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LINKING ORGANISMAL FUNCTIONS, LIFE HISTORY STRATEGIES AND POPULATION PERFORMANCE

High dispersal ability is related to fast life-history strategies

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Abstract

1. Seed dispersal is an essential, yet often overlooked process in plant ecology and evolution, affecting adaptation capacity, population persistence and invasiveness. A species' ability to disperse is expected to covary with other life-history traits to form dispersal syndromes. Dispersal might be linked to the rate of life history, fecundity or generation time, depending on the relative selection pressures of bet-hedging, kin competition or maintaining gene flow. However, the linkage between dispersal and plant life-history strategies remains unknown because it is difficult to observe, quantify and manipulate the influence of dispersal over large spatiotemporal scales.
2. We integrate datasets describing plant vital rates, dispersal and functional traits to incorporate dispersal explicitly into the rich spectra of plant life-history strategies. For 141 plant species, we estimated dispersal ability by predicting maximum dispersal distances using allometric relationships based on growth form, dispersal mode, terminal velocity and seed mass. We derived life-history traits from matrix population models parameterized with field data from the COMPADRE Plant Matrix Database. We analysed the covariation in dispersal ability and life-history traits using multivariate techniques.
3. We found that three main axes of variation described plant dispersal syndromes: the fast-slow life-history continuum, the dispersal strategy axis and the reproductive strategy axis. On the dispersal strategy axis, species' dispersal abilities were positively correlated with aspects of fast life histories. Species with a high net reproductive rate, a long window of reproduction, low likelihood of escaping senescence and low shrinkage tendencies disperse their seeds further. The overall phylogenetic signal in our multidimensional analyses was low (Pagel's $\lambda < 0.24$), implying a high degree of taxonomic generality in our findings.
4. *Synthesis*. Dispersal has been largely neglected in comparative demographic studies, despite its pivotal importance for populations. Our explicit incorporation of dispersal in a comparative life-history framework provides key insights to bridge

the gap between dispersal ecology and life-history traits. Species with fast life-history strategies disperse their seeds further than slow-living plants, suggesting that longer dispersal distances may allow these species to take advantage of habitats varying unpredictably in space and time as a bet-hedging strategy.

KEYWORDS

comparative demography, dispersal syndromes, fast-slow continuum, functional trait, life-history strategy, life-history trait, matrix population model, phylogenetic comparative analysis

1 | INTRODUCTION

The plant kingdom, with over 350,000 extant species (Paton et al., 2008), has evolved a myriad of strategies to overcome the implications of one of its main features: sessility. By far, the most striking strategy to overcome this limitation is the dispersal of propagules such as seeds (Howe & Smallwood, 1982; Janzen, 1970; Levin, Muller-Landau, Nathan, & Chave, 2003). Seed dispersal, the movement of seeds away from the parent, is key in ecological and evolutionary processes (Clobert, Baguette, Benton, & Bullock, 2012). Plants exhibit a variety of different methods to disperse their seeds—ingestion by animals, wind and ballistic are a few examples; these are inferred from fruit and seed morphology and are referred to as dispersal modes (Howe & Smallwood, 1982). Along with dispersal, plants have evolved a myriad of strategies to survive, grow and reproduce in a variety of habitats (Salguero-Gómez et al., 2016; Silvertown, Franco, & Harper, 1997). Only by understanding how dispersal covaries with life-history traits will researchers gain a more complete understanding of plant life-history strategies and the ability of plant species to respond to environmental change (Ronce & Clobert, 2012; Travis et al., 2013; Uemura & Hausman, 2013). In general, however, seed dispersal has traditionally been excluded from assessments of plant life-history evolution (Bonte et al., 2012).

Several evolutionary pressures may have selected for increased dispersal of seeds (Levin et al., 2003). Theoreticians have used evolutionary models to investigate why and how far species disperse (Duputié & Massol, 2013). Results of models show that kin competition (Hamilton & May, 1977; Hovestadt, Messner, & Hans, 2001; Rousset & Gandon, 2002; Starrfelt & Kokko, 2010), specialized natural enemies (Muller-Landau, Levin, & Keymer, 2003), and spatial and temporal unpredictability in the environment (e.g. bet-hedging Gadgil, 1971; McPeek & Holt, 1992; Snyder, 2011) can all select for a higher propensity of organisms to disperse and for longer dispersal distances.

For plants, seed dispersal can influence fitness by determining the seedscape, that is, the abiotic and biotic environment that affects all later stages of recruitment, from seedling establishment to future reproduction (Beckman & Rogers, 2013). Where a seed is deposited determines the degree of competition (Loiselle, 1990; Spiegel & Nathan, 2012), the presence of natural enemies that consume plants (Connell, 1971; Janzen, 1970) and the suitability of the environment for survival and growth (Howe & Miriti, 2004; Schupp, Jordano, & Maria Gomez, 2010). The spatial template created by dispersal influences the persistence of populations and metapopulations (Jordano, 2017), and long-distance dispersal drives the spread of populations into new areas (Kot, Lewis, & van den Driessche, 1996; Neubert & Caswell, 2000), which is important for tracking changing climates (Bullock et al., 2012; Loarie et al., 2009) and species invasions (Buckley et al., 2005; Skarpaas & Shea, 2007). Dispersal is also central to the genetic diversity of populations (Hamrick, Murawski, & Nason, 1993) and their ability to adapt to new conditions (Kremer et al., 2012). Consequently, for sessile organisms such as plants, their ability to disperse and adapt to new environments will influence a species' persistence and migration into new areas under global change.

The repertoire of life-history traits in the plant kingdom is truly vast. Differential investments in maintenance result in mean life expectancies that range between weeks (e.g. *Sanguinaria*, *Arabidopsis*) and thousands of years (e.g. *Pinus longaeva*, *Lomantia tasmanica*; Peñuelas & Munné-Bosch, 2010). Similarly, investments in reproduction can range widely too, with short-lived (e.g. *Bromus tectorum*) and perennial, semelparous species (e.g. *Agave*) at one end of the spectrum and highly iteroparous species (e.g. *Viola*), reproducing several times during their life spans, at the other extreme, with masting somewhere in between (Piovesan & Adams, 2005). Another important reproductive trait is the number of propagules per individual and annum, ranging between a handful (*Cocus nucifera*) to millions (orchids), or the rate of individual growth, which can range between 91 cm/day (bamboos) or 10 cm/day (hybrid Poplar) to merely 10.2 cm over 150 years (*Thuja occidentalis*). Together, how an organism invests its limited resources into maintenance, reproduction and growth defines the type of life-history strategy that it will follow during its lifetime. Using matrix population models (MPMs) from hundreds of plant species in the COMPADRE Plant Matrix Database (Salguero-Gómez et al., 2015), Salguero-Gómez et al. (2016) demonstrated that these life-history strategies can be adequately characterized according to two universal axes of variation: the pace of life of organisms (i.e. fast-slow continuum, Stearns, 1999) and their mode of reproduction (e.g. how intensively, frequently and for how long reproduction lasts).

It has been argued that dispersal may covary with life-history traits to produce integrated strategies or vary independently of other life-history traits (Bonte & Dahirel, 2017). Following Ronce and Clobert (2012), we refer to the covariation of dispersal with

multiple phenotypic traits, including life-history or behavioural traits, as dispersal syndromes, and reserve dispersal mode for the method of dispersal inferred from fruit or seed morphology. While examining the covariation of dispersal with life-history traits, or lack thereof, cannot distinguish the underlying mechanisms or its ultimate causes, evaluating the presence or absence of dispersal syndromes in plants can help elucidate the joint evolution of traits among species and the demographic consequences of dispersal (Ronce & Clobert, 2012). The relationship between dispersal and plant life-history strategies has remained unclear to date due to the fact that quantifying seed dispersal empirically is challenging, and hence, data on dispersal tends to be limited. However, the availability of large volumes of open-access data on demography (Salguero-Gómez et al., 2015), dispersal (Bullock et al., 2017; Tamme et al., 2014) and functional traits (Kattge et al., 2011) is increasing.

By synthesizing available data on life-history traits, as derived from empirical stage-based demographic models, with recent approaches to predict dispersal ability from plant traits, we incorporate dispersal ability into analyses of life-history strategies and examine whether dispersal ability covaries with life-history traits, and if so, how. If dispersal is independent of life-history traits, we predict an independent axis of variation describing dispersal will be added to the existing axes describing the fast-slow continuum and the mode of reproduction. However, if dispersal ability covaries with life-history traits, then we predict that the axes of variation describing life-history strategies will shift with the inclusion of dispersal. We evaluate the following hypotheses regarding how dispersal will covary with life-history traits:

1. If dispersal evolved as a bet-hedging strategy to take advantage of habitats that vary unpredictably in space and time, we predict dispersal distance to correlate positively with life-history traits indicative of fast life-history strategies (e.g. short generation times, high investments on reproduction, high individual growth rates; Baker & Stebbins, 1965; McPeek & Holt, 1992; Roff, 1975; Snyder, 2011).
2. We expect dispersal distance to correlate positively with fecundity, based on classical theories that predict selection for dispersal to escape kin competition under the source parent tree (Hamilton & May, 1977; Hovestadt et al., 2001; Rousset & Gandon, 2002; Starrfelt & Kokko, 2010) and selection for long-distance dispersal to escape specialized natural enemies (Connell, 1971; Janzen, 1970; Muller-Landau et al., 2003).
3. Dispersal distance could also be positively correlated with generation time; species with shorter generation times can maintain gene flow through time (e.g. they have more opportunities to exchange genetic information per unit time), and species with longer generation times are expected to maintain gene flow through space (Stevens, Trochet, Van Dyck, Clobert, & Baguette, 2012). In addition, organisms can evolve longer life spans when their propagules disperse farther, escaping kin competition for space (Dytham & Travis, 2006).

Growth form and plant size can constrain the variation of plant life histories, and, in combination with dispersal modes, could constrain dispersal syndromes. Growth form describes potential constraints due to anatomy (Salguero-Gómez et al., 2016), while dispersal mode, growth form and plant height explain dispersal distances (Tamme et al., 2014; Thomson, Letten, Tamme, Edwards, & Moles, 2018). Salguero-Gómez et al. (2016) found that growth form and matrix dimension—associated with plant size and life cycle complexity—explained the location of species on the axes of variation describing the fast-slow continuum and the mode of reproduction. We examine whether a plant's mode of dispersal, growth form and matrix dimension help explain how species are distributed along axes of variation describing dispersal and life-history traits. If dispersal varies independently of life-history traits, we expect dispersal mode to explain a species' location on the axis of variation that captures dispersal ability (Tamme et al., 2014), and growth form to explain species' locations on the axes capturing the fast-slow continuum and reproductive strategies (Salguero-Gómez et al., 2016), while matrix dimension would be associated with both dispersal and life-history traits.

2 | MATERIALS AND METHODS

To determine how dispersal covaries with life-history traits, we brought together data on demography, dispersal and functional traits. Demographic data were obtained from the COMPADRE Plant Matrix Database (Salguero-Gómez et al., 2015). We defined dispersal ability in terms of maximum dispersal distance and obtained measured maximum dispersal distances from Tamme et al. (2014). The number of species that overlapped between both datasets was 47. To include more species and improve our ability to ascertain general patterns, we predicted maximum dispersal distances for species using information on functional traits, dispersal mode and growth form based on published relationships (Tamme et al., 2014); this resulted in a total of 141 species for which we were able to predict dispersal distances and derive life-history traits.

Species names across datasets were standardized using The Taxonomic Name Resolution Service using all available data sources (Boyle et al., 2013; The Taxonomic Name Resolution Service), including Tropicos (Missouri Botanical Garden), USDA (USDA, NRCS), Global Composite Checklist (Flann, 2009), The Plant List (2013) and the International Legume Database and Information Service. Angiosperm Phylogeny Group III was used for standardization of family and order names (http://www.mobot.org/MOBOT/research/APweb/). Species with unresolved taxonomic names that otherwise matched across datasets were retained in the analysis. We obtained a phylogeny by trimming down the tree made available by Zanne et al. (2014) to the number of species used in each analysis using the package *ape* (Paradis, Claude, & Strimmer, 2004) in R (R Core Team, 2017).

2.1 | Dispersal ability

Dispersal ability in evolutionary models is usually expressed as the propensity to disperse or a summary of dispersal distances (e.g.

statistical moments of distribution, non-local dispersal; Duputié & Massol, 2013; Saastamoinen et al., 2018). Maximum dispersal distance is a useful metric as it represents long-distance dispersal ability, directly relating to the ability to colonize new areas, and due to the high correlation with mean dispersal distances (R^2 = .85–.90 Tamme et al., 2014; Thomson, Moles, Auld, & Kingsford, 2011), it also represents local dispersal ability relevant to within population processes.

We generated maximum dispersal distances using the *dispeRsal* function (version 0.2) developed by Tamme et al. (2014). The function predicts maximum dispersal distances using a linear mixed-effects model that can include information on dispersal mode (i.e. no special mechanism, ballistic, ant, wind, animal), growth form (i.e. herb, shrub, tree), seed mass or terminal velocity (i.e. velocity of the diaspore falling in still air, Greene & Johnson, 1992) as fixed effects, as well as taxonomic family or order as random effects. We obtained trait data from open-access sources as described in the Supplementary Methods in the Supporting Information. A list of data sources from the TRY Plant Trait Database used in this study are provided in the Data sources section. We $\log_{10}$-transformed continuous trait values to meet parametric assumptions, and calculated the mean for each species if more than one value was reported.

To predict maximum dispersal distances, we chose models based on available information for each species that resulted in the highest predictive power as determined by the R^2 reported in Tamme et al.

TABLE 1 Loadings of dispersal and life-history traits on the first three principal components for 141 species. Loadings in bold (≥0.30) have a greater contribution to each PC axis. Descriptions sensu Salguero-Gómez et al. (2016)

Trait	Symbol	Definition	PC1	PC2	PC3
Dispersal					
Dispersal ability	D	Maximum dispersal distance	0.13	**0.43**	−0.19
Turnover					
Generation time	T	Number of years necessary for individuals of a given population to be replaced by new ones	**0.50**	0.25	−0.09
Longevity					
Survivorship curve type	H	Shape of the age-specific survivorship curve, as quantified by Keyfitz' entropy (Wrycza & Baudisch, 2014). H > 1: most deaths occur at early ages. H < 1: number of deaths increases with age	**0.32**	**−0.31**	**−0.43**
Age at sexual maturity	L_α	Number of years that it takes an average individual in the population to become sexually mature	**0.35**	0.25	**−0.38**
Growth					
Progressive growth	γ	Mean probability of transitioning to a larger/more developed stage, weighted by the stable stage distribution (SSD)	**−0.30**	−0.23	**−0.30**
Retrogressive growth	ρ	Mean probability of transitioning to a smaller/less developed stage in the life cycle of species, weighted by the SSD	0.14	**−0.47**	0.10
Reproduction					
Mean sexual reproduction	ϕ	Mean per capita number of established sexual recruits across stages in the life cycle of the species, SSD-weighted	**−0.41**	−0.17	−0.29
Degree of iteroparity	S	Spread of reproduction throughout an individual's life span as quantified by Demetrius' entropy (Demetrius, 1978). Low values of S indicate semelparity, and higher values, higher iteroparity	−0.18	0.17	**−0.43**
Net reproductive rate	R_0	Mean number of established recruits produced during the mean life expectancy of an individual in the population	**−0.39**	**0.31**	**−0.32**
Mature life expectancy	L_ω	Number of years from the mean age at sexual maturity (L_α) until the mean life expectancy of an individual in the population	−0.21	**0.41**	**0.39**
Proportion variance explained			0.26	0.20	0.16
Cumulative proportion of variance explained			0.26	0.46	0.61

(2014). For each species, we included growth form and dispersal mode as fixed effects. In addition, we included seed mass, terminal velocity or taxonomic information when these data were available for a species (taxonomic names had to match data used in the *dispeRsal* predictive model from Tamme et al. (2014); see Supplementary Methods for details).

2.2 | Life-history traits

We obtained demographic information from the COMPADRE Plant Matrix Database (https://www.compadre-db.org, version 4.0.1). Life-history traits were derived from MPMs (Caswell, 2001). Briefly, MPMs are discrete time, discrete stage population models where individuals are categorized according to a mixture of age-, size- and/or ontogenetic classes that define their rates of survival, transition between classes, and rates of sexual/clonal reproduction. Similar to Salguero-Gómez et al. (2016), we included MPMs parameterized with field data from natural populations representing whole individual (genet) plants under unmanipulated conditions, among other criteria described in the Supplementary Methods. In contrast to Salguero-Gómez et al. (2016), we only included non-clonal plants where sexual reproduction had been explicitly quantified as we were interested in movement capacity via seed dispersal by seed-bearing plants. Through various demographic methods described elsewhere (Caswell, 2001; Cochran & Ellner, 1992), multiple summary statistics of vital rates and resulting life-history traits that describe the strategies of different species can be calculated from these MPMs. Nine life-history traits were calculated sensu Salguero-Gómez et al. (2016) related to investments in population turnover (T), longevity (H, L_α), growth (γ, ρ) and reproduction (ϕ, S, R_0, L_ω) as described in Table 1 and Table S1. Specifically, the life-history traits are generation time (T), rate of senescence (H), age at sexual maturity (L_α), progressive growth (γ), retrogressive growth (shrinkage; ρ), mean sexual reproduction (ϕ), degree of iteroparity (S), net reproductive rate (R_0) and mature life expectancy (L_ω).

2.3 | Statistical analyses

We used principal component analyses (PCA) to examine how predicted maximum dispersal distance (D) relates with plant life-history traits as described in Table 1. This allowed us to examine covariation of maximum dispersal distances with life-history traits associated with fast life-history strategies (e.g. short generation times, high reproduction and high progressive growth; Hypothesis 1), high fecundity (high net reproductive rate, mean sexual reproduction; Hypothesis 2) and long generation times (Hypothesis 3). We used parallel analysis to simulate 95th percentile eigenvalues from 100 simulated analyses and determine the number of retained principal components (Franklin, Gibson, Robertson, Pohlmann, & Fralish, 1995; Horn, 1965) using the function *f a.parallel* in the *psych* package (Revelle, 2017) in R (R Core Team, 2017).

To control for non-independence among lineages in our study, we conducted a phylogenetically informed PCA using the package *phytools* (Revell, 2012) in R (R Core Team, 2017). This approach differs from a standard PCA in that it explicitly incorporates the phylogeny into the backbone of the PCA, correcting for the lack of independence and estimating the phylogenetic signal in the examined relationships at the same time. We estimated Pagel's λ, a scaling parameter that quantifies the phylogenetic correlation among species, ranging between 0 (no role of phylogeny in determining trait covariation) and 1 (trait covariation fully explained by phylogenic relationships, assuming Brownian motion; Freckleton, Harvey, & Pagel, 2002).

We first conducted a PCA on life-history traits for the 141 species, not including predicted maximum dispersal distances. Subsequently, we conducted the PCA including life-history traits and predicted maximum dispersal distances to explicitly incorporate dispersal ability into the life-history strategies. We compared the PCA results with and without dispersal distances to examine whether and how variation in axes of life-history strategies shift when including dispersal ability. We also conducted the PCA for the 47 species that had measured maximum dispersal distances in Tamme et al. (2014). For each analysis (Tables S3–S5), the phylogenetic signal as measured by Pagel's λ was low (<0.24), suggesting a weak effect of the ancestral relationships among the examined lineages onto the configuration of life-history traits and dispersal (Freckleton, 2012). Hence, here we report the results for the non-phylogenetically informed PCA.

For each PCA, we used the *imputePCA* function of the *missMDA* (Josse & Husson, 2016) package in R (R Core Team, 2017) to impute missing values. For the of 141 species, a total of 8.2% (116) of the 1,410 possible trait values were missing. Such missing values of life-history traits arose from outliers identified as trait values greater than 3 standard deviations from the mean (after transformation; criteria for outliers sensu Diaz et al., 2016; Salguero-Gómez et al., 2016), as well as some life-history trait calculations having no solutions under certain circumstances, as detailed elsewhere (see Caswell, 2001; Salguero-Gómez et al., 2016; Stott, Franco, Carslake, Townley, & Hodgson, 2010). Life-history traits and dispersal distances were transformed to meet assumptions of linearity in the PCA, as described in the Supplementary Methods, and then standardized by the mean and *SD* before inclusion in multivariate analyses.

To examine whether a plant's mode of dispersal, growth form and matrix dimension (i.e. life cycle complexity) explain the location of a species along the major principal components, we used an ANOVA with Type 1 SS (Hector, Von Felten, & Schmid, 2010) including matrix dimension, dispersal mode, growth form and their two-way interactions as predictors (function *aov* in R, R Core Team, 2017). We controlled for matrix dimension before including additional terms as it is a property of these demographic models known to bias demographic outputs (Enright, Franco, & Silvertown, 1995; Salguero-Gómez & Plotkin, 2010); the order of dispersal mode or growth form did not influence results and are similar to results using Type 2 SS (data not shown). Because of the small sample sizes across most combinations of growth forms and dispersal modes (Table S2), we only include herbs and trees that are dispersed by either wind or animals in this analysis (59 animal-dispersed herbs, 24 animal-dispersed trees, 19 wind-dispersed herbs and 15 wind-dispersed trees).

To ensure our results were not affected by statistical dependence among the principal components, we conducted a permutational ANOVA on the first three principal components using Euclidian distance and 9,999 permutations with the function *adonis* in the package *vegan* (Oksanen et al., 2017) in R (R Core Team, 2017). As the results for the permutational ANOVA (Table S9) were the same as the results for the ANOVA, we report the results obtained from the ANOVA here. All analyses were conducted in R (R Core Team, 2017).

3 | RESULTS

3.1 | Life-history strategies

For life-history traits of the 141 species, the first three principal components were retained (Figure S1) and explain 65% of the variation (Table S6). The first axis of variation, principal component one (PC1), describes the fast-slow pace of life continuum (hereafter, the fast-slow axis), with species characterized by fast individual growth (γ), high mean sexual reproduction (ϕ) and high net reproductive rates (R_0) at one end, and species that postpone their first reproductive event to advanced ages (high L_α), have a low population turnover (high T) and tend to escape from senescence ($H > 1$), at the other end (Figure S2). The second axis of variation (PC2) describes the reproductive window and is associated with species that have a long reproductive window (high L_ω) on one end, and species that have a high likelihood of escaping senescence ($H > 1$), grow fast (high γ), high shrinkage (high ρ) and high mean sexual reproduction (ϕ) at the other end. The third principal component (PC3) describes modes of reproduction (hereafter, the reproductive strategy axis) and is associated with species that are iteroparous (high S), delay sexual maturation (high L_α), and have high net reproductive rate (R_0) vs. those that are semelparous with low net reproductive rates and earlier sexual maturation.

3.2 | Do plants exhibit dispersal syndromes?

After incorporating dispersal ability into the PCA for the 141 species, the first three principal components were retained (Figure S3) and capture 61% of the variation in life-history strategies (Table 1, Table S7). The first principal component is qualitatively similar to the above analyses that do not include maximum dispersal distances, and it depicts the fast-slow continuum (Figure 1). However, the value of the loadings on the second and third principal components shifts with the incorporation of dispersal. Specifically, net reproductive rate (R_0) has a higher loading while mean sexual reproduction (ϕ) and growth (γ) become less important on PC2 after including dispersal. PC2 describes life-history strategies incorporating dispersal ability (hereafter, the dispersal strategy axis) and is associated with species that have longer dispersal distances (high D), tend to have a long window of reproduction (high L_ω), and have high net reproductive rates (R_0) on one end, and species that have a high likelihood of escaping senescence ($H > 1$) and experience high shrinkage (high ρ) on the other end. PC3 describes the reproductive strategy axis and is associated with species that have a high likelihood of escaping senescence ($H > 1$), high frequency of reproductive events (high S), delay their age at sexual maturity (high L_α), high net reproductive rate (high R_0), and high rate of growth of individual plants (high γ) on one end and large reproductive window on the other end (high L_ω). The results are qualitatively similar for the 47 species with measured maximum dispersal distances from Tamme et al. (2014) (Tables S5 and S8).

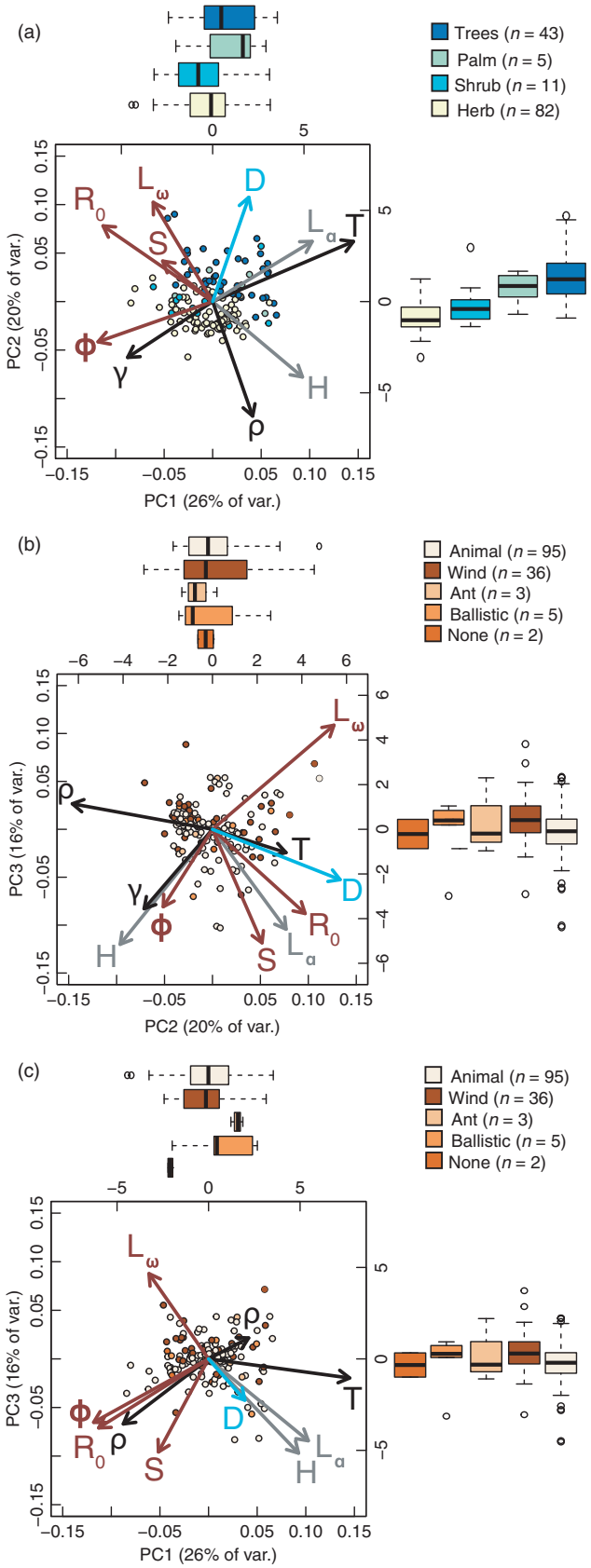
3.3 | Do dispersal mode and growth form explain the distribution of species along dispersal syndromes?

Both dispersal mode and growth form explain variation in a species' location on at least one principal component after controlling for matrix dimension for herbs and trees that are dispersed by either wind or animals. Matrix dimension is significantly larger in trees compared to herbs ($F_{1,113} = 27.73$, $p < .001$)—corresponding naturally to the more complex life cycle of larger species. Matrix dimensions do not differ among dispersal modes ($F_{1,113} = 1.49$, $p = .23$) nor is the interaction between growth form and dispersal mode significant ($F_{1,113} = 2.18$, $p = .14$; Figure S4).

Dispersal mode and growth form do not influence species location on the fast-slow axis (PC1). Species with larger matrix dimensionality have significantly slower life-history strategies as depicted by higher scores on PC1 ($F_{1,109} = 13.35$, $p < .001$; Table 2, Figure S5a,b).

Growth form ($F_{1,109} = 134.85$, $p < .001$) and matrix dimension ($F_{1,109} = 17.83$, $p < .001$) significantly explain the location of species on the dispersal strategy axis (PC2, Table 2). Generally, trees have higher scores on PC2 (Figure 2a), though a significant interaction exists between dispersal mode and growth form ($F_{1,109} = 5.92$, $p < .05$). Trees generally have higher dispersal ability (high D), less frequent shrinkage (lower ρ), a long window of reproduction (high L_ω), high net reproductive rates (R_0) and lower likelihood of escaping senescence ($H < 1$) on the dispersal strategy axis (PC2) compared to herbs. Wind-dispersed trees have the highest mean scores on the dispersal strategy axis (PC2), followed by animal-dispersed trees, while wind-dispersed herbs have the lowest mean scores on the dispersal strategy axis (PC2) with animal-dispersed herbs second to lowest (Figure 2a). There is also an interaction between dispersal mode and matrix dimension ($F_{1,109} = 5.75$, $p < .05$). At higher matrix dimensions, wind-dispersed species have higher scores on PC2 than animal-dispersed species, and this difference becomes smaller and eventually reverses at lower dimensions (Figure S5b,c).

Dispersal mode ($F_{1,109} = 6.28$, $p < .05$) and matrix dimension ($F_{1,109} = 39.87$, $p < .001$) significantly explain the location of species on the reproductive strategies axis (PC3, Table 2). Wind-dispersed species have consistently higher scores on the reproductive strategy axis compared to animal-dispersed species (PC3, Figure 2b). This suggests wind-dispersed species tend to have a large reproductive window (high L_ω), while animal-dispersed species have a high likelihood of escaping senescence ($H > 1$), high frequency of reproductive events (high S), delay their age at sexual maturity (high L_α), high



net reproductive rate (high R_0) and high rate of growth of individual plants (high γ). Species with higher matrix dimensionality have lower scores on the reproductive strategy axis (PC3, Figure S5e,f).

FIGURE 1 The ordination of the first three principal component axes (PC1, PC2 and PC3) of dispersal ability and life-history traits for 141 plant species (See Table 1) show that plants exhibit dispersal syndromes. PC1 describes the fast-slow continuum of life-history strategies, PC2 describes the dispersal strategy axis and PC3 describes the reproductive strategy axis. Box plots show variation in principal component scores within growth forms (a) and dispersal modes (b, c)

4 | DISCUSSION

Our study shows that seed dispersal ability—defined as maximum dispersal distance—has not evolved independently of other life-history traits across plant species. Dispersal seems indeed to be an integral part of a complex suite of traits; dispersal and life-history traits covary to form dispersal syndromes (Ronce & Clobert, 2012), which have also been recognized among animals (Stevens et al., 2014). In our analyses with 141 plant species, dispersal syndromes comprised three main axes of variation related to the fast-slow continuum (PC1), dispersal strategies (PC2) and reproductive strategies (PC3). We found that species dispersal ability was related to values of life-history traits of species that exhibit fast life-history strategies (Prediction 1). Species with high maximum dispersal distances tended to have a long window of reproduction, high net reproductive rates, higher rate of senescence and less frequent shrinkage. As dispersal was positively associated with net reproductive rate R_0, dispersal could also be a strategy to escape competition or natural enemies (Prediction 2). Maximum dispersal distance was not associated with generation times (Prediction 3). For herbs and trees that

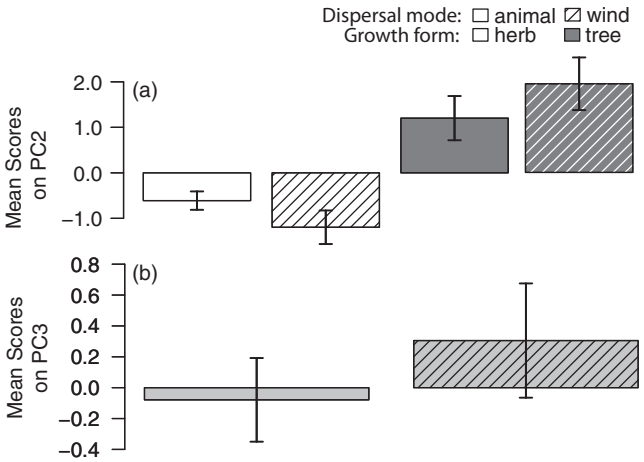


FIGURE 2 The effect of dispersal mode and growth form on species location on the second and third principal components: (a) Trees have higher mean scores on the dispersal strategy axis (PC2) than herbs, with scores of wind- dispersed trees greater than animal-dispersed trees, and scores of animal-dispersed herbs greater than wind-dispersed herbs. (b) Wind-dispersed species have larger mean scores on the reproductive strategy axis (PC3) compared to animal-dispersed species. Shading indicates growth form (dark grey: trees, white: herbs, light grey: both), while stripes indicate wind-dispersed plants and no stripes indicate animal-dispersed plants

TABLE 2 Results of ANOVA including matrix dimension, dispersal mode and growth form as predictors for the first three principal components including life-history traits and dispersal mode for 117 species

Variable	*df*	SS	MS	*F*
Fast-slow continuum (PC1)				
Matrix dimension (MD)	1	29.33	29.33	13.35***
Dispersal mode (DM)	1	1.23	1.23	0.56
Growth form (GF)	1	8.11	8.11	3.69†
Matrix dimension * dispersal mode	1	1.51	1.51	0.69
Matrix dimension * growth form	1	0.14	0.14	0.06
Dispersal mode * growth form	1	2.20	2.20	1.00
MD * DM * GF	1	0.12	0.12	0.05
Residuals	109	239.47	2.20	
Dispersal strategy (PC2)				
Matrix dimension	1	15.37	15.37	17.83***
Dispersal mode	1	0.94	0.94	1.09
Growth form	1	116.25	116.25	134.85***
Matrix dimension * dispersal mode	1	4.95	4.95	5.75*
Matrix dimension * growth form	1	0.62	0.62	0.72
Dispersal mode * growth form	1	5.11	5.11	5.92*
MD * DM * GF	1	0.34	0.34	0.40
Residuals	109	93.97	0.86	
Reproductive strategy (PC3)				
Matrix dimension	1	41.38	41.38	39.87***
Dispersal mode	1	6.51	6.51	6.28*
Growth form	1	0.01	0.01	0.005
Matrix dimension * dispersal mode	1	0.35	0.35	0.34
Matrix dimension * growth form	1	3.90	3.90	3.75†
Dispersal mode * growth form	1	1.07	1.07	1.03
MD * DM * GF	1	0.65	0.65	0.63
Residuals	109	113.14	1.04	

***$p < .001$, **$p < .01$, *$p < .05$, †$p < .1$.

are dispersed by either wind or animals, the location of a species on the fast-slow continuum (PC1), the dispersal strategy axis (PC2) and the reproductive strategy axis (PC3) was significantly explained by a species' matrix dimension, and for the reproductive strategy, a plant's dispersal mode. A species location on the dispersal strategy axis was additionally explained by a plant's growth form and interactions with dispersal mode.

4.1 | Life-history strategies

Our decomposition of the main drivers of life-history strategies in plants is qualitatively similar to previous examinations (Salguero-Gómez et al., 2016). However, a few variables have shifted their importance on each axis of life-history variation. This is most likely because the 141 species included in our analyses do not capture the range of growth forms included in the previous study of 418 species (Table S2). We excluded clonal species and species that did not have sexual reproduction quantified as we wanted to focus on movement ability in terms of seed dispersal by seed-bearing plants. Plant species with a clonal strategy may differ in their life-history strategies compared to non-clonal species (Kroon & Groenendael, 1997). For example, clonal species may have alternative strategies to escape herbivory associated with tolerance (Pellissier et al., 2016), different patterns of senescence due to the accumulation of mutations (Ally, Ritland, & Otto, 2010; Salguero-Gómez, 2017) and trade-offs with investment in sexual reproduction, influencing fecundity (Barrett, 2015).

4.2 | The dispersal syndromes of plants

We found evidence for dispersal syndromes across plant species as the axes of variation of life-history strategies based on life-history traits shifted with the inclusion of maximum dispersal distances. Specifically, we found that high dispersal ability was related to fast life-history strategies. Previous studies in plants have provided evidence for dispersal syndromes based on phenotypic traits, such as plant height, seed mass and dispersal structures (Tamme et al., 2014; Thomson et al., 2011, 2018). Across animal species, Stevens et al. (2014) found that dispersal ability was consistently associated with high fecundity and survival, and, in aerial dispersers, with early maturation, but the strength, direction and functional form of these relationships varied within taxonomic orders. Across animal and plant groups, species seem to have converged on similar dispersal syndromes that relate high dispersal ability with aspects of fast life-history strategies, including high reproductive rates for all organisms studied, early maturation for aerial-dispersing terrestrial animals and a long window of reproduction for terrestrial plants. This could have arisen from two potential mechanisms: (1) a suite of traits evolving as a bet-hedging strategy in response to unpredictable habitats (Prediction 1) or (2) dispersal evolving in response to the negative impacts of high fecundity on fitness via increased kin competition or mortality due to specialized natural enemies (Prediction 2). In each case, dispersal has evolved in tandem with life-history traits.

For this analysis, we predicted dispersal distances for 141 species using dispersal mode and growth form, including functional traits and taxonomic names when possible, to increase the number of species included in the PCA. This approach seemed to capture the covariation in dispersal and life-history traits as the results were qualitatively similar for the 47 species for which there were measured dispersal distances available in Tamme et al. (2014). In previous analyses, major habitat was a significant predictor of the

position of plant species on the fast-slow axis of life-history strategies (Salguero-Gómez et al., 2016). Dispersal ability of a plant species may also vary by habitat as the mode of dispersal can depend on precipitation, temperature and altitude (Almeida-Neto, Campassi, Galetti, Jordano, & Oliveira-Filho, 2008; Chen, Cornwell, Zhang, & Moles, 2017). As data for dispersal and demography continue to grow, future studies can examine how these relationships and dispersal syndromes vary by major habitat.

Here, we have measured but one component of the dispersal process—the maximum dispersal distance of seeds. However, dispersal is made up of several phases, including pre-departure, departure, transfer and settlement. The maximum dispersal distance of seeds is most related to the transfer phase. Each of these phases incur some costs to dispersing (Bonte et al., 2012; Clobert, Le Galliard, Cote, Meylan, & Massot, 2009), and selection will act to optimize fitness by minimizing costs associated across these multiple phases of dispersal (Bonte et al., 2012; Travis et al., 2012). Both the pre-departure and departure phases include costs associated with the investment in dispersal structures, from no specialized structures to plumes or wings for dispersal by wind to fleshy fruits for dispersal by animals. Each of these may have different energy requirements and developmental times, which may covary with other life-history traits, such as traits related to reproduction and growth. During these phases, plants may incur costs from predators and pathogens that reduce their ability to disperse seeds (Tewksbury & Nabhan, 2001; Tiansawat, Beckman, & Dalling, 2017). A plant's ability to deter reductions in dispersal due to predation would be related to its ability to develop and disperse fast enough to escape predation (related to growth strategies), satiate predators (related to number of seeds produced) or otherwise defend themselves. After the settlement phase, seedlings will have to grapple with the local environment, competition with their neighbours, and mortality due to natural enemies which may be related to growth strategies (e.g. tolerance vs. defence) and turnover.

This study suggests that dispersal syndromes exist across plant species, but more work needs to be done in terms of individual variation where dispersal is predicted to be an independent axis (Bonte et al., 2012). Saastamoinen et al. (2018) showed that dispersal is a complex process arising from several interacting traits and a complex genetic architecture; they found that although some genes influence certain aspects of dispersal with moderate to large effect, dispersal traits are typically polygenic. Studies on the genetic correlations of dispersal tend to be scarce, and the topic requires further study. In contrast, within species correlations among dispersal traits as well as between dispersal traits and other traits under selection are more common in animals (Saastamoinen et al., 2018), but less well studied in plants. Future research on the drivers of variance in dispersal distances within species will give additional insight into the fitness benefits of dispersal and potential trade-offs or synergies with life-history traits.

Finally, selection for longer dispersal distances will influence the ability of plant species to invade new habitats (Hastings et al., 2005), track changing climates (Travis et al., 2013) and persist in fragmented landscapes (Williams, Kendall, & Levine, 2016). As dispersal ability covaries with life-history traits to form dispersal syndromes, the selection for dispersal in response to global change may be constrained by or indirectly influence the evolution of life-history traits. For example, evolving populations of *Arabidopsis thaliana* in experimental landscapes spread much faster in fragmented than continuous landscapes due to the selection for dispersal and competitive tolerance (Williams et al., 2016). How global change events influence the evolution of dispersal syndromes requires further investigation and will improve our ability to manage and conserve populations under global change.

4.3 | Dispersal mode and growth form explain how species are distributed along the strategies of dispersal syndromes

Matrix dimension, growth form and dispersal mode significantly explained variation of a species' location on at least one of the main axes of plant dispersal syndromes of herbs and trees dispersed by either wind or animals. Matrix dimension represents the number of life-history stages of an organism. The number of life-history stages represents model complexity based on the informed-decisions of the researchers who assembled the matrices, and, in this study, plant size, as trees had significantly higher matrix dimensionality than herbs. Matrix dimension explained a significant amount of variation across all three axes of variation. On the fast-slow continuum (PC1), species with higher matrix dimensionality, mostly represented by trees, had significantly slower life-history strategies, while species with lower matrix dimensionality, mostly represented by herbs, had significantly faster life-history strategies. These results are similar to previous analyses (Salguero-Gómez et al., 2016).

Growth form and dispersal mode partly determined the dispersal strategy exhibited by different species as depicted by their mean scores on the dispersal strategy axis (PC2). Trees tended to have higher scores on the dispersal strategy axis compared to herbs, suggesting higher dispersal ability of trees compared to herb species. Higher dispersal ability of trees is in-line with previous studies that show, all else being equal, taller plants tend to disperse their seeds farther regardless of dispersal modes (Tamme et al., 2014; Thomson et al., 2011), and trees tend to be the tallest plant species as plant height increases across growth forms (herbs < shrubs < trees; Moles et al., 2009). While taller plants are more likely to invest in the presence of dispersal structures, height alone is a better predictor of dispersal distances (Thomson et al., 2018). In addition, taller trees may have a higher likelihood of dispersing further distances because they produce more seeds (Moles, Falster, Leishman, & Westoby, 2004). We found wind-dispersed trees had higher mean scores on the dispersal strategy axis (PC2), suggesting higher dispersal ability, compared to animal-dispersed trees. These patterns could partly be due to wind-dispersed species being taller than animal-dispersed species as plant height increases across dispersal modes (unassisted < ant < vertebrate < wind; Thomson et al., 2018). For wind-dispersed species, plant height per se can increase dispersal distances due to

canopy wind conditions (Augspurger, Franson, Cushman, & Muller-Landau, 2016; Soons, Heil, Nathan, & Katul, 2004).

Dispersal mode was partly related to the reproductive strategy exhibited by different species as depicted by their mean scores on the reproductive strategy axis (PC3). Wind-dispersed species tended to have higher scores on the reproductive strategy axis (PC3) than animal-dispersed species, suggesting wind-dispersed species have a longer reproductive window, lower frequency of reproductive events, earlier age of sexual maturity and lower net reproductive rate compared to animal-dispersed species. We are unaware of studies that have compared the life-history traits among plants differing in dispersal modes. These results suggest further research should investigate the reproductive strategies and allocation patterns of plants differing in dispersal modes.

5 | CONCLUSIONS

Here, we describe the dispersal syndromes of plants by quantifying the global variation in dispersal ability and life-history traits for 141 species. While dispersal syndromes have been previously described based on phenotypic traits, we show that high dispersal ability is related to aspects of fast life-history strategies. These results may be broadly generalizable across plant species as the phylogenetic signal in our multivariate analyses were low and follow previous findings in patterns of dispersal syndromes across animal species. Growth form and dispersal mode significantly explained variation in species' locations along the major axes of variation in dispersal syndromes, and this may potentially be driven by differences in plant height across growth form and dispersal mode. Understanding the covarying responses of dispersal and life-history traits to selection pressures will be crucial for predicting plant species responses to global change events.

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AUTHORS' CONTRIBUTIONS

All authors contributed to the development of ideas, interpretation of results, and writing of the manuscript. N.G.B. conducted the statistical analyses and wrote the manuscript. R.S.-G. developed the R script from which life-history traits were derived and the phylogenetic tree used in the phylogenetically corrected PCA.

DATA ACCESSIBILITY

All data used in this manuscript were obtained from publicly available sources. Maximum dispersal distances are available from Tamme et al. (2014). Traits are available from the KEW Seed Information Database (Royal Botanic Gardens Kew, 2016, available from http://data.kew.org/sid/), the TRY Plant Trait Database (Kattge et al., 2011, version 3.0, available from https://www.try-db.org), and the LEDA Traitbase (Kleyer et al., 2008, available from http://www.uni-oldenburg.de/en/biology/landeco/research/projects/leda/). Demographic information is available from the COMPADRE Plant Matrix Database (Salguero-Gómez et al., 2015, available from http://www.compadredb.org/). Taxonomic information was obtained from The Taxonomic Name Resolution Service using all available data sources (Boyle et al., 2013; The Taxonomic Name Resolution Service), including Tropicos (Missouri Botanical Garden), USDA (USDA, NRCS), Global Composite Checklist (Flann, 2009), The Plant List (2013), and International Legume Database and Information Service, and the Angiosperm Phylogeny Group III (available from http://www.mobot.org/MOBOT/research/APweb/).

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SUPPORTING INFORMATION

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

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