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 & Tiellberg, 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.

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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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 & Tiellberg, 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 dispersal structure and the occurrence of a seed bank 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
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 apparentness 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 Taxonrand (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 (Poschlod 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 log10-transformed prior to all the analyses.

We compared dispersal potential across dormant and non-dormant species using phylogenetic logistic regression (Ives &
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 ($\beta$ 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 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
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 (Tuckenberg 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 Groenendael 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.

DATA AVAILABILITY STATEMENT

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

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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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