Seed dispersal is a prominent and unique life-history transition that links many ecological, genetic, evolutionary dynamics and processes (Loveless and Hamrick, 1984; Schupp et al., 2010). As such, traits that affect dispersal are expected to be shaped by strong selection pressures (Bonte and Dahirel, 2017). A comprehensive understanding of the evolution of dispersal-linked traits requires addressing several key questions: How is this variation distributed across space, time, and levels of organization? How does this variation relate to, and interact with, variation in other life history traits? And to what extent does this variation eventually influence plant fitness? These questions, which form the backbone of a trait-based approach for understanding the global spectrum of plant form and function, have been addressed mainly at the interspecific level. Nevertheless, much less is known about the sources, extent, and implications of intraspecific trait variation in dispersal-linked traits (Saatkamp et al., 2019), with one notable exception—heterocarpy. Heterocarpy, the production of two or more types of diaspores associated with different dispersal capabilities, has been thoroughly studied at both the interspecific and intraspecific levels (Imbert, 2002; Matilla et al., 2005). Although heterocarpy has been described for only a few families (mainly for the Asteraceae; Imbert, 2002; Fenesi et al., 2019), it occupies a central place in the literature on the evolution of dispersal, with dispersal rate (i.e., proportion of dispersive diaspores) serving as the main depiction of dispersal strategy in both theoretical and empirical studies (Mazer and Lowry, 2003; Mandák and Pyšek, 2005; Hughes, 2018). However, variation in dispersal traits within a seed type (especially dispersive type) is usually overlooked,
despite the fact that such variation may significantly affect dispersal potential and enact an even wider range of dispersal strategies. This neglected facet is the focus of our investigation. In this study, we quantify the variation in both categorical and continuous diaspore morphological traits of a wind-dispersed heterocarpic species at three intraspecific levels of organization (among populations, among individual plants, and among seeds), reflecting different underlying mechanisms and consequences. Further, we tested the effects of diaspore morphological traits on dispersal potential and the subsequent seedling emergence.

Trait-based approaches have been expanded recently in two major directions: (1) from focusing on interspecific variation to including intraspecific and even intra-individual variation (Albert et al., 2010; Bolnick et al., 2011; Viole et al., 2012; Sievert et al., 2015; Des Roches et al., 2018); and (2) from focusing on vegetative traits, mainly those related to leaf and root economics (Wright et al., 2004; Bardgett et al., 2014; Sievert et al., 2015; Umaña et al., 2018), to the inclusion of interspecific and intraspecific variation in diaspore traits and in dispersal traits (Tamme et al., 2014; Thomson et al., 2018; Saatkamp et al., 2019; Snell et al., 2019). The power of using simple measures of plant traits, such as diaspore shape, mass, and investment in dispersal devices, to predict seed dispersal has been comprehensively explored at the interspecific level (e.g., Tamme et al., 2014; Thomson et al., 2018, but rarely at the intraspecific level (Wyse et al., 2019). Thus, a fine-scale examination from the population level to the seed level is an important step toward a better understanding of the ecological and evolutionary implications of intraspecific variation in continuous dispersal traits (Messier et al., 2010; Herrera, 2017; Snell et al., 2019).

Intraspecific variation in diaspore characteristics may also affect post-dispersal performance, such as seedling emergence and potentially competitive abilities at early life stages (Meyer and Carlson, 2001; Albert et al., 2010; Kristenmacher and Gibson, 2016). Seed mass is associated with a wide range of plant functions (Saatkamp et al., 2019), and it plays a major role in some well-studied trade-offs, such as the negative correlation between colonization and competition (Westoby et al., 1996; Coomes and Grubb, 2003). For example, it has long been hypothesized that larger seeds enhance seedling survivorship over a wider range of conditions (Kitajima and Fenner, 2000) and may face difficulties of dispersal (Chen and Moles, 2015; Chen et al., 2019). This is especially the case in wind-dispersed seeds, where heavier seeds disperse poorly, but may have higher emergence potentials and competitive advantage in early establishment stages (Meyer and Carlson, 2001; Jakobsson and Eriksson, 2003; Hahn et al., 2013).

Beyond seed mass, however, little is known about how diaspore traits affect performance at early life stages. Although a trade-off between dispersal and dormancy has been widely proposed, interspecific and intraspecific findings are not consistent in this aspect (De Waal et al., 2016). Relatively little is known about how intraspecific variation in diaspore traits other than dispersal rate and seed mass can be used to predict plant establishment at early life stages, such as seedling emergence (Skarpaas et al., 2011).

Our study capitalizes on noticeable variation both in dispersal rate and in morphology of the dispersive diaspore in the wind-dispersed annual species Geropogon hybridus (Asteraceae), and its relation to various seed functional components (Appendix S1; Chen and Giladi, 2018). We set three objectives. First, we estimated intraspecific variation in easily measured diaspore traits at various hierarchical levels from population to seed. We hypothesized that the combination of genetic differentiation and environmental heterogeneity at both the population level and the plant level will lead to substantial variation in dispersal traits, while developmental constraints within a diaspore and potential benefits from a mixed dispersal strategy will contribute to within-individual variation. Second, we quantified the variation in diaspore morphological traits between years, to see if the population-level variation was consistent across growing seasons. Last, we used univariate and multivariate analyses to test the effects of diaspore morphological traits on dispersal potential (approximated by diaspore terminal velocity, $V_{t}$) and on seedling emergence. We focused the analyses on dispersive diaspores and predicted that (1) dispersal potential will be more tightly associated with traits that shape diaspore geometry, and will be less tightly associated with diaspore mass or within-diaspore mass allocation (to achene and pappus), as the latter are also associated with diaspore functions other than dispersal; (2) seedling emergence will be positively affected by seed mass; and (3) seedling emergence will be positively associated with dispersal capabilities, mirroring the pattern observed in an intraspecific case where a trade-off between dispersal and dormancy is hypothesized (De Waal et al., 2016).

**MATERIALS AND METHODS**

**Diaspore collection and measurement**

*Geropogon hybridus* (L.) Sch. Bip. is an annual heterocarpic herb in the family Asteraceae, which is widespread in the Mediterranean region, including most of southern Europe, the Levant, and all across northern Africa (Wilson, 1982). It grows on calcareous, loamy soils in open habitats. Within our study regions, it is mainly found in natural and seminatural *batha* vegetation, which is typical of the eastern Mediterranean, where annual plant communities evolved in the presence of various human activities for thousands of years (Giladi et al., 2011). It germinates in early winter, flowers in March, and during April–May produces usually one but up to seven capitula that are carried on long (approximately 10–70 cm) stalks (Chen and Giladi, 2018). Flowers are radially symmetrical, with pink to violet corollas and dark purple anthers. Each capitulum consists of 9 to 95 diaspores of two types. Diaspores in the central whorls have plumelike pappi consisting of ~20 unequal bristles that function as parachutes in dispersal by wind (hereafter as dispersive diaspores), while diaspores in the peripheral whorl are heavy and have diminutive pappi of five unequal awns and therefore have reduced dispersal capability (hereafter as non-dispersive diaspores; Bergholz et al., 2017). The non-dispersive diaspores generally have short awns and remain attached to the plant tightly for at least several months (S.-C. Chen and I. Giladi, personal observation). Thus, although a possibility of epizoochory for the non-dispersive diaspores cannot be excluded, it has not been described for this species and is probably rare. We recorded the proportion of dispersive versus non-dispersive diaspores for each capitulum, but the main focus of this study is the yet unstudied variation in the dispersal traits of the dispersive diaspores. These traits are likely to affect dispersal potential, thus affecting the distance to which diaspores will travel, and consequently influence seed fate, which is likely to be...
affected by distance to conspecific individuals. In addition, the fact that G. hybridus might bear zero non-dispersive diaspores but always produces dispersive diaspores prevented comparative studies for non-dispersive diaspores—so we focused our study on morphological traits for dispersive diaspores.

This study took place in 2016 (Year 1) in the southern Judean lowlands in central Israel (34°50'26"N; 31°35'35"E). The study system consists of patches of seminatural vegetation (shrubland and/or grassland) surrounded by a matrix of agricultural land. The study species reaches its southern geographic range edge within our study region (http://www.biogis.huji.ac.il). In the spring of 2016 (Year 1), we collected capitula of G. hybridus from 10 sites, which in previous seasons were marked as sustaining sizable populations (>50 individuals; Bergholz et al., 2017). In each population, we randomly selected 20 individual plants and collected one mature capitulum from each of them prior to the dispersal of any seed. Each capitulum was carefully kept in a separate plastic container, which was sufficiently large to maintain its structure and all the diaspores intact. Later, in the laboratory, we counted numbers of diaspores of the two types in each capitulum to determine dispersal rate. Following that, we randomly selected five of the 20 capitula from each population, and 12 plumed diaspores from each capitulum, to measure their morphological traits and terminal velocities. The total sample size for this year was 600 diaspores.

We viewed each diaspora as consisting of a pappus and an achene (while being fully aware that some authors refer to the latter as cy- psela in Asteraceae species; Marzinek et al., 2008). Diaspores and achenes were weighed to ±0.01 mg on an analytical balance (model AUW220D, Shimadzu Corporation, Kyoto, Japan). Pappus mass was calculated as the difference between diaspora mass and achene mass. Achene width was measured to ±0.01 mm using digital calipers. Diaspore length, achene length, pappus length, pappus width, and pappus opening angle were measured from digital photographs using ImageJ software. The pappus angle equals 180° when the pappus opens to form a flat disk perpendicular to the achene main axis, and 0° when the pappus is fully closed (see Appendix S2 for description of the measurements). Terminal velocity of each diaspora was measured by dropping it in a 0.5 × 0.5 × 1 m (length × width × height) closed chamber at ambient temperature. Diaspore motion was captured by a high-speed camera (model Mako 030C, Allied Vision Technologies, Stadtroda, Thuringia, Germany) that was placed 1 m away from the chamber and recorded the position of the falling diaspora at 300 frame/s for a path length of ~0.7 m within the chamber. Following the procedures in Sirisathitkul et al. (2013), we analyzed the video using Tracker software (http://physlets.org/tracker), determined when instantaneous falling velocity reached a constant value, and referred to that value as terminal velocity.

To quantify inter-annual variation in diaspora traits, capitula from nine of the 10 populations were sampled again in the spring of 2017 (Year 2), using the same procedure as in Year 1. One site was not sampled in Year 2 due to logistical reasons. Diaspore mass, dias- pore length, achene length, pappus length, pappus width, pappus angle, and terminal velocity were measured for these additional 540 diaspores using the same procedures as in Year 1.

In February 2017, the same 600 achenes of Year 1 measured above (pappi removed) were sown in germination trays filled with standard commercial soil mixture (Even Ari, Green 90 potting soil, Farm no. 88 Beil-Ela'azary Village, Israel), in the Sede Boker campus of the Ben-Gurion University of the Negev. Each seed was sown in an individual chamber of the germination trays. They were watered and observed daily for 1 mo. Seedling emergence of each seed was recorded as “yes” or “no.” The positions of germination trays were randomly exchanged every 3 d to avoid potential biases of germination conditions. We also germinated a subset (~20) of non-dispersive diaspores under the same condition, but none of them germinated. We considered them viable and dormant as they remained firm and did not rot. They may show delayed germina- tion just like non-dispersive diaspores of many other heterocarpic species (Venable and Lawlor, 1980). A further investigation on the dormancy and germination of non-dispersive diaspores could be helpful, but this is not the focus of the present study.

Statistical analysis

Variation in diaspora morphological traits was assessed at three hierarchical levels of organization: (1) among populations, (2) among individual plants within a population, and (3) among seeds (diaspores) within an individual plant (i.e., within-individual level). To calculate the variance partitioning of diaspora morphological traits across the three nested levels of organization, variance component analyses were performed with fitted general linear models, following Messier et al. (2010). In each model, the response variable was one of the nine diaspora traits. As the random-effects term in the model, seed level was nested within the plant level, which was nested within the population level. The model was fitted with a restricted maximum likelihood method, using the “nlme” package (Pinheiro et al., 2017) and the “ape” package (Paradis et al., 2004) in R version 3.6.1.

Pearson correlation coefficients were estimated for the relationships between diaspora traits. A diagnostic check on a correlation matrix of the nine diaspora morphological traits revealed a substantial number of statistically significant pairwise relationships (|r| > 0.7). Given this high degree of collinearity among traits, a principal component analysis (PCA) was implemented to transform the trait data into a smaller number of underlying components. Values of diaspora morphological traits were standardized prior to the PCA.

Generalized linear mixed-effects models were fitted to quantify the effects of diaspora morphological traits on terminal velocity and on seedling emergence. Terminal velocity was log_{10}-transformed to normalize the data and ensure homogeneity of variances. In each univariate model, diaspore terminal velocity (Gaussian family model) or seedling emergence (binomial family model) was treated as the response variable, and each morphological trait was treated as the fixed-effect term, with population and plant as random-effects terms. The multivariate effect of diaspora traits was captured by setting the first two principal component axes (PC1 and PC2) as fixed-effect terms in the generalized linear mixed-effects model. All models were fitted using restricted maximum likelihood with the “lme4” package (Bates et al., 2014). The statistical significance of the fixed-effect term in a model was evaluated using a likelihood ratio test of the model with the fixed-effect term against the model without the fixed-effect term. As measures of goodness-of-fit, the proportional variances explained by the fixed-effect term (marginal $R^2$) and by the whole model (conditional $R^2$) were calculated using the method in Nakagawa and Schielzeth (2013) and the “piecewiseSEM” package (Lefcheck, 2015).

The relative importance of diaspora morphological traits in determining terminal velocity or seedling emergence was partitioned using independent-effects analysis (Murray and Conner, 2009). The independent-effects analysis calculates the average contribution of
each predictor to variance in the response variable across all possible models that represent a subset of the predictors (Murray and Conner, 2009). This analysis was suitable to our study, in which predictors exhibited multicollinearity, as it attributed variance in the response variable to independent effects of individual morphological traits through a hierarchical partitioning algorithm (Chevan and Sutherland, 1991). The model was fitted using the “hier.part” package (Walsh and Mac Nally, 2013), using a Gaussian family model for terminal velocity and a binomial family model for seedling emergence.

RESULTS

The number of diaspores in a capitulum of *G. hybridus* varied considerably, between 13 and 84. Among these, the number of dispersive diaspores ranged between 6 and 69, and the number of non-dispersive diaspores ranged between 0 and 17. The dispersal rate (i.e., proportion of dispersive diaspores) varied between 0.429 and 1.0, with a mean of 0.761 (Appendix S3). A majority of variance in dispersal rate and diaspore numbers was found at the individual plant level (>78%; Appendix S3).

Morphological traits of dispersive diaspores varied substantially, up to eightfold (Table 1). The variance partitioning in dias- pore morphological traits was generally well distributed across the three levels of organization (Table 1 and Fig. 1). Variance at the individual plant level was found to be consistently the largest component, and variance at the seed level the smallest, in the traits of diaspore and achene, as well as in pappus length. Population level contributed most to the variance in pappus mass. Population and plant levels contributed equally to the explained variance in pappus width, whereas variance in pappus angle was equally explained by the plant and seed levels.

Pairwise correlations among the nine diaspore morphological traits indicated positive and tight correlations between almost all trait pairs (Appendix S4). The exception was pappus angle, which was significantly correlated with only two other traits—positively with pappus width and negatively with diaspore length. Values of pappus width and pappus angle were significantly and positively correlated between years at the population level (Fig. 2), while values of the other diaspore morphological traits were not correlated between years and are therefore not shown.

PC1 and PC2 explained 64% and 18% of the total variance in diaspore morphological traits, respectively (Table 2 and Appendix S5). PC1 was composed of all traits of diaspore and achene, as well as pappus mass. Therefore, this PC1 value primarily represented the diaspore size. PC2 was mainly composed of pappus width and pappus angle. Therefore, this PC2 value could be interpreted as representing the geometry of the pappus.

Diaspore terminal velocity ranged from 0.465 to 2.313 m/s, with a mean value of 0.787 m/s. Values of terminal velocity (at the population level) were significantly and positively correlated between years (Fig. 2). All morphological traits were significantly correlated with diaspore terminal velocity, though the sign and the magnitude of these correlations varied substantially among morphological traits (Table 3). Diaspore terminal velocity was negatively correlated with pappus geometry (i.e., pappus length, width, and angle) and positively with the other morphological traits. The strongest correlates of terminal velocity were pappus width (marginal $R^2 = 0.549$) and pappus angle (marginal $R^2 = 0.403$), both of which are “shape” rather than “size” traits. In the multivariate model, PC1 and PC2 were both negatively correlated with diaspore terminal velocity ($P = 0.013$ and $P < 0.0001$, respectively), and together they explained 57.54% of the variance in terminal velocity, which was just slightly higher than

| Trait                 | Mean (range) | Magnitude of range | CV (%) | Variance at each level (%) |
|-----------------------|--------------|--------------------|--------|---------------------------|
|                       |              |                    |        | Population    | Plant    | Seed and error |
| Diaspore mass (mg)    | 9.19 (3.40–18.24) | 5.36              | 31.36  | 35.92         | 45.31    | 18.77          |
| Diaspore length (mm)  | 38.24 (22.31–53.31) | 2.39              | 14.64  | 32.08         | 50.83    | 17.09          |
| Achene mass (mg)      | 7.55 (2.96–15.17)  | 5.13              | 31.08  | 30.20         | 47.09    | 22.71          |
| Achene length (mm)    | 25.42 (18.08–33.66) | 1.86              | 13.60  | 39.44         | 50.26    | 10.30          |
| Achene width (mm)     | 0.74 (0.47–1.05)   | 2.23              | 14.03  | 24.67         | 41.79    | 33.54          |
| Pappus mass (mg)      | 1.64 (0.44–3.40)   | 7.73              | 36.71  | 54.57         | 36.98    | 8.45           |
| Pappus length (mm)    | 17.11 (10.18–23.78) | 2.34              | 15.60  | 31.36         | 48.51    | 20.13          |
| Pappus width (mm)     | 28.66 (8.10–43.54) | 5.38              | 20.99  | 37.40         | 36.25    | 26.34          |
| Pappus angle (degree) | 133.93 (26.77–220.94) | 8.25              | 24.47  | 27.43         | 37.27    | 38.00          |

### FIGURE 1

Variance partitioning of seed morphological traits of *Geropogon hybridus* across three nested levels of organization.
that in the univariate relationship between pappus width and diaspore terminal velocity (marginal $R^2 = 0.549$; Table 3). The result of independent-effects analysis was consistent with that of the univariate relationships (Fig. 3). The relative importance of pappus width and pappus angle combined accounted for 69.88% of the variance in diaspore terminal velocity.

Two-thirds of the sown achenes emerged as seedlings (409 of 600; 68%). Only pappus width and pappus angle were significantly, but weakly, correlated with seedling emergence (marginal $R^2 = 0.032$ and 0.027; Table 3). Diaspores with greater width and angle of pappi exhibited increased probability of seedling emergence. In the independent-effects analysis, pappus angle was the most important trait and it explained 25.47% of the variance in seedling emergence, followed by pappus width that accounted for 21.12% of the variance (Fig. 3). Diaspore terminal velocity was significantly and negatively correlated with seedling emergence (Fig. 4). From the fastest diaspore (2.313 m/s) to the slowest diaspore (0.465 m/s), the probability of seedling emergence increased threefold, from 0.294 to 0.848.

**DISCUSSION**

We found substantial variation in, and tight correlations between, continuous diaspore morphological traits of the dispersive diaspores of *G. hybridus*. This variation provides this heterocarpic species a wider range of dispersal potential in addition to the presence of two diaspore types. Trait variance is evenly distributed across all levels of organization, suggesting that processes at the population, individual plant, and seed levels are all important in determining diaspore morphology. The variation in both diaspore morphological traits and terminal velocity was high. For example, both

![FIGURE 2. Inter-annual variation in (A) terminal velocity, (B) pappus width, and (C) pappus angle between Year 1 and Year 2 for *Geropogon hybridus*. Each point represents the mean trait value of a population, with bars representing one standard deviation around the mean (n = 9 populations). Dashed lines show one-to-one relationships. Correlation coefficients for the displayed relationships between years are shown.]

**TABLE 2.** Principal component analysis for nine diaspore morphological traits of *Geropogon hybridus*.

| Eigenvector | Principal component 1 | Principal component 2 |
|-------------|-----------------------|-----------------------|
| Loading     | Percent contribution  | Loading               | Percent contribution  |
| Diaspore mass | −0.40                 | 16.20                 | −0.08                 | 0.69                |
| Diaspore length | −0.35             | 12.32                 | −0.24                 | 5.92                |
| Achene mass   | −0.39                 | 15.47                 | −0.10                 | 0.91                |
| Achene length | −0.39                 | 14.85                 | −0.08                 | 0.56                |
| Achene width   | −0.33                 | 10.69                 | −0.04                 | 0.20                |
| Pappus mass    | −0.39                 | 15.53                 | −0.02                 | 0.06                |
| Pappus length  | −0.30                 | 9.09                  | 0.19                  | 3.64                |
| Pappus width    | −0.24                 | 5.83                  | 0.59                  | 34.98               |
| Pappus angle    | −0.01                 | 0.01                  | 0.73                  | 53.05               |
| Eigenvalue     | 5.76                  | 1.62                  |
| Percent variation explained | 63.99           | 18.00                  |

**TABLE 3.** Univariate relationships between diaspore morphological traits and terminal velocity, and between diaspore morphological traits and seedling emergence, in *Geropogon hybridus*, using generalized linear mixed-effects models with population and plant as random-effects terms.

| Trait            | Terminal velocity (log$_{10}$-transformed) | Seeding emergence |
|------------------|--------------------------------------------|-------------------|
|                  | Intercept | Slope | $\chi^2$ | $P$ | Marginal $R^2$ | Conditional $R^2$ | Intercept | Slope | $\chi^2$ | $P$ | Marginal $R^2$ | Conditional $R^2$ |
| Diaspore mass    | −0.40     | 0.031 | 216.68   | <0.0001 | 0.323 | 0.862 | 1.120 | −0.022 | 0.1858 | 0.667 | 0.001 | 0.219 |
| Diaspore length  | −0.598    | 0.013 | 124.58   | <0.0001 | 0.280 | 0.773 | 1.864 | −0.025 | 0.766 | 0.381 | 0.005 | 0.216 |
| Achene mass      | −0.386    | 0.035 | 232.64   | <0.0001 | 0.315 | 0.852 | 1.111 | −0.026 | 0.178 | 0.673 | 0.001 | 0.220 |
| Achene length    | −0.968    | 0.033 | 199.51   | <0.0001 | 0.375 | 0.908 | 0.964 | −0.002 | 0.001 | 0.971 | <0.0001 | 0.219 |
| Achene width     | −0.607    | 0.662 | 228.09   | <0.0001 | 0.261 | 0.814 | 0.610 | 0.417 | 0.105 | 0.746 | 0.004 | 0.219 |
| Pappus mass      | −0.312    | 0.118 | 62.49    | <0.0001 | 0.239 | 0.790 | 1.095 | −0.109 | 0.163 | 0.686 | 0.001 | 0.217 |
| Pappus length    | 0.182     | −0.018 | 62.47    | <0.0001 | 0.164 | 0.661 | −0.381 | 0.076 | 1.965 | 0.161 | 0.010 | 0.231 |
| Pappus width     | 0.347     | −0.016 | 448.66   | <0.0001 | 0.549 | 0.868 | −0.840 | 0.062 | 6.855 | 0.009 | 0.032 | 0.235 |
| Pappus angle     | 0.144     | −0.002 | 231.74   | <0.0001 | 0.403 | 0.646 | −0.442 | 0.010 | 6.599 | 0.010 | 0.027 | 0.204 |
diaspore mass and achene mass varied up to fivefold, a relatively large range compared to the variation reported for these traits in other species (Sipe and Linnerooth, 1995; Susko and Lovett-Doust, 2000). Along with the finding that diaspore morphological traits are closely correlated with each other, our results also support the hypothesis that diaspore traits evolve in concert with respect to their effect on dispersal potential (Augspurger et al., 2016). Meanwhile, diaspore terminal velocity itself and those diaspore traits that are most important in determining terminal velocity (pappus width and pappus angle) remain fairly consistent from year to year for a given population, and differ significantly among individual plants in a given year. The significant correlation between years (Fig. 2) suggests that the contribution of the population level to overall variance in terminal velocity is not spurious, but rather has to do with a consistency in population-level differences. Although intraspecific variation in plant functional traits is traditionally considered to be relatively low compared to interspecific variation (Siefert et al., 2015; Umaña et al., 2018), recently the magnitude and importance of intraspecific variation in plant traits in general (Albert et al., 2010) and in dispersal traits in particular have received increasing attention (Saatkamp et al., 2019). Our results show not only that intraspecific variation in traits of the dispersive diaspores of Geropogon hybridus is substantially large, but also that the variation originates at different levels of organization from the seed level to the population level. Partitioning the sources of variance in diaspore traits is a necessary step leading to a better understanding of important mechanisms that may affect the fates of individual diaspores, plants, populations, and communities (Herrera, 2017). Furthermore, intraspecific and even more so, intraindividual variation in traits that affect dispersal can be viewed and should be examined as a potentially mixed strategy that enables plants to spread risks (Kistenmacher and Gibson, 2016).

The diaspore traits that we investigated could clearly be classified into two major phenotypic groups: those associated with diaspore size and those associated with pappus geometry. Although diaspore terminal velocity was significantly affected by variables from both groups, it was mostly explained by pappus geometry, as indexed by pappus width and pappus angle. Theoretical considerations, backed by empirical results and experimental manipulation, indicate that seed terminal velocity of plumed seeds, as in the Asteraceae, are highly correlated with the square root of the plume loading, which is the ratio of the pappus area to the diaspore mass (Sheldon and Burrows, 1973; Greene and Johnson, 1989; Andersen, 1993; Soons and Heil, 2002). However, we found that measures of pappus dimensions (width, length) explained more of the variance in seed terminal velocity than measures of mass (diaspore, pappus, or achene), in accordance with Sheldon and Burrows (1973). There could be several
explanations for the greater explanatory power of pappus dimensions than mass to the variation in terminal velocity. First, as plume loading is theoretically correlated with pappus area, it is expected to follow a quadratic relationship with the one-dimensional measures of the pappus (width/length), but a linear relationship with mass. Second, if the variation in measures of geometry is higher than that in mass, there is a higher chance that geometry will explain more of the variance in terminal velocity. However, this explanation is not supported by our data (Table 1), where the CVs for mass are similar to, or even higher than, the CVs for pappus dimensions. Last, the relative importance of pappus area and diaspore mass to terminal velocity may vary with diaspore size in a nontrivial manner. Even though biomass allocation to dispersal (pappus mass) in G. hybridus is tightly correlated with biomass investment in defense and seed reserve (Chen and Giladi, 2018), there is still much flexibility in how the biomass allocated to the pappus is distributed and affects terminal velocity. Plants have evolved complex structures of pappus, where a nearly optimal construction of pappus may provide aerodynamics properties with little investment in biomass, thus decoupling the link between dispersal investment and dispersal performance (Casseau et al., 2015; Tabassum and Bonser, 2017). For example, the weaving of the filamentous structure of pappus in Asteraceae species constructs an efficient dispersal device, where porosity provides stability while boundary layers between filaments enhance flight stability and generate drag four times more efficient than what a simple disk membrane of a comparable surface area would do (Casseau et al., 2015; Cummins et al., 2018). In accordance with an interspecific study (Thomson et al., 2018), our intraspecific data also show that the absolute biomass investment in dispersal device (i.e., pappi or wings) contributed little to diaspore dispersal ability for wind-dispersed species. This consistent finding between the intraspecific and interspecific studies supports a conclusion that pappus geometry is more important in determining dispersal capabilities than pappus mass, for wind-mediated seed dispersal.

Contrary to the expectation from a colonization–establishment trade-off, traits related to diaspore mass (e.g., diaspore mass, achene mass, achene width) were not significantly correlated with seedling emergence in our study. Similar results were reported in Aster umbellatus (Asteraceae), for which diaspore mass did not affect the likelihood of germination (Chmielewski, 1999). Our results differ from those found for a heterocarpic species in a closely related genus, Tragopogon (Mølken et al., 2005), and in a tree species (Pinus sylvestris; Debean et al., 2003). In Tragopogon pratensis, germination is mainly influenced by diaspore mass rather than diaspore morphology across the two diaspore types (both are dispersed by wind; Mølken et al., 2005), in contrast with our result of G. hybridus in which only pappus geometry was correlated with seedling emergence within dispersive diaspores (Table 3). Previous studies have found either negative (Morse and Schmitt, 1985) or no relationship between diaspore dispersal ability and germination ability for some perennial species (Soons and Heil, 2002; Debean et al., 2003; Skarpaas et al., 2011). Nevertheless, seedling emergence’s weak correlation with either pappus width or pappus angle shows, in our case, that individual morphological traits are not good indicators for post-dispersal performance, as the process of germination and establishment could be influenced by a complexity of factors (Kitajima and Fenner, 2000). If diaspore traits indeed affect germination, their effects are probably integrated to form a complex relationship between dispersal and post-dispersal function (Fig. 4). These findings indicate that how diaspore traits affect germination needs to be further disentangled.

The correlation between diaspore terminal velocity, as a proxy for dispersal capability, and seedling emergence can also be, with some restrictive assumptions, viewed in light of an expected trade-off between two risk-reducing mechanisms: dispersal and dormancy (Venable and Brown, 1988; Rees, 1993). Relying implicitly or explicitly on the assumption that long-term dormancy is either low or independent of short-term seedling emergence, many previous studies have used fraction of seedling emergence as a continuous measure of seed dormancy that further represents an important axis of temporal dispersal (Rees, 1993; De Waal et al., 2016). Using similar variables to those that we used (diaspore terminal velocity and germination fraction), De Waal et al. (2016) interpreted the results as indicating a marginally significant dispersal–dormancy trade-off across 15 annuals and a significant trade-off across 12 perennials of wind-dispersed Asteraceae species. However, they didn’t reveal such negative correlation between dispersal and dormancy within species. In contrast, our results suggest that such trade-off could also be observed at the intraspecific level for an annual species. It has been suggested that an intraspecific trade-off between spatial and temporal dispersal is the basic level of organization for bet-hedging resulting from physical and biochemical constraints or sibbling competition (Rees, 1993; Buoro and Carlson, 2014). The difference between our result and others’ findings may lie in the fact that G. hybridus exhibited a considerably high variation in diaspore terminal velocity itself and in the associated traits, compared to the species considered in previous studies. The bet-hedging strategies of this species are not only enacted by its heterocarpy—a seed type with distance dispersal and quick germination, and a seed type with reduced dispersal and delayed germination—but also in the potential dispersal–dormancy trade-off within its dispersive diaspores. These strategies could help spread the risk associated with regeneration failure in heterogeneous environments where the species grows.

This study is one of the few to quantify properties of continuous dispersal-related traits of individual diaspores and distinguish explicitly their effects on ecological characteristics. Our approach and findings allow us to evaluate which of the measured traits correlates to differences in terminal velocity and seedling emergence. The answer to this question will indicate which traits can be potentially controlled by the mother plant, likely to be amenable for selection, and/or considerably affect fitness.

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AUTHOR CONTRIBUTIONS

S.-C.C. analyzed the data. S.-C.C. and I.G. designed the study, collected the data, and wrote the manuscript.
DATA AVAILABILITY

All raw data are uploaded to the Figshare data repository (https://doi.org/10.6084/m9.figshare.11409429).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

APPENDIX S1. Plumed diaspores of Geropogon hybridus.

APPENDIX S2. Illustration of diapspore measurement for Geropogon hybridus.

APPENDIX S3. Proportion and numbers of dispersive and non-dispersive diaspores.

APPENDIX S4. The correlation matrix of the Pearson’s correlation coefficients between seed morphological traits.

APPENDIX S5. Scree plot and biplot of principal component analysis.

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