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RESEARCH ARTICLE

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Wind dispersed tree species have greater maximum height

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Abstract

Aim: We test the hypothesis that wind dispersal is more common among emergent tree species given that being tall increases the likelihood of effective seed dispersal.

Location: Americas, Africa and the Asia-Pacific.

Time period: 1970–2020.

Major taxa studied: Gymnosperms and Angiosperms.

Methods: We used a dataset consisting 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 compared differences in tree species maximum height between biogeographic regions and examined the relationship between species maximum height and wind dispersal using logistic regression. We also tested whether emergent tree species, that is species with at least one individual taller than the 95% height percentile in one or more plots, were disproportionally wind dispersed in dry and wet forests within each biogeographic region.

Results: Our dataset provides maximum height values for 5314 tree species, of which more than half (2914) 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 those in Africa and the Asia Pacific. The probability of wind dispersal increased significantly with tree species maximum height and was significantly higher among emergent than non-emergent tree species in both dry and wet forests in all three biogeographic regions.

Main conclusion: Wind dispersal is more prevalent in tall, emergent tree species than in non-emergent species and may thus be an important factor in the evolution of tree species maximum height. By providing the most comprehensive dataset so far of tree species maximum height and wind dispersal strategies, this study 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

1 | INTRODUCTION

Tree species maximum height is closely linked to competition for light, a fundamental resource for tree growth, survival and reproduction. Yet, if light exerted the predominant selection pressure on trees in closed-canopy forests, one would expect to find little variation in interspecific maximum heights as smaller species would be shaded out and eventually disappear from the community (D'Andrea et al., 2019, 2020; Scheffer & van Nes, 2006). On the other hand, species emerging above the canopy are subject to other selective pressures like exposure to wind, lightning and elevated levels of evaporation, which also limit their abundance (Jackson et al., 2021; Larjavaara, 2014; Margrove et al., 2015; Olson et al., 2018). However, maximum heights of co-existing tree species vary considerably, reflecting a range of life history strategies (Kohyama, 1993; Kohyama et al., 2003; Rüger et al., 2020; Souza, 2021). Some species complete their entire life cycle in the forest understorey, while others tower above their neighbours as emergents (Banin et al., 2012; Iida et al., 2014). Selective pressures in addition to light and to the risks associated with emergence must therefore account for the variation found in tree maximum heights.

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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 favourable 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 (de Santana et al., 2017; Smith et al., 2015, 2016). Release of wind dispersed fruits and seeds at elevated heights increases the probability of long-distance dispersal, which can facilitate successful establishment (Heydel et al., 2014; Nathan et al., 2002; Wu et al., 2023). Therefore, wind-dispersed tree species likely have an evolutionary advantage by being emergent, as this condition may offset the increased mortality risks that result from their size (Jackson et al., 2021; Larjavaara, 2014; Margrove et al., 2015; Olson et al., 2018). 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 (Cazzolla Gatti et al., 2022; Slik et al., 2015). We also provide an appendix containing maximum heights for more than 5000 tree species to promote further study on the ecology and evolution of tree species maximum height.

2 | MATERIALS AND METHODS

2.1 | 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 (Figure 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 7913 tree species. To ensure an adequate sample size for each species, we only considered those with a minimum of 10 reported height values, which reduced the number of species for analysis to 5314 (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). Together these databases contained 2400 of the species included in our dataset, of which 926 had lower and 1474 had higher maximum height than the 90-percentile height value calculated from our plots (Appendix 2). Our dataset thus provided maximum height values for an additional 2914 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.

2.2 | 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

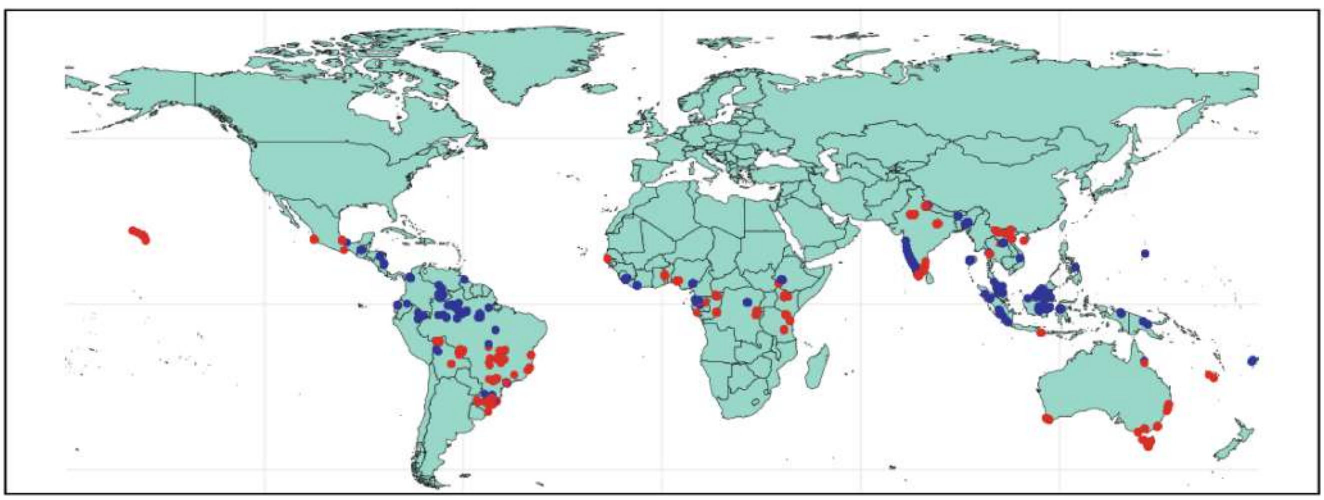

FIGURE 1 Location of 246 one-degree latitude/longitude locations comprising 2821 forest plots with tree height data used in this study. Sites were classified as wet (annual rainfall ≥1800 mm, blue dots) and dry (<1800 mm, red dots) forests.

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 given that dispersal type is a phylogenetically conserved trait that is generally shared among congenerics (Chazdon et al., 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. This procedure allowed us to classify all species in a binary format as either wind dispersed or not (Appendix 2).

2.3 | Tree species maximum height between biogeographic regions

We used a Kruskal–Wallis test followed by Dunn's post-hoc test to determine whether species maximum tree heights differed between the three main biogeographic regions (Africa, Americas and Asia-Pacific). To avoid potential bias resulting from the higher prevalence of dry forests among the biogeographic regions (Miles et al., 2006), with dry forests tending to have smaller trees than wet forests, we repeated this analysis including only the 10% tallest tree species in each biogeographic region. To map patterns in species maximum height across sample locations, we used the species list of each location in combination with the species' 90-percentile height values to determine the median maximum height for each location in our dataset.

2.4 | Tree species maximum height and wind dispersal

To compare the portion of species overall with that of wind-dispersed species across height classes, we partitioned the tree species of each biogeographic region into 5-m maximum height intervals. To examine the relationship between 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 height (continuous variable) of tree species with a maximum height >15 m. We accounted for the potential bias due to physiognomic structural differences between dry and wet forests by analysing 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 1800 mm, respectively (Figure 1).

2.5 | 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 was 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 et al., 2001) and R 4.3.1 (R Core Team, 2023).

3 | RESULTS

3.1 | Maximum tree height differences between biogeographic regions

Maximum height of all tree species was largest in the Asia-Pacific region (median = 23.9 m), followed by Africa (median = 22.0 m) and the Americas (median = 18.0 m) (Kruskal–Wallis test $H = 377.8$, $n = 5290$, $p < 0.0001$) (Figure 2). According to Dunn's post-hoc 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. Maximum height of the 10% tallest species was largest 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 $H = 272.0$, $n = 529$, $p < 0.0001$) (Figure 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.

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 and non equatorial regions (Figure 3).

3.2 | Tree species maximum height and wind dispersal

The percentage of wind-dispersed tree species increased towards higher maximum height classes in all biogeographic regions, despite the declining portion of species in those classes. The percentage of wind-dispersed species also increased slightly towards the smallest maximum height classes, especially in the Americas (Figure 4).

Analysing 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 all three biogeographic regions and in dry and wet forests (Figure 5). This relationship was strongest in the Asia-Pacific region, followed by Africa and the Americas.

3.3 | Emergent tree species and wind dispersal in dry versus wet forests

When tree species were classified as emergent versus non-emergent based on heights measured within each region-forest type

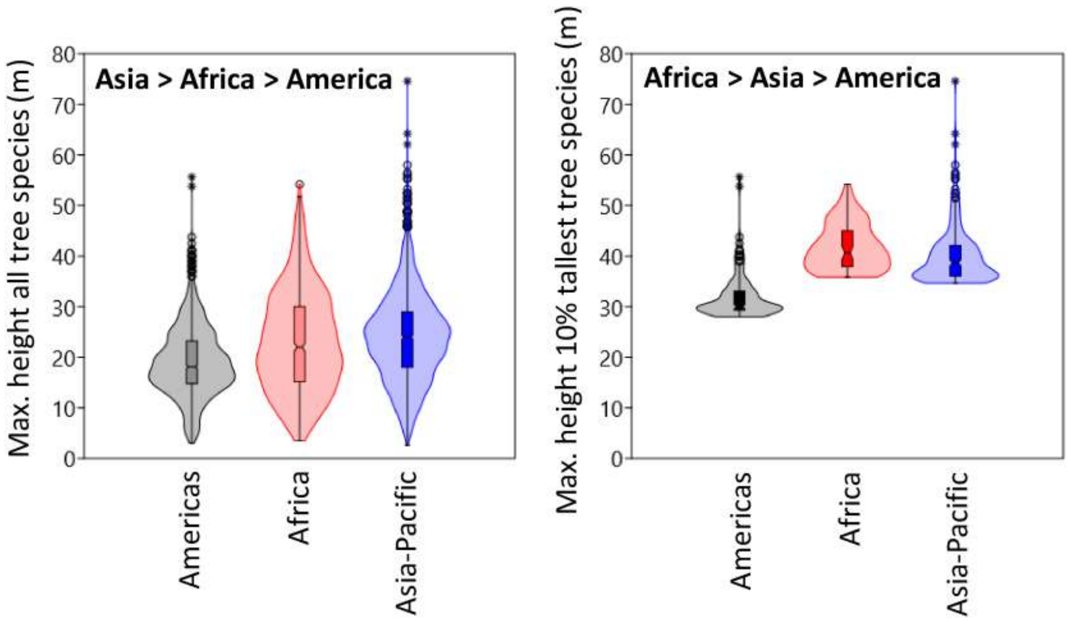

FIGURE 2 Distribution of species maximum heights across the three biogeographical regions for all tree species (left) and the 10% tallest tree species (right). The middle line represents the median and the lower and upper boxes represent the first and third quartiles, respectively. The lighter-coloured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

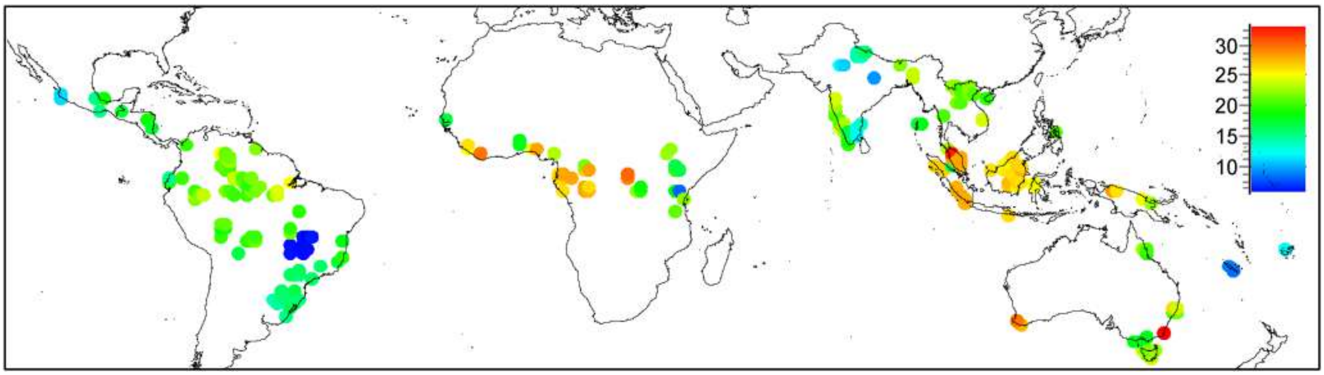

FIGURE 3 Median of tree species maximum height (m) based on species lists per location.

combination, emergent species were significantly more likely to be wind-dispersed than non-emergent species in both dry and wet forests across all three biogeographic regions (Figure 6).

4 | DISCUSSION

4.1 | Tree species maximum height among biogeographic regions

Tree species in the Americas had lower maximum heights, on average, than those in Africa and the Asia-Pacific. This difference was especially pronounced when only the 10% tallest tree species in each biogeographic region were compared, with the median height approximately 10 m taller in Africa and the Asia-Pacific than in the Americas. This does not appear to be related to the proportion of wind-dispersed tree species on each continent, which, based on our data, was 10.4% in Africa, 14.0% in the Americas and 17.5% in the Asia-Pacific. It does, however, agree with earlier findings that tropical American forests are generally shorter, show less variation in tree height and contain less tree biomass than their African and Asian-Pacific counterparts (Banin et al., 2012; Dial et al., 2004; Dudley & DeVries, 1990; Slik et al., 2013). Even after accounting for environmental variation between these three regions, Banin et al. (2012) found that the tree height differences persisted, with trees typically shorter in the Americas.

Ascertaining why maximum tree heights are generally lower in the Americas remains an intriguing question. Studies show that canopy level and tree heights are highest in areas with stable climates that have sufficient rainfall to offset transpiration (Banin et al., 2012; Givnish et al., 2014; Gorgens et al., 2020; Larjavaara, 2014; Mao et al., 2020; Marks et al., 2016; Venter et al., 2017), that is areas

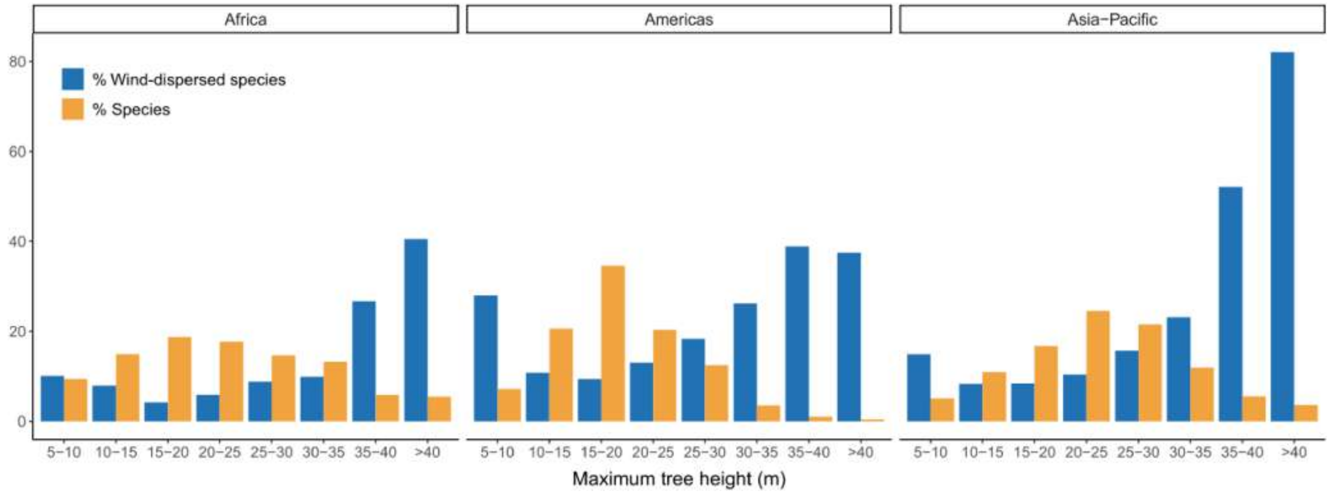

FIGURE 4 Comparison of the percentage of tree species in each biogeographic region in 5 m maximum height intervals (orange bars) and the percentage of those species that are wind dispersed (blue bars). Number of tree species included in the analysis: Africa, 769; Americas, 1879; and Asia-Pacific, 2642.

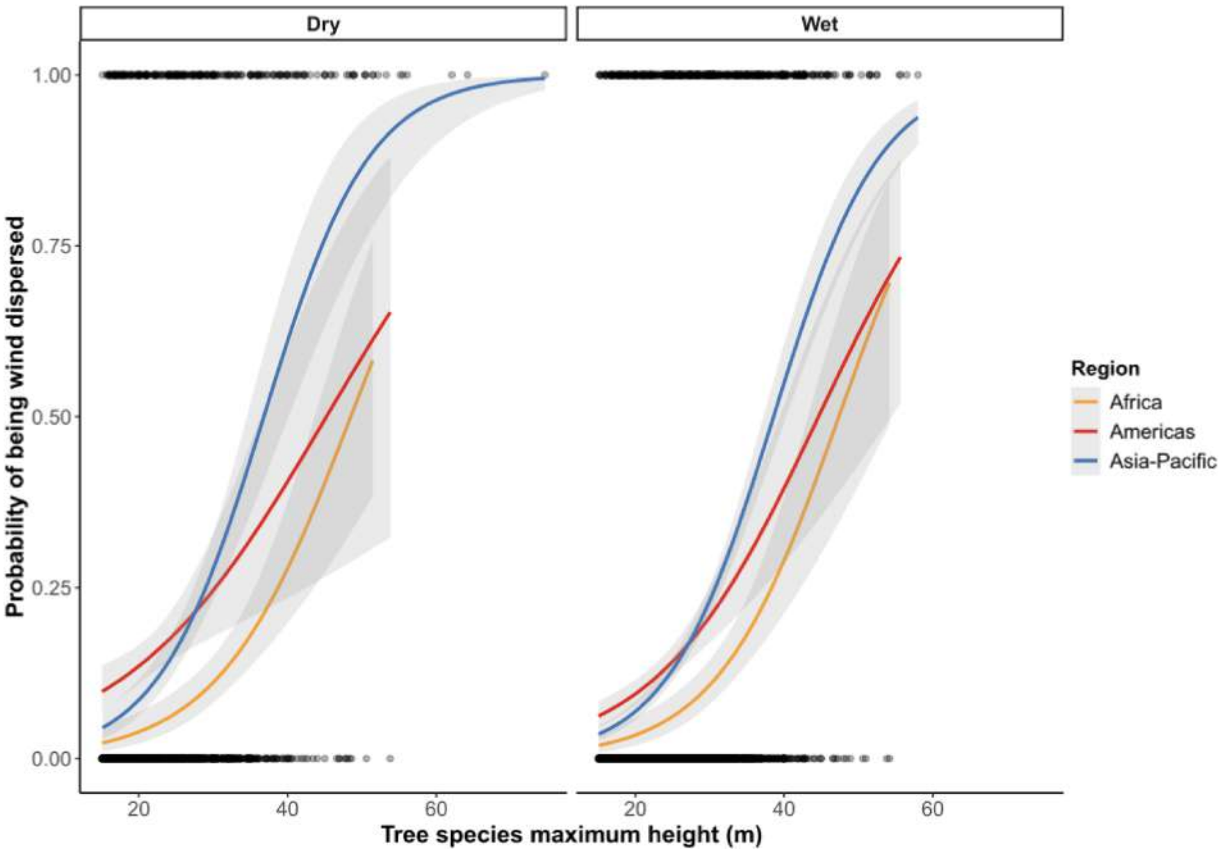

FIGURE 5 Logistic regressions of the probability of being wind dispersed as a function of tree species maximum height for the three biogeographic regions in dry and wet forests, for species with a maximum height ≥15 m. Asia-Pacific dry: Estimate 0.141, Std. Error 0.017, *z*-value 8.525, $p < 2e{-}16$,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

where hydraulic vulnerability is lowest (Olson et al., 2018), as well as fertile, stable soils that are not located on alluvial sites (Gorgens et al., 2020; Jackson et al., 2021; Margrove et al., 2015). Tall forests also tend to occur in areas where wind speeds and the number of lightning strikes are low and that enjoy at least 130 sunny days per year (de Lima et al., 2023; Gorgens et al., 2020). Differences in

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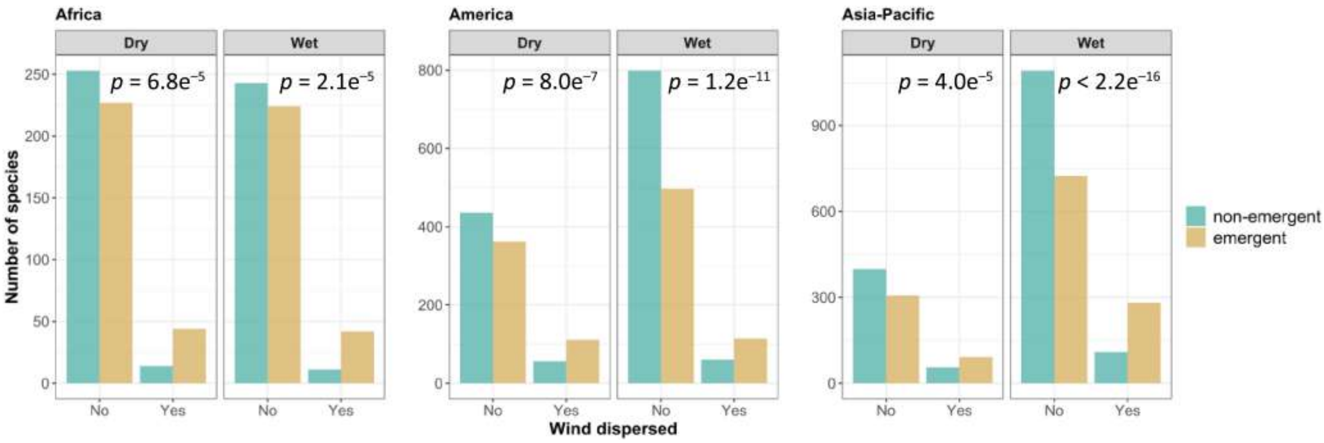

FIGURE 6 Comparison of the number of emergent species among trees that are non-wind and wind-dispersed in dry and wet forests across the Asia-Pacific, Africa and Americas. Emergent species were significantly more likely to be wind-dispersed in both forest types within all three regions (Pearson's Chi-squared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

maximum tree heights among biogeographic regions is thus likely related to environmental conditions conductive for growing tall, which suggests that American forests generally lack such favourable conditions relative 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.

4.2 | Probability of wind dispersal increases with tree species maximum height

While a positive association between tree species' maximum height and wind dispersal has long been observed in closed canopy forests at local scales (Chazdon et al., 2003; Hughes et al., 1994; Slik et al., 2013; Suzuki & Ashton, 1996; Yamada & Suzuki, 1999), we found this association to be widespread in both dry and wet forests throughout three large biogeographic regions that have limited species overlap (Cazzolla Gatti et al., 2022; Slik et al., 2015). This relationship makes sense ecologically as tree height is physically linked to dispersal distance in wind-dispersed trees, even in the absence of wind (Augspurger et al., 2017; Hughes et al., 1994; Smith et al., 2015, 2016). Being emergent aids wind dispersal because these trees are more exposed to wind above the canopy, especially during storms (Heydel et al., 2014). Wind-dispersed seeds can be lifted to great heights during storms and be dispersed over distances of several hundred meters or even farther (Heydel et al., 2014). Although such events are infrequent, most trees live for hundreds of years and thus a few such storm events over the reproductive lifespan of a tree might be enough for successful long-distance dispersal and establishment.

Interestingly, we also detected an increase in the proportion of wind-dispersed tree species towards the smallest maximum height classes, especially in the Americas. This may reflect species occurring in open woodlands and savannah-like habitats where maximum tree height is often limited to 5–15 m and trees are spaced far apart. Wind dispersal is likely to provide a successful strategy under such conditions given that individual trees, despite their relatively short stature, would still be exposed to wind.

4.3 | 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 forests 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 much obstructed 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 et al., 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 (Augspurger et al., 2017; Hughes et al., 1994; Smith et al., 2015, 2016; Thomson et al., 2011).

4.4 | Areas of future inquiry

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 (Cazzolla Gatti et al., 2022; Slik et al., 2015, 2018), implying largely independent evolutionary histories. Borrowing from work on traits impinging on tree height, such as 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 in the supplementary material will stimulate research to address these and other interesting questions on the relationship between wind dispersal and tree maximum height.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data used in this study are provided in Appendices 1–3.

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SUPPORTING INFORMATION

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

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