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RESEARCH ARTICLE

The multiple dimensions of intraspecific variation in seed dispersal

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Abstract

1. Seed dispersal plays a central role in plant ecology and evolution, and understanding its variation is key to predicting species demography and range dynamics. However, dispersal is difficult to measure, and most modelling and field studies assume uniform dispersal within species, ignoring individual variation. Yet dispersal potential can differ strongly among individuals within species. More empirical data at the individual level are therefore needed to quantify the magnitude of intraspecific variation and its ecological underpinnings.
2. We developed a wind dispersal trial to capture full individual seed dispersal distributions for 107 *Arabidopsis thaliana* genotypes originating across the species' European range. We used these data to (1) assess variation in seed dispersal patterns via dispersal kernel, (2) estimate dispersal kernel heritability, (3) identify how strong and widespread are the major phenotypic drivers of intraspecific variation in dispersal kernel, including (4) the relative contribution of intra-individual versus inter-individual phenotypic variation and (5) test whether spatial, demographic or environmental factors structure dispersal traits.
3. Dispersal kernel properties, mean distance, skewness, kurtosis and standard deviation, varied significantly across genotypes and showed considerable heritability. These components were not uniformly controlled by the same set of traits. Mean distance, skewness and kurtosis that reflect aspects of average and longer distance dispersal were primarily driven by a few tightly linked traits, especially plant height and fecundity. In contrast, standard deviation (SD), which captures the variability in dispersal distance, was influenced by a broader and more complex set of predictors, including within-individual variation in seed roundness and seed size.
4. We found no clear geographic or demographic structure of dispersal kernel properties. However, SD, which is related to post-dispersal sibling distance, was significantly associated with environmental unpredictability, suggesting it may represent an environmentally responsive and potentially adaptive strategy.
5. Our findings reveal that, even within a single species and dispersal mode, dispersal varies substantially and is shaped by distinct trait dimensions. We highlight the

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need to account for intraspecific variation in seed dispersal potential and suggest that incorporating variation in kernel properties or the underlying trait complexity could improve predictions of species spread, persistence and adaptive capacity in changing environments.

KEYWORDS

Arabidopsis thaliana, dispersal kernel, dispersal-related traits, intraspecific variation, seed dispersal, wind dispersal

1 | INTRODUCTION

Dispersal is a fundamental ecological and evolutionary process that shapes species' distributions, population dynamics, community structure and adaptation (Clobert et al., 2012; Ronce, 2007). In flowering plants, which comprise the majority of terrestrial plant diversity, population demography and the colonization of new habitats occur primarily through reproductive propagules, most commonly seeds, although vegetative propagules can play a substantial role. Because dispersal is tightly coupled to reproduction, opportunities for expansion and colonization are limited to the periods when these propagules are produced and released. Although individual plants may produce many seeds, the temporal window during which dispersal occurs remains restricted relative to the organism's lifetime. As a result, the conditions under which seeds are released, and the traits of both the parent plant and the propagules, play a disproportionate role in shaping dispersal outcomes. Understanding how dispersal varies within species is therefore essential for predicting how plant populations persist, adapt and respond to environmental change.

Seed dispersal is often modelled using a single mean value per species or assuming all individuals disperse similarly (e.g. Miller & McGill, 2018), despite considerable variation within species. This simplification overlooks the variability driven by spatial, temporal and genetic factors, with implications for phenotypic selection and rates of spread. A growing body of work highlights that intraspecific variation in dispersal is not merely noise and can have major ecological and evolutionary consequences (Snell et al., 2019). Studies that ignore such variation may obscure differences in seed dispersal effectiveness or underestimate actual dispersal distances (Jordano, 2017; Schupp et al., 2019). While recent advances emphasize the importance of explicitly considering individual-level variation in dispersal potential, this remains underexplored in empirical plant studies.

Dispersal can be described using the probability distributions (kernels) representing the spatial deposition pattern of dispersal units from a common source (Nathan et al., 2008). These kernels are commonly parameterized using statistical moments (e.g. mean, variance, skewness and kurtosis), which capture different aspects of dispersal potential (Clark et al., 1999; Kot et al., 1996). For example, the mean and variance describe the average dispersal distance and

spread, while tail behaviour, reflected in kurtosis, indicates the frequency of long-distance dispersal (LDD) events. The use of dispersal kernels has since expanded considerably, especially used to differentiate between short- and long-distance dispersal strategies (e.g. Klein et al., 2006; Liu, 2021; Marco et al., 2011). Fitting kernels to empirical data enables a detailed quantification of dispersal distance distributions, potentially reflecting underlying variation in dispersal strategies. While dispersal kernels are commonly used in ecological and evolutionary studies across diverse taxa (Bullock et al., 2017; Nathan et al., 2012), natural variation within species, and whether it reflects distinct, evolvable differences, remains poorly understood.

Measuring direct dispersal distance is difficult, especially in natural settings. Many studies thus rely on associations between dispersal and suites of phenotypic traits (dispersal syndromes) that reflect consistent trait covariation underlying different dispersal strategies, particularly among species (Cote et al., 2022; Schupp et al., 2010). Across species, body size is often a key predictor of dispersal syndromes, with larger or taller individuals generally exhibiting greater seed dispersal potential (Augspurger et al., 2017; Thomson et al., 2011, 2018). For wind-dispersed species in particular, greater release height leads to longer dispersal distances (Thomson et al., 2011). Fecundity has also been proposed as a primary driver for seed dispersal and its variation among populations (Clark et al., 1999; Kaproth et al., 2023; Norgauer et al., 2011), while other work shows that dispersal syndromes can be structured by seed morphology, for instance, with more consistent associations with seed size across species (Leslie et al., 2017). However, the identity and relative importance of the traits most strongly shaping dispersal remain debated.

Many traits influencing seed dispersal, such as seed and fruit size, vary not only among individuals but also within individuals. Despite growing interest in the ecological consequences of individual dispersal variation, we still know little about how within- versus among-individual variation in dispersal-related traits contributes to overall seed dispersal patterns (Schupp et al., 2019). Moreover, dispersal outcomes, including dispersal distance and the spatial distribution of seeds, emerge from the combined and often interacting effects of multiple plant and seed traits. When dispersal is quantified using dispersal kernels, there is therefore an increasing need to identify which specific traits shape different components of the kernel (Ronce, 2007). Such an approach

is essential, particularly given that dispersal syndromes are not always reliable predictors of realized dispersal outcomes (Green et al., 2022).

Dispersal-related traits are often geographically structured along environmental or latitudinal gradients, consistent with local adaptation, as geographic variation in climate, life-history strategies and demographic history may impose different selective pressures on dispersal traits (Sobral et al., 2013; Darling et al., 2008; Bastias et al., 2024). At the individual level, intra-individual trait variation has been proposed as one form of diversifying bet-hedging, where a single individual produces a range of propagule phenotypes potentially suited to different environmental conditions (Simons, 2011; Starrfelt & Kokko, 2010). By increasing phenotypic diversity among seeds, such as variability in seed size, individuals may buffer reproductive success across unpredictable environments (Pélabon et al., 2021). While bet-hedging is most strongly supported in seed dormancy studies, its role in shaping dispersal variation remains largely unexplored. Dispersal is known to respond to environmental factors; for instance, dispersal kernels vary with abiotic and biotic drivers like temperature (Drees & Shea, 2024) and competition (McHugh et al., 2024). Additionally, a recent study found that species with fast life histories tend to disperse seeds farther than slow-living species, suggesting that longer dispersal distances may serve as a bet-hedging strategy to exploit habitats that vary unpredictably in space and time (Beckman et al., 2018). However, the extent to which variation in dispersal kernels reflects adaptive strategies like bet-hedging remains an open question. A first step towards understanding how dispersal might respond to future environmental change is to examine how dispersal varies across a species' geographic range.

In *Arabidopsis thaliana*, a model annual plant, trait differences have been linked to historical population structure. Genomic studies have revealed that a few *A. thaliana* genotypes from Iberic peninsula and North Africa belong to ancient, genetically distinct lineages known as relicts. In contrast, most genotypes across central and northern Europe (and globally) descend from a more recently evolved lineage (non-relict hereafter) that rapidly expanded out of Central Europe (Alonso-Blanco et al., 2016; Durvasula et al., 2017; Hsu et al., 2019; Lee et al., 2017). During this expansion, non-relicts often replaced or admixed with local relict populations. Previous studies have shown that these lineages differ in life-history traits such as flowering time, as well as in dispersal-related traits, including plant height, seed size and seed number (Alonso-Blanco et al., 1999, 2016; Bastias et al., 2024), suggesting that dispersal potential may also have diverged during range expansion. However, whether dispersal kernels also vary across environmental gradients or among geographically structured lineages remains unknown. There is still a paucity of research directly addressing intraspecific variation in seed dispersal, partly due to the complexity of its underlying drivers (Schupp et al., 2019). In this study, we addressed several questions: (1) To what extent do dispersal kernels vary within species? (2) Are they heritable? (3)

Which major phenotypic traits predict variation in dispersal kernels, and how strong and widespread are their effects? (4) What is the relative contribution of intra- versus inter-individual trait variation to dispersal outcomes? (5) Finally, do dispersal kernels exhibit spatial, demographic or environmental structure, and could they reflect adaptive strategies?

It is highly challenging to collect seeds and identify their sources in the wild. Moreover, dispersal in natural settings is driven by many unknown environmental factors, which limit our ability to estimate the extent of genetic variation and test associations with the traits of the disperser individual. To overcome these limitations, we conducted a controlled experiment to quantify individual-level seed dispersal. Specifically, we built a wind tunnel equipped with a high-resolution camera to record the complete dispersal pattern of seeds released from single plants under standardized conditions. Using 465 individuals from 107 *A. thaliana* genotypes originating across the species' European range, we quantified individual seed dispersal distances to estimate dispersal kernels. We then assessed correlations between kernel properties, plant and seed traits, heritability and spatial-environmental variables to address our questions. By integrating fine-scale, individual-level dispersal data with detailed phenotypic trait analyses, our study revealed variation in dispersal that was shaped by distinct trait dimensions and their potential adaptive significance. Our study provides novel insights into the ecological and evolutionary importance of intraspecific variation in seed dispersal.

2 | MATERIALS AND METHODS

2.1 | Plant materials and lineage classification

We initially selected 120 natural genotypes of *A. thaliana* sampled across its native range in Europe. All genotypes are part of the initial germplasm from the 1001 Genomes Project (<http://1001genomes.org/>), which provides a comprehensive resource on the genetic diversity and demographic history of the species. This project identified fine-scale population structure and assigned each genotype to specific genetic clusters. Following the classification scheme established by the 1001 Genomes Project, we assigned each genotype in our study to its corresponding genetic cluster. To capture broad geographic and genetic variation in dispersal traits, we sampled genotypes from southern, central and northern regions, each represented by 40 accessions (See Figure S1 in Supporting Information). The southern set included both non-relict genotypes and Iberian relicts. The origin of the seeds used in the experiment was distributed by Nottingham Arabidopsis Stock Center (NASC). To reduce potential maternal effects, these seeds were first grown for one generation under standardized conditions. Seeds from this generation were then used in all subsequent experiments.

We established five replicates per genotype (120 genotypes $\times$ 5 replicates = 600 pots). During the experiment, some individuals died or failed to complete their life cycle (e.g. failure to germinate or to bolt). After excluding these individuals, 465 plants remained suitable for dispersal measurements, resulting in a final dataset comprising 107 genotypes. The list of analysed genotypes, together with those excluded due to mortality or reproductive failure, is provided in [Table S1](#), where excluded genotypes are indicated in red.

2.2 | Greenhouse and wind dispersal experiment

The experiment was conducted in a greenhouse, where plants were sown and grown individually in round pots (5 cm diameter) filled with commercial peat moss (Neuhaus N2). Three seeds were sown per pot, and the largest centrally located germinated seedling was retained and grown under well-watered conditions, maintained by regular irrigation throughout the experiment. Plants were kept under cold conditions ($\sim 10^{\circ}\text{C}$) with continued watering for the first month after sowing (late November to late December 2024) to ensure establishment and vernalization of all genotypes (i.e. release genotypes from flowering suppression due to low temperatures). After this vernalization period, the temperature in the greenhouse was gradually increased to $\sim 20^{\circ}\text{C}$ during the day and $\sim 15^{\circ}\text{C}$ at night. Pots were fully randomized and placed on trays, which were evenly distributed across four Tables (150 pots per table). The tables were rotated among greenhouse compartments and turned twice per week to minimize microclimatic heterogeneity and positional effects. Plants were grown until they reached reproductive maturity, defined as the stage when most fruits (siliques) were dry and ready for the wind dispersal trial. On average, this stage was reached ~ 50 days after the onset of flowering (the emergence of the first white flower buds).

Each plant was individually subjected to a wind dispersal trial. Before exposure, we photographed the plant to document its condition prior to seed release (pre-dispersal). The plant was then placed inside a custom-built wind tunnel ([Figure 1a](#)) and exposed to standardized wind conditions ($\sim 0.8\text{ m s}^{-1}$). This wind speed was previously tested to be sufficient to generate turbulence and trigger seed release. To simulate additional natural mechanical disturbance, purple paper flags were installed between the wind inlet and the plant ([Figure 1b](#)). During the trial, the plant was positioned near the wind source, in a black round pot placed at a fixed location, and seeds were allowed to disperse freely onto a sticky carpet lining the floor of the wind tunnel. After wind exposure, we photographed the entire seed deposition pattern on the carpet using an overhead camera fixed to the wind tunnel roof and then took a photo of the plant to document its condition after dispersal (post-dispersal). Seed deposition images were analysed using ImageJ. For each image, we extracted the coordinates of all dispersed seeds, with the X-axis representing distance along the wind direction and the Y-axis indicating lateral spread ([Figure 1c](#)).

2.3 | Trait measurement

2.3.1 | Dispersal measure

Variation in seed dispersal among individuals was quantified in distance units. First, we measured the maximum dispersal, based on the distance of the furthest seed dispersed in the wind tunnel for each individual. We also calculated the distance between seeds (at the individual level) using the `dist` function in R, based on the x and y coordinates of each seed deposited by one individual in the wind tunnel.

Subsequently, dispersal distances were analysed in the form of dispersal kernels, which describe the probability distribution of seed distances from the source. We estimated individual-level dispersal kernels ([Figure 1d](#), [Figure S2](#)) by fitting parametric models to the Euclidean distance of each seed from its release point (seed deposition). This parametric approach has statistical moments that shape the kernel, which may capture different aspects of dispersal capacity, including: mean (average dispersal distance), standard deviation (dispersal variability), skewness (distribution asymmetry) and kurtosis (tail weight, indicating longer distance dispersal potential).

Previous studies have shown that commonly used models like the Gaussian and exponential distributions often fail to adequately capture real dispersal patterns, particularly their high leptokurtosis and fat tails (Nathan et al., 2012). To address this, we used the R package `dispsfit` (Proença-Ferreira et al., 2023), that was recently developed to fit and compare dispersal kernels from different functions adapted to species dispersal. We fitted eight functions provided in `dispsfit`, which are the functions most used in dispersal studies (Nathan et al., 2012). Among these, the log-normal, generalized normal and gamma distributions most frequently provided the best fits based on Akaike information criterion (AIC) values ([Figure S3](#)). We finally selected the generalized normal distribution for further analysis. This distribution has previously been applied in seed dispersal studies (Schurr et al., 2008), shown to perform well in comparative studies (Bullock et al., 2017), and can model both short- and long-tailed dispersal (Nathan et al., 2012; Proença-Ferreira et al., 2023).

The generalized normal (also known as exponential power) distribution used in `dispsfit` for the dispersal location kernel, $K_L(r)$, is defined as:

$$f(x) = \frac{b}{2a\Gamma(1/b)} \exp\left(-\left|\frac{x}{a}\right|^b\right) \quad (1)$$

where parameter a is the scale parameter, b is the shape parameter that determines the tail behaviour, and Γ is the gamma function. The dispersal distance kernel used by `dispsfit` is measured as $K_D(r) = 2\pi r K_L(r)$. For further details on the kernel functions and the equations of the moments (mean, standard deviation, skewness and kurtosis), we refer readers to the `dispsfit` package documentation and publication (Proença-Ferreira et al., 2023).

Pearson's pairwise correlation tests showed that the parameters a and b were highly correlated with each other ($r = 0.97$, $p < 0.001$;

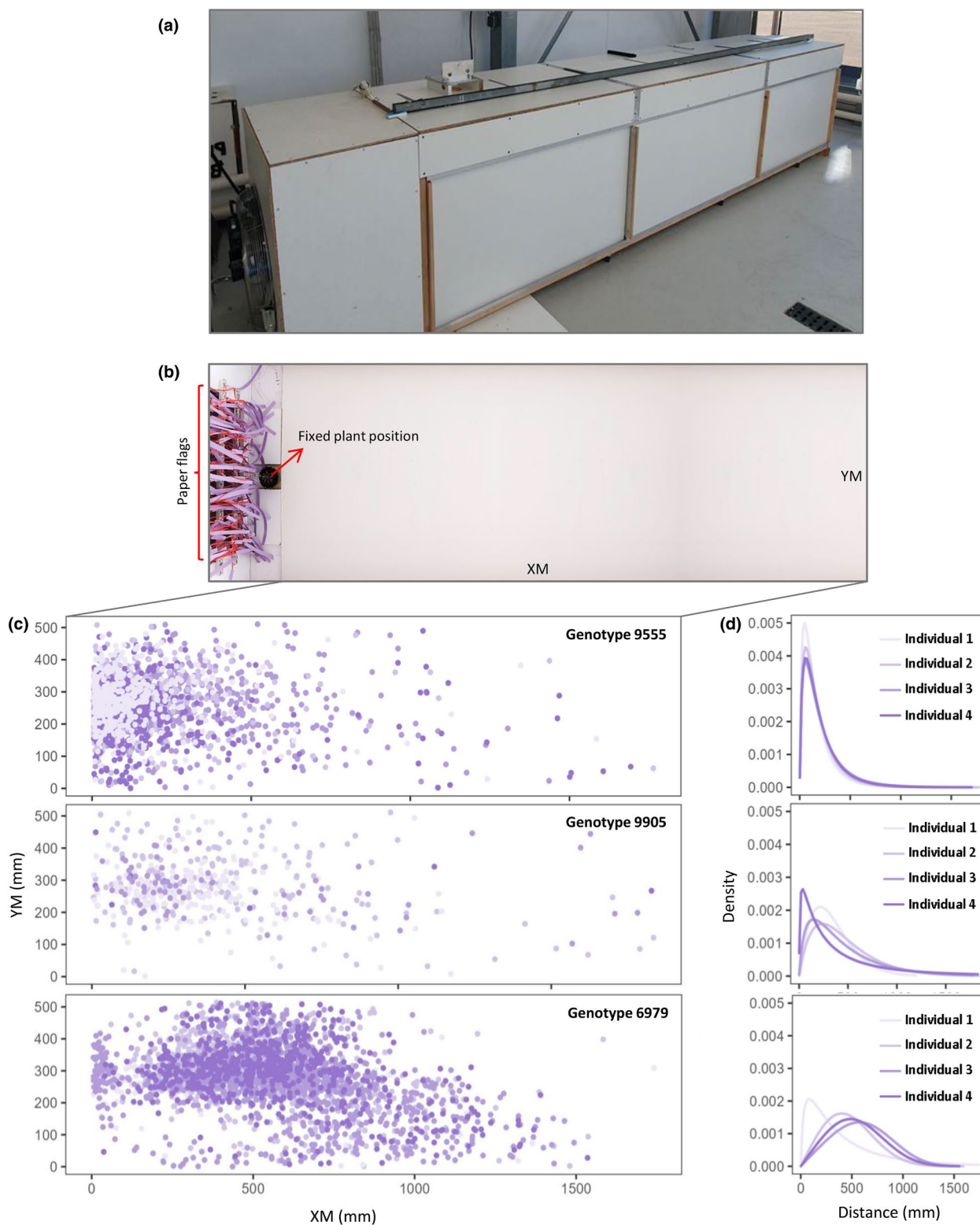


FIGURE 1 Experimental setup for measuring individual-level dispersal kernel. (a) External view of the wind tunnel used for the dispersal experiment. The roof includes fixed camera mounts to capture images of seed dispersal. (b) Top-down camera view of the inside of the wind tunnel. Seeds are dispersed from a plant positioned near the wind source (black round pot, fixed in place) and are trapped on a sticky carpet lining the tunnel floor. Purple paper flags, placed between the wind entrance and the plant, simulate mechanical disturbance. (c) Projection example of all dispersed seeds from individual plants. Each panel represents four individuals from a genotype, with each colour corresponding to a different individual. Seed coordinates were obtained from image analysis (ImageJ), with XM showing distance along the wind axis and YM the lateral spread. (d) Corresponding fitted dispersal distributions (kernels) for the genotypes and individuals shown in C. Distributions were inferred from the Euclidean distance of each seed from the release point and fitted using an exponential power distribution model to extract individual-specific dispersal properties.

Figure S4), and both were also strongly correlated with several moments, specifically, the mean, skewness and kurtosis ($r \geq 0.75$, $p < 0.001$; Figure S4). Therefore, we focused our analysis on the four statistical moments (kernel properties).

2.3.2 | Plant traits

We quantified plant traits using standardized digital images collected at specific stages of the experiment and processed later using image analysis. Photographs of each plant were taken immediately before the wind dispersal trial, and these images were used to measure plant height, the number of secondary branches, total number of siliques and average silique size, with a scale reference included for calibration. A second photograph of the plant was taken immediately after the wind trial, to measure silique resistance as the proportion of siliques that dehisced during the wind dispersal trial relative to the total number of siliques. Seed deposition on the sticky carpet was photographed to quantify the number of seeds dispersed, their distance to the mother plant, as well as to measure seed traits (seed area and roundness) using the Analyse Particles tool in ImageJ (<https://imagej.net/software/imagej/>). All images were processed using standardized thresholding parameters, and background noise was minimized by retaining only particles within a seed size range of 0.10–0.60 mm² and roundness greater than 0.4. Seed production per individual was estimated by dividing the number of dispersed seeds by the number of siliques that dehisced and multiplying by the total number of siliques. Within-individual variation in seed size and shape was quantified as the variance in seed area and roundness, across all seeds measured from a given plant.

2.4 | Environmental data

Temperature is widely used in studies of environmental variability and climate-related ecological responses, and temperature has documented effects on plant dispersal processes (e.g. Drees & Shea, 2024). We extracted from WorldClim version 2.1 at a spatial resolution of 2.5 arc-minutes (approximately 21 km² at the equator) the mean annual temperature (MAT, °C) at each genotype's location, as well as historical monthly temperature data (1970–2000) to quantify temperature unpredictability. Following Pélabon et al. (2021), monthly temperature time series were decomposed into seasonal, trend and random components using the decompose function in R, which applies a moving-average seasonal decomposition. The random (residual) component was then mean-scaled by the square of the average monthly temperature over the entire time series. The variance of this mean-scaled residual component was used as an index of short-term environmental unpredictability, with higher values indicating greater unpredictability. This index captures interannual variability in monthly temperature

after removal of the seasonal signal, reflecting non-seasonal, year-to-year fluctuations.

2.5 | Statistical methods

2.5.1 | Trait variation among genotypes and lineages

To assess variation in dispersal ability among *A. thaliana* genotypes, we first examined the range (maximum–minimum) of maximum seed dispersal distance as well as the four kernel properties, the mean, standard deviation, skewness and kurtosis. For each trait, we also calculated the overall mean and 95% confidence intervals. To test for significant differences among genotypes, we fitted a linear model with genotype identity as a fixed effect. Standard deviation, skewness and kurtosis were log-transformed prior to analysis to meet normality assumptions. In addition, we tested a linear mixed-effects model that included block as a random effect (nested within experimental table). However, a likelihood ratio test (LRT) comparing the mixed model to the simpler model revealed no significant improvement in model fit. Therefore, we retained the simpler linear model for subsequent analyses.

2.5.2 | Heritability

We calculated broad-sense heritability (H^2) for each dispersal trait to estimate the proportion of phenotypic variation attributable to genetic differences among genotypes. Broad-sense heritability is defined as:

$$H^2 = V_G / V_P \quad (2)$$

where V_G is the genetic variance, and V_P is the total phenotypic variance. This measure captures the contribution of all genetic effects, including additive, dominance and epistatic interactions. We fitted linear mixed-effects models with genotype identity as a random effect to partition the observed variance into genetic and residual components. Heritability estimates were then derived as the ratio of genotypic variance to total variance.

2.5.3 | Relationships between dispersal kernel and plant traits

We first ran genotypic mean correlations among measured phenotypic traits, without assuming causal relationships. Before calculating correlations and fitting models, we log-transformed the total number of siliques, number of secondary branches, seed production, seed size variance and seed roundness variance to better approximate normality. Since the total number of siliques and seed production were highly correlated ($r^2 > 0.8$; $p < 0.001$) and both represent plant fecundity, we retained only seed production for further analyses. To test how plant phenotypic traits predict variation in dispersal, we fitted linear models between each dispersal

kernel property (mean, standard deviation, skewness and kurtosis) and each plant trait using genotypic means. For each model, we extracted the coefficient of determination (r^2) and p -value, and we assessed the normality of residuals using the Shapiro–Wilk test.

To complement the univariate analyses, we performed multivariate analysis using Random Forest (RF) models to identify the relative importance of plant phenotypic traits in predicting each of the four kernel properties. For each property, we constructed a separate RF model using a specific subset of phenotypic predictors that had shown significant associations in prior univariate analyses. Models were trained on 80% of the dataset (with stratified sampling) using 2000 trees and default parameters. We extracted the percentage increase in mean squared error (%IncMSE) as a measure of variable importance and normalized these values to obtain relative importance scores for comparison across traits and models.

2.5.4 | Relationship between dispersal kernel and geographical-environmental characteristics

To examine how dispersal metrics (kernel properties and inter-seed distance) relate to geography, MAT and temperature unpredictability, we ran linear models using genotypic means of kernel properties as response variables and latitude, longitude and the temperature unpredictability described in section 2.4 as predictors. For each trait–predictor pair, we fitted both linear and quadratic models and extracted r^2 , AIC and p -values. The same model structure was used to test relationships between inter-seed distance with SD and temperature unpredictability. All analyses were performed in R v. 4.4.2.

3 | RESULTS

3.1 | Intraspecific variation of dispersal in *a. thaliana*

We quantified individual-level dispersal kernel properties by fitting a generalized normal (exponential power) distribution model. The resulting kernels revealed substantial variation in shape among individuals and genotypes. Kernel properties varied widely among

individuals (mean: 221.5–815.8 mm; SD: 164.3–748.5 mm; skewness: 6.5–21.0; kurtosis: 28.9–75.1), whereas maximum dispersal distance showed large individual-level variation (648.99–2742.18 mm) but did not differ significantly among genotypes (ANOVA, $p > 0.1$) and exhibited low heritability ($H^2 = 0.08$). By contrast, kernel properties displayed higher variance between genotypes than within genotypes (ANOVA, $p < 0.001$; Table 1), consistent with broad-sense heritability estimates ranging from 0.16 to 0.51.

Some genotypes exhibited limited dispersal distances, with consistently low mean and standard deviation values (e.g. Figure 1d, top panel). In contrast, certain genotypes tended to disperse seeds over longer distances, as reflected by higher mean, skewness and kurtosis values (Figure 1d, bottom panel). Others displayed greater variability in dispersal distance, characterized by higher standard deviation values (Figure 1d, middle panel).

3.2 | Relationships between dispersal kernels and plant traits

Significant linear and log-linear relationships were observed between dispersal kernel properties and multiple plant reproductive traits, although the strength and direction of these associations varied depending on both the kernel property and the trait considered (Figure 2a,b).

Overall, plant architectural traits explained more variation in dispersal kernel properties than seed-level traits. Reproductive height emerged as the strongest explanatory variable for skewness, kurtosis and mean distance ($r^2 = 0.60, 0.46, 0.41$; all $p < 0.001$), although it showed, in contrast, a weaker negative relationship with SD ($r^2 = 0.06$; $p < 0.01$). The number of secondary branches followed a similar pattern, showing stronger relationships with skewness ($r^2 = 0.18$, $p < 0.01$) and kurtosis ($r^2 = 0.18$, $p < 0.01$) than with mean distance ($r^2 = 0.09$, $p < 0.01$) or SD ($r^2 = 0.04$, $p < 0.05$). Silique resistance was negatively related to skewness ($r^2 = 0.10$, $p < 0.001$) and kurtosis ($r^2 = 0.14$, $p < 0.001$), but positively related to SD ($r^2 = 0.12$, $p < 0.001$), and was unrelated to mean distance ($p > 0.5$). Total seed production showed strong positive relationships with skewness and kurtosis ($r^2 = 0.49$ and 0.42 ; $p < 0.001$), and a weaker positive relationship with mean

TABLE 1 Intraspecific variation in seed dispersal kernel properties and their heritability.

Variation between dispersal parameters	Accessions p -value	Range value	Mean [95% CI]	Heritability	Relict vs. non-relict p -value
Maximum distance (mm)	0.11	648.99–2742.18	1590.4 [1565.9–1614.97]	0.08	0.19
Mean distance (mm)	<0.001	221.51–815.77	434.19 [424.76–443.63]	0.47	0.07
Standard deviation	<0.001	164.25–748.47	286.09 [278.93–293.25]	0.16	0.08
Skewness	<0.001	6.54–21.02	10.52 [10.22–10.83]	0.51	0.13
Kurtosis	<0.001	28.85–75.14	37.56 [36.74–38.38]	0.42	0.05

Note: The range column shows the minimum and maximum values observed among individuals, and mean indicates the overall average across individuals. The Heritability column reports broad-sense heritability (H^2). The last two columns present p -values from ANOVA and/or Kruskal–Wallis tests assessing the significance of variation among accessions and lineages, respectively.

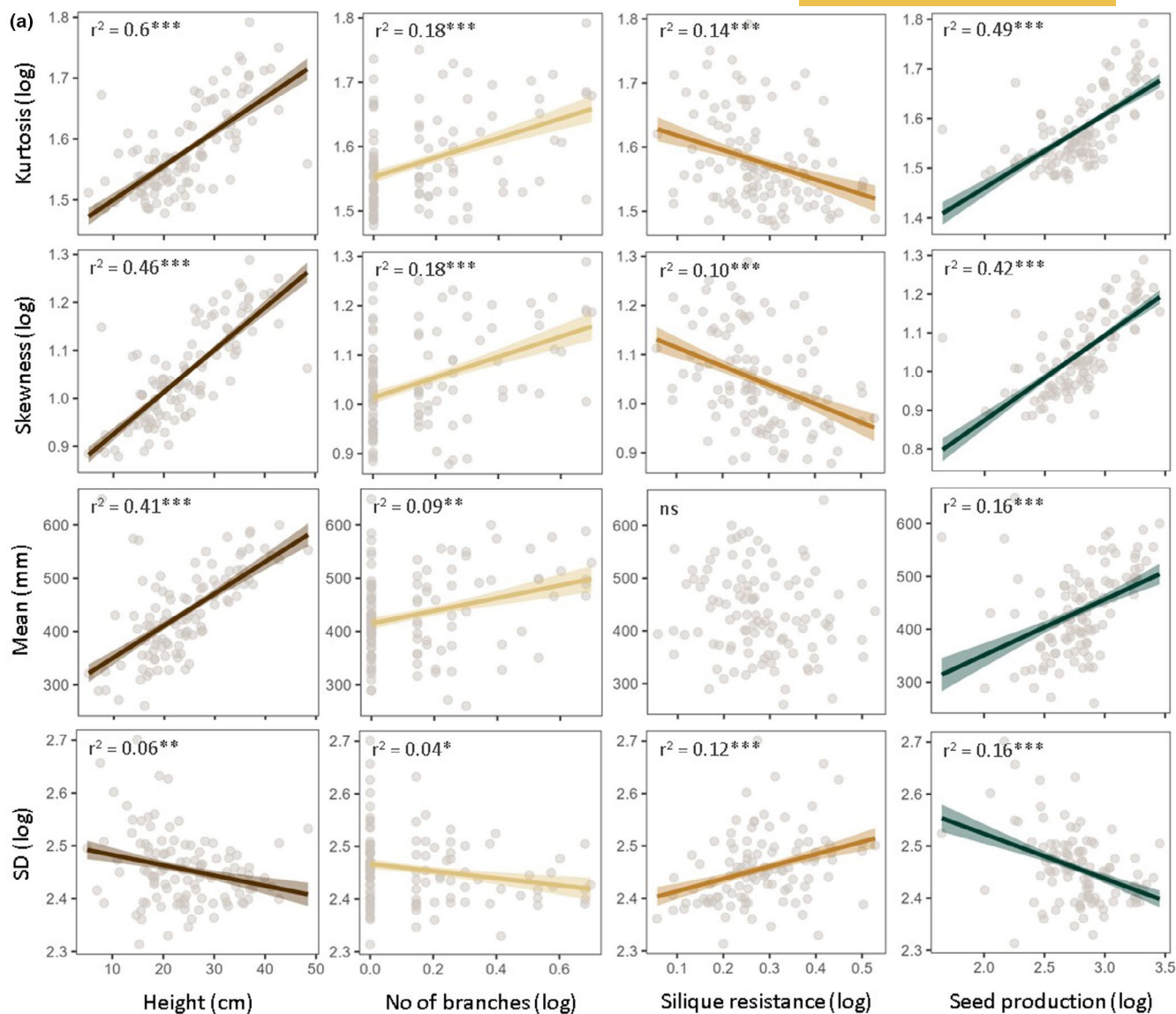


FIGURE 2 (a) Relationships between plant-level traits and dispersal kernel. Each panel shows a linear regression between a plant trait (columns: Plant height, number of secondary branches, silique resistance and seed production) and dispersal kernel properties (rows: Kurtosis, skewness, mean distance and standard deviation of seed dispersal). Each point represents a genotype. Shaded bands show 75% confidence intervals around the regression lines. R^2 values indicate the proportion of variance in the dispersal properties explained by each trait (** $p < 0.01$, *** $p < 0.001$, ns = non-significant). (b) Relationships between seed-level traits and dispersal kernel properties. Each panel shows a linear regression between a seed trait (columns: Seed size, within-plant seed size variance, seed roundness and within-plant seed roundness variance) and a dispersal kernel properties (rows: Kurtosis, skewness, mean distance and standard deviation of seed dispersal). Each point represents a genotype. Shaded bands show 75% confidence intervals around the regression lines. R^2 values indicate the proportion of variance in the dispersal properties explained by each trait (** $p < 0.01$, *** $p < 0.001$, * $p < 0.05$, ns = non-significant).

distance ($r^2 = 0.16$; $p < 0.001$), but a negative relationship with SD ($r^2 = 0.16$; $p < 0.001$).

Seed-level traits showed generally weaker and more trait-specific associations with dispersal kernel properties. Seed roundness was negatively related to both standard deviation (SD; $r^2 = 0.10$, $p < 0.001$) and mean distance ($r^2 = 0.09$, $p < 0.01$). Seed size was positively associated with SD ($r^2 = 0.09$, $p < 0.1$) but negatively with skewness ($r^2 = 0.04$, $p < 0.05$). Seed size variance within individual emerged as the strongest predictor of SD ($r^2 = 0.23$, $p < 0.001$), while its relationships with other kernel properties were weak

or non-significant. In contrast, seed roundness variance showed broader associations, such as a positive relationship to mean distance ($r^2 = 0.24$, $p < 0.001$) and, to a lesser extent, to SD, kurtosis and skewness ($r^2 = 0.09$, 0.06 , 0.05 ; all $p < 0.05$).

Random Forest analysis highlighted plant height and seed production as key drivers of mean distance, skewness and kurtosis (Figure 3). For skewness and kurtosis, key contributors included plant height, seed production, silique resistance and branching. For mean distance, a similar set of traits was important, except that seed roundness emerged as a predictor instead of silique resistance. In

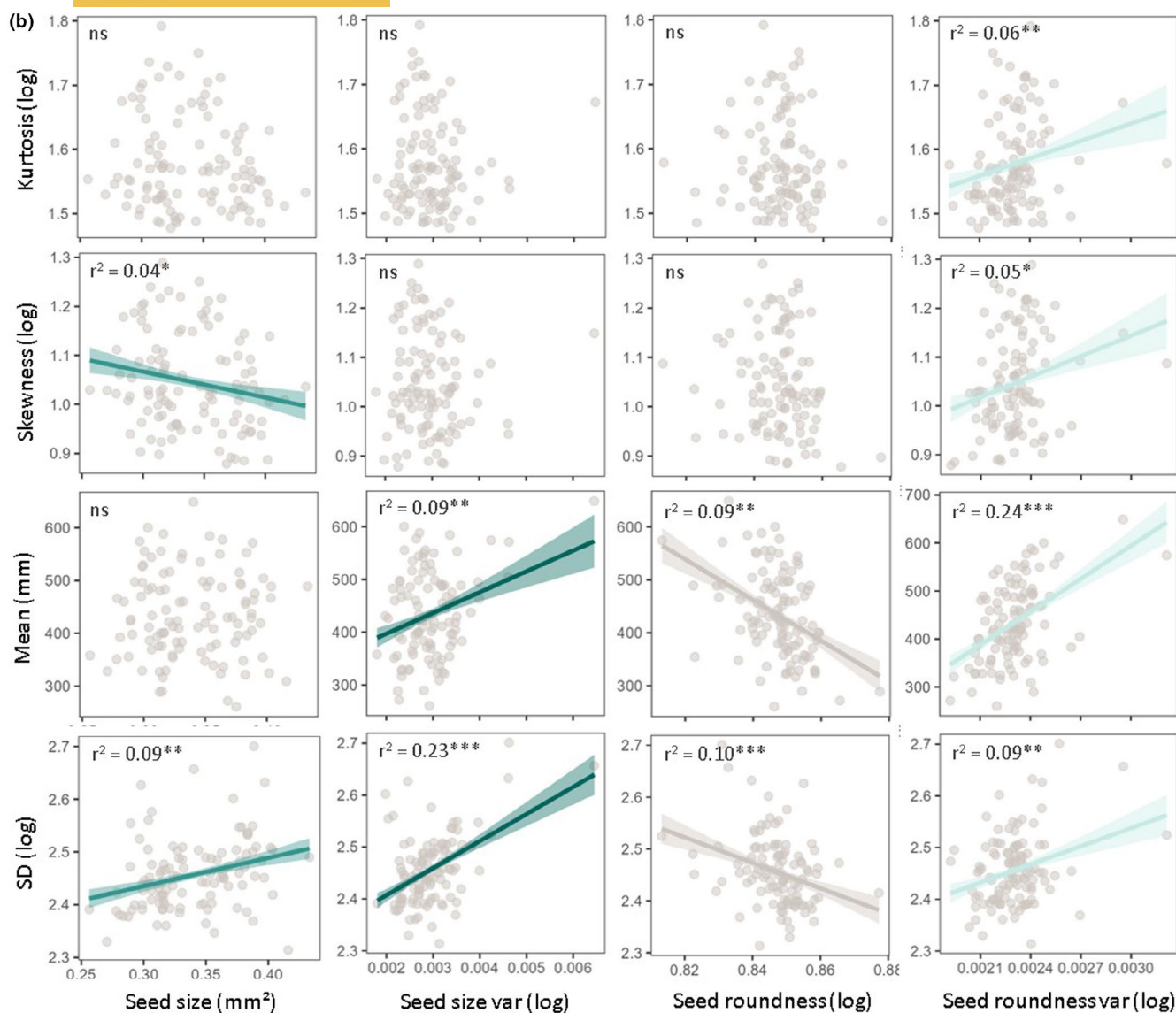


FIGURE 2 (Continued)

contrast, SD had a distinct and more complex predictor profile, with a greater emphasis on seed-related traits. Seed roundness was the strongest contributor to SD, followed by seed production, roundness variance, silique resistance, seed size, plant height, seed size variance and branching. Seed size, in particular, was only a relatively minor contributor to mean distance, skewness and kurtosis but had slightly greater importance for SD.

3.3 | Effects of demographic history, geography and climate on dispersal kernel variation

Despite genetic differences among *A. thaliana* genotypes, we detected no significant differences in any dispersal kernel property between relict and non-relict lineages (all $p > 0.1$; Table 1). Similarly, dispersal traits showed no clear geographic structuring, with no significant associations with latitude or longitude (all $p > 0.05$; Figure 4).

Overall, associations between dispersal traits and climatic variables were weak. Nevertheless, dispersal standard deviation (SD) showed significant positive relationships with both mean annual temperature (MAT; $r^2 = 0.10$, $p < 0.01$) and temperature unpredictability ($r^2 = 0.06$, $p < 0.01$; Figure 4d). By contrast, mean dispersal distance, skewness and kurtosis were not significantly related to either MAT or temperature unpredictability (all $p > 0.05$).

4 | DISCUSSION

Growing evidence highlights the importance of individual variation in dispersal and its ecological and evolutionary consequences (Nanninga & Berumen, 2014; Schreiber & Beckman, 2020; Teller et al., 2015). Such variation, for example, can generate leptokurtic population-level dispersal kernels, as variation among individuals inflates both the central peak and the tails of dispersal distributions

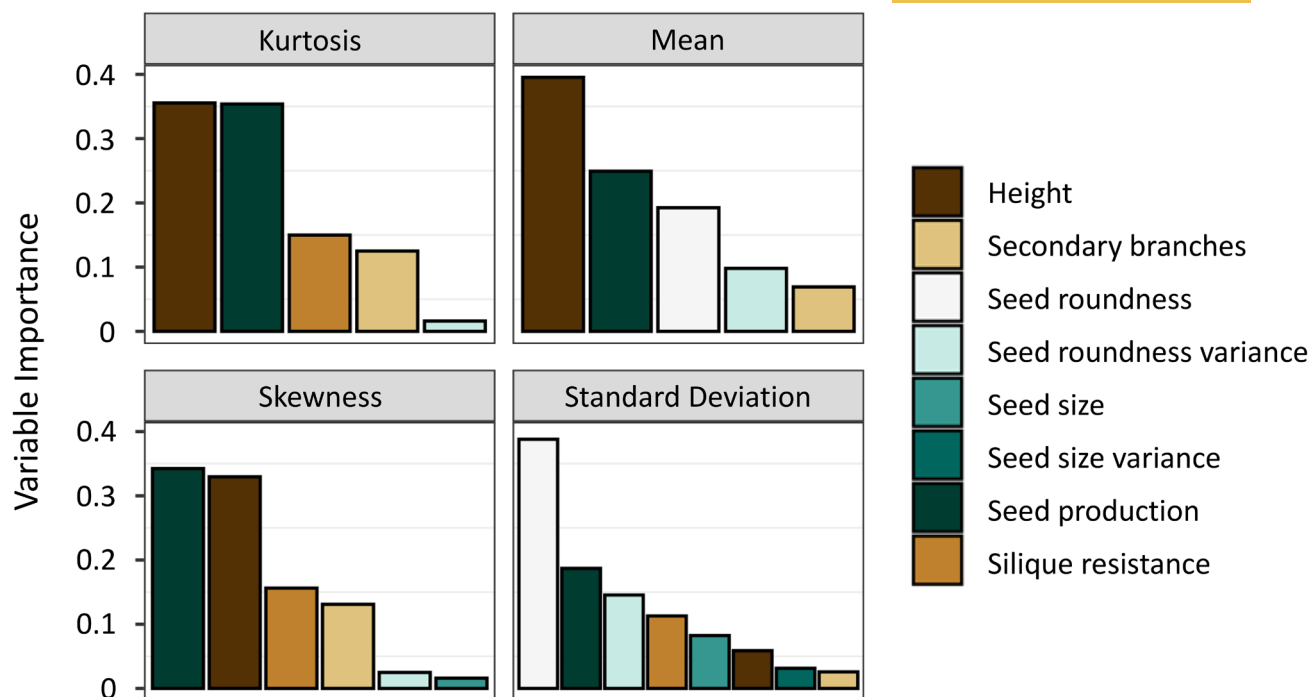


FIGURE 3 Traits importance for predicting dispersal kernel properties. Each panel represents the results of Random Forest analysis for each dispersal kernel property, showing the relative importance of morphological and reproductive traits. Bars indicate the importance score of each trait (colour-coded by trait category), with taller bars representing greater influence on the corresponding kernel property.

(Brown & Crone, 2016; Clark et al., 2001; Schupp et al., 2019). This body of work emphasizes the need to examine dispersal at the individual level and to characterize the full distribution of dispersal distances rather than relying on summary metrics alone. Here, we quantified full individual-level dispersal kernels and show that dispersal patterns vary significantly among *A. thaliana* genotypes. This variation is expressed through significant differences among genotypes in all kernel properties, that is, mean distance, standard deviation, skewness and kurtosis. These properties carry distinct biological meanings and together provide a multidimensional framework for characterizing dispersal potential and identifying components that contribute to broader dispersal strategies at the intraspecific level.

Complete dispersal kernels are rarely available due to the difficulty of capturing full distributions under field conditions. As a result, many empirical studies have focused on maximum or mean distances as proxies for dispersal ability. However, our results show that maximum distance varies relatively little among individuals and genotypes, suggesting that it may be less informative than often assumed. Similarly, although dispersal kernels have become more commonly used in ecological modelling, empirical studies tend to focus on tail behaviour and properties (e.g. kurtosis) as proxies for rare long-distance dispersal (LDD) events, but mostly used in the context of colonization, expansion processes (Klein et al., 2006; Liu, 2021; Marco et al., 2011). While this focus has proven valuable for understanding rare dispersal events, it has also contributed to a conceptual dichotomy between short- and long-distance dispersers (SDD vs. LDD), potentially obscuring more subtle and continuous patterns of

variation. Our study overcomes these limitations through a uniquely controlled experimental setup. Using a custom-built wind tunnel and high-resolution tracking of individual seeds, we generated full dispersal kernels at the individual level that enable us to characterize the entire shape of the distribution, not just its extremes. This enables us to identify and interpret distinct combinations of each kernel property (mean, standard deviation, skewness and kurtosis) that define the diverse dispersal patterns among individuals and genotypes.

Each kernel property showed distinct associations with reproductive traits, suggesting that different components of the dispersal kernel are shaped by partially independent trait syndromes. Plant height emerged as a strong predictor of both mean dispersal distance and kurtosis, consistent with previous work identifying height as a key determinant of dispersal potential (Tamme et al., 2014; Thomson et al., 2011, 2018). In contrast to Donohue et al. (2005), who reported a negative association between height and kurtosis, we observed strong positive relationships, indicating that taller plants may enhance longer dispersal distance. By contrast, the standard deviation, which reflects the spatial spread of dispersal outcomes, was more strongly associated with seed-level traits, particularly seed roundness, although seed number also contributed. These results suggest a dual dispersal syndrome, one promoting longer dispersal distances via plant architecture and another promoting broader spatial spread through variability in seed traits.

We estimated the broad-sense heritability (H^2) of dispersal kernel and found moderate to high values for all properties, consistent

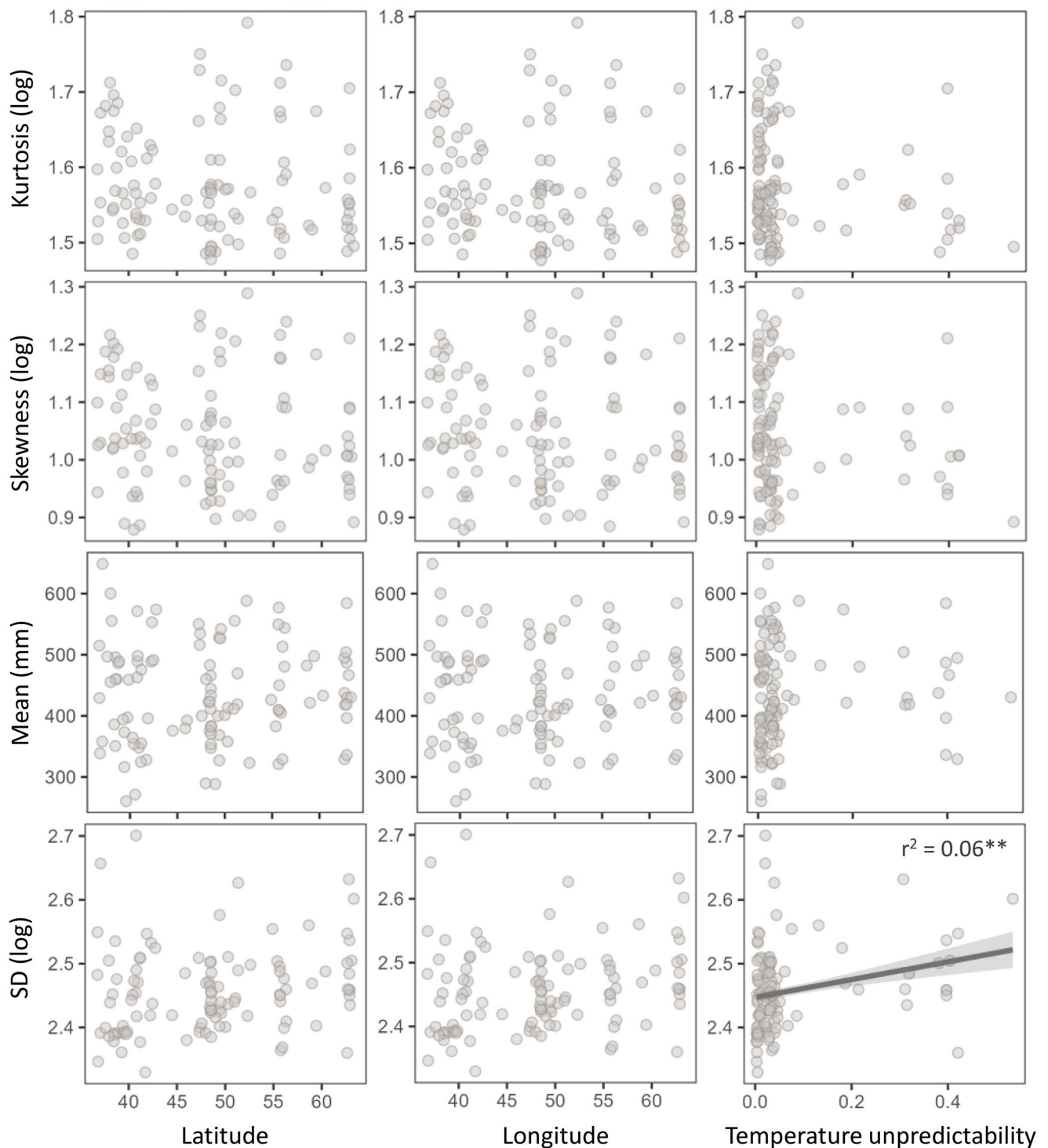


FIGURE 4 Dispersal kernel and the relationship with latitude, longitude and environmental unpredictability. Almost no significant relationship is detected, except for the relationship between temperature unpredictability and SD. The bottom right panel shows that higher temperature unpredictability leads to more variation of within-individual dispersal distance ($**p < 0.01$).

with previous findings in *A. thaliana* (Donohue et al., 2005) and other species (Keena et al., 2007; Lobón et al., 2011; Matthysen et al., 2005; Teyssier et al., 2014). To place this variation in an evolutionary and biogeographical context, we examined associations between dispersal kernel properties, geographic origin (latitude and longitude) and demographic lineage (relict vs. non-relict). Previous

studies have shown trait divergence between lineages (e.g. relict and the non-relict), including in the life-history traits that relate to dispersal (Alonso-Blanco et al., 1999; Bastias et al., 2024; Borevitz et al., 2002), and this has been presumed to reflect the dispersal and competition strategies (Bastias et al., 2024). In addition, theoretical and empirical work suggests that dispersal ability may follow a

peripheral–core hypothesis, whereby increased dispersal is favoured at range edges to facilitate colonization and range expansion (Bastias et al., 2024; Travis & Dytham, 2002). We are not aware, however, of studies demonstrating clear geographic patterning in direct dispersal ability itself (e.g. dispersal distance), even though traits related to dispersal often vary systematically with latitude and climatic factors such as temperature, such as seed size or mass (e.g. Darling et al., 2008; Murray et al., 2004; Sobral et al., 2013).

Here, we found no clear geographic structure in dispersal kernel properties, nor significant differences between demographic lineages' history. However, dispersal variation was associated with climatic conditions at the sites of origin, such as MAT. Correlations with temperature-related climatic variables suggest that temperature is an important driver of dispersal processes. Previous studies have shown that temperature can influence dispersal dynamics, including dispersal distance (e.g. Drees & Shea, 2024; Kuparinen et al., 2009). However, beyond mean conditions, temperature unpredictability, which captures temporal variability in thermal environments, is expected to impose selection on variance-related traits. Accordingly, the standard deviation of the dispersal kernel, our proxy for within-individual dispersal variance, was most consistently associated with temperature unpredictability, suggesting that dispersal variance may be particularly sensitive to environmental fluctuations rather than to average conditions alone. This pattern aligns with predictions from bet-hedging theory, which posits that organisms inhabiting unpredictable environments can increase long-term fitness by producing variable offspring phenotypes. In plants, bet-hedging has primarily been documented through variation in germination timing or seed size (e.g. Childs et al., 2010; Pélabon et al., 2021). Our results extend this framework by suggesting that within-plant variation in seed dispersal distance may represent an additional bet-hedging axis, allowing offspring to encounter spatially heterogeneous and temporally variable habitats. Consistent with this interpretation, genotypes with higher within-individual seed size variance also tended to produce seeds that were more widely spaced (Figure S6), and these genotypes originated from regions characterized by higher temperature unpredictability. Increased seed spacing may reduce sibling competition or enhance establishment across variable microsites under fluctuating climatic conditions.

Overall, our findings reveal that even within a single species and dispersal mode, dispersal varies substantially and is shaped by distinct trait dimensions. We highlight the importance of accounting for intraspecific variation in seed dispersal strategies and suggest that incorporating variation in dispersal kernel properties and underlying trait complexity can improve predictions of species spread, persistence and adaptive capacity under changing environments. Notably, dispersal variance emerges as a potentially adaptive trait under climatic unpredictability, likely functioning as a bet-hedging strategy. We acknowledge that given the small spatial scale of dispersal observed in our study, it remains unclear whether this variance effectively buffers offspring against meaningful environmental differences. Future research is needed and should test the fitness consequences of dispersal variance under contrasting environmental

conditions, such as through experimental evolution, to better understand how this component of dispersal evolves in response to environmental uncertainty.

AUTHOR CONTRIBUTIONS

All authors conceived the study and designed its methodology; Catharina Y. Utami collected and analysed the data and wrote the initial manuscript; all authors significantly contributed to revisions of the manuscript and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest. Cyrille Violle is an Associate Editor of Functional Ecology, but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

All data used in the manuscript are available from the Zenodo Digital Repository: <https://doi.org/10.5281/zenodo.18315060> (Utami et al., 2026).

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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. Map of the geographic origin of the *A. thaliana* genotypes used in the experiment.

Figure S2. Individual seed dispersal kernels in *A. thaliana*.

Figure S3. Frequency of best and second-best fitting distribution models for individual-level seed dispersal kernels.

Figure S4. Pairwise correlations between phenotypic traits.

Figure S5. Variation in dispersal traits across 107 widely distributed *A. thaliana* genotypes in Europe.

Figure S6. Relationship between within-individual inter-seed distance and dispersal standard deviation (SD) and temperature unpredictability.

Table S1. Summary of the geographical and genetic characteristics of the genotypes of *A. thaliana* chosen in our study from the 1001 Genomes project.

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