

## RESEARCH ARTICLE

# Simulated climate warming decreases fruit number but increases seed mass

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## Abstract

Climate warming is changing plant sexual reproduction, having consequences for species distribution and community dynamics. However, the magnitude and direction of plant reproductive efforts (e.g., number of flowers) and success (e.g., number and mass of fruits or seeds) in response to warming have not been well-characterized. Here, we generated a global dataset of simulated warming experiments, consisting of 477 pairwise comparisons for 164 terrestrial species. We found evidence that warming overall decreased fruit number and increased seed mass, but little evidence that warming influenced flower number, fruit mass, or seed number. The warming effects on seed mass were regulated by the pollination type, and insect-pollinated plants exhibited a stronger response to warming than wind-pollinated plants. We found strong evidence that warming increased the mass of seeds for the nondominant species but no evidence of this for the dominant species. There was no evidence that phylogenetic relatedness explained the effects of warming on plant reproductive effort and success. In addition, the effects of warming on flowering onset negatively related to the responses in terms of the number of fruits and seeds to warming, revealing a cascading effect of plant reproductive development. These findings provide the first quantification of the response of terrestrial plant sexual reproduction to warming and suggest that plants may increase their fitness by producing heavier seeds under a warming climate.

## KEYWORDS

climate warming, flowering phenology, meta-analysis, plant sexual reproduction, reproductive effort, reproductive success

## 1 | INTRODUCTION

Global surface air temperatures have risen approximately 1°C above pre-industrial levels, and the climate warming is expected to reach 3.3–5.7°C above pre-industrial levels by the end of the 21st century (IPCC, 2021). A growing body of evidence is showing that climate

warming changes plant sexual reproduction performance, including flowering phenology and reproductive effort (the proportion of the resources of an organism allocated to reproduction, e.g., flower number) and success (the final outcome of resource investment, e.g., fruit and/or seed number) (Arft et al., 1999; Bazzaz et al., 2000; Dorji et al., 2013; Molau, 1993). Changes in sexual reproduction

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performance may affect plant demographics (Jones & Henry, 2003; Walker & Chapin, 1987; Welker et al., 1997), offspring genetic variability (Steltzer et al., 2008), species distributional range (Dainese et al., 2017; Valdés et al., 2019), community composition, and many other ecosystem functions (Solomon et al., 2007; Walther et al., 2005). However, to date, the influence of climate warming on plant reproductive effort and success on a global scale remains poorly understood.

Climate warming affects the reproductive efforts in several ways. Climate warming often reduces flower number because higher temperatures decrease floral transition by accelerating somatic growth (Liu et al., 2012; Tromp, 1984). Warming also decreases flower production through a reduction in soil moisture (Hedhly et al., 2009; Kuppler et al., 2021), which is associated with flowering requiring the consumption of large amounts of water (Burke & Runyon, 2016; Gallagher & Campbell, 2017; Kuppler et al., 2021). In addition to changes in environmental conditions, warming may change plant reproductive effort via affecting flowering phenology. Rising temperatures in spring tend to advance the onset of plant flowering by accelerating ecodormancy breaks in northern high-latitude ecosystems (Wolkovich et al., 2012). Earlier flowering onset favors flower production by prolonging the duration of flowering, but negatively influences flower number due to the increased risks of frost damage (Cook et al., 2012; Inouye, 2008; Prevey et al., 2019). In contrast, winter warming can delay the onset of flowering through devernization, because many temperate and boreal species require prolonged winter chilling to initiate flowering (O'Neill et al., 2019; Penfield et al., 2021). Late flowering onset negatively influences flower formation and development (O'Neill et al., 2019).

Climate warming can influence plant reproductive success by disrupting fertilization. For instance, high-temperature stress shortens the duration when the stigmas of flowers are receptive to pollen, so reduces the chances of successful fertilization (Zinn et al., 2010). The number of fruits or seeds also decreases if climate warming reduces the quality and number of flowers (Bogdziewicz et al., 2020). Fruit and seed production requires fully developed flowers, and the number of flowers and ovules is a prerequisite for fruit and seed set per individual plant (Bykova et al., 2012). Additionally, the reproductive success of entomophilous species can be regulated by pollinators (Bennett et al., 2020; Rodger et al., 2021). When pollinators cannot track an earlier flowering phase under warming, the mismatch between the timing of flowering and pollinator occurrence leads to reductions in seed and fruit production (CaraDonna et al., 2014; Gérard et al., 2020; Gezon et al., 2016; Kudo & Cooper, 2019; Rafferty & Ives, 2011). In addition to the number of fruits or seeds, climate warming may influence fruit or seed mass by changing plant phenology. An extended growing season under warming conditions enhances the investment of resources into reproduction and prompts heavier fruits and seeds (Bolmgren & Cowan, 2008; Menzel et al., 2011; Moles & Westoby, 2003). Moreover, warming also potentially influences the fruit or seed mass of plants by altering their reproductive strategies. A trade-off between fruit and seed number and mass is ubiquitous for terrestrial species (Aarssen & Jordan, 2001; Dani & Kodandaramaiah, 2017; Henery & Westoby, 2001).

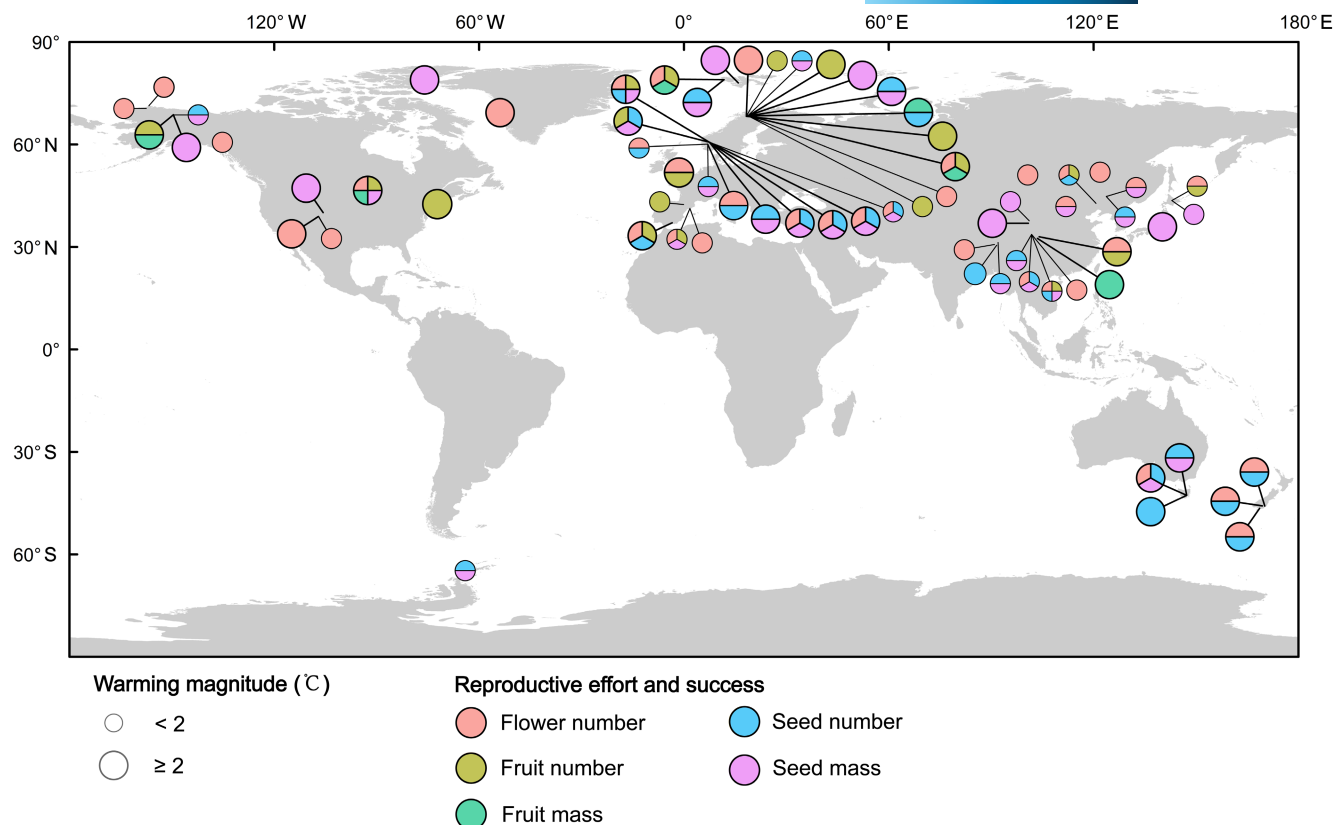
Previous manipulative experiments have produced inconsistent findings regarding how climate warming influences plant reproductive efforts and success, which may be owing to differences in ecological and experimental factors. For instance, the pollination type of a plant regulates the effects of warming on reproductive success, as entomophilous species are often more sensitive to warming than anemophilous species (Fitter & Fitter, 2002). Reproductive effort and success are more affected by long-term than short-term warming because the former leads to the depletion of plant belowground carbohydrates and nutrient stores over time (Arft et al., 1999; Barrett & Hollister, 2016; Dorji et al., 2013; Klady et al., 2011; Lambrecht et al., 2007). In contrast, an understudied factor potentially influencing the responses of plant reproduction to warming is the species dominance in a community. Generally, the dominant species monopolizes light, nutrients and water, and enough resources may allow them to exhibit a stronger reproductive response to warming than the rare species (Avolio et al., 2019; Liu et al., 2012). In addition, it also remains unclear whether the phylogenetic relatedness of plants regulates the effects of warming on reproductive effort and success, although the evolutionary history of a species partly explains its reproductive strategy (Vargas et al., 2018).

Here, we conducted a global meta-analysis of 61 manipulative warming studies, focusing on 164 terrestrial species, to examine how climate warming influences plant reproductive effort and success (Figure 1). We tested the following hypotheses (Table 1): First, we predicted that warming decreases the reproductive effort (e.g., flower number) by reducing plant water availability and devernization, and further reduces the number of fruits and seeds through cascading effects (Gérard et al., 2020; Kudo & Cooper, 2019; Liu et al., 2012). Second, we predicted that warming increases the mass of fruits and seeds, in addition to reducing fruit and seed number, because the offspring size and number tradeoffs are ubiquitous for many terrestrial species (Dani & Kodandaramaiah, 2017; Jakobsson & Eriksson, 2000; Moles, 2018). Finally, we predicted that the dominance and evolutionary history of species explain the effects of warming on reproductive effort and success, as they partly reflect plant resource acquisition ability (Doudová & Douda, 2020) and reproductive strategy (Ashman et al., 2004).

## 2 | METHODS

### 2.1 | Data compilation

We collected data on the effects of experimental warming on reproductive effort (e.g., flower number) and success (e.g., fruit number, fruit mass, seed number, and seed mass) from peer-reviewed articles published before December 31, 2020. Specifically, we conducted a systematic literature search on Web of Science (Thompson Reuters), Google Scholar (Google Inc.), and China National Knowledge Infrastructure (CNKI) using the terms (warm\* OR increased temperature OR elevated temperature OR temperature gradient OR heating) AND (reproduction OR seed OR fruit OR flower). We used the following criteria to extract data: (1) we



**FIGURE 1** Geographical distribution of the experimental warming studies in our meta-analysis.

included species from natural terrestrial ecosystems, and we excluded species from agricultural (e.g., transplanted individuals and seed germination) or aquatic ecosystems; (2) the biotic (e.g., vegetation structure) and abiotic (e.g., climatic and soil properties) conditions in the control and warming plots were the same at the beginning of the experiments; (3) we selected only the data from control and warming plots in the multifactor experimental manipulation studies; and (4) we directly obtained the means, standard deviations, and sample sizes from tables or we indirectly extracted them from digitized figures. Based on the four standards, we obtained a meta-dataset covering 61 published papers, which consisted of 477 pairs of observations for 164 terrestrial species (Table S1). These observations comprised 177 pairs for flower number, 48 pairs for fruit number, 16 pairs for fruit mass, 100 pairs for seed number, and 136 pairs for seed mass.

As the phenology of flowering often influences reproductive effort and success, we extracted data on the onset (97 pairs) and duration of flowering (53 pairs) from the 61 selected papers (Table S1). In addition, we collected ancillary ecological and experimental information, including latitude, longitude, elevation, annual mean air temperature (MAT), mean annual precipitation (MAP), ecosystem types (arctic/alpine tundras, boreal forests, [semi]arid grasslands, temperate grasslands, and temperate forests), warming methods (open-top chambers, infrared radiators, and greenhouses), warming season (year-round and seasonal warming), warming magnitude (<2 and ≥2°C; holding global warming at 2°C above pre-industrial

temperature was considered as a “safe level” of warming; Joshi et al., 2011), and experimental duration (≤2, 2–5, and >5 years; warming effects on vegetation composition were often detected in the first two experimental years (Walker et al., 2006), whereas most warming experiments lasted less than 5 years (Liu et al., 2021)) (Table S2). We obtained the MAT and MAP from the WorldClim v2.0 database (<http://www.worldclim.org/>) when they were not reported in the source papers (Fick & Hijmans, 2017).

We also collected biological information on the study species, including species name, dominance (dominant species and non-dominant species; the classification was based on the description of the study species in the papers), functional group (graminoids, leguminosae, forbs, and woody species), and pollination type (entomophily and anemophily; the study species were classified based on the papers or some websites, e.g., <https://plants.usda.gov>). We extracted the phylogenetic tree of these species from a global phylogenetic tree using Phylomatic software (version 3.0; <http://phylodiversity.net/phyloomatic>) (Zanne et al., 2014).

## 2.2 | Statistical analyses

To quantify the warming effect on plant sexual reproduction, we used the Hedges' *d* metric as recommended by Gurevitch et al. (2001). We calculated the Hedges' *d* value of each reproductive index for each study:

TABLE 1 Potential mechanisms underlying the effects of climate warming on reproductive effort and success

Variables	Definition	Direction	Mechanism	Key references
Flower number	The number of flowers per plant individual or the total number of flowers per unit area for the target species.	Decreased	<ol style="list-style-type: none"> <li>1. Climate warming disrupts the vernalization requirement for flower formation</li> <li>2. Warming decreases soil moisture, and plants produce smaller, fewer, and/or short-lived flowers under low water availability</li> <li>3. Earlier onset of flowering under warming increases risk of plants being exposed to frost damage during early-flowering season, which may cause reduced reproductive effort</li> </ol>	<p>Liu et al. (2012)</p> <p>Burkle and Runyon (2016), Kuppler et al. (2021) and Sherry et al. (2007)</p> <p>Inouye (2008)</p>
Fruit/seed number	The number of fruits/seeds per plant individual or the total number of fruits/seeds per unit area for the target species.	Decreased	<ol style="list-style-type: none"> <li>1. High-temperature stress negatively influences reproductive tissues through (i) shortened duration when flower stigmas are receptive to pollen, (ii) asynchrony of male and female reproductive development, (iii) defects in parental tissue, and/or (iv) defects in male and female gametes</li> <li>2. Warming reduced number of fruits or seeds through reduction in flower number</li> <li>3. Warming causes mismatch between timing of plant flowering and pollinator occurrence</li> </ol>	<p>Bheemanahalli et al. (2019), Lobell et al. (2015) and Zinn et al. (2010)</p> <p>Liu et al. (2012)</p> <p>Gérard et al. (2020) and Hegland et al. (2009)</p>
Fruit/seed mass	The mass of fruits/seeds per plant individual or the total mass of fruits/seeds per unit area for the target species.	Increased	<ol style="list-style-type: none"> <li>1. Extended growing season under warming increases accumulation of biomass and resource allocation to reproduction</li> <li>2. Trade-off exists between seed mass and seed number</li> </ol>	<p>Jacques et al. (2015) and Wolkovich et al. (2012)</p> <p>Smith and Fretwell (1974)</p>

$$d = \frac{X_e - X_c}{\sqrt{\frac{(N_e - 1)S_e^2 + (N_c - 1)S_c^2}{N_e + N_c - 2}}} J \quad (1)$$

$$J = 1 - \frac{3}{4(N_e + N_c - 2)} \quad (2)$$

where  $X_c$  and  $X_e$  are the mean values,  $S_c$  and  $S_e$  are the standard deviations, and  $N_c$  and  $N_e$  are the sample sizes for the control and warming plots, respectively;  $J$  is a weighting factor based on the sample size (Hedges, 1981). For studies that did not report the standard deviations, we used the Bracken (1992) approach to impute the missing standard deviations (the "impute\_SD" function; R package "metagear," version 0.7).

We also calculated the within-case variation of Hedges'  $d$ :

$$v_d = \frac{N_e + N_c}{N_e N_c} + \frac{d^2}{2(N_e + N_c)} \quad (3)$$

In this study, we calculated Hedges'  $d$  values and their within-case variations using the "escals" function (R package "metafor," version 3.0-2).

As some studies included multiple cases, we used hierarchical random-effects meta-analyses to quantify the mean effect sizes of warming and their confidence intervals (CIs). We performed the meta-analyses using the "rma.mv" function (R package "metafor," version 3.0-2), taking the variable "Reference/ID" as a nesting factor (Nakagawa et al., 2017; Viechtbauer, 2010). We considered the mean effect sizes of warming to be significant if the 95% CIs did not overlap by zero.

We tested the heterogeneity of warming effect sizes across studies using  $Q$  statistics, which are the weighted square sums compared with the  $\chi^2$  distribution (Hedges & Olkin, 1985). We divided the total heterogeneity ( $Q_T$ ) into the heterogeneity explained by the predictor variable examined in the model ( $Q_M$ ) and residual heterogeneity ( $Q_E$ ) using the "rma.mv" function (R package "metafor" version 3.0-2; Harrison, 2011). For each continuous variable (latitude, MAT, MAP, and elevation), we examined their relationship with the effect of warming on reproductive effort and success. For each categorical variable (e.g., warming magnitude), we compared the warming effects on reproduction between its different categories (e.g.,  $<2$  and  $\geq 2^\circ\text{C}$ ). We considered that the predictor variable regulated the effect sizes of warming when the  $p$ -values for  $Q_M$  were  $<0.1$ . In addition, we assessed whether evolutionary history was a key predictor of the effects of warming on reproduction using Blomberg's  $K$  metric (R package "phytools," version 4.1.3) (Blomberg et al., 2003; Chamberlain et al., 2012; Han & Zhu, 2021). A  $p$ -value for Blomberg's  $K$  lower than .05 indicated that evolutionary history contributed to the variance in the warming effect size.

To explore whether the linkages of reproductive indices exist under warming, we picked up the two groups of studies: (1) that simultaneously containing the data of the onset or duration of flowering and the reproductive effort or success and (2) that simultaneously including the information of number and mass of fruits

or seeds. We further examined the relationships between flowering phenology and reproductive effort or success and between offspring number and mass using the linear regression.

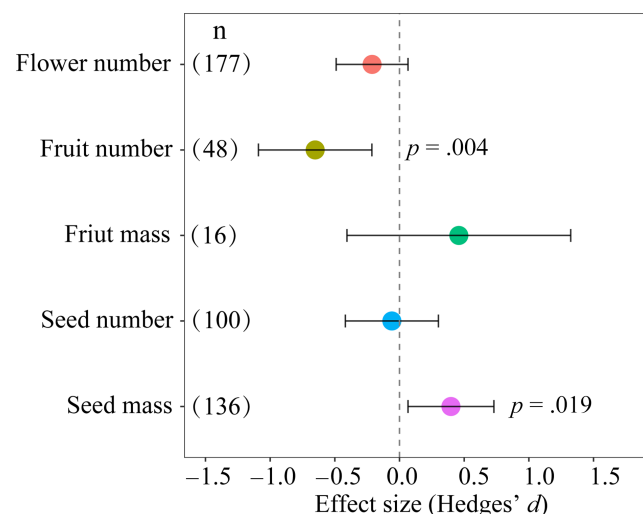
We tested for potential publication bias using Rosenberg fail-safe numbers and funnel plots. If the fail-safe number is larger than  $5 \times n + 10$ , where  $n$  is the sample size, publication bias does not exist (Rosenberg, 2005). In this study, we did not find any publication bias for most reproductive indices (Figure S1; Table S3). We conducted all statistical analyses using R 4.1.2 (R Core Team, 2021).

We presented our results using a gradual language of evidence, which has been recommended by Muff et al. (2021). Compared to significance testing with an arbitrary  $p$ -value cutoff, the language of evidence allows us to communicate scientific findings in a more nuanced form.

### 3 | RESULTS

Across all species examined, we found strong or moderate evidence that experimental warming decreases fruit number (Hedges'  $d = -0.65$ ,  $p = .004$ ) and increases seed mass (Hedges'  $d = 0.40$ ,  $p = .019$ ; Figure 2). In contrast, we found little evidence that warming overall influences flower number (Hedges'  $d = -0.21$ ,  $p = .135$ ), fruit mass (Hedges'  $d = 0.46$ ,  $p = .298$ ), or seed number (Hedges'  $d = -0.06$ ,  $p = .749$ ). However, the  $Q$  statistics showed that the evidence is very strong that the variances in warming effects on flower number ( $Q_t = 464.80$ ;  $p < .001$ ), fruit number ( $Q_t = 198.75$ ;  $p < .001$ ), fruit mass ( $Q_t = 91.02$ ;  $p < .0001$ ), seed number ( $Q_t = 284.77$ ;  $p < .001$ ), and seed mass ( $Q_t = 571.86$ ;  $p < .0001$ ) were large among the different studies (Figure S2).

Variances in the effects of warming on reproductive effort (i.e., flower number) across studies could be partly explained by latitude and elevation (Table 2). Specifically, we found very strong evidence



**FIGURE 2** Effect sizes (Hedges'  $d$ ) of experimental warming on reproductive effort and success. Points indicate mean effect sizes across all studies, and the bars indicate 95% confidence intervals. Values on left represent sample sizes.

**TABLE 2** Q-statistics results for whether the effect of experimental warming on reproductive effort and success is regulated by the examined predictor variables

Predictor variable	Flower number		Fruit number		Fruit mass		Seed number		Seed mass	
	$Q_M$	$p$	$Q_M$	$p$	$Q_M$	$p$	$Q_M$	$p$	$Q_M$	$p$
Latitude	<b>12.56</b>	<b>&lt;.001</b>	1.13	.287	2.61	.106	2.05	.152	<b>9.95</b>	<b>.002</b>
Mean annual temperature	1.87	.172	0.23	.634	0.21	.645	0.57	.449	1.88	.170
Mean annual precipitation	2.52	.113	<b>7.68</b>	<b>.006</b>	<b>21.12</b>	<b>&lt;.001</b>	0.06	.803	0.07	.796
Elevation	<b>7.94</b>	<b>.005</b>	0.01	.919	<b>7.32</b>	<b>.007</b>	0.01	.916	<b>6.70</b>	<b>.010</b>
Ecosystem type	5.89	.207	1.30	.862	—	—	0.10	.953	5.31	.151
Warming method	0.27	.602	<b>8.75</b>	<b>.013</b>	<b>13.05</b>	<b>.002</b>	0.03	.985	0.16	.924
Warming magnitude	2.10	.147	0.25	.615	—	—	0.01	.921	0.00	.981
Warming season	0.02	.876	1.93	.164	0.54	.464	0.39	.533	1.03	.310
Experimental duration	1.81	.405	1.13	.568	—	—	0.90	.235	0.18	.914
Functional group	3.96	.266	1.31	.728	<b>17.58</b>	<b>&lt;.001</b>	1.55	.672	2.66	.447
Pollination type	0.07	.798	1.01	.315	—	—	0.50	.481	<b>2.88</b>	<b>.090</b>
Species dominance	1.22	.270	0.21	.645	<b>15.15</b>	<b>&lt;.001</b>	0.00	.986	1.34	.247

Note: Note that bold sizes are shown when there are weak ( $p < .1$ ), moderate ( $p < .05$ ), strong ( $p < .01$ ), or very strong evidence ( $p < .001$ ) for the regulatory effects of predictor variables. "—" indicates that data are not available because the predictor variables are less than two categories.

that warming effects on flower number positively correlate with latitude ( $Q_M = 12.56$ ,  $p < .001$ ), but negatively correlate with elevation ( $Q_M = 7.94$ ,  $p = .005$ ; Figure 3). In addition, we noted moderate evidence that warming decreases flower number in (semi)arid grasslands (Hedges'  $d = -1.02$ ,  $p = .012$ ), but we found no evidence of this in other ecosystems ( $p > .1$ ; Figure 4). There was moderate evidence that low-level warming ( $<2^\circ\text{C}$ ) decreases the flower number (Hedges'  $d = -0.37$ ,  $p = .038$ ), but little evidence that high-level warming influences the flower number ( $p = .195$ ). The evidence was weak that the flower number reduces in studies that lasted longer than 5 years (Hedges'  $d = -0.63$ ,  $p = .065$ ), and we found no evidence of this in short-term studies ( $\leq 5$  years;  $p > .1$ ). We found no evidence that phylogenetic relatedness regulates the effects of warming on flower number ( $K = 0.08$ ,  $p = .142$ ; Figures 5; Table S4).

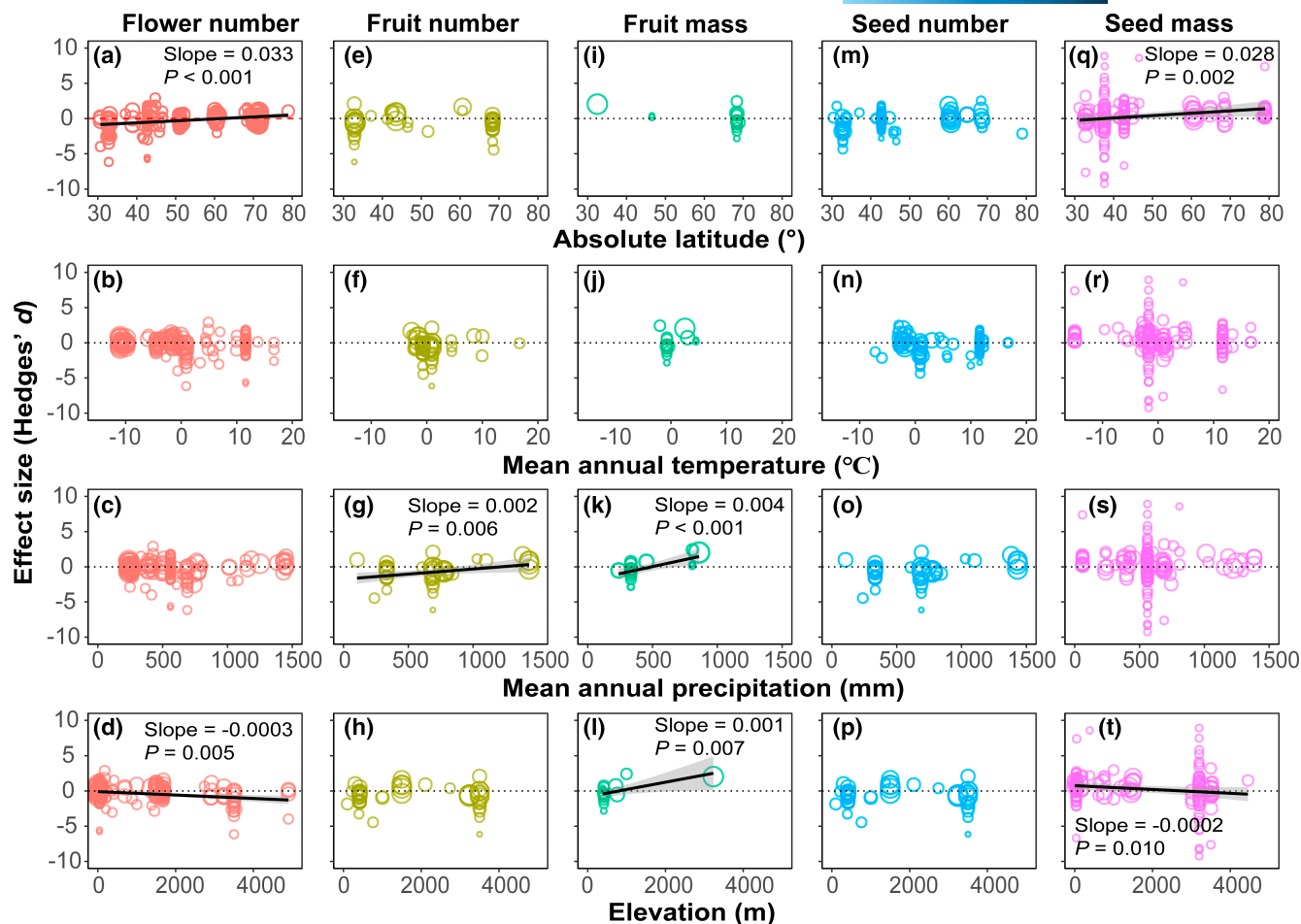
Key predictors of the effects of warming on reproductive success differed among the indices. For fruit number, there was strong evidence that the negative effects of warming diminish with increasing MAP ( $Q_M = 7.68$ ,  $p = .006$ ; Figure 3). The evidence was strong that warming decreases the fruit number in Arctic/alpine tundras (Hedges'  $d = -0.68$ ,  $p = .006$ ) but not in other ecosystems ( $p > .1$ ; Figure 4). There was moderate evidence that warming decreases the fruit number in studies using infrared radiators (Hedges'  $d = -0.67$ ,  $p = .042$ ), but no evidence of this in studies using open-top chambers ( $p = .124$ ). In addition, we found moderate evidence that the fruit number decreases under high-level warming ( $\geq 2^\circ\text{C}$ ) (Hedges'  $d = -0.73$ ,  $p = .014$ ), but no evidence under low-level warming ( $<2^\circ\text{C}$ ) ( $p = .200$ ; Figure 4). The evidence was very strong that the fruit number of entomophilous species reduces under climate warming (Hedges'  $d = -0.66$ ,  $p < .001$ ) and weak that the fruit number of anemophilous species decreases under warming (Hedges'  $d = -1.46$ ,  $p = .059$ ). We also found moderate evidence that warming reduces the

fruit number of the dominant species (Hedges'  $d = -0.71$ ,  $p = .014$ ), but not for the nondominant species ( $p > .1$ ; Figure 4). In contrast, we found no evidence that the warming effects on seed number were modulated by the examined predictor variables (Table 2).

For fruit mass, we found strong evidence that warming effects positively correlate with MAP ( $Q_M = 21.12$ ,  $p < .001$ ) and elevation ( $Q_M = 7.32$ ,  $p = .007$ ; Figure 3). We noted moderate evidence that warming enhances the fruit mass of forb species (Hedges'  $d = 1.21$ ,  $p = .017$ ), but reduced it for woody species (Hedges'  $d = -0.50$ ,  $p = .045$ ; Figure 4). In addition, we did not find any evidence that phylogenetic relatedness influences the effects of warming on fruit mass ( $K = 0.39$ ,  $p = .355$ ; Figure 5, Table S4). For seed mass, the evidence was strong that warming effects positively correlate with latitude ( $Q_M = 9.95$ ,  $p = .002$ ) and negatively correlate with elevation ( $Q_M = 6.70$ ,  $p = .010$ ; Figure 3). We also found strong evidence that warming increases seed mass for entomophilous species (Hedges'  $d = 0.53$ ,  $p = .004$ ) and nondominant species (Hedges'  $d = 0.54$ ,  $p = .009$ ; Figure 4), but no evidence that warming influences the seed mass of anemophilous species and dominant species ( $p > .1$ ).

We found weak evidence that warming advances flowering onset across the examined studies (Hedges'  $d = -0.38$ ,  $p = .056$ ; Figure S3). The effect sizes of warming on flowering onset negatively correlated with the effect sizes of flower number ( $p = .016$ ), fruit number ( $p = .045$ ), and seed number ( $p = .001$ ) (Figure S4). In contrast, there was no evidence that warming changes flowering duration (Hedges'  $d = 0.05$ ,  $p = .791$ ; Figure S3). In addition, we found very strong evidence that the effect sizes of warming on flower number positively correlate with those of fruit number ( $p < .001$ ) and seed number ( $p < .001$ ), and moderate evidence that the effects





**FIGURE 3** Relationships between warming effect sizes of reproductive effort and success and latitude, mean annual temperature, mean annual precipitation, and elevation. The reproductive indices include flower number (a–d), fruit number (e–h), fruit mass (i–l), seed number (m–p), and seed mass (q–t). Point size is proportional to weight in the meta-analysis. Regression lines and 95% confidence intervals are shown when there are weak ( $p < .1$ ), moderate ( $p < .05$ ), strong ( $p < .01$ ), or very strong evidence ( $p < .001$ ) for the regulatory effects of predictor variables.

of warming on seed number positively correlate with those of seed mass ( $p = .037$ ; Figure S5).

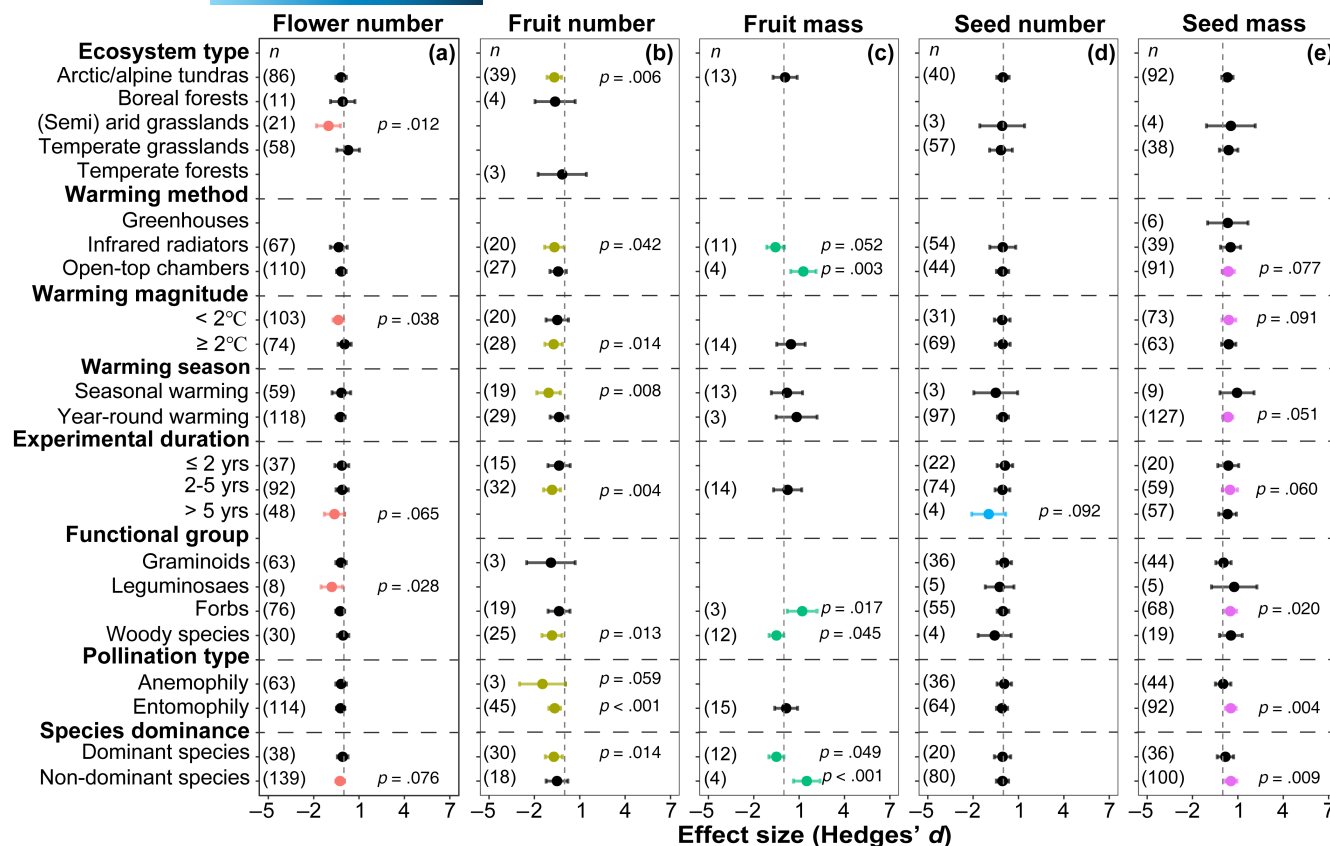
## 4 | DISCUSSION

Our meta-analysis provides the first quantification of the effects of climate warming on plant reproductive effort and success on a global scale. Our first hypothesis received mixed support from the global meta-analysis, with strong evidence that warming overall reduced fruit number but little evidence for a reduction in flower number (Figure 2). There was moderate evidence that warming resulted in heavier seeds across terrestrial species, which supported the second hypothesis. Regarding our third hypothesis, we found evidence that the dominance of species modulated the effect of warming on fruit mass, and no evidence that the evolutionary history of species regulated warming effects on reproductive indices. These findings deepen our understanding of plant sexual reproduction in a warmer world, and suggest that climate warming may benefit the

reproduction of terrestrial species by resulting in their producing heavier seeds.

### 4.1 | Limited change in flower number under warming

The results of our meta-analysis showed no evidence that experimental warming changed the flower number across all terrestrial species (Figure 2). This limited warming effect may be related to the number of flowers set before flowering (Molau, 1993; Sorensen, 1941). The flower buds of many species form one or several seasons before flowering (Diggle, 1997). This speculation also means that long-term experimental warming may produce a more pronounced effect on flower number, which is supported by our result that in studies lasting longer than 5 years, researchers observed a larger reduction in flower number than those conducting short-term studies (Figure 4a). In addition, the limited change in flower number may be associated with our finding that experimental warming did not change



**FIGURE 4** Comparisons of warming effects on reproductive effort and success among different categories of predictor variables. Reproductive indices include flower number (a), fruit number (b), fruit mass (c), seed number (d), and seed mass (e). Predictor variables include ecosystem type, warming method, warming magnitude, warming season, experimental duration, functional group, pollination type, and dominance of species. Solid points and error bars indicate mean effect sizes and 95% confidence intervals, respectively. Values on left represent number of synthesized cases. Black points are shown when there is no evidence of warming effects ( $p > .1$ ); other colors are shown when there are weak ( $p < .1$ ), moderate ( $p < .05$ ), strong ( $p < .01$ ), or very strong evidence ( $p < .001$ ).

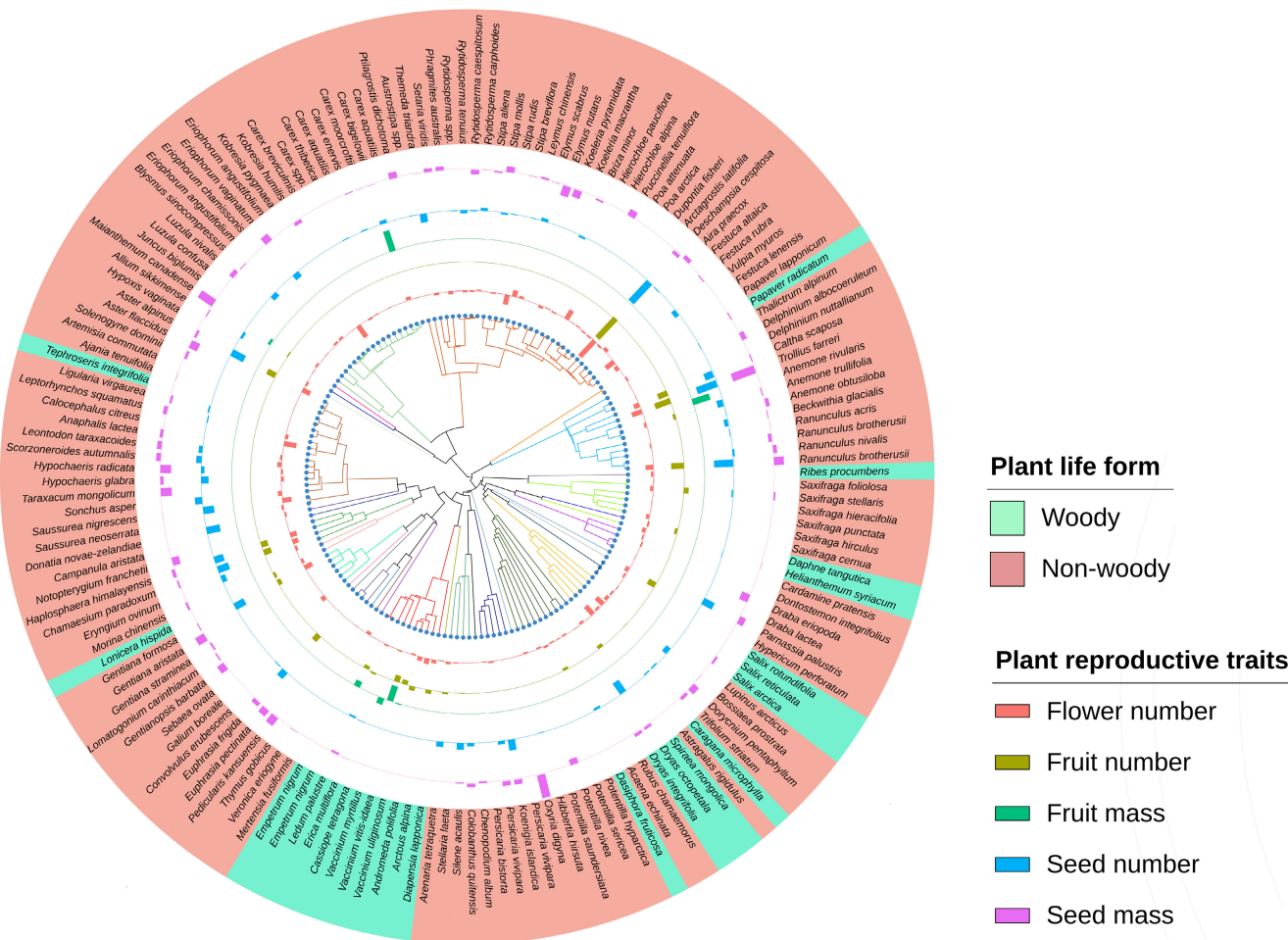
flowering duration (Figure S3). Flowering duration is an important factor influencing the number of flowers because a longer flowering period provides an opportunity for more flowers to be produced (Dorji et al., 2020; Nagahama et al., 2018).

However, we found moderate evidence that flower number decreased in response to experimental warming in (semi)arid ecosystems (Figure 4a), which likely occurred because warming reduced plant water availability and thus negatively influenced flower production (Dolezal et al., 2021; Dorji et al., 2013; Sherry et al., 2007). In contrast, we found no evidence that warming changed the flower number in Arctic/alpine tundras or temperate grasslands, although rising temperatures caused an earlier flowering onset (Figure S6). This likely occurred because the positive effect of earlier flowering on flower number was counteracted by the negative effect of increased risk of frost damage (Inouye, 2008; Wipf et al., 2009). Additionally, we found strong evidence that the warming effect size on the number of flowers positively correlated with latitude and negatively correlated with elevation (Figure 3a, d), suggesting that climate warming may result in a larger flower number shift at lower latitudes and higher elevations.

## 4.2 | Reduced fruit number and unchanged seed number under warming

Our result showed strong evidence that experimental warming overall reduced the fruit number, which is consistent with previous findings in Tibetan alpine (Liu et al., 2012) and semiarid Mediterranean grasslands (Valencia et al., 2016). One explanation for the negative effect of warming on fruit number is that high-temperature stress disrupts the development of the embryo and endosperm (Srinivasan et al., 1999). This speculation is supported by our finding that a reduced fruit number occurred only when experimental warming increased more than 2°C (Figure 4b). This reduction in fruit number was also likely related to changes in reproductive efforts under warming. Although we found that experimental warming caused limited changes in flower number in the present meta-analysis, it may have reduced the quality of flowers, which, in turn, reduced fruit production. It has been reported that climate warming decreases the number of fully developed flowers in the subalpine meadows of the Colorado Rocky Mountains (Saavedra et al., 2003).





**FIGURE 5** Phylogenetic trees of studied species and effects of warming on their reproductive effort and success. Warming effects on flower number, fruit number, fruit mass, seed number and seed mass are shown following the order from inner cycle to outer cycle. Length of bar is proportional to effect size of warming, which represents a positive (negative) value if the bar points toward outer (inner) cycle. Branch colors of phylogenetic tree represent family. Background colors of tip labels represent plant life form.

There was no evidence from our global meta-analysis that warming overall changed the seed number, which is inconsistent with previous findings based on herbarium specimens in China that climate warming has increased the seed number per pod of legume species over the past century (Duan et al., 2019). The discrepancy between the two findings may be associated with the researchers applying different seed number observation methods. Duan et al. (2019) only focused on the number of seeds per pod, whereas most researchers in our meta-analysis quantified the number of seeds by monitoring the seeds per unit area or per individual plant.

### 4.3 | Increased seed mass under warming

We found moderate evidence that warming increased seed mass across terrestrial species, which may have resulted from a larger reproductive investment associated with an enhancement in biomass production. It is well known that rising temperatures

stimulate the photosynthetic activity and biomass production by accelerating the rate of Rubisco carboxylation (Crous et al., 2018; Gunderson et al., 2010). In addition, increased seed mass is likely associated with earlier seed development following earlier flowering onset. Seed development often requires completion before frost damage occurs in autumn (Ida & Kudo, 2021). Earlier-onset seed development can provide plants with more time to produce heavier seeds.

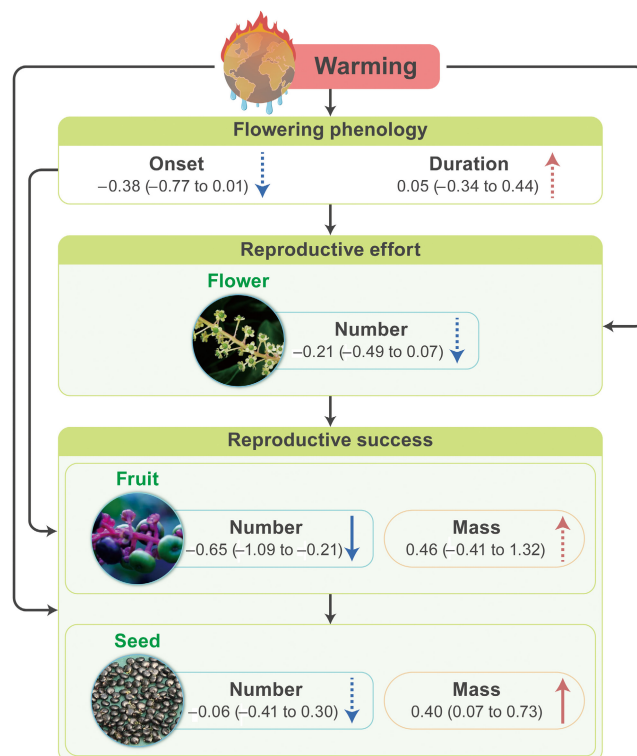
Our finding of a positive relationship between seed mass and seed number did not support the offspring number and mass trade-off. In contrast, the increased seed mass but unchanged seed number we found revealed another plant reproductive strategy under a warmer climate, that is, the mother plants not only allocate more resources to reproduction but also prefer to improve seed mass (Dani & Kodandaramaiah, 2017). An explanation for the observed reproductive strategy is that the offsprings of larger seeds have advantages in terms of survival and growth potential compared with smaller seeds, so have a higher probability of survival (Bergholz et al., 2015; Metz et al., 2010; Thompson & Hodgson, 1993). For

instance, an increase in seed mass may more easily satiate seed predators, thus leading to plants to experience a lower proportion of seed predation (i.e., “predator satiation hypothesis”; Bogdziewicz et al., 2020; Jansen et al., 2004; Janzen, 1971; Linhart et al., 2014). In addition, the observed reproductive strategy may favor the migration and diffusion of species under climate warming. Generally, terrestrial plants shift their distribution ranges to keep track with their climatic niches by seed dispersal, and most species rely on animals to disperse their seeds because animal-dispersed seeds are dispersed farther (Fricke et al., 2022; Gallagher, 2013; González-Varo et al., 2017; Tamme et al., 2014). In this study, plant seeds with a heavier mass under warming could attract more seed dispersers and have wider dispersal and hoard (i.e., “animal dispersal hypothesis”; Fricke et al., 2022; Gallagher, 2013; González-Varo et al., 2017; Janzen, 1971; Kelly, 1994; Vander Wall, 2002).

Notably, from this meta-analysis, we found strong evidence that warming overall increased the seed mass of the nondominant species but no evidence of this for the dominant species. Although this result did not derive from the same plant communities, it suggested that climate warming may exert different impacts on the fitness of the dominant and nondominant species. Further research is required to explore how climate warming differentially influences the reproduction of dominant species and nondominant species, given that it may be a key to shifts in community composition and biodiversity under a changing climate. In contrast, we did not find an important role for the evolutionary history of species in regulating the effects of warming on reproductive effort and success. This indicated that the response of plant reproduction to climate warming may not be phylogenetically conserved (Liu et al., 2022). Therefore, using simple phylogenetic relatedness to predict the dynamics of terrestrial species' sexual reproduction and its consequences in warmer climates may be inappropriate.

Overall, our global meta-analysis suggested that climate warming reduced fruit number of terrestrial plants but increased their seed mass. These findings have three important implications. First, our findings did not support the trade-off between offspring size and mass under warming conditions, but revealed a potentially increased fitness of terrestrial species due to their production of heavier seeds. Second, our findings provided evidence that the effects of warming on plant sexual reproduction are regulated by species dominance. Thus, examining whether the reproduction of rare species responds differently from dominant species may improve biodiversity conservation outcomes. Finally, we found complex linkages between flowering phenology and reproductive effort and success (Figure 6), suggesting the necessity of elucidating the whole plant life history for predicting the future dynamics of plant populations and communities.

However, our dataset lacks evidence from subtropical and tropical ecosystems, although it covers a wide range of terrestrial plants. Our study was also limited by the lack of some potentially important measurements (i.e., height and biomass of plant and quantity or quality of pollen) for completely elucidating the mechanisms underlying the effects of climate warming on



**FIGURE 6** Overview of the effects of warming on plant sexual reproductive effort and success across terrestrial species. Mean effect sizes of warming (Hedges'  $d$ ) and 95% confidence intervals are shown for flowering phenology (onset and duration of flowering), reproductive effort (flower number), and reproductive success (fruit and seed number and mass). Red and blue arrows indicate that warming increased and decreased reproductive effort and success, delayed and advanced flowering onset, or extended and shortened the flowering duration, respectively. Solid and dashed arrows beside numbers are shown when there is evidence ( $p < .1$ ) or no evidence of warming effects ( $p > .1$ ), respectively. We use *Phytolacca americana* as an example.

plant sexual reproduction. For instance, plant height and biomass often positively correlate with reproductive effort (Bolmgren & Cowan, 2008); however, a reduction in pollen quantity or quality reduces reproductive success (Ashman et al., 2004). In addition, self-compatibility is an important biological character, and the reproduction of only self-incompatible plants may be negatively influenced by the phenological mismatch between pollinator occurrence and flowering under climate warming. So far, how this biological character of species regulates the reproductive responses of terrestrial plants to warming remains poorly understood. Filling these gaps will help us to identify broad patterns of plant reproductive efforts and success in climate warming across geography and taxonomy.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Figshare at <https://doi.org/10.6084/m9.figshare.21302934.v1>.

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## SUPPORTING INFORMATION

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

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