific 2642.

When mapped across locations, the equatorial regions of Africa and the Asia Pacific as well as sites in southern Australia showed higher median tree species maximum heights than forests in the Americas (Fig. 3).

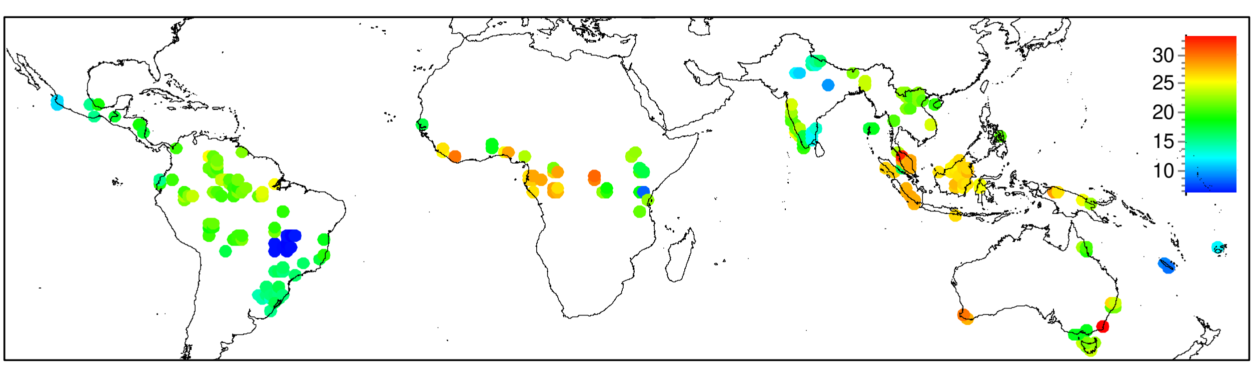

Figure 3. Median of tree species maximum height based on species lists per location.

Wind dispersal and tree species maximum height

The percentage of wind dispersed tree species increased towards higher maximum height classes in all biogeographic regions, despite the declining number of species in these classes. Percentage of wind dispersed species also increased slightly towards the smallest maximum tree heights, especially in the Americas (Fig. 4).

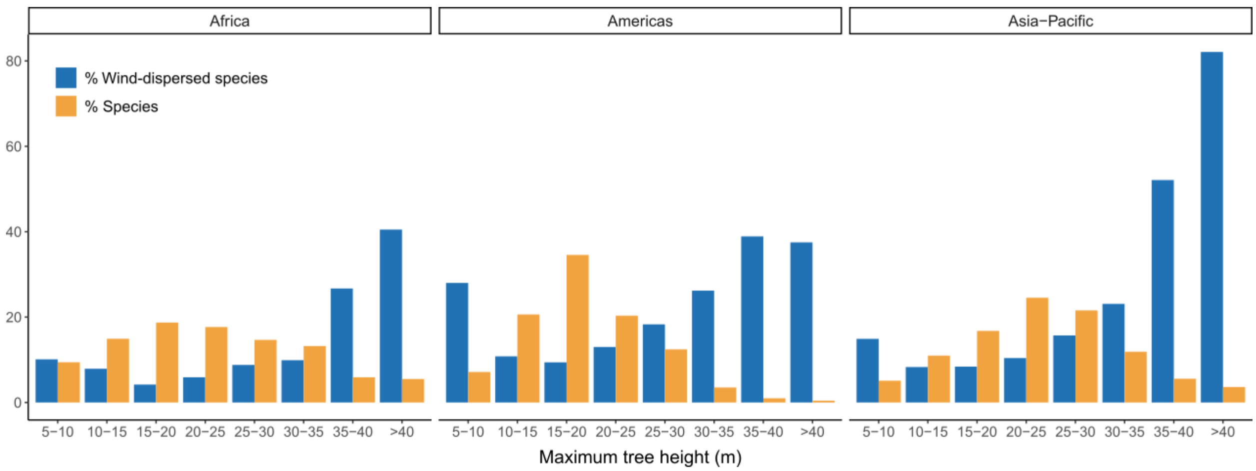

Figure 4. Comparison of the percentage of tree species in 5 m maximum height intervals (in orange) and the percentage of those species that are wind dispersed (in blue). Number of tree species included in the analysis: Africa 769; Americas 1879, Asia-Pacific 2642.

Using only tree species with a maximum height ≥ 15 m, we found a strong and significant increase in the probability of being wind dispersed with increasing species maximum height in each of the three biogeographic regions in dry and wet forests (Fig. 5). This pattern was strongest in the Asia-Pacific region, followed by Africa and the Americas.

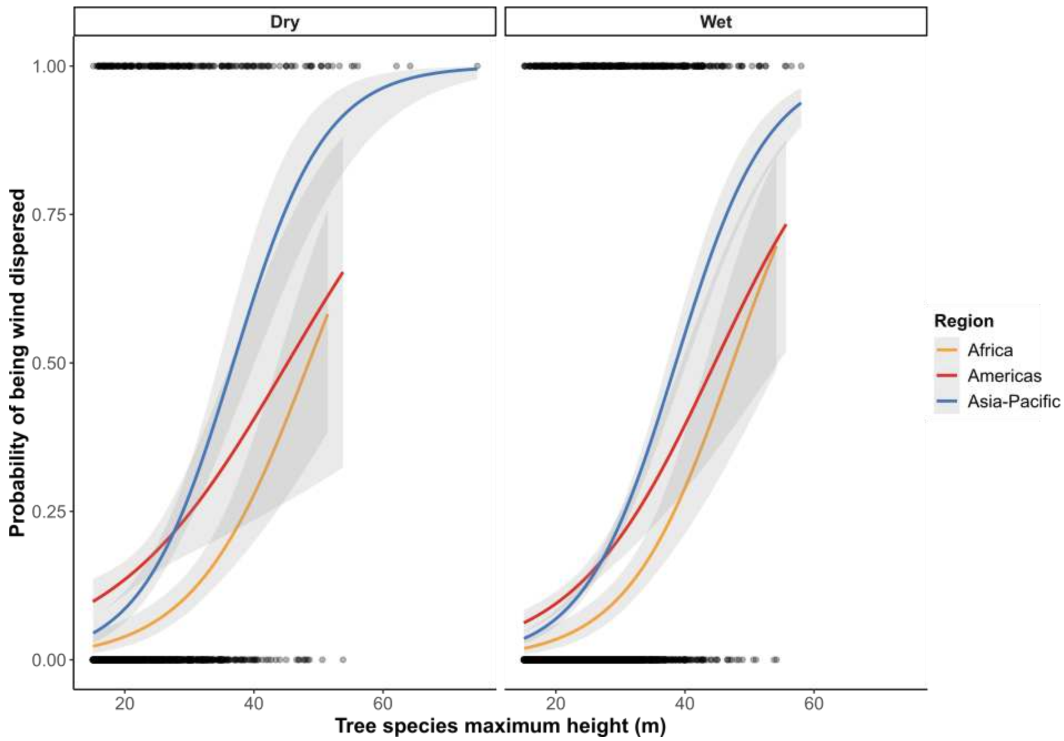

Figure 5. Logistic regression of the probability of being wind dispersed as a function of tree species maximum height for the three biogeographic regions in dry and wet forests, for species with a maximum height ≥ 15 m. Asia-Pacific dry: Estimate 0.141, Std. Error 0.017, z-value 8.525, Pr(>|z|) <2e-16, R2 0.177; Asia-Pacific wet: Estimate 0.140, Std. Error 0.010, z-value 14.650, Pr(>|z|) <2e-16, R2 0.137; Americas dry: Estimate 0.074, Std. Error 0.022, z-value 3.391, Pr(>|z|) <0.0007, R2 0.022; Americas wet: Estimate 0.092, Std. Error 0.015, z-value 6.157, Pr(>|z|) <7.42e-10, R2 0.044; Africa dry: Estimate 0.112, Std. Error 0.020, z-value 5.698, Pr(>|z|) <1.21e-08, R2 0.128; Africa wet: Estimate 0.122, Std. Error 0.020, z-value 6.179, Pr(>|z|) <6.46e-10, R2 0.140.

Emergent tree species and wind dispersal in dry versus wet forests

When tree species were classified into emergent versus non-emergent based on their actual height as observed over all locations, emergent tree species were significantly more likely to be wind-dispersed than non-emergent species in both dry and wet forests across all three biogeographic regions (Fig. 6).

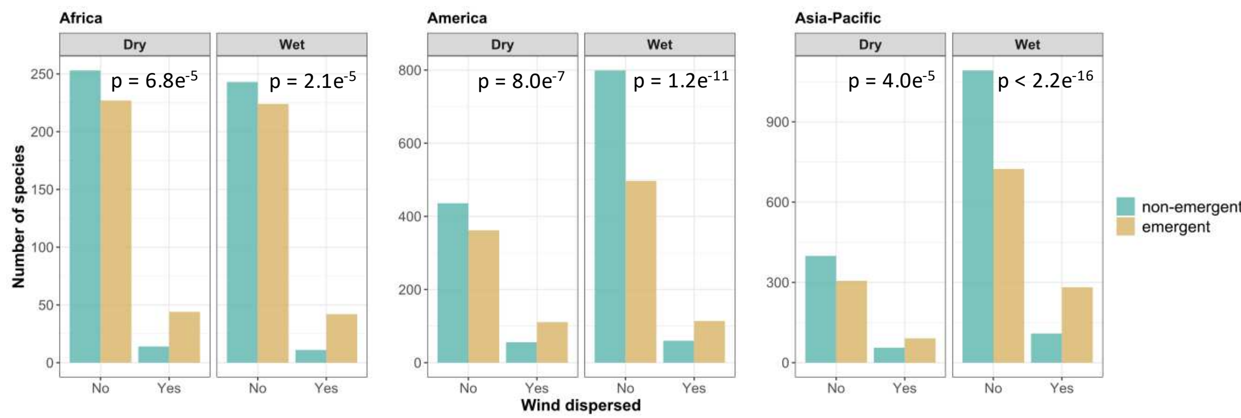

Figure 6. Comparison of the number of emergent species among non-wind and wind dispersed tree species for dry and wet forests in the Asia-Pacific, Africa and Americas. Emergent species were significantly more likely to be wind-dispersed in all three regions and forest types (Pearson's Chi-squared test with Yates' continuity correction).

Discussion

Comparisons of tree species maximum height among biogeographic regions

The Americas differed from their African and Asian-Pacific counterparts in having tree species with smaller maximum heights. This difference was especially pronounced when only the 10% tallest tree species in each biogeographic region were compared, with the median height of these species approximately 10 m taller in the Asia-Pacific and Africa than the Americas. This does not appear to be related to the proportion of wind dispersed tree species in the three continents, which is 10.4% in Africa, 14.0% in the Americas and 17.5% in the Asia-Pacific. It does, however, correspond to earlier findings that tropical American forests are generally less tall, show less variation in tree height and contain less tree biomass than their African and Asian-Pacific counterparts (Dudley & DeVries, 1990; Dial, Bloodworth, Lee, Boyne & Heys, 2004; Banin et al. 2012; Slik et al. 2013). Banin et al. (2012) found that even after accounting for environmental differences between the three biogeographic regions, the maximum tree height differences persisted, with the Americas having shorter trees.

Explaining why maximum tree heights are generally lower in the Americas remains an intriguing problem. Studies comparing canopy and tree heights along environmental gradients have found that these were highest in areas with stable climates that have sufficient rainfall to offset transpiration (Banin et al. 2012; Larjavaara, 2014; Givnish, Wong, Stuart-Williams, Holloway-Phillips & Farquhar, 2014;

Marks, Muller-Landau & Tilman, 2016; Venter at al. 2017; Mao et al. 2020; Gorgens et al. 2020), i.e., areas where hydraulic vulnerability is lowest (Olson et al. 2018), as well as fertile, stable soils that are not located on alluvial sites (Margrove et al. 2015; Gorgens et al. 2020; Jackson et al. 2020). Tall forests also tend to occur in areas with the lowest wind speeds and number of lightning strikes and at least 130 sunny days per year (Gorgens et al. 2020; de Lima et al 2023). Differences in the distribution of maximum tree heights among biogeographic regions may thus be related to environmental conditions conductive for growing tall, suggesting that American forests generally lack such conditions compared to their African and Asian-Pacific counterparts. Further research is needed to determine how the relationship between tree species maximum heights and particular environmental conditions has played out at both the continental scale and over evolutionary time scales.

Tree species maximum height and wind dispersal

A positive association between tree species' maximum height and wind dispersal has long been suspected and observed at local scales in closed canopy forests (Hughes et al. 1994; Suzuki & Ashton, 1996; Yamada & Suzuki, 1999; Chazdon et al. 2003; Slik et al. 2013). We found that there is indeed a strong and positive association between tree species' maximum height and being wind dispersed, and that this pattern is present in dry and wet forests of three large biogeographic regions that have limited species overlap (Slik et al. 2015; Gatti et al. 2022). The detected association makes sense ecologically as tree height is physically linked to dispersal distance in wind dispersed tree species, even in the absence of wind (Hughes et al. 1994; Smith et al. 2015, 2016; Augspurger, Franson & Cushman, 2017). Being emergent also aids wind dispersal as the trees would be better exposed to wind, especially during storms (Heydel et al. 2014). Wind dispersed seeds can be lifted to great heights during storms and be dispersed over long distances of at least several hundred meters, but possibly much farther (Heydel et al. 2014). Although the chance of this happening may be low, most trees live for hundreds of years and thus only a few such storm events over the reproductive lifespan of a tree might be enough for successful dispersal over long distances.

Interestingly, we also detected an increase in the proportion of wind dispersed tree species in species with the smallest maximum heights, especially in the Americas. This may reflect species in more open, savannah-like vegetation types. In savannas the maximum tree height is often limited to 5-15 m and trees are spaced far apart. Under such conditions wind dispersal may be a successful strategy as individual trees, despite their relatively short stature, would still be exposed to wind.

Emergent tree species are disproportionately wind dispersed in dry and wet forests

Emergent tree species were significantly more likely to be wind-dispersed than non-emergent species in both dry and wet forests across the three biogeographic regions. Based on the p-values from our chi-squared tests, the association between emergent species and wind dispersal was stronger in wet than dry forests in the Asia-Pacific and Americas. This is not surprising given that being emergent is probably not as important in dry (especially deciduous) forests where wind is not as hindered by a dense canopy compared to wet forests. Other factors like water stress in tall trees, strong winds, and the relative scarcity of animal frugivores are also likely to affect the strength of this relationship in dry forests (Correa, Alvarez, & Stevenson, 2015). Nevertheless, the consistency of the association across forest types and regions is probably a result of the fact that height is positively related to dispersal distance in wind dispersed tree species (Hughes et al. 1994; Thomson, Moles, Auld, & Kingsford, 2011; Smith et al. 2015, 2016; Augspurger et al. 2017).

Further research

Our results raise several questions for further research. First, they suggest that wind dispersal may be an important factor in the evolution of maximum tree height. The three biogeographic regions have negligible species overlap and also differ considerably in their generic compositions (Slik et al. 2015; Slik et al. 2018; Gatti et al. 2022), implying largely independent evolutionary histories. Borrowing from work on traits impinging on tree height, like hydraulic efficiency (Liu et al. 2019) and those related to seed dispersal, like terminal velocity and seed release timing (Wright et al. 2008), phylogenetic comparative analysis could provide a more integrated picture of the evolution of different life-history traits and reproductive associations in trees. A related question is how this association evolved, for example, whether wind dispersal facilitated the evolution of emergence or vice versa? Phylogenetic methods using tests of contingent evolution could trace the evolutionary pathways that led to this association in different wind dispersed lineages (Larson-Johnson 2016). Another area of inquiry is how maximum height and wind dispersal covary across finer biogeographic and environmental gradients than those explored here, for example in habitats with different canopy structures. We hope that this study and the large list of tree species maximum heights provided will stimulate research to address these and other open questions.

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Data Accessibility Statement

All data used in this study are provided in Appendices 1 & 2.

Appendices

Appendix 1: List of locations with tree heights used in this study.

Appendix 2: Listing of the following information per species: Family, Genus, Species, Region (Region where species was observed), Region.native (the native region of the species), Wind.dispersed..1. (whether a species was wind dispered (1) or not (0)), N (sample size), X90.percentile.dbh..cm. (90-percentile diameter (cm)), X90.percentile.height..m. (90-percentile height (m)), max_dbh..cm. (maximum diameter reported (cm)), max_height..m. (maximum height reported (m)), Hmax_TRYBIEN (maximum height reported in TRY or BIEN (m)), Hmax_higher (talles height reported in either TRY, BIEN or our data set (m)), emerg_loc (whether a species is emergent (1) or not (0)).

Appendix 3: Listing of the following information per species: Region (Americas, Africa, Asia-Pacific), Type (dry (mean annual precipitation < 1800 mm) versus wet (MAP >= 1800 mm)), Species (Scientific species name), emerg_loc (Classification as emergent (1) or non-emergent (0)), WDisp (Wind dispersal (1) or not (0)).