

# Seed dispersal distance is more strongly correlated with plant height than with seed mass

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## Summary

1. It is often assumed that there is a trade-off between maternal provisioning and dispersal capacity, leading small-seeded species to disperse further than large-seeded species. However, this relationship between dispersal distance and seed mass has only been quantified for species from particular sites or with particular dispersal syndromes.

2. We provided the first large-scale, cross-species quantification of the correlations between dispersal distance and both seed mass and plant height. Seed mass was positively related to mean dispersal distance, with a 100-fold increase in seed mass being associated with a 4.5-fold increase in mean dispersal distance ( $R^2 = 0.16$ ;  $n = 210$  species;  $P < 0.001$ ). However, plant height had substantially stronger explanatory power than did seed mass, and we found a 5-fold increase in height was associated with a 4.6-fold increase in mean dispersal distance ( $R^2 = 0.54$ ;  $n = 211$  species;  $P < 0.001$ ).

3. Once plant height was accounted for, we found that small-seeded species dispersed further than did large-seeded species ( $R^2 = 0.54$ ;  $n = 181$  species; slope =  $-0.130$ ;  $P < 0.001$ ); however, seed mass only added 2% to the  $R^2$  of the model. Within dispersal syndromes, tall species dispersed further than did short species, while seed mass had little influence on dispersal distance.

4. *Synthesis.* These findings enhance our understanding of plant life-history strategies and improve our ability to predict which species are best at colonizing new environments.

**Key-words:** dispersal, dispersal mechanism, dispersal syndrome, long-distance dispersal, maximum dispersal, plant dispersal, plant height, seed mass, seed size

## Introduction

Dispersal, the movement of seeds or diaspores away from the parent plant, is a key life-history stage in plants. Persistence, migration and seedling recruitment are all affected by seed dispersal distances (Howe & Smallwood 1982; Hyatt *et al.* 2003; Levin *et al.* 2003). There are correlations between most life-history traits (Wright *et al.* 2004; Moles & Leishman 2008), and some traits may affect species' dispersal distances (Muller-Landau *et al.* 2008). Understanding how species' traits are related to dispersal distance is crucial for understanding the evolution and ecology of plant dispersal systems. However, there is limited information about how life-history traits and dispersal distance are correlated. Plant species may modify particular traits to enhance dispersal or conversely trade off

between dispersal capacity and other important life-history stages.

Our first aim was to quantify the cross-species relationship between seed mass and dispersal distance. Seed mass influences many different life-history stages in plants. Small-seeded species have low rates of survival in the early stages of establishment (Moles & Westoby 2004). Small-seeded species also tend to have high annual seed output, but short lifespans (Moles & Westoby 2004; Moles *et al.* 2004). Relationships between seed mass and dispersal distances are less well understood than relationships between seed mass and other life-history stages. This is surprising, because seed mass is important for species' life-history strategies, and dispersal is a major life-history stage.

There is a perception that small-seeded species should disperse better than large-seeded species, trading off seed mass (maternal provisioning) with dispersal capacity (Venable & Brown 1988; Greene & Johnson 1993; Cornelissen *et al.* 2003). Small-seeded species may increase their probability of survival by dispersing further from the parent plant than do

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large-seeded species (Janzen 1970; Hyatt *et al.* 2003). High annual seed production of small-seeded species may enhance the likelihood of rare long-distance dispersal events, resulting in dispersal curves with fat, long tails and increased mean and maximum dispersal distances. We therefore predicted that small-seeded species would have greater dispersal distances than large-seeded species.

The relationship between seed mass and dispersal distance has been quantified before, but only within single species, dispersal syndromes or vegetation communities (Greene & Johnson 1993; Xiao, Zhang & Wang 2005; Muller-Landau *et al.* 2008). The cross-species relationship between seed mass and dispersal distance was negative for 41 tropical tree species, including wind-, ballistically and animal-dispersed species (Muller-Landau *et al.* 2008). Within wind-dispersed species, relationships between seed mass and dispersal capacity have been negative for winged achenes (Greene & Johnson 1993) and nonsignificant across seed-morphology types (Greene & Johnson 1986). There was no relationship between maximum dispersal distance and propagule mass for 320 species of passively dispersed organisms (Jenkins *et al.* 2007), but this study combined plants, marine larvae and pollen reproductive bodies, making it impossible to identify the plant contribution. Our study is the first to provide a large-scale, cross-species quantification of the relationships between seed mass and dispersal distance across and within seed dispersal syndromes.

Our second aim was to quantify the cross-species relationship between plant height and dispersal distance. Plant height is another important trait for species' life-history strategies, affecting species' abilities to capture light (Falster & Westoby 2005). Tall species tend to have higher annual seed production, larger seeds, greater longevity and greater reproductive lifespans than do short species (Moles & Leishman 2008). However, tall species take longer to reach maturity (Moles & Leishman 2008). Taller species presumably release seeds at greater heights than do shorter species, and for wind-dispersed species, greater release heights result in increased dispersal distances (Tackenberg, Poschlod & Bonn 2003; Soons *et al.* 2004; Travis, Smith & Ranwala 2010). Beyond wind-dispersed species, the relationship between plant height and dispersal distance is largely unknown, although there was a positive relationship between plant height and mean dispersal distance for 41 tropical tree species (Muller-Landau *et al.* 2008). If taller plants have wider crowns than shorter species (King 1990), then seeds released at the crown edge would disperse further from the parent plant base for tall species (Muller-Landau *et al.* 2008). We therefore predicted that seeds from taller species would disperse further than would seeds from shorter species.

Plant height may mask the true relationship between seed mass and dispersal distance, because taller species tend to have larger seeds than shorter species (Thompson & Rabinowitz 1989; Moles *et al.* 2004). Consequently, our third aim was to investigate the relationship between seed mass and dispersal distance after controlling for plant height. Subsequently, we predicted that there would be no relationship between seed mass and dispersal distance because of (predicted) opposing relationships between dispersal distance and seed mass and plant height.

## RELATIONSHIPS WITHIN DISPERSAL SYNDROMES

It has been stated that dispersal syndromes produce distinct ranges in dispersal distances, varying in the orders of magnitude (Willson 1993; Vittoz & Engler 2007). This is largely based on multiple single-species studies or studies within a particular dispersal syndrome (Gomez & Espadaler 1998), vegetation type (Cain, Damman & Muir 1998; Clark *et al.* 2005) or region (Vittoz & Engler 2007). Generalizations are that wind-, water- and vertebrate-dispersed species have longer-distance dispersal capabilities than species with ant, ballistic and unassisted dispersal (Willson 1993; Gomez & Espadaler 1998; Vittoz & Engler 2007). The studies that have examined dispersal distances globally have been primarily descriptive, with distances not quantified for dispersal syndromes (Willson 1993; Hughes *et al.* 1994). Therefore, our fourth aim was to quantify cross-species dispersal distances within each dispersal syndrome.

In addition to differences in the mean dispersal distance associated with each dispersal syndrome, there may be differences in the relationship between dispersal distance and seed mass and/or plant height between dispersal syndromes. We predicted that seed mass and dispersal distance would be positively related for species dispersed by ants and seed-caching vertebrates and negatively related for species that are ballistically or wind dispersed or dispersed through ingestion by vertebrates. We predicted that there would be no relationship between seed mass and dispersal distance for species dispersing by attachment or with unassisted dispersal. The reasoning behind these predictions is explained in Appendix S1 in Supporting Information. For plant height and dispersal distance, we predicted positive relationships for wind and unassisted dispersal because greater release heights increase dispersal distances and taller species may have wider canopies than shorter species, thereby increasing fall distance. We predicted no relationship for ballistic species because Beer & Swaine (1977) demonstrated in a theoretical paper that release height had little influence on seed dispersal distance. Lastly, for species using biotic dispersal (ants, seed-caching ingestion and attachment), we predicted no relationship between plant height and dispersal distance. Changes in animal vector traits are more important than variation within a particular species for dispersal kernels (Will & Tackenberg 2008), and we predicted that this would extend to cross-species relationships.

In summary, we tested four main hypotheses:

- 1 Small-seeded species disperse further than large-seeded species.
- 2 Tall species disperse further than short species.
- 3 Once plant height is accounted for, small-seeded and large-seeded species will disperse to similar distances.
- 4 Within dispersal syndromes, relationships between dispersal distances and plant traits will vary.

## Materials and methods

We searched ISI Web of Science for papers published in English, using two search strings: (i) 'seed' and 'dispersal distance' or 'seed

dispersal' and 'distance' and (ii) 'dispersal kernel', 'dispersal curve' or 'seed shadow'. Papers with seed dispersal distance data from published sources (Willson 1993; Hughes *et al.* 1994; Cain, Damman & Muir 1998; Gomez & Espadaler 1998; Bullock & Clarke 2000; Ness *et al.* 2004; Vittoz & Engler 2007) were used to gather additional peer-reviewed articles. We included studies that measured dispersal distance from the base of the plant or from the edge of the canopy of the parent plant. However, we excluded studies that only measured distance from the mother plant to established offspring, because this measure is influenced by mortality and establishment ability. We also excluded studies that measured dispersal distance from seed to nearest adult, when dispersal curves of other adults may have influenced results (Willson 1993). We preferentially chose dispersal distances estimated for natural habitats because direct or indirect anthropogenic disturbances can alter dispersal kernels (Andersen & Morrison 1998). We left out species that had invasive biotic vectors because species did not co-evolve, potentially affecting dispersal distances (Ness 2004). Dispersal distance had to be related to individual species, so studies that amalgamated species or used artificial seeds were not included. To avoid circularity, we excluded studies that used seed mass to model dispersal distances. We included studies examining secondary dispersal syndromes because morphologies adapted for one dispersal syndrome can aid multiple dispersal syndromes. For example, *Rhinanthus minor* (Orobanchaceae), a grassland annual, has moderately large-winged disc seeds dispersed by wind (Bullock *et al.* 2003) and attachment to animals (Kiviniemi & Eriksson 1999). We classified species into eight dispersal syndrome categories: unassisted, wind, water, ballistic, ingestion, attachment, seed-caching and ant. These classifications were based on the vector that moved seeds in the source papers. We used empirical studies, except for some species dispersed by ingestion.

Percentiles are the preferable measure for reporting dispersal distances because dispersal curves are usually skewed and leptokurtic in shape. However, we found percentiles were not commonly reported and the value of the maximum percentile reported varied, usually as the 90th, 95th or 99th percentiles. Therefore, we collected mean and maximum dispersal distances, which were more widely reported, preferentially from text or tables; otherwise, data were extracted from graphs using DataThief III (B. Tummers 2006; <http://datathief.org/>).

We used maximum recorded dispersal distance data for each species. Researchers are highly unlikely to have recorded the actual longest dispersal event for each species, and so observed maxima will be less than the species' lifetime maximum dispersal distance. However, these real observations are the best information available. Species with < 5 seed movement observations were excluded. Seed mass data were acquired preferentially from the study from which dispersal distance was taken and then from Moles *et al.* (2005) or the Royal Botanic Gardens Kew's Seed Information Database (Liu *et al.* 2008). Seed mass data collection followed the criteria outlined by Moles *et al.* (2005). Seeds and diaspores were not always distinguished in the literature and seed mass data resources; therefore, we did not attempt to convert 'diaspore' masses into 'seed' masses. Seed mass rather than diaspore mass was preferentially chosen wherever possible, to facilitate comparison of our results with the results of other studies, and because seed mass data are more abundant. We collected maximum height and growth form data from the study from which dispersal distance data were taken, or from Moles *et al.* (2009), Chew (1989), Hickman (1993), eFlora of China (Brach & Song 2006), the LEDA Traitbase (Kleyer *et al.* 2008) or the United States Department of Agriculture PLANTS Database (<http://plants.usda.gov>). Maximum plant height, not mean height, was used to maximize the probability

of representing sexually mature adults, as mean height could include seedlings or juveniles.

Our study spanned eight orders of magnitude in seed mass, from 0.0071 mg (*Striga hermonthica* – Purple witchweed) to 0.5 kg for *Borassus aethiopum* (African fan palm). Our range for maximum plant height was also broad, from 5 cm for *Hexastylis arifolia* up to 73 m for our largest species *Pinus lambertiana*. The recorded mean dispersal distances across all species ranged from 3 cm for *Viola olifera* with secondary dispersal by ants to 4.05 km for the water-dispersed species *Ailanthus altissima*. Maximum dispersal distances reached by species ranged from 15 cm for *Viola olifera* (secondary ant dispersal) to 400 km for several species attached to the wool of migrating sheep (Manzano & Malo 2006).

#### DATA ANALYSIS

Seed mass, dispersal distance (mean and maximum) and maximum plant height data were log<sub>10</sub>-transformed before analyses. We calculated the geometric means when species had multiple mean distance values, from either multiple studies, or several treatments within a study. Species with more than one dispersal syndrome were weighted in the analyses. For example, a species with mean dispersal distances for two dispersal syndromes (ant and ballistic) received a 0.5 weighting for the ant mean dispersal value and 0.5 weighting for the ballistic value.

We used ordinary least-squares regressions to quantify relationships between dispersal distance and seed mass and between dispersal distance and plant height across all species. We used multiple linear regressions to examine the influence of plant height on the relationship between seed mass and dispersal distance. We then used a reduced data set containing species with known dispersal syndromes. We ran analysis of covariance (ANCOVA), with dispersal syndrome as a categorical variable and seed mass and/or plant height as covariates. Water-dispersed species were excluded because of insufficient data ( $n = 8$ ), and mean dispersal distance data for species using attachment were insufficient for analyses ( $n = 4$ ). We found significant interaction terms for all analyses, indicating heterogeneous slopes. Therefore to quantify relationships between seed mass, plant height and dispersal distances within dispersal syndromes, we used ordinary least-squares regressions and multiple linear regressions. Data sets for the multiple regressions (combining seed mass and plant height) were smaller than singular regression data sets, because seed mass and plant height data were needed for each species. Results for the linear regressions were similar when we used the reduced data sets from the multiple regression analyses.

We used an ANCOVA to quantify the relationship between mean and maximum dispersal distance, with dispersal syndrome as a covariate (Appendix S2). We also asked whether the plant height and dispersal distance relationships held within woody and nonwoody species using ANCOVA, where growth form (woody or nonwoody) was the categorical variable. All regression and ANCOVA analyses were conducted using JMP version 5 (SAS institute, Cary, NC, USA).

We performed phylogenetic regressions on the cross-species relationships across dispersal syndromes between plant height, seed mass and dispersal distances. We used PHYLOMATIC (Webb, Ackerly & Kembel 2008) to arrange species on a phylogenetic tree and then used the 'Analysis of Traits' (aot) module in PHYLOCOM to create phylogenetically independent contrasts of the data (Webb, Ackerly & Kembel 2008). We then analysed the contrasts using linear regression (forced through the origin; Garland, Harvey & Ives 1992).

## Results

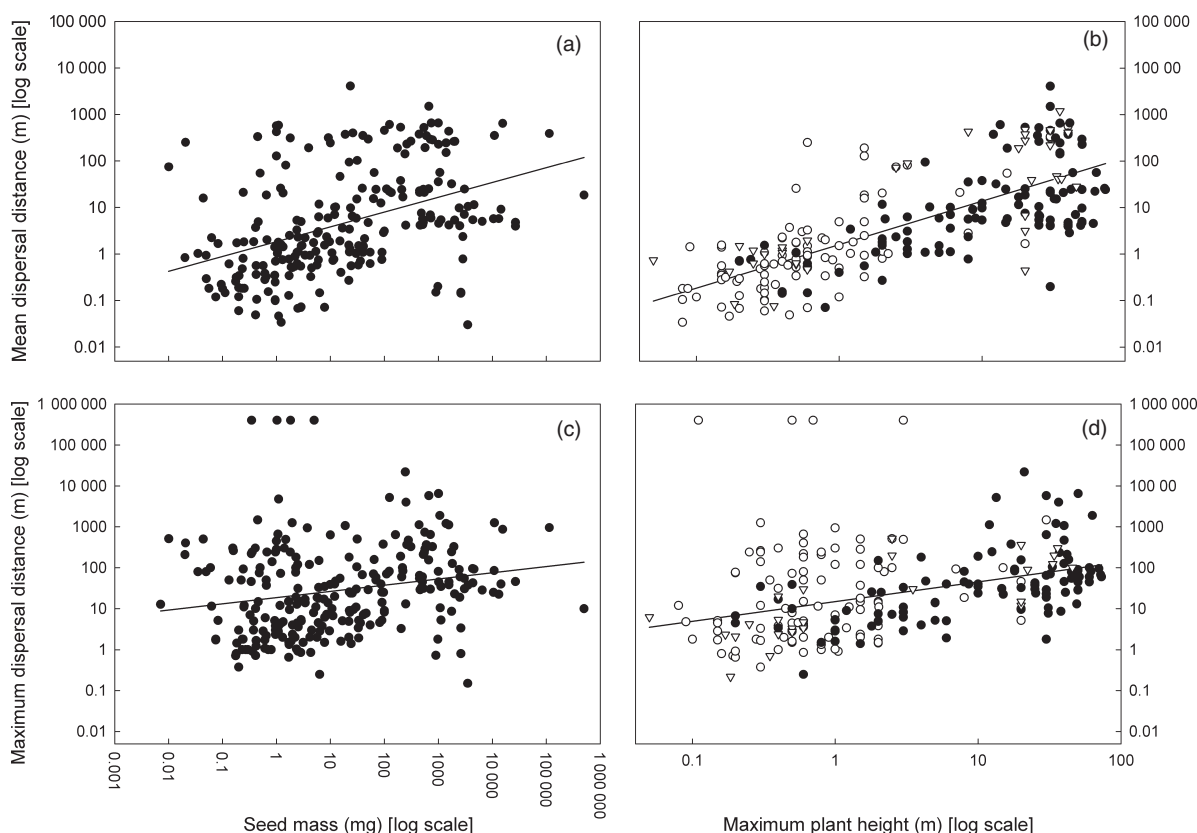
### CROSS-SPECIES RELATIONSHIPS BETWEEN SEED MASS AND PLANT HEIGHT

Our initial hypothesis that small-seeded species would disperse further than large-seeded species was not supported. Species with heavier seeds had greater mean dispersal distances, but seed mass only accounted for a small amount of the variation in mean dispersal distance ( $R^2 = 0.16$ ;  $n = 210$  species; slope =  $0.326 \pm 0.049$  SE;  $P < 0.001$ ; Fig. 1a). The regression slope indicated that a 100-fold increase in seed mass was associated with a 4.5-fold increase in dispersal distance. We found that larger seeds also had greater maximum dispersal distances ( $R^2 = 0.04$ ;  $n = 245$  species; slope =  $0.159 \pm 0.047$  SE;  $P \leq 0.001$ ; Fig. 1c), although the strength of this relationship was low.

Our hypothesis that tall species disperse further than short species was supported for both mean and maximum dispersal distance. Taller species had greater mean dispersal distance than shorter plant species ( $R^2 = 0.54$ ;  $n = 211$  species; slope =  $0.936 \pm 0.057$  SE;  $P < 0.001$ ; Fig. 1b). A 5-fold increase in height was associated with a 4.6-fold increase in mean dispersal distance. Taller species also had greater maximum dispersal distances than did shorter species, although the relationship was weak ( $R^2 = 0.13$ ;  $n = 235$  species; slope =  $0.472 \pm 0.076$  SE;

$P \leq 0.001$ ; Fig. 1d). Interestingly, plant height had substantially greater explanatory power than did seed mass (the  $R^2$  for the relationship between mean dispersal distance and plant height was 0.54, compared with only 0.16 for seed mass). There was no significant interaction between plant height and growth form (woody or nonwoody) for mean ( $P = 0.96$ ;  $n = 207$  species) and maximum ( $P = 0.68$ ;  $n = 227$  species) dispersal distance; this indicates taller species disperse further than shorter species, regardless of growth form.

Once we controlled for plant height, there was a negative relationship between seed mass and dispersal distance, with smaller-seeded species having greater mean (slope =  $-0.130 \pm 0.050$  SE;  $P = 0.001$ ) and maximum (slope =  $-0.469 \pm 0.095$  SE;  $P \leq 0.001$ ) dispersal distances. A combination of seed mass and plant height explained over 50% of the variation in mean dispersal distance ( $R^2 = 0.54$ ;  $n = 181$  species;  $P \leq 0.001$ ), but this was close to the variation explained by plant height alone using this reduced data set where both trait data were available for all species ( $R^2 = 0.52$ ;  $n = 181$  species). The combination of seed mass and plant height improved the model for maximum dispersal distance ( $R^2 = 0.22$ ;  $n = 208$  species;  $P \leq 0.001$ ). We found a positive relationship between mean and maximum dispersal distance, with a large amount of the variation explained by the overall model ( $R^2 = 0.90$ ;  $n = 220$  species; slope =  $0.836 \pm 0.031$  SE;  $P < 0.001$ ; Appendix S2).



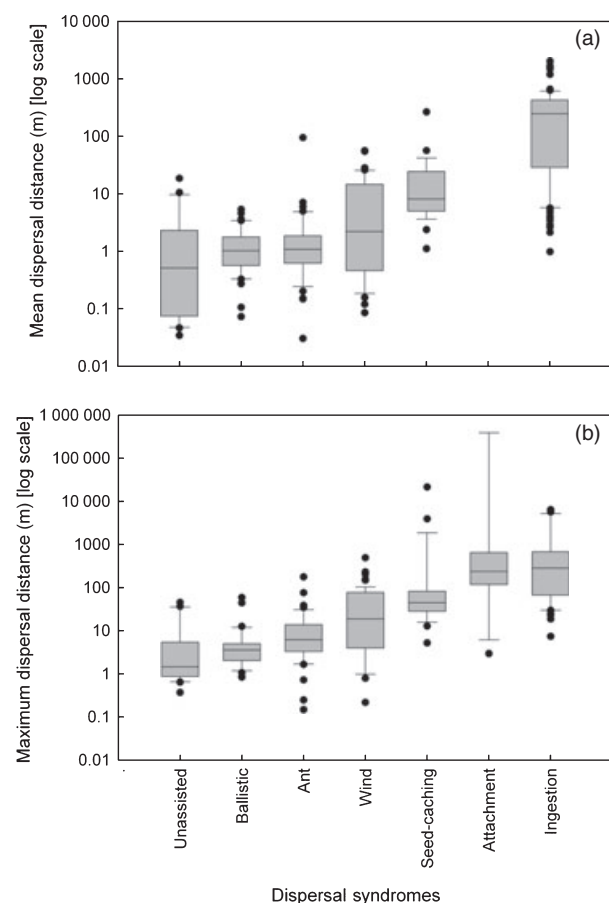
**Fig. 1.** Relationships between mean dispersal distance and (a) seed mass ( $n = 210$  species) and (b) maximum plant height ( $n = 211$  species); and between maximum dispersal distance and (c) seed mass ( $n = 245$ ) and (d) maximum plant height ( $n = 235$  species). For maximum height graphs (b) and (d), seeds < 6 mg (6 mg was the median for species' seed mass data in our study) are marked as white circles, seeds > 6 mg are marked as black circles and seeds with no seed mass data are marked with grey triangles.



Results of phylogenetic regressions on relationships between mean dispersal distance and seed mass (slope =  $0.191 \pm 0.062$ ;  $P = 0.003$ ) or plant height (slope =  $0.925 \pm 0.089$ ;  $P \leq 0.001$ ) were qualitatively similar to the results of cross-species regressions. However, once we accounted for phylogeny, the relationship between maximum dispersal and both seed mass and plant height altered. Phylogenetic regressions for maximum dispersal distance showed no relationship with seed mass ( $P = 0.56$ ) or plant height ( $P = 0.11$ ). The difference between cross-species and phylogenetic results suggests that the cross-species relationships for maximum dispersal distance might be attributable to one or a few divergences deep in the phylogenetic tree.

#### RELATIONSHIPS BETWEEN SEED MASS AND PLANT HEIGHT WITHIN DISPERSAL SYNDROMES

The median value for mean dispersal distance was greatest for species using ingestion for dispersal (245 m) followed by seed-caching (8.0 m), wind (2.1 m), ant (1.1 m), ballistic (1.0 m)



**Fig. 2.** Relationships between (a) mean dispersal distance ( $n = 302$ ) and (b) maximum dispersal distance ( $n = 317$ ) and dispersal syndromes: unassisted, wind, ballistic, ingestion, attachment, seed-caching and ant dispersal. Whiskers represent 10th and 90th percentiles, while the grey box represents the 25th, 50th (median) and 75th percentiles. Water (mean and maximum) and attachment (mean) were excluded because of small sample size.

and lowest for unassisted species (0.5 m) (Fig. 2a; Appendix S3). Results for maximum dispersal distance were qualitatively similar (Fig. 2b). The mean dispersal distance of species using biotic vectors (ant, seed-caching, ingestion and attachment;  $203 \pm 26$  m SE;  $n = 190$  species) was significantly greater than the mean dispersal distance of abiotically dispersed species (wind, ballistic, unassisted, water;  $44 \pm 34$  m SE;  $n = 115$  species;  $t = 12.38$ ; d.f. = 270;  $P < 0.001$ ).

Unassisted and wind-dispersed species had significant positive relationships between seed mass and mean dispersal distance ( $R^2 = 0.37$ ;  $P = 0.002$  and  $R^2 = 0.19$ ;  $P = 0.003$ , respectively; Fig. 3a,b), and ballistic species also showed a positive trend ( $R^2 = 0.07$ ;  $P = 0.07$ ; Fig. 3c). None of the remaining relationships between seed mass and mean dispersal distance were statistically significant (Fig. 3d–f; Appendix S4). There were also significant positive relationships between maximum dispersal distance and seed mass for species with unassisted ( $R^2 = 0.35$ ;  $P < 0.003$ ) and ballistic dispersal ( $R^2 = 0.51$ ;  $P < 0.001$ ; Appendix S4). All other dispersal syndromes had nonsignificant relationships between maximum dispersal distance and seed mass (Appendix S4).

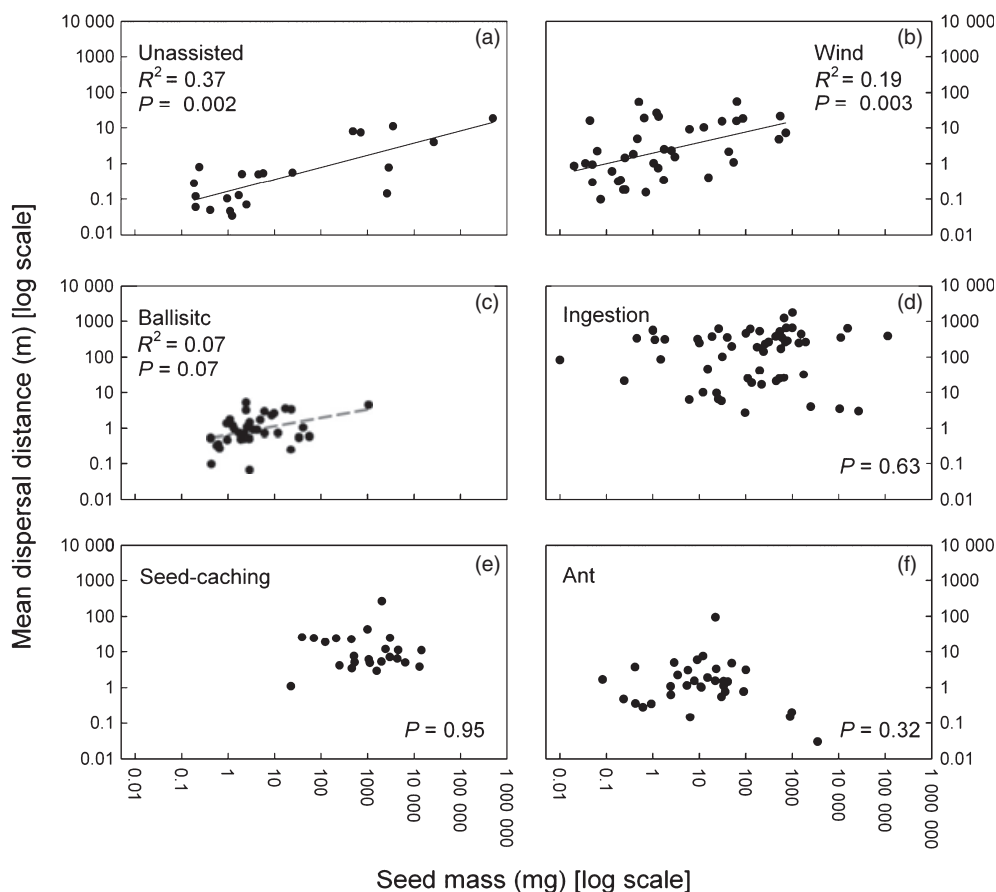
We found positive relationships between plant height and mean dispersal distance within all dispersal syndromes (Fig. 4; Appendix S4). Positive relationships were found between maximum dispersal distance and plant height for wind, ballistic and unassisted dispersal (Appendix S4). Once we accounted for the variation owing to plant height, seed mass was not significantly related to mean dispersal distance within any dispersal syndrome (see Appendix S5 for overall models). Only ballistic (positive;  $P < 0.001$ ) and wind-dispersed (negative;  $P < 0.01$ ) species showed significant relationships between seed mass and maximum dispersal distance once we controlled for plant height (Appendix S5).

## Discussion

#### CROSS-SPECIES RELATIONSHIPS BETWEEN SEED MASS, PLANT HEIGHT AND DISPERSAL DISTANCE

Our most important finding is that plant height is a much stronger predictor of seed dispersal distance than is seed mass. This was surprising, because seed mass, not plant height, has traditionally been considered as the major trait relating to seed dispersal distance (Howe & Smallwood 1982; Venable & Brown 1988), except in wind-dispersed species (Tackenberg, Poschlod & Bonn 2003; Soons *et al.* 2004; Travis, Smith & Ranwala 2010). This result indicates that plant height would be better than seed mass for predicting species dispersal distances and which species would be better at colonizing new environments.

Our findings suggest that the positive relationship between maximum tree height and mean dispersal distance found by Muller-Landau *et al.* (2008) across 41 tropical tree species might be a general phenomenon. This positive relationship might reflect the selective pressure on tall species with broad canopies, requiring increased dispersal distances to escape the reduced survival associated with parental proximity (Janzen



**Fig. 3.** The relationships between seed mass and mean dispersal distance within dispersal syndromes: (a) unassisted, (b) wind, (c) ballistic, (d) ingestion, (e) seed-caching and (f) ant dispersal. Solid regression lines represent significant linear relationships, and dashed grey lines represent strong trends. Water and attachment were excluded because of small sample sizes. Each data point represents one species.

1970; Hyatt *et al.* 2003). The long fall distance for abiotically dispersed seeds on tall species would also contribute to long dispersal distance. For biotic dispersal, tall species with large fruits may attract highly mobile dispersers such as birds and bats, which can take seeds long distances.

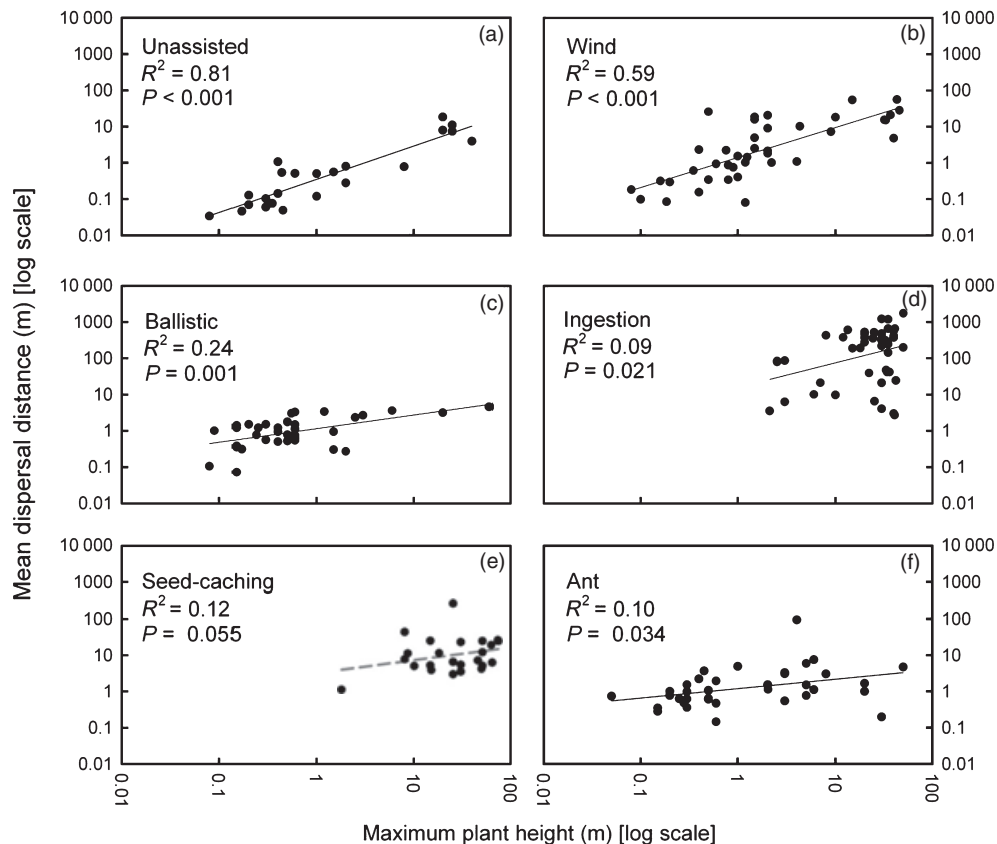
Contrary to our expectations, we initially found a positive relationship between seed mass and seed dispersal distance. However, this might be a secondary correlation, driven by a positive relationship between seed mass and plant height (Thompson & Rabinowitz 1989; Moles *et al.* 2004), combined with the positive relationship between plant height and dispersal distance. The negative relationship we found once we controlled for plant height was also found between seed mass and mean dispersal distance by Muller-Landau *et al.* (2008) with tree species whose maximum heights varied less than threefold. These findings help support the general perception that small-seeded species are better dispersers than large-seeded species, and they are indicative of a trade-off between maternal provisioning and dispersal capacity.

Our findings on species' dispersal distances can be put into the context of plant life-history strategy. Tall species tend to have longer lifespans than short species (Moles & Leishman 2008). Small, short-lived species with persistent seed banks are thought to disperse through time rather than space (Venable

*et al.* 2008). We found that small species had low mean dispersal distances, which may reflect a strategy for temporal rather than spatial dispersal. Our finding of tall (long-lived) species dispersing further than short species contradicts Bossuyt & Honnay's (2006) suggestion that long-lived species require less investment in dispersal capacity than short-lived species to avoid extinction. Our findings suggest that there will be correlations between species longevity and dispersal distance, but further work is needed to quantify this relationship. This would add to our understanding of species' life-history strategies.

#### RELATIONSHIPS BETWEEN SEED MASS, PLANT HEIGHT AND DISPERSAL DISTANCE WITHIN DISPERSAL SYNDROMES

Surprisingly, seed mass had little influence on mean and maximum dispersal distances within dispersal syndromes, especially after accounting for plant height. This lack of relationships could be because species adjust their investment in energetic rewards for dispersers or dispersal structures (primary or secondary) to increase dispersal distances (Appendix S1). We examine relationships between seed mass and dispersal distances within each dispersal syndrome in Appendix S1.



**Fig. 4.** The relationships between maximum plant height and mean dispersal distance within dispersal syndromes: (a) unassisted, (b) wind, (c) ballistic, (d) ingestion, (e) seed-caching and (f) ant. Solid regression lines represent significant linear relationships, and dashed grey lines represent strong trends. Water and attachment were excluded because of small sample size. Each data point represents one species.

There was a positive relationship between mean dispersal distance and plant height within all dispersal syndromes, even for ant-dispersed and seed-caching species where experimental depots are commonly used (Fig. 4). Seeds dispersed from experimental depots negate the influence of canopy width, because dispersal distance is measured from a depot and not the plant base. This suggests that the positive relationship for tall species is not dependent on the drop distance from the canopy edge, but in fact tall species have adapted to disperse long distances, possibly to escape the reduced survival associated with parental proximity (Janzen 1970; Howe & Smallwood 1982; Hyatt *et al.* 2003).

Wind is often considered a long-distance dispersal syndrome, but we found that species dispersed by animals through ingestion, attachment or seed-caching actually disperse much further than do species with wind-dispersed seeds (Fig. 2). Our findings could be attributed to certain dispersal syndromes being easier to track for long distances (ant or seed-caching) compared with other types of syndromes (wind and water). However, overall, species that disperse seeds using biotic vectors appear to be better dispersers, gaining long dispersal distances, than species using abiotic dispersal vectors.

We found few studies that gave the total dispersal distance of combined dispersal syndromes for species that use multiple dispersal syndromes (e.g. Beaumont, Mackay & Whalen 2009). Most studies only examined dispersal distances of par-

ticular dispersal syndromes within species or conversely used seed traps without defining all the vectors. Therefore, our data were typically species' dispersal distance for one syndrome and did not represent entire dispersal kernels of individual species. Broadening research from singular syndromes to more complete dispersal kernels for species is an important future research direction (Vander Wall & Longland 2004).

There are multiple definitions for dispersal capacity, which can include or exclude survival to reproductive maturity (Howe & Smallwood 1982; Levin *et al.* 2003). Our study used two measures of dispersal capacity that excluded recruitment: mean and maximum seed dispersal distance. However, some species use directed dispersal, where seeds are dispersed to local sites with relatively higher probabilities of survival over sites that are further away from the parent plant (Howe & Smallwood 1982). Species using directed dispersal may have higher seedling and juvenile survival rates over passively dispersed seeds, making them more efficient dispersers with greater dispersal capacities (Wenny 2001). Our use of simple dispersal distance meant we excluded other sources of variation, such as seed predation and germination rates, but we could not account for directed dispersal. Despite this and differences between methodologies, our results indicated underlying trends between dispersal capacity and plant traits. Future work using measures of dispersal that include recruitment would complement our findings.

Mean and maximum dispersal distance produced distinctive results. Plant height and seed mass were more strongly correlated with mean dispersal distance than with maximum dispersal distance. This is probably because maximum distances are outliers which are notoriously difficult to measure (Nathan 2006). The accuracy of all dispersal distance data depends on sample size and the inclusion of methods to detect rare long-distance dispersal events. It is important to remember that our data are maximum observed dispersal distances, rather than species' true maxima. Nonetheless, data for maximum distance were included because they are an important part of the dispersal process, as long-distance dispersal can be critical for plant migration and colonization rates (Cain, Damman & Muir 1998; Levin *et al.* 2003). Furthermore, seed dispersal distance varies so much among species (maximum dispersal distance in our study ranged from just 15 cm to 400 km) that even if researchers' best efforts in the field do yield imperfect measures, the bigger picture from a compilation like this is still expected to be informative. The only potential bias would be if long-distance dispersal events were harder to track for small-seeded than large-seeded species. However, as researchers tend to use methods appropriate to the size of the seeds that they are tracking (e.g. threads on large seeds and seed traps for small seeds), we do not expect this to be a serious problem for our analysis.

Our compilation of mean and maximum dispersal distances for over 200 species from 148 studies around the world has given novel information about the relative effectiveness of different dispersal syndromes and provided surprising insights into correlations between seed dispersal distance and two crucial plant traits, seed mass and plant height. Our most important finding is that seed dispersal distance is more closely correlated with plant height than with seed mass. Our data also show that plant height should be considered when examining the dispersal ability of species within all types of dispersal syndromes, not just for wind-dispersed species. Plant traits play a key role in our understanding of ecological systems. We hope that future work will expand our findings to explore the possible trade-offs between dispersal capacities and other important life-history traits of species, such as longevity and reproductive output.

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## Supporting Information

Additional supporting information may be found in the online version of this article:

**Appendix S1.** Predicted and actual relationships between seed mass and dispersal distance within dispersal syndromes with explanations.

**Appendix S2.** Relationship between mean and maximum dispersal distance.

**Appendix S3.** Dispersal distance data within dispersal syndromes.

**Appendix S4.** Ordinary least square regressions results for individual dispersal syndromes.

**Appendix S5.** Multiple regression results for individual dispersal syndromes.

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