


LETTERS


Trade-off between seed dispersal in space and time

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Abstract

Seed movement and delayed germination have long been thought to represent alternative risk-spreading strategies, but current evidence covers limited scales and yields mixed results. Here we present the first global-scale test of a negative correlation between dispersal and dormancy. The result demonstrates a strong and consistent pattern that species with dormant seeds have reduced spatial dispersal, also in the context of life-history traits such as seed mass and plant lifespan. Long-lived species are more likely to have large, non-dormant seeds that are dispersed far. Our findings provide robust support for the theoretical prediction of a dispersal trade-off between space and time, implying that a joint consideration of risk-spreading strategies is imperative in studying plant life-history evolution. The bet-hedging patterns in the dispersal–dormancy correlation and the associated reproductive traits have implications for biodiversity conservation, via prediction of which plant groups would be most impacted in the changing era.

Keywords

Annual, dormancy, germination, iteroparity, lifespan, longevity, perennial, seed bank, seed dispersal.

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INTRODUCTION

The ecology of dispersal is key for a vast range of scientific and practical applications. Understanding how species differ in their ability to disperse has implications for predicting the invasiveness risk of plants, the restoration potential of natural ecosystems, the assembly of plant communities and species persistence in the Anthropocene (Howe & Smallwood, 1982; Poschlod *et al.* 2013). Seeds can be dispersed in space or in time (Poschlod *et al.* 2005). Spatial dispersal is achieved by transporting seeds away from parental plants, up to a few or even hundreds of kilometres (Shilton *et al.* 1999; Manzano & Malo, 2006). Temporal dispersal can be achieved by delayed seed germination, through either or both of dormancy (Venable & Lawlor, 1980; Gremer & Venable, 2014) and long-term persistence in soil seed banks (Grime, 1989; Honda, 2008; Saatkamp *et al.* 2014). With these potentials, seeds can be dispersed to a distant habitat or germinate after centuries (Priestley, 1986; Shen-Miller *et al.* 1995; Sallon *et al.* 2008; Yashina *et al.* 2012). Thus, both the spatial and temporal dimensions of dispersal have diverse consequences for gene flow and demography (Rubio de Casas *et al.* 2015; Saastamoinen *et al.* 2018). They are strategies to reduce parent-offspring and kin competition, to avoid inbreeding, to spread risks among offspring, and to persist through changing environments (Cohen & Levin, 1987; Poschlod *et al.* 2005; Siewert & Tielbörger, 2010; Buoro & Carlson, 2014). Here, we perform the first global test of the long-standing hypothesis that there is a trade-off between these two dispersal strategies.

Despite the broad importance of understanding patterns and determinants of seed dispersal, only a few studies have explored the species-level relationship between spatial dispersal (hereafter referred to as dispersal) and temporal dispersal (hereafter referred to as dormancy). These attempts have provided mixed results, as they have been restricted to certain modelling contexts or limited to certain plant taxa (synthesised in Buoro & Carlson, 2014). Theoretical studies have expected a negative correlation between optimal dispersal and optimal dormancy in environments with low variability, and a positive correlation in environments with high variability (Snyder, 2006; Siewert & Tielbörger, 2010). Empirical studies have reported various patterns using different proxies, in specific plant groups (mostly in herbaceous plants and Asteraceae species) and/or in single regions (Venable & Levin, 1983; Eriksson, 1992; Rees, 1993; Willson, 1993; Eriksson, 1996; Dostál, 2005; de Waal *et al.* 2016). For example, de Waal *et al.* (2016) found a significant negative relationship between diaspore falling velocity and germination fraction across 27 Asteraceae species in South Africa, whereas Eriksson (1992) found no relationship between the presence of a dispersal structure and the occurrence of a seed bank across 61 Swedish clonal species. Although a joint consideration of dispersal and dormancy is imperative in studying plant life-history evolution, current evidence covers a limited scale, as the characterisation and quantification of seed dispersal is challenging. Previous examinations have relied on surrogate indicators of dispersal, such as the presence of wings or falling velocity among wind-dispersed diaspores, instead of real

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distances covered. Therefore, little is known about the exact shape of the correlation even if there is one.

The other axes along the dispersal–dormancy trade-off are two important components in plant life-history strategies: adult plant lifespan and seed mass. First, lifespan broadly affects whether a plant can reproduce more than once in a lifetime (i.e. polycarpic; with a few notable, long-lived monocarpic exceptions). Extended lifespan has a crucial consequence, allowing the plant to spread the risk of reproduction across seasons as a persisting seed source (van Groenendael *et al.* 1998). It has been well-documented that seed dormancy is a bet-hedging strategy in annual plants (Gremer & Venable, 2014; de Waal *et al.* 2016). In contrast, perennial plants are assumed to favour distance dispersal to avoid parent-offspring competition and potential inbreeding (Venable & Levin, 1983), while also spreading the risk of potentially unsuccessful dispersal by substituting dormancy with multiple reproduction (Wilbur & Rudolf, 2006). Theoretical models predict a negative correlation between dispersal and dormancy in annual plants (Venable & Lawlor, 1980), while predictions are sparse in perennial plants. In de Waal *et al.* (2016), dispersal–dormancy correlation in annuals versus perennials showed contrasting patterns, depending on whether evolutionary history is accounted for. These clues indicate that long lifespan may evolve in response to environmental uncertainty, together with dormancy and dispersal. Second, seed mass is a central trait linking these three life-history strategies – dispersal, dormancy and plant lifespan (Venable & Brown, 1988). Generally, annuals produce small seeds that are dispersed close and persist long compared to perennials (Rees, 1994; Thomson *et al.* 2011). As perennials are more apparent in space and time ('plant apparency theory'; Feeny, 1976), the (generally) larger seeds of perennials are assumed to suffer higher seed predation than the smaller seeds of annuals (Thompson, 1987; Chen & Moles, 2018), and therefore dormancy may be selected against (Rees, 1993; Jurado & Flores, 2005). However, there is also evidence among Israeli annuals showing more dormancy in species with larger seeds (Harel *et al.* 2011). Correlations between these traits are usually examined in bivariate relationships. Thus, the roles of plant lifespan and seed mass in this puzzle are not yet resolved.

In this study, we compile a novel global data set to test if species with dormant seeds exhibit reduced spatial dispersal. We deploy both qualitative and quantitative metrics of seed dispersal that are generally intuitive and commonly used. We also test if a dispersal–dormancy correlation is a general pattern across both short-lived (annuals and biennials) and long-lived (perennials) species, and use piecewise structural equation models to examine the direct and indirect effects of plant lifespan and seed mass on this correlation.

MATERIALS AND METHODS

Data collection

Data on seed dormancy were from the database in Baskin & Baskin (2014). This data set is based on combined information on germination time and embryo/seed characteristics from an exhaustive review of literature over decades, and thus

provides a reliable and comprehensive data set of seed dormancy class. Species were classified as having non-dormant seeds, if more than half of the seeds germinated within 4 weeks and the seeds had fully developed embryos. Non-dormant seeds germinate under the widest range of conditions possible immediately after dispersal (Willis *et al.* 2014). Otherwise, species were assigned to one of the dormancy classes (Baskin & Baskin, 2014) and classified as having dormant seeds.

The qualitative metric of seed dispersal (short- vs long-distance dispersal; hereafter dispersal potential) can be applied to a broad range of species. Data on seed dispersal potential were compiled from the Seed Information Database (SID) of the Royal Botanic Gardens Kew (<https://data.kew.org/sid>) and following the methodology in Heleno & Vargas (2015). Species were classified to have long-distance dispersal if they are dispersed by vertebrate ingestion, by external adhesion to vertebrate fur or feathers, by wind or by oceanic current, while species lacking specialised dispersal structures relevant for long-distance dispersal were classified as having short-distance dispersal (details in Heleno & Vargas, 2015). Atypical and human-mediated seed dispersal were excluded.

The quantitative metric of seed dispersal (mean and maximum dispersal distances) allows adequate exploration of the relationship. Data on seed dispersal distance were obtained from the data set compiled by Chen *et al.* (2019b), a study focusing on the geographic aspects of seed dispersal distance. We followed the same data selection criteria in the present study as in Chen *et al.* (2019b), but also included records of seed dispersal distance from inexplicit locations (Appendix S1). Being highly correlated, mean and maximum dispersal distances respectively capture information about the average and the long-tailed movement of seeds (Chen *et al.* 2019b).

We resolved nomenclatural issues against the Plant List using the R package *Taxonstand* (Cayuela *et al.* 2012), and cross-referenced species in the data sets of seed dormancy and seed dispersal. As this is a species-level study, we excluded species with polymorphic seeds. In the final data sets, seed dormancy data could be matched to 1655 species of dispersal potential data, 323 species of mean dispersal distance data and 493 species of maximum dispersal distance data (Fig. 1).

When possible, seed mass and plant lifespan (annual vs perennial) were collected from the source papers of dispersal distance (Chen *et al.* 2019b). Otherwise, we acquired these data from SID, the BIOPOP database (Poschlo *et al.* 2003) and the TRY database (Kattge *et al.* 2020). The geometric mean of seed mass was used if there was more than one record for a given species. Annual and biennial species were grouped as annuals, in contrast to the life strategies of perennials characterised by multiple reproductive cycles over a lifetime (polycarpic *sensu lato*; Appendix S1).

Data analysis

Seed mass and dispersal distance were \log_{10} -transformed prior to all the analyses.

We compared dispersal potential across dormant and non-dormant species using phylogenetic logistic regression (Ives &

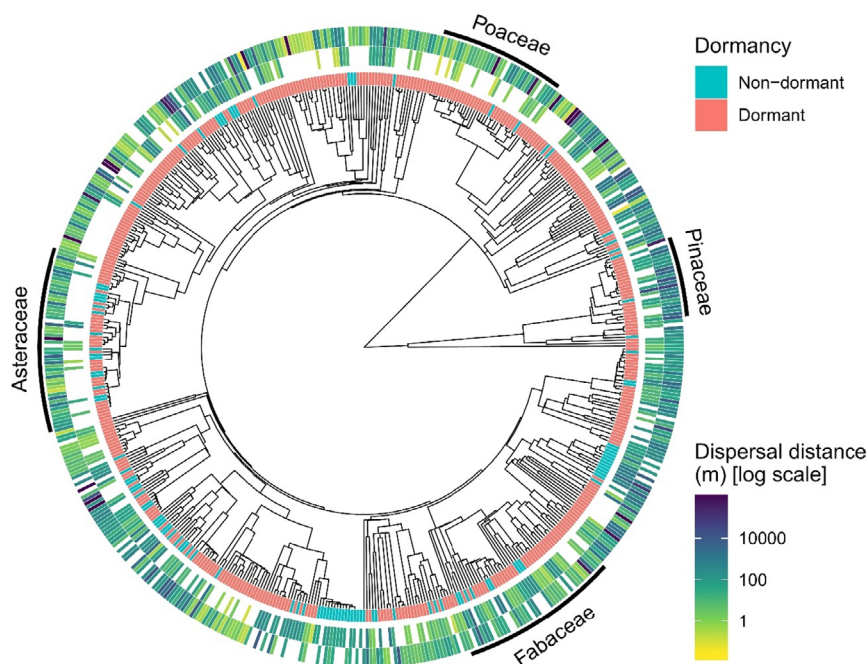


Figure 1 Phylogeny of study species with available information of seed dispersal distance and dormancy ($N = 558$). The innermost ring of the heatmap presents seed dormancy. The two outer rings (shown in the viridis palette) are mean and maximum measures of seed dispersal distance respectively. Families with information for more than 20 species are labelled. Graph with species names is provided in Appendix S4.

Garland, 2010). A phylogeny of the studied species was generated from the largest dated mega-tree for vascular plants (Open Tree of Life) using the R packages *V.PhyloMaker* (Jin & Qian, 2019). Model parameters and their 95% confidence intervals (CI) were estimated with 1000 bootstrap replicates using the penalised likelihood of the logistic regression via the R package *phylolm* (Ho & Ané 2014).

We compared mean and maximum seed dispersal distances respectively across dormant and non-dormant species using phylogenetic generalised least square (PGLS) models (Symonds & Blomberg, 2014). Because a species might have more than one record of seed dispersal distance in the data set, we randomly selected one record of dispersal distance for each species and repeated the sampling process for 1000 times to generate the distributions of model coefficients, as in Chen & Moles (2018). We calculated the mean values and 95% CI of coefficients. We derived a phylogeny of all the studied species (Fig. 1) and fitted PGLS assuming the Brownian motion model of trait evolution with Pagel's λ transformation (Pagel, 1999). The PGLS models were performed using the R packages *ape* (Paradis & Schliep 2018) and *nlme* (Pinheiro *et al.* 2020). In each run of the model, we also calculated the predicted average of dispersal distance in species with non-dormant seeds and the predicted average of dispersal distance in species with dormant seeds. We compared their paired difference with bootstrapping 95% CI using the R package *dabestr* and the method in Ho *et al.* (2019). With an expanding recognition of the limitations of using only statistical significance in hypothesis testing, this approach estimates effect sizes and their uncertainty, drawing attention away from dichotomous thinking (i.e. P -value statistics) and

towards quantitative reasoning of the result (Ho *et al.* 2019; Appendix S2).

To determine whether the dispersal–dormancy trade-off still existed regardless of plant lifespan, we repeated the above approaches to quantify the relationships between seed dormancy and seed dispersal within annual species and within perennial species respectively.

To evaluate both direct and indirect effects of plant lifespan and seed mass on the dispersal–dormancy correlation, we performed piecewise structural equation models (SEM) using the R package *piecewiseSEM* (Lefcheck, 2016). This approach offers a means of confirmatory path analysis and accommodates non-normal distributions of response variables (Lefcheck, 2016), which suits the seed dormancy and dispersal potential data in our study. Due to the data structure, we used the mean value of mean seed dispersal distances and the maximum value of maximum seed dispersal distances across available records for each species. Based on the causal hypotheses, we predicted that: (1) plant lifespan affects seed mass, dormancy and dispersal; (2) seed mass affects dormancy and dispersal; (3) dormancy and dispersal share a correlated error, which was our focus in this intercorrelated network. We started with this saturated model, as all paths were based on a plausible hypothesis. To assess goodness-of-fit, we constructed a final model by stepwise eliminating a non-significant path in (a) and (b), until the rest paths became significant and the model had an adequate overall fit through Fisher's C statistic. A small and non-significant C value ($P > 0.05$) indicates the acceptance of the null hypothesis that the model fits the observed data (Shipley, 2009).

RESULTS

Seed dormancy and dispersal potential showed a significant and negative correlation (Fig. 2). The probability of having short-distance dispersal increased from 17.3% in non-dormant species to 25.7% in dormant species (β coefficient = -0.50 , 95% CI = -0.75 to -0.26 , $P < 0.001$, $\alpha = 0.02$). That is, species with dormant seeds are more likely to have short-distance dispersal.

There was a substantial variability in seed dispersal distances for species within either dormant or non-dormant seeds. Although species with dormant seeds showed a broader range of seed dispersal distances at both extremes, these species generally had reduced seed dispersal ability compared to species with non-dormant seeds. Mean dispersal distance decreased from an average of 12.0 m in non-dormant species to an average of 5.7 m in dormant species ($P = 0.03$, $\lambda = 0.90$; Fig. 3). That means, non-dormant seeds are dispersed more than twice as far as dormant seeds, with a mean difference of 6.3 m (95% CI = 6.2–6.4; Appendix S2). Similarly, maximum dispersal distance decreased from an average of 84.8 m in non-dormant species to an average of 46.1 m in dormant species ($P = 0.13$, $\lambda = 0.60$; Fig. 3). In other words, non-dormant seeds were dispersed nearly twice as far as dormant seeds, with a mean difference of 38.7 m (95% CI = 38.0–39.4; Appendix S2).

Within either annuals or perennials, the negative correlation between dormancy and dispersal was not significant. Nevertheless, species with dormant seeds always have reduced

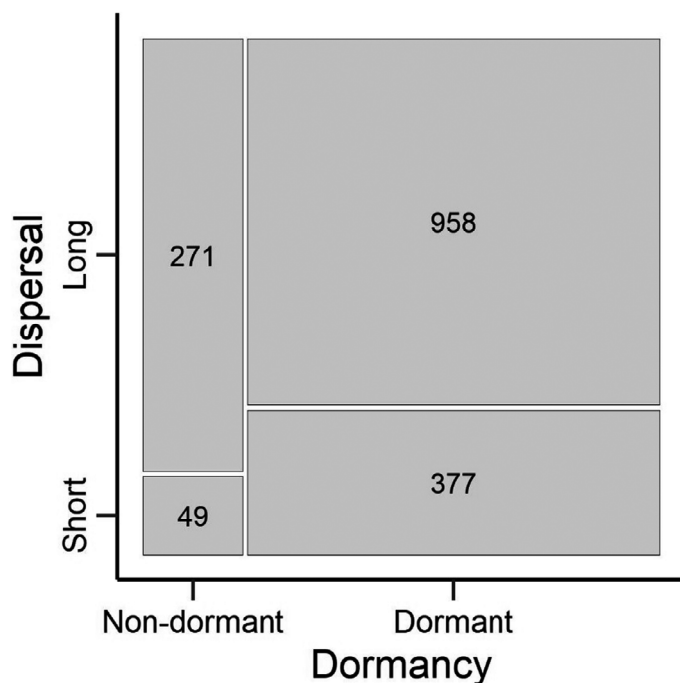


Figure 2 Mosaic plots showing short- or long-distance dispersal across species with non-dormant or dormant seeds. The numbers of species in each group are provided in each box. Species with dormant seeds are more likely to have short-distance dispersal than do species with non-dormant seeds.

dispersal distance or dispersal potential, compared to species with non-dormant seeds (Appendix S3).

All our piecewise SEM models had adequate fit to the data (Fig. 4). The dispersal–dormancy correlation was consistently negative, regardless of how we measured seed dispersal, although such correlation was marginally non-significant between seed dormancy and maximum dispersal distance ($P = 0.06$; Fig. 4c). In accordance with traditional expectations, seeds of perennial species were more likely to be larger, dispersed further and less likely to be dormant. The negative effect of plant lifespan on seed dormancy could be either direct (Fig. 4a) or indirect via seed mass (Fig. 4b & c).

DISCUSSION

Our study demonstrates a significant trade-off between dispersal in space and dispersal in time, based on the taxonomically and geographically broadest data sets to date. This finding provides rigorous support for the theoretical prediction that spatial dispersal and temporal dispersal represent alternative strategies to reduce risks of reproductive failure, implying that selection for one strategy could constrain evolution of the other. This study also represents by far the most comprehensive quantification to disentangle the roles of plant lifespan and seed mass in the dispersal–dormancy trade-off. The results provide empirical support for the hypothetical trade-offs among traits associated with dispersal, colonisation and extinction (van Groenendael *et al.* 1998). According to the triangular relations of the three characteristics, short-lived plants with non-dormant seeds and long-distance dispersal are most vulnerable to habitat fragmentation (van Groenendael *et al.* 1998). Meanwhile, strong dispersal capability and delayed germination are characteristics of many invasive species and are likely to offer escape from weed management practices (Donohue *et al.* 2010). Therefore, our result also has implications for biodiversity conservation to predict which plant groups concerning functional trait composition would be mostly impacted in global changes.

Dispersal trade-off

On average, species with dormant seeds disperse their seeds a substantially shorter distance than those with non-dormant seeds. This trend is consistent and conspicuous across data sets and analyses, suggesting a robust conclusion. The consistent results of a trade-off between dormancy and dispersal are in concert with a previous suggestion that dispersal strategies, either spatial or temporal, are guided by similar sources of information and cues in ecology and evolution (Buoro & Carlson, 2014). In addition to the risk-spreading purpose, either producing an extended seed shadow or germinating gradually could avoid a burst and subsequent crowding, which virtually relieves seeds from parent-offspring competition and/or sibling competition (Venable & Brown, 1988).

Besides regulating germination, seed dormancy could be functionally similar to seed dispersal in ecology (Venable & Lawlor, 1980; Venable & Brown, 1988). Seed dormancy is the adaptive strategy where growing season is ephemeral (Rubio

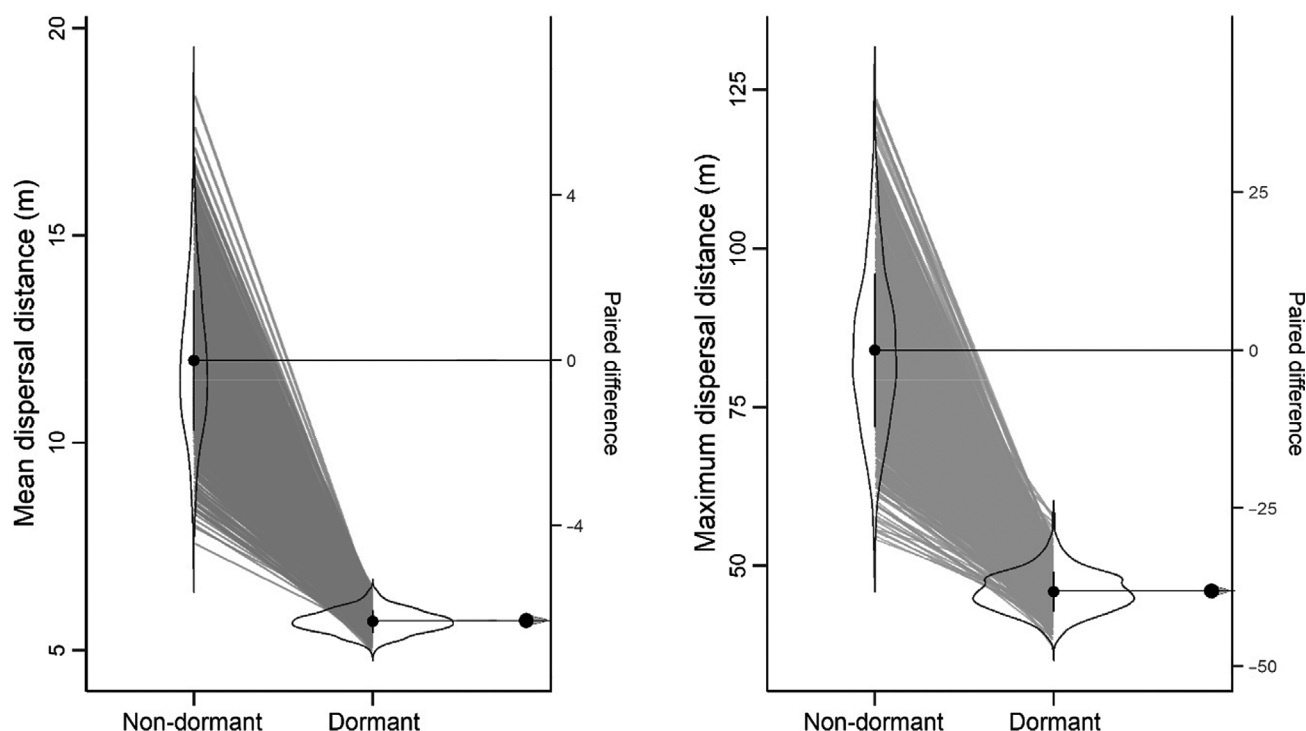


Figure 3 The estimation graphs and the difference axes depicting mean and maximum seed dispersal distances across species with non-dormant versus dormant seeds. The violin and line plots show predicted dispersal distances and their paired differences based on 1000 random selections of one dispersal distance record for each species in PGLS models. The dots and bars within the violin plots show the mean and the standard deviation of each group. The narrow curves and the big dots near the difference axes indicate the paired mean differences with bootstrapping 95% CIs. Species with non-dormant seeds have much greater dispersal distances than species with dormant seeds.

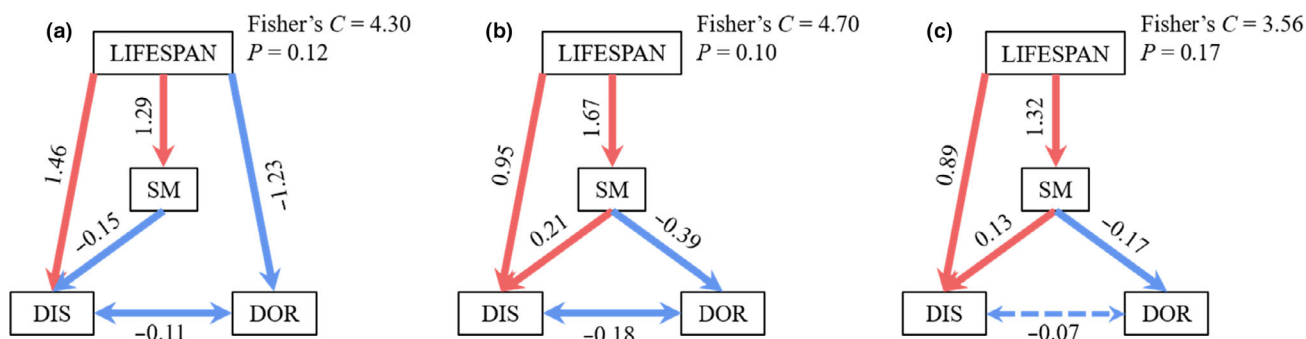


Figure 4 Piecewise structural equation models showing direct and indirect effects of adult plant lifespan (LIFESPAN) and seed mass (SM) on the correlation between seed dispersal (DIS) and dormancy (DOR). Three measures of seed dispersal are used: (a) dispersal potential; (b) mean dispersal distance; and (c) maximum dispersal distance. Solid red and blue arrows indicate significantly negative and positive effects ($P < 0.05$) respectively. The dashed arrow indicates a non-significant effect ($P = 0.06$). Overall model fits are also shown (all 2 degrees of freedom). In these analyses, seed dispersal and dormancy always show a negative correlation.

de Casas *et al.* 2017), such as in desert plants where adaptations for long-distance dispersal are rare and poor dispersibility is common (Ellner & Shmida, 1981; Gremer & Venable, 2014). In theoretical predictions, environmental uncertainty could play a potential role in the existence of the dispersal–dormancy trade-off (Venable & Lawlor, 1980; Cohen & Levin, 1987; Wilbur & Rudolf, 2006). However, we note that a high level of environmental variability is not a necessary condition of unsuitable environments. Our global study strongly suggests that this trade-

off is a general phenomenon (see the latitude effect in Appendix S1). As environmental variation could be a continuum to plants and reducing environmental impacts is a continuing quest, our results reconcile the contracting patterns of dispersal–dormancy correlation under high vs low levels of environmental variability (Snyder, 2006; Siewert & Tielbörger, 2010). It could still be possible that the effect of environmental uncertainty on optimal dormancy and optimal dispersal works at within-species levels (Chen & Giladi, 2020).

Perennials vs annuals

The dispersal–dormancy trade-off is predominantly mediated through the effects of plant lifespan and seed mass, and persists in the networking of life-history traits (Fig. 4). The selective interactions of these traits indicate that organisms spread the risks of reproductive failure in different ways (Buoro & Carlson, 2014). Besides having long-distance dispersed or dormant seeds, being perennial also provides a hedge, thus these three strategies (being dormant, dispersing far and living long) can be partly substitutable (Rohde & Bhalerao, 2007). Long-lived species average risks across time (Rees, 1996). They are more likely to have long-distance dispersed and non-dormant seeds to colonise new habitats (Fig. 4), since the benefits of dispersal may be negated by dormancy, and *vice versa* (de Waal *et al.* 2016). The positive relationship between seed dispersal and plant lifespan is consistent with the fact that the potential to be dispersed over long distances is higher in taller species which are generally long-lived woody plants (Tackenberg *et al.* 2003; Thomson *et al.* 2011; Chen *et al.* 2019b).

We provide the first global documentation that perennials select for less dormancy than annuals (Fig. 4b and c; Rees, 1996), which is consistent with the evidence in some regional studies on much fewer species (Rees, 1993; de Waal *et al.* 2016). Although previous studies have discussed the effect of plant lifespan on dormancy or dispersal respectively, an important omission is the quantification of the dispersal–dormancy correlation separately for annuals and perennials, probably due to their relatively small sample sizes.

We show that, the relationship between dormancy and dispersal remains negative within both perennials and annuals (Appendix S3). Although *P*-values are not statistically significant, species with non-dormant seeds still show a dispersal distance twice as far as species with dormant seeds, within either perennials or annuals (Appendix S3). We note the possibility that annuals may generally have greater annual seed production than perennials (Vico *et al.* 2016). The high seed production in annuals could serve as a buffer and bet-hedge spreading risks across a high number of offspring, just as the polycarpic nature of perennials spreading risks across adult lifespan. In addition, the greater number of seeds dispersed away from mother plants enhances the likelihood of dispersal events and extends seed shadow (Chen *et al.* 2019b), which remedies the trade-off with temporal dispersal to a certain degree. The effect of seed production could be another axis in these selective trade-offs and needs further investigations.

Seed mass

There is a clear pattern that smaller seeds are rather dormant than non-dormant (Fig. 4). This finding substantiates a recent notion that dormancy is an important adaptive strategy of seeds in response to short growing season and thus evolutionarily stable in lineages with small seeds (Rubio de Casas *et al.* 2017). On the other hand, seed mass is contentious in determining seed dispersal. Large seeds are maladaptive for long-distance dispersal under the same condition with the dispersal of small seeds (Thomson *et al.* 2011). However, the dispersal

difficulties for species with large seeds are often counterbalanced by their advantages on seed release height, resource allocation and dispersal mode (Thomson *et al.* 2011; Chen *et al.* 2019a). This leads to the discrepancy of the lasting assumption that large seeds face difficulties of dispersal potential and the fact that large seeds actually reach further dispersal distances than small seeds (Thomson *et al.* 2011), as shown in our SEM models. The increased dispersal distance in large seeds contributes to explain the dispersal–dormancy trade-off via the effect of seed mass (Fig. 4b and c).

The trade-off between dormancy and dispersal might arise from seed biophysical constraints (Rees, 1993; Buoro & Carlson, 2014). An investment in seed coat that may induce dormancy and an investment in dispersal structure that facilitates long-distance dispersal may compete for the same limiting resources (de Waal *et al.* 2016). Large seeds are equipped with proportionally thinner seed coat due to a negative allometry between seed coat and seed reserve (Wu *et al.* 2019). Species with large seeds are predicted to have reduced dormancy because their seedlings can draw on a larger seed reserve, and hence thrive in relatively unfavourable environments (Rubio de Casas *et al.* 2017). In contrast, small-seeded species may possess elongated lifetimes of both vegetative and reproductive organs in order to persist long in degrading habitats (Butterfield *et al.* 2019). As seed dormancy and dispersal are associated with colonisation and extinction (van Groenendaal *et al.* 1998), our result supports the hypothesis that seed mass may influence interspecific variation in both the rate at which species colonise newly suitable habitats and the rate at which species go locally extinct from deteriorating habitats (Butterfield *et al.* 2019).

Methodological and data considerations

Examining the intercorrelated network of partial mediation reveals the importance of proper measures of variables in the selective interactions. We used three measures of seed dispersal that are the most widely used in studies on seed dispersal. Compared with the simple, qualitative data (i.e. dispersal potential) used in most previous literature and this study, our use of a quantitative metric of seed dispersal (i.e. dispersal distance) in the present study is a critical step forward in disentangling the maze of plant dispersal ecology. As the models showed (Fig. 4), mean dispersal distance overrode maximum dispersal distance and binary dispersal potential to demonstrate the dispersal–dormancy trade-off. Thus, a possible explanation of conflicting evidence among previous studies could be associated with the various dispersal indices selected (e.g. Venable & Levin, 1983).

Another measure that could have been considered for inferring temporal dispersal is seed persistence. Delayed germination, as a risk-spreading strategy over time (Rees, 1994), can be achieved not only by displaying dormancy, but also by having a persistent seed bank (Poschlod *et al.* 2005). Dormancy enhances the formation of a seed bank by including seeds in soil, reducing germination percentage during germination season and preventing germination under unfavourable conditions (Poschlod *et al.* 2013). However, there seems to exist no close relationship between dormancy and persistence (Thompson *et al.* 2003; Long

et al. 2015) – probably a situation similar to the relationship between dispersal potential and dispersal distance. Although seed longevity in the seed bank (transient vs persistent) could be a surrogate of temporal dispersal, real-time seed longevity is notoriously difficult to measure and broad-scale data on seed bank persistence are not available.

In summary, there is a strong tendency for dormant seeds to have low spatial dispersal. This study advances our knowledge on the joint evolution of dispersal through space and time in the context of plant life-history traits. To our knowledge, this is the first attempt to expand the episodic understandings of dispersal–dormancy correlation based on certain plant taxa to the global scale. Our findings resolve the mixed evidence at much smaller scales and highlight a necessity for macroecological tests of theoretical predictions.

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AUTHORSHIP

S.-C.C. and U.L. collected the data; S.-C.C. designed the study, analysed the data and wrote the first draft of the manuscript with substantial contribution from P.P., A.A. and J.B.D.

OPEN RESEARCH BADGES



This article has earned Open Data badge. Data is available at (<https://doi.org/10.6084/m9.figshare.12709229>)

DATA AVAILABILITY STATEMENT

Compiled data sets used in this manuscript are archived in the Figshare repository: <https://doi.org/10.6084/m9.figshare.12709229>

REFERENCES

- Baskin, C.C. & Baskin, J.M. (2014). *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination*. Elsevier Academic Press, London, UK.
- Buoro, M. & Carlson, S.M. (2014). Life-history syndromes: Integrating dispersal through space and time. *Ecol. Lett.*, 17, 756–767.
- Butterfield, B.J., Holmgren, C.A., Anderson, R.S. & Betancourt, J.L. (2019). Life history traits predict colonization and extinction lags of desert plant species since the Last Glacial Maximum. *Ecology*, 100, e02817.
- Cayuela, L., Granzow-de la Cerda, Í., Albuquerque, F.S. & Golicher, D.J. (2012). Taxonstand: An R package for species names standardisation in vegetation databases. *Methods Ecol. Evol.*, 3, 1078–1083.
- Chen, S.-C. & Giladi, I. (2020). Variation in morphological traits affects dispersal and seedling emergence in dispersive diaspores of *Geropogon hybridus*. *Am. J. Bot.*, 107, 436–444.
- Chen, S.-C. & Moles, A.T. (2018). Factors shaping large-scale gradients in seed physical defence: Seeds are not better defended towards the tropics. *Glob. Ecol. Biogeogr.*, 27, 417–428.
- Chen, S.-C., Pahlevani, A.H., Malíková, L., Riina, R., Thomson, F.J. & Giladi, I. (2019a). Trade-off or coordination? Correlations between ballochorous and myrmecochorous phases of diplochory. *Funct. Ecol.*, 33, 1469–1479.
- Chen, S.-C., Tamme, R., Thomson, F.J. & Moles, A.T. (2019b). Seeds tend to disperse further in the tropics. *Ecol. Lett.*, 22, 954–961.
- Cohen, D. & Levin, S.A. (1987). The interaction between dispersal and dormancy strategies in varying and heterogeneous environments. In: *Mathematical Topics in Population Biology, Morphogenesis and Neurosciences, Lecture Notes in Biomathematics* (eds Teramoto, E., Yumaguti, M.). Springer, Berlin, Heidelberg, pp. 110–122.
- de Waal, C., Anderson, B. & Ellis, A.G. (2016). Dispersal, dormancy and life-history tradeoffs at the individual, population and species levels in southern African Asteraceae. *New Phytol.*, 210, 356–365.
- Donohue, K., Rubio de Casas, R., Burghardt, L., Kovach, K. & Willis, C.G. (2010). Germination, postgermination adaptation, and species ecological ranges. *Annu. Rev. Ecol. Evol. Syst.*, 41, 293–319.
- Dostál, P. (2005). Is the population turnover of patchy-distributed annuals determined by dormancy dynamics or dispersal processes? *Ecography*, 28, 745–756.
- Ellner, S. & Shmida, A. (1981). Why are adaptations for long-range seed dispersal rare in desert plants? *Oecologia*, 51, 133–144.
- Eriksson, O. (1992). Evolution of seed dispersal and recruitment in clonal plants. *Oikos*, 63, 439–448.
- Eriksson, O. (1996). Regional dynamics of plants: a review of evidence for remnant, source-sink and metapopulations. *Oikos*, 77, 248–258.
- Feeny, P. (1976). Plant apparency and chemical defense. In: *Recent Advances in Phytochemistry* (eds Wallace, J.W. & Mansell, R.L.). Plenum Press, New York, pp. 1–40.
- Gremer, J.R. & Venable, D.L. (2014). Bet hedging in desert winter annual plants: optimal germination strategies in a variable environment. *Ecol. Lett.*, 17, 380–387.
- Grime, J.P. (1989). Seed banks in ecological perspective. In: *Ecology of Soil Seed Banks* (eds Leck, M.A., Parker, V.T., & Simpson, R.L.). Academic Press, Inc., San Diego, CA, pp. XV–XXXIII.
- Harel, D., Holzapfel, C. & Sternberg, M. (2011). Seed mass and dormancy of annual plant populations and communities decreases with aridity and rainfall predictability. *Basic Appl. Ecol.*, 12, 674–684.
- Heleno, R. & Vargas, P. (2015). How do islands become green? *Glob. Ecol. Biogeogr.*, 24, 518–526.
- Ho, J., Tumkaya, T., Aryal, S., Choi, H. & Claridge-Chang, A. (2019). Moving beyond P values: data analysis with estimation graphics. *Nat. Methods*, 16, 565–566.
- Ho, L.S.T. & Ané, C. (2014). A linear-time algorithm for Gaussian and non-Gaussian trait evolution models. *Syst. Biol.*, 63, 397–408.
- Honda, Y. (2008). Ecological correlations between the persistence of the soil seed bank and several plant traits, including seed dormancy. *Plant Ecol.*, 196, 301–309.
- Howe, H.F. & Smallwood, J. (1982). Ecology of seed dispersal. *Annu. Rev. Ecol. Syst.*, 13, 201–228.
- Ives, A.R. & Garland, T. (2010). Phylogenetic logistic regression for binary dependent variables. *Syst. Biol.*, 59, 9–26.
- Jin, Y. & Qian, H. (2019). VPhyloMaker: an R package that can generate very large phylogenies for vascular plants. *Ecography*, 42, 1353–1359.
- Jurado, E. & Flores, J. (2005). Is seed dormancy under environmental control or bound to plant traits? *J. Veg. Sci.*, 16, 559–564.

- Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P. *et al.* (2020). TRY plant trait database – enhanced coverage and open access. *Glob. Change Biol.*, 26, 119–188.
- Lefcheck, J.S. (2016). piecewiseSEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods Ecol. Evol.*, 7, 573–579.
- Long, R.L., Gorecki, M.J., Renton, M., Scott, J.K., Colville, L., Goggin, D.E. *et al.* (2015). The ecophysiology of seed persistence: a mechanistic view of the journey to germination or demise. *Biol. Rev.*, 90, 31–59.
- Manzano, P. & Malo, J.E. (2006). Extreme long-distance seed dispersal via sheep. *Front. Ecol. Environ.*, 4, 244–248.
- Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, 401, 877–884.
- Paradis, E. & Schliep, K. (2018). ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, 35, 526–528.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team (2020). nlme: linear and nonlinear mixed effects models, R package version 3.1-140. <https://CRAN.R-project.org/package=nlme>
- Poschlod, P., Abedi, M., Bartelheimer, M., Drobnik, J., Rosbakh, S. & Saatkamp, A. (2013). Seed ecology and assembly rules in plant communities. In: *Vegetation Ecology* (2nd Edition) (eds van der Maarel, E. & Franklin, J.). Wiley-Blackwell (John Wiley & Sons, Ltd.), Chichester, pp. 164–202.
- Poschlod, P., Kleyer, M., Jackel, A.-K., Dannemann, A. & Tackenberg, O. (2003). BIOPOP—a database of plant traits and internet application for nature conservation. *Folia Geobotanica*, 38, 263–271.
- Poschlod, P., Tackenberg, O. & Bonn, S. (2005). Plant dispersal potential and its relation to species frequency and coexistence. In: *Vegetation Ecology* (ed. van der Maarel, E.). Blackwell, Oxford, pp. 147–171.
- Priestley, D.A. (1986). *Seed Aging: Implications for Seed storage and persistence in the soil*. Cornell University Press (Comstock Publishing Associates), Ithaca and London.
- Rees, M. (1993). Trade-offs among dispersal strategies in British plants. *Nature*, 366, 150–152.
- Rees, M. (1994). Delayed germination of seeds: a look at the effects of adult longevity, the timing of reproduction, and population age/stage structure. *Am. Nat.*, 144, 43–64.
- Rees, M. (1996). Evolutionary ecology of seed dormancy and seed size. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 351, 1299–1308.
- Rohde, A. & Bhalerao, R.P. (2007). Plant dormancy in the perennial context. *Trends Plant Sci.*, 12, 217–223.
- Rubio de Casas, R., Donohue, K., Venable, D.L. & Cheptou, P.-O. (2015). Gene-flow through space and time: dispersal, dormancy and adaptation to changing environments. *Evol. Ecol.*, 29, 813–831.
- Rubio de Casas, R., Willis, C.G., Pearse, W.D., Baskin, C.C., Baskin, J.M. & Cavender-Bares, J. (2017). Global biogeography of seed dormancy is determined by seasonality and seed size: a case study in the legumes. *New Phytol.*, 214, 1527–1536.
- Saastamoinen, M., Bocedi, G., Cote, J., Legrand, D., Guillaume, F., Wheat, C.W. *et al.* (2018). Genetics of dispersal. *Biol. Rev.*, 93, 574–599.
- Saatkamp, A., Poschlod, P. & Venable, D.L. (2014). The functional role of soil seed bank in natural communities. In: *Seeds: The Ecology of Regeneration in Plant Communities* (ed Gallagher, R.S.). CABI Wallingford, UK, pp. 263–295.
- Sallon, S., Solowey, E., Cohen, Y., Korchinsky, R., Egli, M., Woodhatch, I. *et al.* (2008). Germination, genetics, and growth of an ancient date seed. *Science*, 320, 1464.
- Shen-Miller, J., Mudgett, M.B., Schopf, J.W., Clarke, S. & Berger, R. (1995). Exceptional seed longevity and robust growth: ancient sacred lotus from China. *Am. J. Bot.*, 82, 1367–1380.
- Shilton, L.A., Altringham, J.D., Compton, S.G. & Whittaker, R.J. (1999). Old World fruit bats can be long-distance seed dispersers through extended retention of viable seeds in the gut. *Proceedings of the Royal Society B: Biological Sciences*, 266, 219–223.
- Shipley, B. (2009). Confirmatory path analysis in a generalized multilevel context. *Ecology*, 90, 363–368.
- Siewert, W. & Tielbörger, K. (2010). Dispersal-dormancy relationships in annual plants: putting model predictions to the test. *Am. Nat.*, 176, 490–500.
- Snyder, R.E. (2006). Multiple risk reduction mechanisms: can dormancy substitute for dispersal? *Ecol. Lett.*, 9, 1106–1114.
- Symonds, M.R.E. & Blomberg, S.P. (2014). A primer on phylogenetic generalised least squares. In: *Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology* (ed Garamszegi, L.Z.). Springer, Berlin Heidelberg, pp. 105–130.
- Tackenberg, O., Poschlod, P. & Bonn, S. (2003). Assessment of wind dispersal potential in plant species. *Ecol. Monogr.*, 73, 191–205.
- Thompson, K. (1987). Seeds and seed banks. *New Phytol.*, 106, 23–34.
- Thompson, K., Ceriani, R.M., Bakker, J.P. & Bekker, R.M. (2003). Are seed dormancy and persistence in soil related? *Seed Sci. Res.*, 13, 97–100.
- Thomson, F.J., Moles, A.T., Auld, T.D. & Kingsford, R.T. (2011). Seed dispersal distance is more strongly correlated with plant height than with seed mass. *J. Ecol.*, 99, 1299–1307.
- van Groenendael, J.M., Ouborg, N.J. & Hendriks, R.J.J. (1998). Criteria for the introduction of plant species. *Acta Botanica Neerlandica*, 47, 3–13.
- Venable, D.L. & Brown, J.S. (1988). The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. *Am. Nat.*, 131, 360–384.
- Venable, D.L. & Lawlor, L. (1980). Delayed germination and dispersal in desert annuals: escape in space and time. *Oecologia*, 46, 272–282.
- Venable, D.L. & Levin, D.A. (1983). Morphological dispersal structures in relation to growth habit in the Compositae. *Plant Syst. Evol.*, 143, 1–16.
- Vico, G., Manzoni, S., Nkurunziza, L., Murphy, K. & Weih, M. (2016). Trade-offs between seed output and life span – a quantitative comparison of traits between annual and perennial congeneric species. *New Phytol.*, 209, 104–114.
- Wilbur, H.M. & Rudolf, V.H.W. (2006). Life-history evolution in uncertain environments: Bet hedging in time. *Am. Nat.*, 168, 398–411.
- Willis, C.G., Baskin, C.C., Baskin, J.M., Auld, J.R., Venable, D.L., Cavender-Bares, J. *et al.* (2014). The evolution of seed dormancy: environmental cues, evolutionary hubs, and diversification of the seed plants. *New Phytol.*, 203, 300–309.
- Willson, M.F. (1993). Dispersal mode, seed shadows, and colonization patterns. In: *Frugivory and Seed Dispersal: Ecological and Evolutionary Aspects* (eds Fleming, T.H. & Estrada, A.). Springer, Dordrecht, pp. 261–280.
- Wu, L.-M., Chen, S.-C. & Wang, B. (2019). An allometry between seed kernel and seed coat shows greater investment in physical defense in small seeds. *Am. J. Bot.*, 106, 371–376.
- Yashina, S., Gubin, S., Maksimovich, S., Yashina, A., Gakhova, E. & Gilichinsky, D. (2012). Regeneration of whole fertile plants from 30,000-year old fruit tissue buried in Siberian permafrost. *Proc. Natl Acad. Sci.*, 109, 4008–4013.

SUPPORTING INFORMATION

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

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