Seeds of future past: climate change and the thermal memory of plant reproductive traits

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ABSTRACT

Plant persistence and migration in face of climate change depend on successful reproduction by seed, a central aspect of plant life that drives population dynamics, community assembly and species distributions. Plant reproduction by seed is a chain of physiological processes, the rates of which are a function of temperature, and can be modelled using thermal time models. Importantly, while seed reproduction responds to its instantaneous thermal environment, there is also evidence of phenotypic plasticity in response to the thermal history experienced by the plant's recent ancestors, by the reproducing plant since seedling establishment, and by its seeds both before and after their release. This phenotypic plasticity enables a thermal memory of plant reproduction, which allows individuals to acclimatise to their surroundings. This review synthesises current knowledge on the thermal memory of plant reproduction by seed, and highlights its importance for modelling approaches based on physiological thermal time. We performed a comprehensive search in the *Web of Science* and analysed 533 relevant articles, of which 81 provided material for a meta-analysis of thermal memory in reproductive functional traits based on the effect size *Zr*. The articles encompassed the topics of seed development, seed yield (mass and number), seed dormancy (physiological, morphological and physical), germination, and seedling establishment. The results of the meta-analysis provide evidence for a thermal memory of seed yield, physiological dormancy and germination. Seed mass and physiological dormancy appear to be the central hubs of this memory. We argue for integrating thermal memory into a predictive framework based on physiological time modelling. This will provide a quantitative assessment of plant reproduction, a complex system that integrates past and present thermal inputs to achieve successful reproduction in changing environments. The effects of a warming environment on plant reproduction cannot be reduced to a qualitative interpretation of absolute positives and negatives. Rather, these effects need to be understood in terms of changing rates and thresholds for the physiological process that underlie reproduction by seed.

Key words: climate warming, dormancy, functional traits, germination, global change, phenotypic plasticity, seed mass and number, seedling establishment, thermal time.

CONTENTS

I. INTRODUCTION

In a climate change context, the ability of a plant species to persist in its current habitat or to migrate to new sites will depend on successful reproduction by seed. Seed traits affect all levels of plant ecology from population dynamics (Huang *et al.*, 2016) to community assembly (Larson & Funk, 2016) and species distributions (Bykova *et al.*, 2012). Seeds are also the basis for human activities such as agriculture, *ex situ* conservation (Li & Pritchard, 2009) and ecological restoration (Merritt & Dixon, 2011). Recently, Walck *et al.* (2011) highlighted how climate change is altering the major post-dispersal seed-germination cues: temperature and water availability. However, seed responses to these cues are not fixed species traits. As Cochrane *et al.* (2015) showed, there is ample intraspecific variability in seed traits, which can provide the raw material for acclimatisation and/or adaptation to new climates. Intraspecific variability can be the result of either genetic differences (Fernández-Pascual *et al.*, 2013) or phenotypic plasticity (Fenner, 1991), but the latter provides the fastest way for plants to adjust to their environment (Nicotra *et al.*, 2010). Importantly, phenotypic plasticity allows plants to take into account their thermal history, integrating both the pre- and the post-dispersal environments into cross-generational plasticity (Auge *et al.*, 2017). We define thermal history as the past thermal environments experienced by the seed and its recent ancestors (generally the parental and grandparental generations), as opposed to the current thermal environment reviewed by Walck *et al.* (2011). Phenotypic plasticity in response to thermal history amounts to a 'thermal memory' of plant reproductive traits. Remembering their thermal history would inform seeds to germinate in the most convenient conditions for seedling establishment and allow individuals to acclimatise to new surroundings.

This review has the double objective of promoting a physiological thermal time framework to study plant reproduction, and highlighting the importance of thermal memory in such a framework. As ectotherm life forms, most plant physiological processes are a function of environmental temperature, and suitable for quantification using a thermal time approach (Garcia-Huidobro, Monteith, & Squire, 1982). Each process has an optimal temperature at which its rate is maximal. Below and above this optimum, the rate progressively decreases until the temperature reaches base and ceiling thresholds beyond which the process stops. The optimal, base and ceiling temperatures are the cardinal temperatures of this process. For the process to be completed, a certain number of thermal units must accumulate, but this accumulation only happens within the limits of the cardinal temperatures. As we will see in this introduction, these thermal time concepts apply to the successive steps of plant reproduction by seed,

from seed production to seedling emergence. Through these concepts, plant reproduction becomes measurable by a set of thermal time traits: the cardinal temperatures and the required thermal time. This approach contributes to a predictive framework for plant reproduction, one that relates directly to the environmental thermal inputs *via* process-based models (Donohue *et al.*, 2015). But if we want to use this framework to predict plant reproduction under changing climates, it is essential to acknowledge that thermal time traits are not fixed species traits but have a thermal memory. To support this critical point, this review synthesises the available evidence on the thermal memory of plant reproductive traits by means of a meta-analysis. We begin by providing a brief state-of-the-art regarding plant reproduction under climate warming; followed by an exploration of thermal time models of plant reproduction. We then perform a meta-analysis of the thermal memory of plant reproductive traits. Finally, we integrate current knowledge towards a predictive framework of plant reproduction, and highlight future avenues for research.

(1) Climate warming and plant reproduction

Evidence of the effect of climate change on plant reproduction is accumulating rapidly. Warming will generally advance plant reproduction in a wide variety of habitats (Wookey *et al.*, 1993; De Frenne *et al.*, 2011), but delays are also possible as a result of regional specificities (Del Cacho, Peñuelas & Lloret, 2013*b*; Bjorkman *et al.*, 2015). These changes in reproductive phenology will have a cascading effect on the phenology and thermal history of subsequent life stages. Seed yield (i.e. the reproductive output of plants) will increase or decrease depending on whether the current limiting factor for a species is temperature (Richardson *et al.*, 2005) or drought (Mutke, Gordo & Gil, 2005). Once seed production is affected, dispersal limitations will determine the future distributions of plant species (Engler *et al.*, 2009), and dispersal distances themselves will be modified by changing wind patterns (Kuparinen *et al.*, 2009). Climate warming will likewise disrupt the natural cycles of seed dormancy (Ooi, Auld & Denham, 2009), which is in essence a form of dispersal in time. The germination of non-dormant seeds will also be affected, with faster rates expected in warm-cued seeds from cold regions (Milbau *et al.*, 2009) and delayed emergence in cold-cued seeds from dry regions (Cochrane, Daws & Hay, 2011). Above all, we must stress that a higher germination percentage – and an advanced or delayed emergence – are not positive or negative *per se*: the essential question is whether emergence will stay matched with the favourable establishment season. Moderate warming, by itself, tends to favour seedling establishment (De Frenne *et al.*, 2012; Cheesman & Winter, 2013; Stevens *et al.*, 2014;

Mondoni *et al.*, 2015). But a seedling that emerges before its time can find itself dealing with frost–thaw events (Huelber, Bardy & Dulinger, 2011), drought (Del Cacho *et al.*, 2013*a*) or increased competition (Caron *et al.*, 2015).

(2) Thermal time and plant reproduction

All the climate change disturbances described above are ultimately a function of environmental temperature, and thus are suitable for thermal time modelling (Donohue *et al.*, 2015). In a thermal time framework (also referred to as growing degree-day), physiological processes involve the accumulation of thermal time units towards the completion of a developmental phase. This phase can be flowering, attaining seed physiological maturity, or germination. Measuring the reproductive process in thermal time has the advantage of integrating time and temperature into a single physiological currency (Romo & Eddleman, 1995), and provides quantifiable units for the emerging framework of ecological energetics (Tomlinson *et al.*, 2014). Five thermal time traits suffice to describe the thermal control of each reproductive step: the three cardinal temperatures or thermal thresholds (base, optimal, and ceiling) and the thermal time (sub- and supra-optimal) required to reach completion. These thermal time traits have two powerful applications. First, parameters calculated in a restricted set of experimental treatments give comprehensive estimations of reproduction in complex environments (Hardegree *et al.*, 1999). This allows, for example, an exploration of plant reproduction in climate change scenarios (Orrù *et al.*, 2012). Second, thermal time parameters are comparable in a standard way across seed individuals, populations and species (Trudgill, Squire & Thompson, 2000). As such, thermal time traits provide the broadest base to conduct comparative studies and meta-analyses of germination (Arène *et al.*, 2017), as well as to integrate reproduction into broader fields of modelling such as community assembly (Larson & Funk, 2016) or species distribution models (Bykova *et al.*, 2012).

Individual models for almost all the individual steps of plant reproduction already exist. In agronomy, there is a long tradition of using growing degree-day models to predict crop phenology (Nesmith & Bridges, 1992) and yield (Ney & Turc, 1993). García-Huidobro *et al.* (1982) developed a thermal time model to describe the rate of germination as a function of temperature, and many authors have subsequently applied this concept to estimate the field emergence of weeds (Steinmaus, Prather & Holt, 2000). Later research extended the framework to physiologically dormant wild species, considering dormancy loss in thermal time terms (Pritchard, Tompsett & Manger, 1996). Gama-Arachchige *et al.*

(2013) modelled periodical changes in coat permeability (i.e. physical dormancy). Most recently, Porceddu *et al.* (2017) made a first attempt to model embryo growth (i.e. morphological dormancy) by quantifying cardinal temperatures specific to embryo growth inside the seed. Post-germination seedling growth also has its own specific thermal time traits (Adam *et al.*, 2007).

All these approaches have in common the use of thermal time traits to quantify the temperature stimuli that the plant or seed is instantaneously experiencing. The main issue we now want to highlight is that thermal time traits are themselves dependent on thermal history, i.e. the temperatures experienced by the plant or seed – or by its ancestors – during previous life stages. In this way, plants have a 'thermal memory' that can keep track of long-term climatic trends (Trewavas, 2003). Therefore, an integrated model of plant reproduction needs to account for the interactive effects of present thermal environment and past thermal history. To contribute to this task, we conducted a meta-analysis of thermal memory in plant reproductive traits.

II. META-ANALYSIS METHODOLOGY

(1) Literature search

We conducted a meta-analysis of the thermal memory of plant reproductive traits following the principles outlined by Koricheva, Gurevitch & Mengersen (2013). The objective of the meta-analysis was to test whether there is a relationship between seed traits and thermal history, either directly or through other seed traits. To gather a comprehensive sample of the available evidence, we performed a literature search in the Thomson Reuters Web of Science™. We constructed a Boolean search string (see online Supporting information, Appendix S1) by grouping key words in three blocks: (1) climate change, (2) thermal time models, and (3) the relationship between the maternal thermal environment and seed production, dispersal, dormancy, germination, and seedling development. We chose not to review seed longevity in the soil, as this has been the subject of a recent comprehensive review (Long *et al.*, 2015). In addition, because many works have studied the effect of post-dispersal temperature in regulating dormancy loss and germination, for these traits we restricted the search to those investigations that used a thermal time approach. Furthermore, we restricted the search to journal articles written in English and classified in a relevant subject area (listed in Appendix S1).

In April 2016, we ran a search whose steps are documented in a PRISMA chart provided as Appendix S2 (Moher *et al.*, 2009). The search returned 10,242 results. We did not add articles

known to us but not found by the search, because the objective was to obtain a representative and unbiased sample of current knowledge, rather than to collect every source. We performed four consecutive screenings of the results. In a first screening of titles and a second screening of abstracts, we removed non-relevant studies. The title screening reduced the list to 1,487 articles, and the abstract screening to 533. In a third screening, we extracted the following information from the abstract: (1) the reproductive trait or process studied; (2) the factor exerting an effect on this trait or process, which could be temperature or another trait; (3) whether the study reported an experimental manipulation of temperature or not; and (4) whether the temperature represented an instantaneous response to the current thermal environment, or a response to the previous thermal history experienced by the plant (i.e. thermal memory). We then removed articles not reporting experimental manipulation of temperature or not addressing the effect of thermal memory, reducing the list to 205 articles. We performed a fourth and final screening of the text of these articles to determine which had actual measurements of temperature and plant traits. In the fourth screening, we rejected 94 articles because they did not provide data of interest; and another 30 articles not reporting sufficient information to perform a weighted meta-analysis (i.e. the standard deviation or an alternative way of calculating it). We included data for 'wild-type' *Arabidopsis thaliana* laboratory populations but excluded mutants with seed functions supressed.

(2) Data extraction and calculation of effect sizes

Since the goal of our meta-analysis was to test the relationship between pairs of quantitative variables (e.g. maternal temperature and seed mass), the most appropriate effect size measure was Pearson's correlation coefficient, r (Rosenberg, Rothstein & Gurevitch, 2013). Experiments in our selection of references, however, presented two caveats to the application of r. Firstly, most of the experiments treated the experimental variable (e.g. temperature) as a categorical variable with two or a few experimental levels. Secondly, our study variables were not expected to have a linear relationship; but rather a unimodal one. As an example, the value of seed mass should peak at the optimal maternal temperature and decrease at sub-optimal and supra-optimal temperatures. If an article used three temperature levels representing the optimum, sub-optimum, and supra-optimum; analysing the overall effect size could indicate no relationship; when in fact the data showed both a positive relationship (between the sub-optimum and the optimum) and a negative relationship (between the optimum and the supra-optimum).

Taking these caveats into consideration, we adopted the following procedure to extract effect sizes. When an article reported values for more than one species, population, or seed accession; we treated these values as separate experimental units nested within the reference. When an article treated the experimental variable as a factor with more than two levels, we only used the two treatments that produced the highest and the lowest value of the study variable (or the two extreme treatments in the case that the study variable showed no change). This assumed that the highest value was close to the optimum, and the lowest value represented a sub- or supra-optimal situation. While it is true that the true optimum might have been somewhere between the highest and lowest values, this should not affect the main outcome of the analysis, which aimed to detect a relationship rather than to define its cardinal values (i.e. the optimum, base and ceiling treatments) or its strength (i.e. the slope). In other words, what was relevant was whether the regression coefficient was different from zero, rather than its actual value. In practice, this approach means that the relationships might have been stronger than reported here.

For these two treatments we extracted the mean, standard deviation, and number of replicates; or calculated them from other parameters if absent. When the study variable was the germination proportion or percentage, we used the mean germination and the number of seeds to create 2×2 contingency tables. In a few cases, the reference treated the experimental variable as a quantitative variable and reported the full set of values in a figure or table; we then calculated r directly using the full data set. When any of the aforementioned measurements were provided graphically, we used WebPlotDigitizer v3.12 (Rohatgi, 2017) to extract the values. We compiled the extracted measures in a table (Appendix S3). We transformed the extracted values to effect sizes (Fisher's Z transformation of r) and weights (the inverse of Zr's variance) using the packages 'esc' (Lüdecke, 2017) and 'metafor' (Viechtbauer, 2010) of R (R Core Team, 2017) (see script in Appendix S4). The calculated effect sizes are provided in Appendix S5. When calculating the effect sizes, we considered the lower value of the experimental variable as the control, and the higher value as the treatment. Therefore, positive effect sizes indicated a positive or sub-optimal relationship, and negative effect sizes a negative or supra-optimal relationship. Since our main objective was to test for a relationship independently of the sign, we transformed all effect sizes to absolute values to pool them in the analyses; but retained the information on whether they were derived from a positive, negative, or neutral (no effect) relationship.

(3) Phylogenetic correlation matrices

The calculated effect sizes could not be regarded as independent, as they were from plant species linked by a common evolutionary history (Chamberlain *et al.*, 2012; Lajeunesse, Rosenberg & Jennions, 2013). Therefore, before proceeding with the analyses, we constructed a phylogenetic correlation matrix. We extracted a phylogenetic tree including all the species in our analysis from the R20120829 tree of Phylomatic v3 (Webb & Donoghue, 2005). We adjusted branch lengths with the exponential node ages of Bell, Soltis & Soltis (2010), using the ages file provided by Gastauer & Meira-Neto (2016) and the 'bladj' function of Phylocom (Webb, Ackerly & Kembel, 2008). The tree is provided in Appendix S6. Finally, we created phylogenetic correlation matrices using 'geiger' (Harmon *et al.*, 2008). We adjusted one such matrix to the specific list of species included in each of the models described below.

(4) Multi-variate meta-analysis models

The nature of our data set, encompassing different plant species from different ecosystems, as well as laboratory and field experiments, made it highly unlikely that the effect sizes shared a common true mean. Furthermore, the data set had two sources of non-independence. Firstly, as discussed above, phylogenetic relatedness. Secondly, the fact that some studies provided more than one experimental unit (species, populations, or seed accessions). We therefore chose a multi-level or hierarchical random model to analyse our effect sizes (Koricheva *et al.*, 2013). We fitted separate models to each relationship between pairs of variables, as there was relatively little overlap between studies and effect sizes. Each model included a random factor for reference, a nested random factor for experimental unit within reference, and a correlated error structure represented by the phylogenetic correlation matrix. We fitted the models using the rma.mv function of 'metafor' (see script in Appendix S7 and tabulated model outputs in Appendix S8).

(5) Heterogeneity in effect sizes

To estimate the heterogeneity or inconsistency in effect sizes (Senior *et al.*, 2016), we calculated two statistics: Q, which tests whether there is a significant amount of variance among studies; and I^2, which indicates which percentage of the total variance can be attributed to the different random terms in the model (Nakagawa & Santos, 2012; Nakagawa *et al.*, 2017). Considering the low number of references for some of our relationships, and wanting to avoid over-complicated models, we decided against including explicit moderators in the models to explore the causes of heterogeneity. Instead, we fitted separate models and calculated effect sizes for subgroups of the data representing different groupings. The first grouping considered the nature of the relationship (i.e. the original sign of the effect size), which could be positive/sub-optimal, neutral, or negative/supra-optimal. The second grouping considered the type of study species as reported in the reference: (*i*) wild, including weeds and exotics; (*ii*) domesticated, including crops and plantation trees; and (*iii*) *Arabidopsis thaliana* 'wild-type' laboratory populations, which represented a sizable portion of the data set and can be argued to be either wild or domesticated. The third grouping considered the experimental setting, either the laboratory (including greenhouses and experimental agricultural fields) or natural field sites.

(6) Publication bias

To test for publication bias or small-study effect we used the random-effects version of Egger's regression test (Rothstein *et al.*, 2005). Because the standard error of our effect size r is a function of the effect size itself, we used as a precision measure the inverse of the sample size (Peters *et al.*, 2006). Thus, we refitted the multi-variate meta-analysis models using the inverse of the sample size as a moderator. A relationship between the effect size and the precision measure could be interpreted as an indication of publication bias.

(7) Sensitivity analysis

Sensitivity analysis for multi-variate meta-analysis models is an active field of research. Following the procedure of recent investigations in plant sciences (Habeck & Schultz, 2015), we conducted ours by refitting the models after removing influential and outlier effect sizes. We defined influential effect sizes as those with hat values (i.e. diagonal elements of the hat matrix) greater than two times the average hat value; and outlier effect sizes as those with standardised residual values exceeding 3. We also tested the sensitivity of the analysis to the phylogenetic component by fitting alternative models with a tree calibrated with log-normal rather than exponential ages; as well as models without a phylogenetic correlation structure.

III. META-ANALYSIS OF THE THERMAL MEMORY OF PLANT REPRODUCTIVE TRAITS

(1) General meta-analysis diagnostics

Our literature search resulted in a set of 81 articles representing 73 taxa from 26 plant families. These articles are marked with asterisks in the reference list. From these articles, we were able to extract 433 effect-size records for the following 11 relationships:

maternal temperature with seed mass, seed number, germination proportion, time to 50% germination, and seedling growth; seed mass with germination proportion, time to 50% germination, and seedling growth; dormancy loss treatment with base germination temperature, base germination water potential, and thermal time for 50% germination. We conducted a meta-analysis (i.e. a quantitative synthesis) of these 11 relationships. In addition, during the literature search we found reports of other relationships or aspects of thermal memory that are worth considering as part of a qualitative synthesis (Appendix S2), even though we were unable to extract the data to include them in the meta-analysis. In the following sections, we combine the quantitative and qualitative syntheses in a narrative account of the successive processes of plant reproduction by seed, including the analysis of effect sizes and significant references for other processes that could not be analysed. First, we present the assessment of heterogeneity, publication bias and sensitivity.

Effect sizes had a generally high level of heterogeneity (Figs 1–3), as may be expected for a data set representing species across the diversity of seed plants. The only cases in which heterogeneity (as measured by Q) was not significant were the relationships of maternal temperature with seedling growth, and dormancy status with base water potential. These two cases were small data subsets dominated by a few species. For the most part, the major source of heterogeneity as estimated by I^2 was at the reference level. Phylogenetic relatedness was the largest contributor to heterogeneity in the relationships between seed mass and germination proportion and time, as well as dormancy and base germination temperature. Given the heterogeneity inherent in our data set, we believe that these heterogeneity values are only an indication of the patterns in the specific set of effect sizes that we gathered, rather than an indication of any general trend. Consistent with expectations, there was a consistent pattern of larger effect-size averages in laboratory vs. field experiments (Figs 1–3), although the confidence intervals largely overlapped. The species categories (wild, domesticated and *Arabidopsis*) tended to have the same effect sizes. Only one relationship (between maternal temperature and germination proportion) showed a stronger effect in the sub-optimal range of temperatures, coinciding with a large difference in the number of records (117 sub-optimal *versus* 8 supra-optimal).

The regression test for publication bias was negative in all cases ($P > 0.10$), indicating no relationship between outcome and precision. The sensitivity analysis identified 44 out of 433 records as influential, and one record as an outlier. The models fitted without these records, with an alternative phylogenetic tree, or with no tree (Appendix S9) did not deviate much from the conclusions of the full models, other than by an increased effect size or reduced confidence interval. Such differences are discussed in the specific sections below.

(2) Reproductive phenology

Several studies suggested that the phenology of reproduction (flowering and seed development) has thermal memory. For example, previous exposure to cold temperatures can enhance or be a requisite for flowering (Nesmith & Bridges, 1992). Flowering can be responsive to temperatures experienced as early as the seed maturation stage (Rubio de Casas *et al.*, 2012), or even by previous generations (Clapham, Willcott & Fedders, 2000). Furthermore, flowering time can be affected by seed mass (Elwell *et al.*, 2011). Such limited examples, however, meant that there was insufficient data to run a meta-analysis.

(3) Seed yield: mass and number

Thirty references from 30 species recorded the mass of seeds that had matured at different temperatures (Fig. 1A) with an even representation of records across temperature range, species category and experimental setting. The overall effect size was significantly different from zero and had a mean 68% correlation, indicating a strong thermal memory for seed mass. Similarly, 23 references from 22 species measured seed number in response to maternal temperature, finding an overall correlation of 68% (Fig. 1B). In this case there was a preponderance of supra-optimal records coming from investigations of extraordinary warming on crop yield. Both the higher contribution of phylogeny to the heterogeneity of mass, and the high inconsistency of number across studies, support the general assumption that seed number is a more plastic trait than seed mass (Baker, 2004). Within a given species, both components of yield generally have neutral or positive correlations, as both depend positively on plant size and resource availability (Venable, 1992).

Although the data made it impossible to dissect the different stages of maturation, individual references showed that the temperature dependence of yield can be specific to very precise stages, e.g. to tissue differentiation (early development events) but less so to filling and maturation (late events) (Wagner & Mitterhofer, 1998). Furthermore, thermal memory can last several years in masting tree populations (Kelly *et al.*, 2013), and be observed generations after in seed mass (Elwell *et al.*, 2011) and number (Bloedner *et al.*, 2007).

(4) Seed dispersal

Dispersability depends on diaspore traits such as terminal velocity, floatability and seed shape (Jacobs & Lesmeister, 2012) which depend strongly on yield traits. In particular, lighter seeds disperse longer distances (Ghamari *et al.*, 2010), while more seeds increase the chances of long-distance dispersal events (Higgins & Richardson, 1999). While we did not find studies testing the direct effect of maternal temperature on dispersal distance, it is clear that there is an indirect effect of thermal memory through seed yield.

(5) Morphological dormancy and embryo growth

Morphological dormancy is a trait in which the seed cannot germinate at the time of dispersal because the embryo is undifferentiated or underdeveloped. Seed maternal temperatures could affect morphological dormancy by determining: (a) the degree of embryo differentiation/development at dispersal; and/or (b) the rate of embryo growth in response to post-dispersal temperatures. Evidence of this is, however, scarce. Mondoni *et al.* (2008) compared morphological dormancy between mountain and lowland populations of the temperate woodland forb *Anemone nemorosa*. Embryo size at dispersal was similar in both populations, but embryo growth was faster in the mountain population. Unfortunately, it was not possible to conclude whether this difference in growth rate was due to different seed development temperatures (i.e. thermal memory), or to genetic differences among sites.

(6) Physical dormancy and coat permeability

Physical dormancy is a block to seed imbibition (and consequently, to germination) imposed by an impermeable seed coat. Coat impermeability to water results from one or more layers of palisade cells in the testa, and in certain cases by specialised structures that regulate water uptake such as the hilum. It is relevant to consider whether seed development temperature could affect the development of these structures, thus determining the degree of physical dormancy at dispersal. There is evidence for variation in physical dormancy among individuals of the same population (Liyanage & Ooi, 2015), but as yet no proof that this variation is influenced by seed maternal temperatures.

(7) Primary physiological seed dormancy and germination traits

The level of physiological dormancy is difficult to measure *per se*, with the majority of studies quantifying it as a lack of germination. Thus, physiological dormancy and germinability become two faces of the same phenomenon, which can be measured in a variety of traits that include the germination proportion, germination rate or speed, cardinal temperatures, and thermal time. Pre-dispersal thermal memory could affect these traits in two ways. First, it could determine their values at the time of dispersal (i.e. primary dormancy level). Second, it could determine their sensitivity to dormancy loss. It is important to note that this second case is a different situation from the effect of post-dispersal temperatures driving dormancy loss and re-imposition (see Section III.8).

The germination proportion (or final germination percentage) is by far the most widely used measure of seed dormancy and germinability. Twenty-seven studies of 24 taxa investigated the germination proportion of seeds from different maternal temperatures (Fig. 1C). Out of 156 records, a sizable proportion arose from laboratory *Arabidopsis* experiments. Most of the records indicated a positive relationship, and the average effect size was higher for sub-optimal temperature increases. It seems well established that warmer maternal environments result in higher germination (Fenner, 1991), but it is reasonable to assume that extraordinary warming could impair viability. A characteristic of germination proportion data sets was a high number of neutral or no-effect records, coming from experiments in which germination was 0 or 100% at both temperatures. Individual studies also suggested that seeds lose dormancy faster in response to warmer maternal environments (Hoyle *et al.*, 2008*a*), although there were not enough data for meta-analysis. Six references of seven species analysed the effect of maternal temperatures on germination time (Fig. 1D), again with a majority of laboratory *Arabidopsis* trials. Although we found a significant overall effect size ($P = 0.012$), the confidence intervals were wider than for other relationships, and significance was lost when influential effect sizes were excluded (Appendix S9, Fig. S7D). We found no articles that measured the effect of maternal temperature on hydrothermal traits.

We were able to conduct a meta-analysis on the effect of seed mass on the germination proportion (23 studies, 24 species) and time (8 studies, 9 species) (Fig. 2A, B). These relationships had a high contribution of phylogeny to heterogeneity, perhaps as a result of constraints on seed mass. The effect for germination proportion was the same as for the relationship between temperature and proportion (38%). For germination time, the number of records was low, heterogeneity high, and the effect non-significantly different from zero (although it was marginally significant when using an alternative phylogenetic tree, and highly significant when considering no phylogenetic relatedness or excluding influential and outlier effect sizes,

Appendix S9, Figs S2B, S5B, S8B). We found a few reports of seed mass affecting hydrothermal time traits, with heavier seeds having lower base temperatures for germination (Wang, Bai & Tanino, 2004) and lower base water potentials (Brunel *et al.*, 2009).

(8) Post-dispersal seed dormancy cycles

Once dispersed, seeds undergo cyclic changes in their dormancy levels. Depending on their post-dispersal thermal history, these can decrease (dormancy loss) or increase (secondary dormancy). Our meta-analysis showed that these changes are in fact due to alteration of the germination hydrothermal parameters (Fig. 3A, B): accumulation of time in dormancy loss conditions changes the germination base temperature (8 references, 7 species), base water potential (10 references, 8 species) and required thermal time for 50% germination (5 references, 8 species). Negative effect sizes here represent a widening of the conditions that will make the seed germinate: as dormancy is released, seeds can germinate at lower temperatures and water potentials, and require less accumulation of thermal time. Conversely, positive relationships indicate that secondary dormancy operates by increasing the base temperature or the required thermal time. In fact, individual studies showed that not only long-term stratification or after-ripening function in this way. Similar changes in hydrothermal traits are elicited by other factors such as fluctuating temperatures (Fernández-Pascual, Seal & Pritchard, 2015) and light (Hu *et al.*, 2013).

(9) Seedling growth

We found three references (four species) dealing with the effect of maternal temperatures on seedling growth. These references provided five records for a meta-analysis, which indicated a marginally significant effect (Fig. 1E). The effect of seed mass on seedling growth was the topic of four references from four species, with a stronger overall effect size (Fig. 2C).

IV. SYNTHESIS

(1) The first hub of thermal memory: seed yield

There is an extensive literature on the thermal memory of seed mass and number, and relating these two traits to a wide range of other reproductive traits (Fig. 4). It is beyond doubt that a warming climate will affect seed yield, and the key question is whether this warming will occur within the sub-optimal temperature range or push species into the supra-optimal range. A specific case of concern is determinate crops, for which it is widely expected that warming – in the absence of other limiting factors – will accelerate all reproductive phases and thus reduce yield (Wheeler *et al.*, 2000). This reduction is expected to be greater for seed number, since this is a more plastic trait than seed mass, especially in crops that have been subject to artificial selection (Sadras, 2007). In non-determinate plants, growth depends on the length of the season with suitable temperatures, and thus sub-optimal warming could improve yields. A key goal for future research will thus be to measure the yield thermal thresholds for a variety of ecologically significant species. As we have seen, another knowledge gap to fill is to dissect the role of different stages of thermal history, including previous generations and specific stages of flowering and seed development (Wagner & Mitterhofer, 1998). Another important step will be to integrate the thermal memory of seed yield into projections of species dispersal and future distributions. Yield improvements can reduce the dispersability of individual seeds (by increasing their mass and terminal velocity) while increasing the chances of an individual dispersing a small fraction of its progeny to long distances (by increasing its seed number, and likely seedling vigour). The overall outcome of these two seemingly opposite trends is not clear. The effect of mass on germination and seedling growth also needs clarification. For example, we found reports of heavier seeds having lower germination, but it is unclear whether this indicates that they are less viable or have deeper dormancy. At least in some cases, heavier and more-developed seeds seem to have deeper dormancy (Wang *et al.*, 2010). It is also unclear if there is a causal relationship between mass and germination, or an indirect correlation because both traits are influenced by maternal temperature. Overall, our meta-analysis reflects the importance of seed mass as a central hub for studies of the thermal memory of plant regeneration. In community ecology, articles considering physical seed traits, in particular seed mass, have increased fourfold in the last ten years (Jiménez-Alfaro *et al.*, 2016). This preponderance of reports on seed mass presumably reflects the ease of measurement of this trait as opposed to seed physiological thresholds and thermal times.

(2) The second hub of thermal memory: seed dormancy

The study of germination as a response to post-dispersal temperatures has reached maturity within the thermal time approach, and thermal time traits are accumulating for an ever-increasing number of species (Seal *et al.*, 2017). Nonetheless, the study of pre-dispersal temperatures and the thermal memory of germination lags behind. As we have seen, most experiments investigating maternal temperature have measured germination as the final proportion of

germinated seeds, a trait which provides little information on the relationships between temperature and reproduction. In a way, pre- and post-dispersal studies are speaking different languages: the former describing proportions and the latter thermal-time. This is a huge handicap to the incorporation of thermal memory into post-dispersal emergence models. It is important for future research on the effect of maternal temperature to adopt a hydrothermal approach, to allow us to develop integrated pre-dispersal/post-dispersal modelling of seed dormancy and germination.

We show one such model in Fig. 5. At the most basic level, germination thermal traits respond to the immediate post-dispersal thermal environment and drive progress towards germination. A first complication involves post-dispersal dormancy cycling, which produces changes in the hydrothermal thresholds and thermal time required for seed germination. During dormancy loss, the thresholds widen and the thermal time required is reduced, hence seeds become 'easier to germinate'; the opposite occurs during the imposition of secondary dormancy (Jones, Ellis & Gosling, 1997). In terms of thermal time, the rate of dormancy change is a function of exposure to post-dispersal temperatures (Pritchard *et al.*, 1996). The rate of dormancy loss is proportional to the difference between the actual temperature and a thermal threshold for dormancy change (Ceccato, Daniel Bertero & Batlla, 2011), and thus can be incorporated into the model by considering a separate set of dormancy-change thermal traits.

Further development of the model allows the integration of pre-dispersal maternal temperatures, which can affect: (1) the initial level of dormancy at dispersal; and (2) the rate of dormancy loss. This second aspect particularly requires further investigation, as little is known about the relationship between maternal temperature and the thermal thresholds for dormancy loss. One likely hypothesis is that these thresholds (for example, the ceiling temperature below which dormancy loss can occur) are dependent on the maternal temperatures experienced during seed development. Much remains to be clarified regarding the thermal memory of physiological dormancy, and very few data are available for species with physically and morphologically dormant seeds.

(3) Implications for modelling: an example

The thermal memory of plant reproduction has profound ecological implications, especially in climate change scenarios, where it has the potential to facilitate acclimatisation to new environments. For example, one concern is that future winters may not be cold enough to break physiological dormancy (Orrù *et al.*, 2012). Warmer climates could also result in more shallow physiological dormancy (Huang *et al.*, 2018). To illustrate the importance of this point, we provide an example in which future seed germination is projected under six different models that differ in their assumptions regarding thermal memory (Fig. 6). To simplify matters, in these models we show changes produced by thermal memory only as changes in the thermal time required for 50% germination (θ_{50}), although in a real scenario both θ_{50} and the cardinal temperatures could change.

In the simplest model with non-dormant seeds (model ND0 in Fig. 6), dispersed seeds accumulate thermal time (red triangles) until they reach θ_{50} (green lines), at which point they germinate. In a warmer future (model ND1), thermal time accumulates faster, leading to earlier seed germination. We can extend this model by including the effect of pre-dispersal thermal memory on seed mass (see Fig. 4) (model ND2). If we assume that a future increase in temperature will be in the sub-optimal range, this would lead to heavier seeds. If we also assume that heavier seeds germinate faster (Fig. 4), we can expect θ_{50} to be reduced, and thus earlier germination than in model ND1.

A more realistic simulation for many plant species should incorporate the role of physiological seed dormancy. In our first example (model D0), dormancy is represented by a decrease in θ_{50} during exposure to cold winter temperatures (blue bars). In practice, this means that, after chilling, seeds need to accumulate less thermal time to germinate. If a warmer future reduces the length of the overwintering season, dormancy loss could be compromised (model D1). After a shortened winter, θ_{50} would remain too high, potentially preventing the seed from germinating. In the final model (model D2), we integrate the effect of thermal memory on seed mass and dormancy (see Fig. 5). In this case, a warmer future would produce seeds that start with a lower θ_{50}. Even if the amount of dormancy loss they receive decreases because of a shortened winter, it might be sufficient to reduce θ_{50} to a level that allows adequate timing of germination. The key difference between D1 and D2 is within the seed: in both scenarios, the external environment provides the same signals for dormancy loss and germination. Through thermal memory, D2 seeds can adjust their 'expectations' to the new climate. D1 seeds can not, and thus fail to germinate.

In conclusion, thermal memory should allow seeds to adjust their germination phenology to climatic changes. In this example we have seen how increasing environmental temperatures can reduce the amount of cold stratification that a seed *receives*, but also the amount it *needs to receive* to break dormancy. This feedback will likely ensure some successful reproduction even if warming goes beyond the current thermal thresholds. In any event,

the effect of temperatures experienced during maternal can influence future germination traits, and climate change simulations should take this into account.

(4) Future priorities

One role for biology in these times of global change is to provide general rules that predict the behaviour of complex ecosystems. A key tool in this pursuit is trait-based models, which provide a predictive framework for the relationships between biodiversity and the environment (Funk *et al.*, 2017). For plant reproduction by seed, incorporating quantitative physiological traits into multi-species studies remains a difficult task, hindered by the lack of reliable trait databases and comparable methodologies for wild species (Jiménez-Alfaro *et al.*, 2016). In stark contrast with other functional traits, there is no standard template for physiological thermal-time studies. A widely followed handbook on the measurement of plant functional traits (Pérez-Harguindeguy *et al.*, 2013) deals only with seed mass and shape, and does not mention germination as a trait. Thus, seed ecology remains fundamentally disconnected from comparative and functional ecology. A modelling approach such as that described herein, applied to a global range of species characteristic of well-defined vegetation types, could provide a basis for a research agenda on global plant reproduction.

Ultimately, understanding plant reproduction by seed means being able to answer several questions. When are seeds produced? How many and how heavy are these seeds? How far do they disperse in space, but also in time through seed dormancy? When do they germinate? How many achieve successful seedling establishment? None of these questions have binary answers, all are a matter of degree. Their quantitative answers depend on physiological seed traits: the cardinal temperatures and thermal times of the different reproductive processes. These traits integrate the climatic inputs of the environment to produce reproductive outputs in the form of timing and success. It is crucial to understand these traits not as fixed numbers, but as having their own thermal memory, sometimes extending over several generations. This complex system – in which seed thermal-time traits are not static but in permanent change as a function of thermal history – ensures phenological integration of plant reproduction. We suggest that such a system will offer a degree of resilience and acclimatisation to climate change, until certain tipping points are passed, and reproduction becomes unsuccessful. Identifying these resilience thresholds remains a chief task for plant biologists and global change researchers. We believe that meeting this challenge will move us towards a more quantitative framework that sees changes in plant life not in absolute terms of positives and negatives, but as the acceleration or deceleration of physiological rates.

V. CONCLUSIONS

(1) Plant reproduction by seed is a complex process that integrates past and present climatic inputs to achieve successful establishment outputs. The successive steps of seed production, dispersal, dormancy, and germination respond to instantaneous thermal cues; but they also have a thermal memory (*via* phenotypic plasticity) that incorporates information from past thermal history.

(2) Seed yield is the first hub of thermal memory. Models of future dispersal and distribution should consider how the future climate will affect seed mass and number, as these two traits determine the dispersability of individuals and populations, as well as the vigour of their seedlings.

(3) Seed dormancy is the second hub of thermal memory, playing a key role in the acclimatisation of establishment timing. Research must link pre-dispersal and post-dispersal thermal histories by using a common thermal-time framework. Physical and morphological dormancy warrant particular efforts.

(4) This integrated system makes plant reproduction from seed relatively resilient to climatic changes, as long as certain tipping points are not passed. The thermal time approach offers a valuable methodological framework to identify such tipping points. Future progress will depend on the adoption of a standardised and simplified methodology for the calculation of thermal time traits, and the application of this methodology to large numbers of ecologically relevant species in a range of habitats.

VI. ACKNOWLEDGEMENTS

VII. REFERENCES

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VIII. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Appendix S1. Boolean search string used in the *Web of Science*.

Appendix S2. PRISMA chart showing the flow of information through the phases of the literature review.

Appendix S3. Data set with the values extracted from the references used in the meta-analysis. This data set can be used together with the R script in Appendix S4 to repeat the effect size calculations.

Appendix S4. R script used to calculate effect sizes from the data in Appendix S2.

Appendix S5. Data set with the calculated effect sizes for the studies in the meta-analysis, with information on the family, species accession number/strain, experimental setting, temperature ranges investigated and wild/domesticated status. This data set can be used together with the phylogenetic tree in Appendix S6 and the R script in Appendix S7 to repeat the meta-analysis model fitting.

Appendix S6. Newick phylogenetic tree used to fit the meta-analysis models.

Appendix S7. R script used to fit the meta-analysis models to the effect sizes in Appendix S5.

Appendix S8. The full output of the meta-analysis models.

Appendix S9. Results of the sensitivity analyses. Figures showing the results of models fitted with a different phylogenetic tree (Figs S1–S3), with no tree (Figs S4–S6), or by removing influential and outlier effect sizes (Figs S7–S9).

(A) Temperature and seed mass
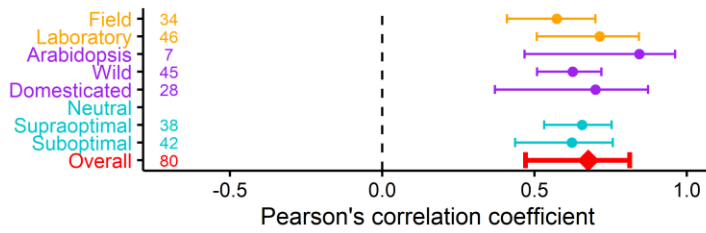
(B) Temperature and seed number

(C) Temperature and germination proportion

(D) Temperature and germination time

## (E) Temperature and seedling growth
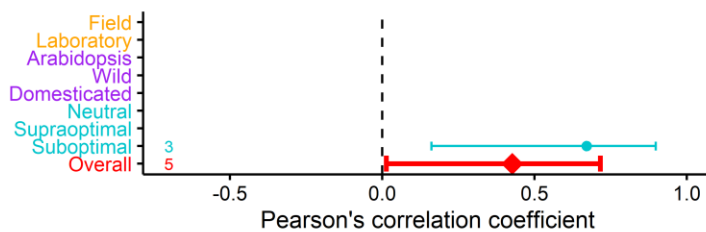
Fig. 1 Results of the meta-analyses for the effect of maternal temperature on several seed traits. The forest plots on the left show the estimated effect sizes (Pearson's correlation coefficient) with their 95% confidence intervals. The overall effect for the whole data set is represented by red diamonds. The partial effects according to different groupings of the data set (experimental setting, type of species and type of effect) are represented by circles of different colours. The number of review units (seed accessions within references) that contributed to the calculation of the effect size of each grouping is given to the right of the y axis. The tables on the right give the main parameters of each model: z is the Z-statistic, k is the number of review units in the model, I2 and Q are heterogeneity parameters. The total heterogeneity I2 can be calculated by adding the values for Phylogeny, Reference and Accession.
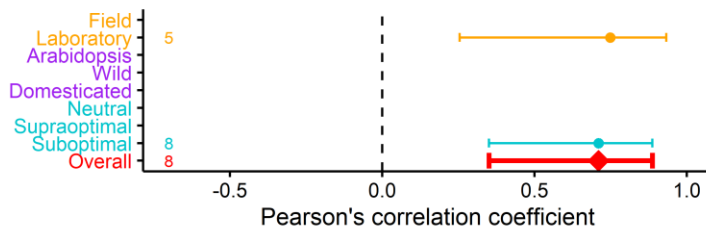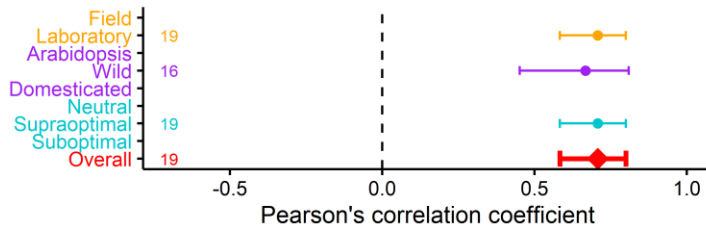
(A) Seed mass and germination proportion
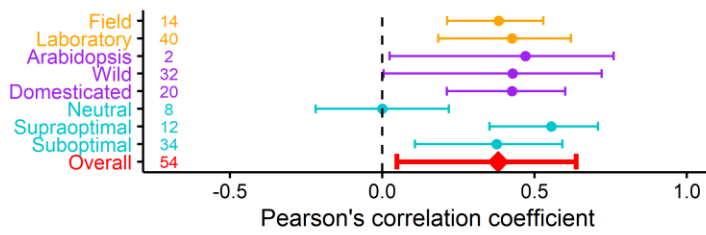
Effect size	0.381	I^2 *(Phylogeny)*	42
SE	0.178	I^2 *(Reference)*	39
z	2.228	I^2 *(Accession)*	13
p	0.026	Q	796.289
k	54	Q (p)	3.3e-133

(B) Seed mass and germination time
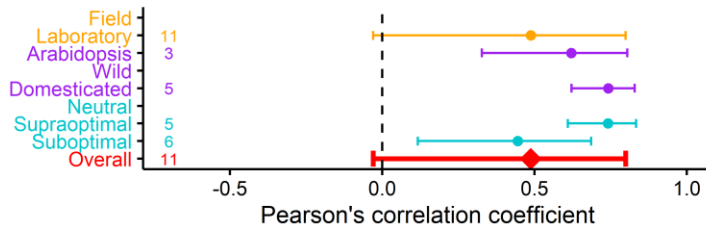
Effect size	0.488	I^2 *(Phylogeny)*	73
SE	0.280	I^2 *(Reference)*	0
z	1.857	I^2 *(Accession)*	0
p	0.063	Q	18.945
k	11	Q (p)	0.041

(C) Seed mass and seedling growth

Effect size	0.710	I^2 *(Phylogeny)*	0
SE	0.260	I^2 *(Reference)*	85
z	3.333	I^2 *(Accession)*	7
p	0.00086	Q	122.774
k	8	Q (p)	2e-23

Fig. 2. Results of the meta-analyses for the effect of seed mass on several seed traits. The forest plots on the left show the estimated effect sizes (Pearson's correlation coefficient) with their 95% confidence intervals. The overall effect for the whole data set is represented by red diamonds. The partial effects according to different groupings of the data set (experimental setting, type of species and type of effect) are represented by circles of different colours. The number of review units (seed accessions within references) that contributed to the calculation of the effect size of each grouping is given to the right of the y axis. The tables to the right give the main parameters of each model: z is the Z-statistic, k is the number of review units in the model, I2 and Q are heterogeneity parameters. The total heterogeneity I2 can be calculated adding the values for Phylogeny, Reference and Accession.
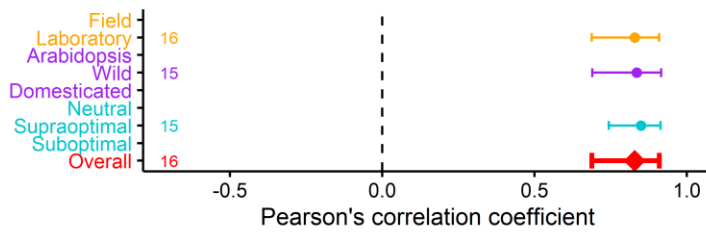
Fig. 3. Results of the meta-analyses for the effect of change in dormancy status on several seed traits. The forest plots on the left show the estimated effect sizes (Pearson's correlation coefficient) with their 95% confidence intervals. The overall effect for the whole data set is represented by red diamonds. The partial effects according to different groupings of the data set (experimental setting, type of species and type of effect) are represented by circles of different colours. The number of review units (seed accessions within references) that contributed to the calculation of the effect size of each grouping is given to the right of the y axis. The tables to the right give the main parameters of each model: z is the Z-statistic, k is the number of review units in the model, I2 and Q are heterogeneity parameters. The total heterogeneity I2 can be calculated adding the values for Phylogeny, Reference and Accession.

Fig. 4. Thermal memory of seed yield. Temperature increases in the sub-optimal range result in the production of more, heavier seeds; while the opposite occurs in the supra-optimal range. In turn, these two yield traits have a lasting effect on subsequent stages of plant reproduction. In the case of dispersal, increases of temperature in the sub-optimal range can decrease the dispersability of individual seeds, but increase the chance of some seeds dispersing over long distances. Sub-optimal range temperature increases also tend to favour faster seed germination and seedling establishment.
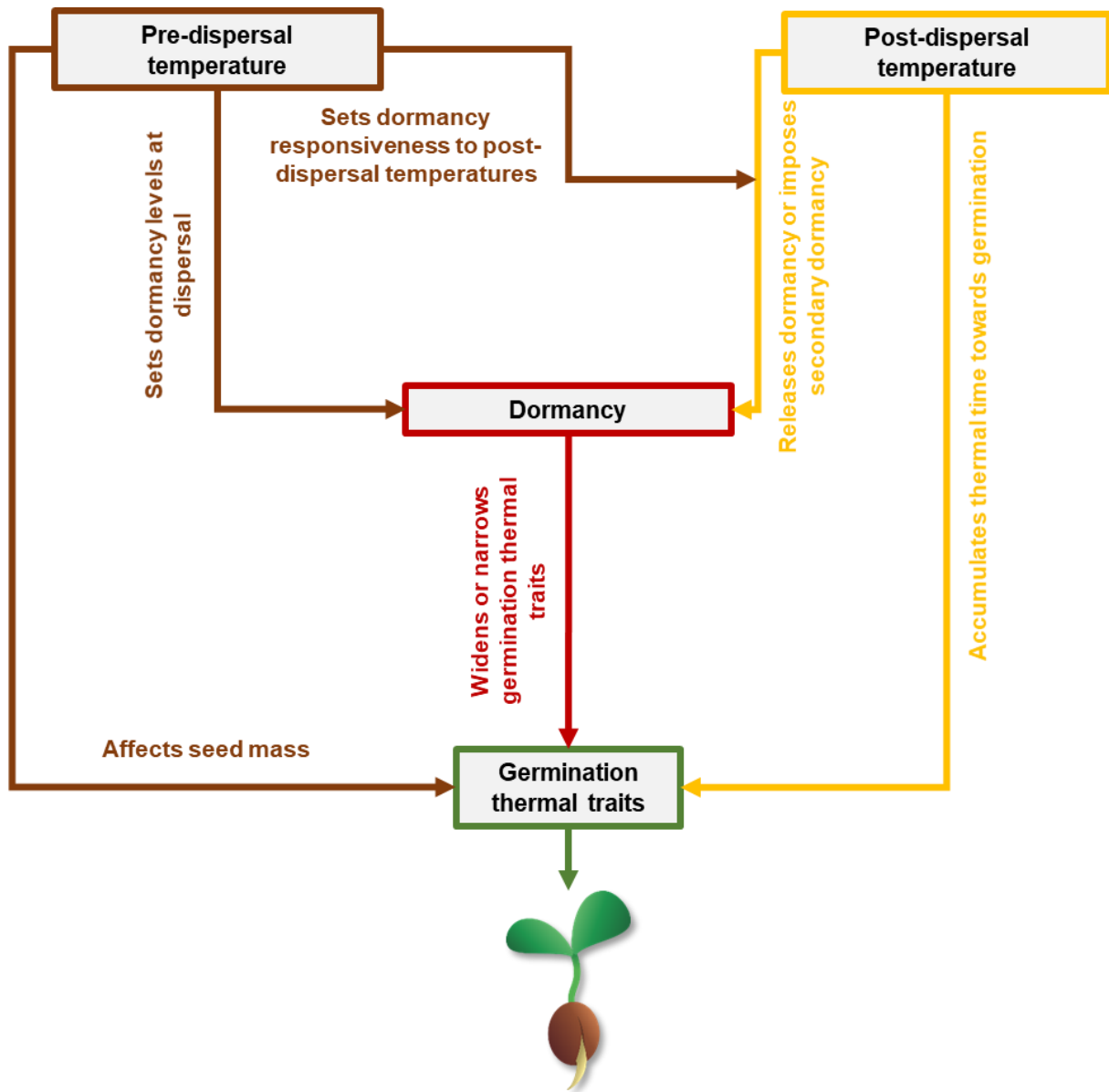
Fig. 5. Thermal memory of seed dormancy and germination. Post-dispersal temperatures (e.g. dormancy loss temperatures experienced in the soil seed bank) change the hydrothermal thresholds and the thermal time required for germination. Pre-dispersal temperatures (e.g. maternal temperatures experienced during seed maturation) can affect hydrothermal traits in two ways: (1) through an effect of seed mass on the hydrothermal traits; (2) through seed dormancy, as maternal temperature could (i) set the level of dormancy that the seeds have at dispersal; and (ii) set the sensitivity to dormancy loss/induction in response to the post-dispersal temperatures. In a practical scenario, seeds maturing in a warmer environment would have less dormancy at dispersal, and would lose this dormancy faster. As dormancy is released, seeds would become able to germinate at wider ranges of temperature and water potential, and would require less accumulation of thermal time before they germinate.
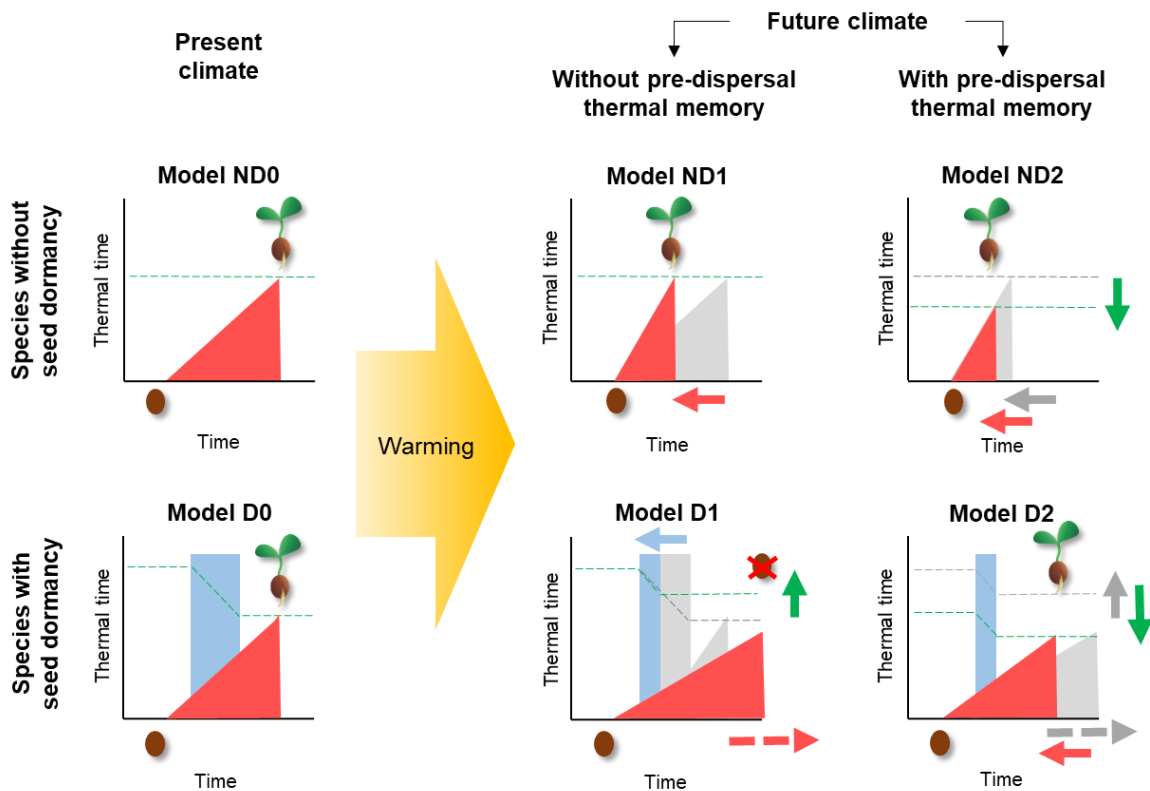
Fig. 6 Modelling of seed germination under climate change scenarios. Six models are presented that differ in their assumptions about seed dormancy and thermal memory. Field emergence of non-dormant seeds (ND) can be modelled using the cumulative sum of environmental temperatures (red areas) and the median thermal time for germination (θ50, dashed green lines). The case of dormant seeds (D) can be considered by incorporating a chilling period (blue bars) that reduces θ50. These models can take into account present temperatures (models ND0 and D0) and future climate change scenarios. They can ignore pre-dispersal thermal memory (models ND1 and D1) or take it into account (models ND2 and D2). In this simplification, dormancy loss and thermal memory are assumed to affect only the value of θ50. Arrows highlight changes due to the predicted increase in environmental temperatures (e.g. from ND0 to ND1) or, within future scenarios, due to the inclusion of thermal memory (e.g. from ND1 to ND2). Grey areas and arrows represent previous conditions and directions of changes. See Section IV.3 for further discussion. The germinated seed indicates the moment of germination, in model D1 the seed fails to germinate due to insufficient dormancy loss.