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Untangling the Complexity of Climate Change Effects on Plant Reproductive Traits and Pollinators: A Systematic Global Synthesis

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ABSTRACT

Climate change is expected to affect the morphological, physiological, and life-history traits of plants and animal pollinators due to more frequent extreme heat and other altered weather patterns. This systematic literature review evaluates the effects of climate change on plant and pollinator traits on a global scale to determine how species responses vary among Earth's ecosystems, climate variables, taxonomic groups, and organismal traits. We compiled studies conducted under natural or experimental conditions (excluding agricultural species) and analyzed species response patterns for each trait (advance vs. delay or no change for phenology, decrease vs. increase or no change for other traits). Climate change has advanced plant and animal phenologies across most Earth's biomes, but evidence for temporal plant–pollinator mismatches remains limited. Flower production and plant reproductive success showed diverse responses to warming and low water availability in Alpine and Temperate ecosystems, and a trend for increased or neutral responses in Arctic and Tropical biomes. Nectar rewards mainly experienced negative effects under warming and drought across Alpine and Temperate biomes, but scent emissions increased or changed in composition. Life form (woody vs. nonwoody species) did not significantly influence trait response patterns to climate change. Pollinator fecundity, size, life-history, developmental, and physiological traits mostly declined with warming across biomes; however, animal

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abundance and resource acquisition traits showed diverse responses. This review identified critical knowledge gaps that limit our understanding of the impacts of climate change, particularly in tropical/subtropical biomes and southern latitudes. It also highlights the urgent need to sample across a greater range of plant families and pollinator taxa (e.g., beetles, wasps, vertebrates). The diversity of climate change effects should be assessed in the context of other anthropogenic drivers of global change that threaten critically important pollination interactions.

1 | Introduction

Global climate change is a major environmental crisis that has direct impacts on living organisms and their ecological interactions (Parmesan and Yohe 2003; Díaz et al. 2019). Rising temperatures, greater variability in surface temperature regimes, changes in precipitation patterns, and more frequent extreme weather events (IPCC 2023) are expected to affect the complex processes involved in plant and animal growth and reproduction (Gray and Brady 2016; Hedhly et al. 2009; Hegland et al. 2009). Plants being immobile have evolved diverse mechanisms to maintain physiological processes across a range of climatic conditions (Yamori et al. 2014); however, specific changes in temperature, humidity, and CO_2 levels have complex consequences on plant metabolism (Borghi et al. 2019; Dusenge et al. 2019). Above certain temperature thresholds, changes in temperature or water availability negatively impact plant growth and reproduction (Jagadish et al. 2021). Climate change may also influence floral trait morphology and physiology, which in turn may affect plant–pollinator interactions (e.g., Carbone et al. 2021; Carbone and Aguilar 2021; Ferreira et al. 2023; Harrison 2000; Nicholson and Egan 2020).

Animal pollination is one of the key ecological interactions on the planet, with around 90% of angiosperms depending on pollinators for sexual reproduction (Tong et al. 2023). Pollinators also have mechanisms to cope with temperature variation (e.g., Johnson et al. 2023; Powers et al. 2017); however, a higher frequency of extreme heat events may surpass species' thermal tolerances, restricting pollinator foraging, or threatening the survival of vulnerable juvenile stages (reviewed by Johnson et al. 2023). Furthermore, plant and animal fertility may decline at temperatures beyond their critical thermal limits (Walsh et al. 2019). Thus, changing climates are expected to affect plant reproduction and pollinator health and survival worldwide. However, the effects of climate change may differ depending on species traits and geographic locations.

The climate variability hypothesis proposes that organisms adapt to the range of thermal conditions in their environment by developing physiological mechanisms that enable them to cope with this variability (Addo-Bediako et al. 2000; Gaston and Chown 1999). Consequently, species that have evolved under seasonally variable climatic conditions in temperate zones are likely to exhibit broader thermal tolerances than species that occur in more stable temperature regimes, like tropical regions (Janzen 1967; Stevens 1989). An extension of the climate variability hypothesis suggests that, in addition to temperature variability, extreme temperatures play a crucial role in the evolution of species' critical thermal limits (Sunday et al. 2019). Although research on geographic ranges and thermal limits in terrestrial ectotherms and certain vertebrate groups provides strong support for this idea (Deutsch et al. 2008; Sunday et al. 2019), the evidence for plants remains scarce.

In the case of higher arctic latitudes or alpine montane regions, global warming may result in higher productivity, longer growing seasons (Berner et al. 2020), and higher insect activity, potentially enhancing plant reproductive success (e.g., Sletvold and Ågren 2015; Urbanowicz et al. 2018). However, greater warming rates at higher elevations and latitudes (Pepin et al. 2015; Post et al. 2018), and more frequent extreme events (IPCC 2023), also expose plants to extreme temperatures, drought and frost, which can negatively impact growth and reproduction (Iler et al. 2019).

In contrast to organisms in Temperate and Alpine biomes, tropical plants are expected to be more susceptible to climate change due to (1) relatively narrow thermal niches, (2) temperatures near the optimal for photosynthesis, and (3) limited access to cool refugees, particularly in lowland habitats (Doughty and Goulden 2008; Perez and Feeley 2018; Wright et al. 2009). Plant species from water-limited subtropical regions, such as Mediterranean ecosystems and deserts, generally exhibit a greater degree of heat tolerance and drought resistance; however, the higher temperatures and lower precipitation expected in the Mediterranean region (Lionello and Scarascia 2018) increase the risk of water stress and threaten plant growth and reproduction (Aronne et al. 2020; del Cacho et al. 2013; Peñuelas et al. 2004). Overall, climate change variables are expected to change across biomes, differentially impacting plant reproduction and pollinator traits. Specific physiological or life-history traits and the capacity for phenotypic plasticity may either facilitate adaptation to new environments or buffer against the impacts of climate change (Nicotra et al. 2010).

An expanding body of literature is available on the effects of climate variables on plant reproduction and pollination interactions, with several reviews focusing on specific topics (e.g., phenology—Byers and Chang 2017; Inouye 2022; Zhou et al. 2023; flower physiological and metabolic responses—Borghi et al. 2019; floral traits and pollination interactions—Kuppler and Kotowska 2021; Alchirique-Rojas et al. 2024; plant–pollinator mismatches—Gérard et al. 2020; insect pollinators—Johnson et al. 2023; see Table S1 for summary of literature reviews). Studies conducted in temperate latitudes show a trend toward advancing spring phenologies for plants and animals (Collins et al. 2021; Inouye 2022; Post et al. 2018); however, there is still a knowledge gap on how phenologies and other reproductive or life-history traits vary across latitudes and among plant life forms and animal groups.

In this review, we evaluate for the first time how climate change affects plant reproduction and pollinator traits across world biomes. Specifically, we investigate how changes in temperature, water availability, and snowmelt patterns influence flowering and pollinator phenologies, plant reproductive success, floral attraction and reward traits, pollinator characteristics, and plant–pollinator interactions among world biomes, plant life forms, and pollinator taxonomic groups. Given the limited number of studies available for most world ecosystems, we evaluated the following groups of biomes: (1) Arctic tundra, (2) Mediterranean ecosystems, (3) Alpine ecosystems (alpine and subalpine grasslands and meadows), (4) Temperate biomes (forests, grasslands, and shrublands), and (5) Tropical and Subtropical biomes (forests, grasslands, and shrublands). We identify knowledge biases and highlight critical gaps that warrant further research.

2 | Review Methods

We conducted a literature search in the online database Web of Science (Core Collection), comprising the period from January 1900 to December 2023 using the following keyword combination: ("climate change" OR "global warming" OR "greenhouse effect") AND (flower* OR pollinat* OR "floral visitor" OR "plant-pollinator") AND (bat* OR bee* OR bumblebee* OR beetle* OR "brush-tongued parrot*" OR butterfl* OR fly OR diptera OR honeyeater* OR honeycreeper* OR hummingbird* OR lemur* OR moth* OR rodent* OR sunbird* OR wasp* OR nectar OR scent* OR odor* OR fragrance* OR volatile* OR "fruit set" OR "seed set" OR "plant reproductive success" OR "seed mass" OR "plant fecundity" OR "plant-pollinator mismatch*" OR "pollinator mismatch*" OR interaction* OR network*). These keywords capture the range of plant reproductive traits and pollinator groups mostly assessed in the scientific literature. We read the abstracts of all retrieved articles and excluded studies that did not directly evaluate climate change effects on these variables. We extended our search with relevant articles cited in the literature. We focused our survey on wild animal-pollinated plant species; thus, we excluded wind-pollinated and agricultural species, as well as mathematical modeling of nonliving systems.

We obtained 340 articles that evaluated climate change variables on plant or pollinator traits at population and community levels or at large taxonomic scales (Supporting Information references: Data S1). We also obtained a list of review studies and summarized their findings (Table S1). For each study, we recorded the taxonomic identity (species, family, order), and plant life form considering two broad categories: woody (trees, shrubs, lianas, woody succulents) and nonwoody (herbs, vines, and nonwoody succulents). We recorded the response of plant reproductive variables assessed in each study and classified traits into the following groups: (1) flowering phenology: onset or mean flowering time (mean was used when available as it was reported in > 70% of species); (2) flower production, flowers produced per plant/inflorescence or flowers per unit area; (3) plant reproductive success, encompassing fruit or seed production, seed germination/progeny viability, and pollen production and viability; (4) pollinator visitation; and (5) attraction and reward traits that encompassed: (a) flower size and inflorescence height, (b) reward production, (c) floral volatile organic compounds (VOCs), and (d) floral pigmentation. We also recorded spatial or temporal pollinator mismatches. For statistical analyses, we excluded variables with small and geographically biased sample sizes (floral VOCs and color), and pooled variables with similar response patterns (plant reproductive success and pollinator visitation; floral size and nectar production). This categorization groups functionally related traits while maintaining adequate sample sizes for statistical analyses.

For animal pollinators, we recorded the following response variables: pollinator phenology (recorded by authors as emergence, first flight day, or peak abundance), species abundance (obtained by direct insect sampling, floral visitation rates, or progeny counts in social insects), health (incidence of disease or parasite infection), life-history traits (longevity, reproduction, survival), morphology (size and weight), physiological traits (heat stupor time, pupal developmental time, diapause time, and body protein content), and resource acquisition traits (time dedicated to foraging, diversity of pollen grains collected while foraging). Due to the limited number of studies that evaluated animal traits across different biomes, for statistical analyses, we pooled trait responses other than pollinator phenology, into a single category labeled "other animal traits" (including abundance, health, life-history, morphology, physiology, and resource acquisition traits).

Initially, we categorized response directions to climate change based on the results reported by each article. This classification included whether the response of a plant or animal species was significantly higher, lower, or unchanged compared to historical data or an experimental control. For flowering phenology, responses were classified as *advance*, *delay*, and *no change*; for other plant traits, responses were categorized as *decrease*, *increase*, and *no change*. If a species had the same response in more than one study within the same biome, it was considered a single entry; if a species was evaluated in different biomes or showed different responses to a climate variable, each response was considered a separate entry. For statistical analyses, we simplified phenological responses into *advance* or *no advance* (delay + no change) and the remaining trait responses into *decrease* and *no decrease* (increase + no change). This was necessary due to the small sample sizes in some response categories and biomes. Due to limited sampling of species and biomes, or lack of *decrease* responses, we excluded pollen quality, floral VOCs, floral pigmentation, pollinator mismatches, and wasps from statistical analyses. These variables are included in the database with their response indicated as "not analyzed" (Martén-Rodríguez et al. 2025). Studies reporting only community-level metrics were summarized and discussed but not included in statistical analyses.

We recorded the climate variables assessed in each study and categorized them for statistical analyses as (a) temperature, including temperature changes over time and warming experiments; (b) water availability, historical analyses of rainfall, and humidity or water stress experiments; and (c) snowmelt time, observed or experimental changes in snowmelt date. Other variables with limited sample sizes, such as indirect effects through ecological interactions or synergistic effects of climate with other global change drivers, are discussed but not included in statistical analyses.

We classified study sites into their corresponding biomes according to Dinerstein et al.'s (2017) classification of major world ecoregions. We adjusted this classification to include all montane ecosystems above the treeline, as well as subalpine grasslands and meadows within the Montane grasslands and shrublands biome (hereafter referred to as Alpine biome). For some statistical analyses and due to limited sampling, a small number of desert and arctic animal species were included in the Temperate biome category.

2.1 | Statistical Analyses

Using the database compiled through the review (Martén-Rodríguez et al. 2025), we conducted multinomial logistic regressions using PROC LOGISTIC in SAS (SAS Institute Inc., 2023, Cary, North Carolina, USA) to evaluate the impact of climate change on plant phenology and plant reproductive traits across biomes (Alpine, Arctic, Mediterranean, Temperate, Tropical/Subtropical), climate variables (warming, reduced water availability, and snowmelt time), and plant life forms (woody or nonwoody). When added water or precipitation was tested instead of drought, we reversed the response direction, so that all results indicate responses to reduced water availability. Analyses were conducted for the following response variables: flowering time, flower production, reproductive success/pollinator visitation, and floral size/nectar production. In the latter two cases, we also included the specific response (reproductive success vs. pollinator visitation, flower size vs. nectar volume) as a predictor in the analysis. Likelihood-ratio tests were used to determine the statistical significance of each predictor variable in the model. We chose the most parsimonious model based on likelihood-ratio tests and AIC values (i.e., the model with the lowest AIC was selected). The categorical response for phenology had two levels: *advance* and *no advance*; the remaining variables had *decrease* and *no decrease* as response levels. The *no advance* and *no decrease* categories were selected as baseline responses. For predictor variables, we selected reference categories with a large sample size that showed weak or no specific trends (e.g., when the *advance* or *decrease* states accounted for less than 50% of the responses). Thus, the reference categories for multinomial regressions were *Alpine* for biome, *temperature* for climate variable, and *nonwoody* for life form. Life form was excluded from some analyses based on likelihood-ratio tests.

We also conducted multinomial logistic regressions to evaluate the impact of climate change on animal phenology and "other animal traits" across biomes and animal groups (predictors). The analysis of climate variables was excluded because sample sizes were low for variables other than temperature. The model for "other animal traits" included the specific trait as a predictor variable with the following states: abundance, fecundity and survival, health, physiology, resource acquisition, and size. Response levels were classified as above, with the *no advance* and *no decrease* considered as baseline categories for phenology and "other animal traits," respectively. Due to small sample sizes, alpine and arctic species were included in the Temperate biome, and wasps were excluded from the statistical analyses conducted for "other animal traits." Reference categories were set to *Mediterranean* for biome, *Butterflies* for animal group, and *Abundance* for animal trait. In all models, Wald tests were used to assess the statistical significance of each regression coefficient. We report regression coefficients and standard errors for each response variable.

3 | Results

3.1 | Geographic and Taxonomic Sampling

The analysis of 340 scientific articles that reported the effects of climate change on plants and pollinators revealed a predominant focus on Temperate biomes (49% of studies), followed by Alpine (17%), Tropical (13%), Arctic Tundra (8%), Mediterranean (9%), and Deserts (4%) (Figure 1). We obtained species-level information for 551 plant species (275 Temperate, 124 Alpine, 78 Mediterranean, 41 Arctic, 38 Tropical), distributed in 95 plant families and 35 orders. We constructed a phylogeny to illustrate the diversity of plant species across orders; this was done with the R package V.PhyloMaker (Jin and Qian 2019), grounded in Smith and Brown's (2018) comprehensive dated phylogeny of seed plants. The families with the greatest number of surveyed species were Asteraceae, Fabaceae, Rosaceae, and Orchidaceae (Figure S1). Nonwoody plants accounted for 67% of the study species. We also obtained information for 574 pollinator species studied across biomes (474 Temperate, 67 Mediterranean, 36 Tropical, 28 Alpine, and 5 Arctic). The most frequently studied pollinator groups were flies, bees, and butterflies, with fewer studies on moths, wasps, and vertebrates (birds and bats; Figure S2).

3.2 | Plant Responses to Climate Change

For flowering phenology, we obtained 484 responses to climate change across biomes (Temperate 43%, Alpine 32%, Mediterranean 13%, Arctic 8%, Tropical 4%). Overall, advanced phenologies comprised 65% of species responses, whereas the remaining species did not advance (delayed 9%, no change 26%; Figure 2). A significant association was found between flowering time and predictors biome (Wald's $\chi^2=9.96$, $p=0.04$), climate variable (Wald's $\chi^2=8.51$, $p=0.014$), but not life form (Wald's $\chi^2=1.89$, $p=0.170$; Figure S3). Specifically, against the Alpine reference biome, plants across most biomes had a significantly higher likelihood of advancing than not advancing their flowering times (Table 1; Figure 2a). For climate variables, the probability of advanced flowering was significantly lower under water limitation than under warming temperatures (reference category; Table 1; Figure 2b).

For flower production, there were 122 responses to climate change (Temperate 35%, Alpine 30%, Tropical 12%, Arctic 11.5%, Mediterranean 11.5%). Overall, flower production decreased in 39% of species, whereas 22% of species showed increased production, and 39% remained unchanged (Table S2; Figure 3a). No significant associations were found between species responses and any of the predictor variables: biome (Wald's $\chi^2=4.7$, $p=0.312$), climate variable (Wald's $\chi^2=2.68$, $p=0.261$), or life form (Wald's $\chi^2=0.30$, $p=0.584$).

For plant reproductive success and pollinator visitation, we obtained 198 responses to climate change (Temperate 37%, Alpine 26%, Tropical 14%, Arctic 13%, Mediterranean 10%). Across

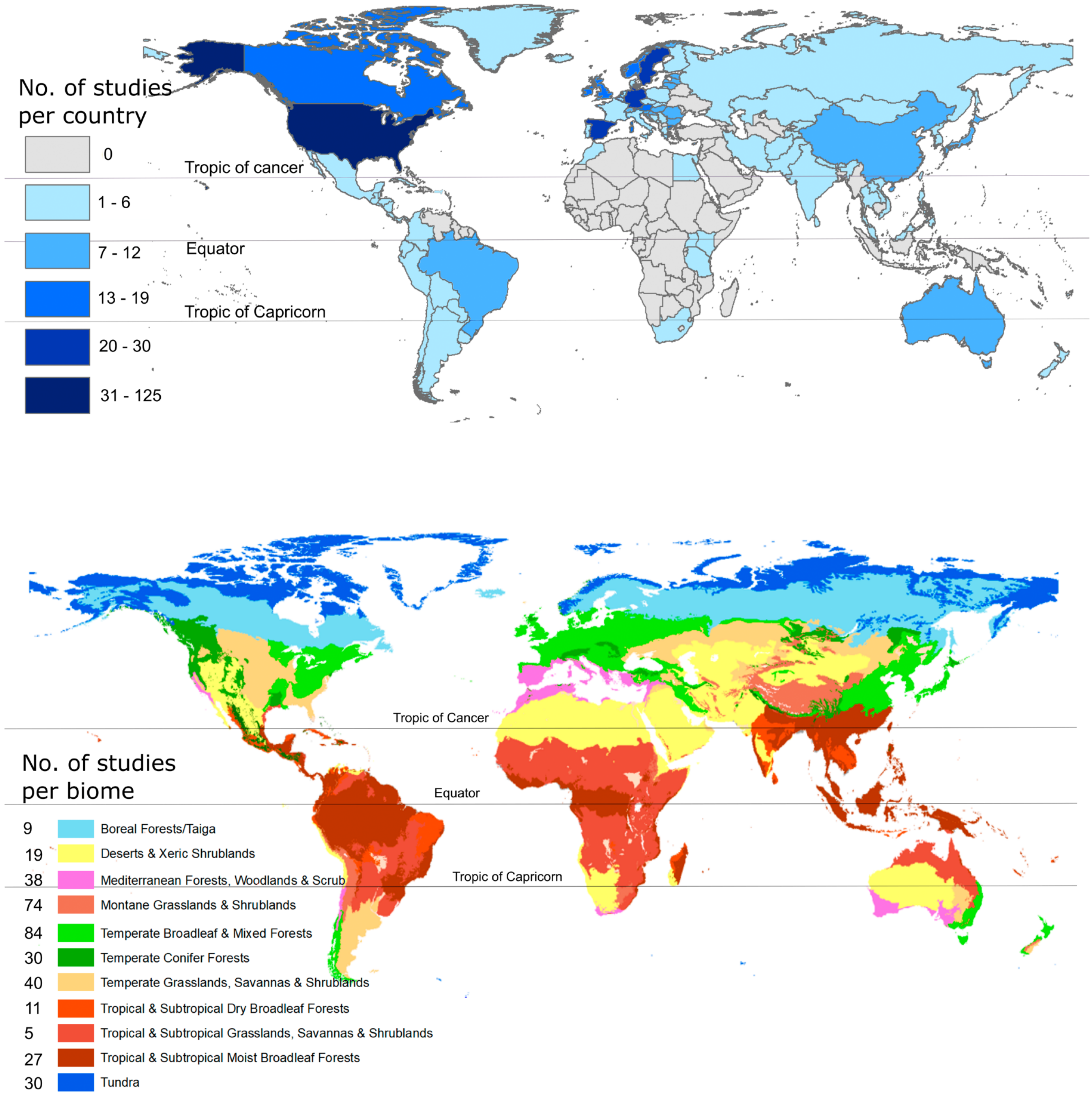


FIGURE 1 | Distribution of studies that evaluate the impact of climate change on plant reproductive traits and pollinator traits across world countries (top panel) and biomes (bottom panel). Map lines delineate study areas and do not necessarily depict accepted national boundaries. Maps were generated using ArcGIS (Esri 2025).

biomes, fruit set and seed set responses accounted for 55%–75% of all cases, followed by pollinator visitation (10%–30%), germination/offspring viability (0%–15%), and pollen production or viability responses (0%–2%). Overall, 41.5% of species showed *decrease* responses, followed by *no change* (36.5%) and *increase* responses (22%; Figures 3b and S3). Biome was a significant predictor of species responses (Wald's $\chi^2 = 13.38$, $p = 0.01$); Arctic and Tropical plant species had significantly lower likelihoods of having decreased reproductive success under climate change than Alpine species (reference biome; Table 2). Neither climate variable (Wald's $\chi^2 = 1.62$, $p = 0.444$), life form (Wald's $\chi^2 = 0.29$, $p = 0.590$), or specific reproductive trait (fecundity vs. pollinator visitation; Wald's $\chi^2 = 0.34$, $p = 0.562$; Figure S4) were significant predictors in this analysis.

For floral attraction and reward traits (flower size, nectar, pollen quality, floral VOCs, and pigmentation), we obtained 103 responses to climate change (Temperate 56%, Alpine 21%, Mediterranean 20%, Tropical 3%; Figure 3c,d). Traits included in statistical analyses, flower size, and nectar production, consisted of 67% *decrease* responses, followed by *no change* (23%) and *increase* responses (10%); in contrast, floral VOCs and pigments showed 61% *increase* and 39% *no change* responses (Figure 3c). No significant associations were found between

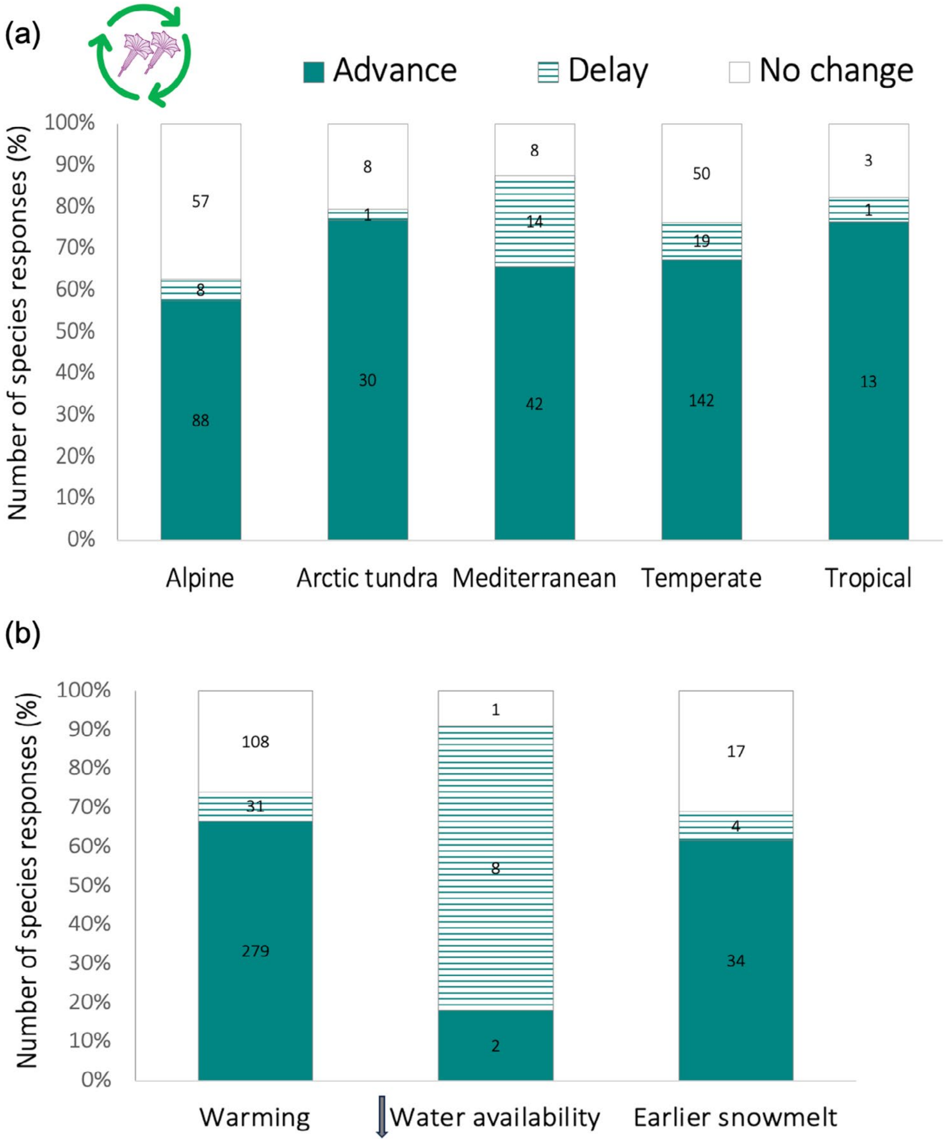


FIGURE 2 | Flowering time responses to climate change obtained in the literature review. (a) Comparison among the most studied earth biomes—Alpine/subalpine montane biomes; Arctic tundra; Mediterranean ecosystems; Temperate forests, grasslands, and shrublands; and Tropical/Subtropical forests, grasslands, and shrublands. (b) Comparison among the most frequently assessed climate variables. Numbers within bars represent the number of species responses per category.

species responses and any predictor variable: biome (Wald's $\chi^2 = 2.34$, $p = 0.310$), climate variable (Wald's $\chi^2 = 0.61$, $p = 0.738$), and specific response (flower size vs. reward, Wald's $\chi^2 = 0.30$, $p = 0.583$; Table S2).

Large-scale studies that did not provide species-level responses were included in a qualitative assessment of "community-level studies" in Tables S3 (Plants), S4 (Animals), and S5 (pollination networks). These studies report results for community-level variables or large taxonomic groups (e.g., species richness, overall abundance, mean changes in flowering time, or animal phenologies across communities or large databases). Most community-level studies show a trend of advancing flowering phenologies associated with higher temperatures in Desert, Mediterranean, and Temperate biomes. In Temperate and Tropical biomes, drought reduced the number of blooming species. Studies showed diverse responses in flowering duration and synchrony (Table S2). Twenty-one studies assessed changes in the network structure driven by climate change variables (temperature, drought, and snowmelt) and the extent of coextinctions caused by climate-driven spatial or temporal mismatches. They also explored factors that may affect network responses (Table S5). In pollination network studies, drought also reduced the number of blooming species, pollinator species, and pollinator and flower abundance ($N = 4$, all in Temperate biomes).

3.3 | Pollinator Responses to Climate Change

We obtained 498 phenological responses (timing of emergence, first flight day, and peak abundance date) to climate change for insect pollinators (bees, butterflies, and flies), distributed among Temperate (85%), Mediterranean (10%), and Alpine biomes (5%). Advanced phenologies accounted for 53% of all species responses, followed by unchanged (37%) and delayed

TABLE 1 | Results from multinomial logistic regression testing for variation in flowering time responses to climate change across predictor variables: (a) biome, (b) climate variable driving response (warming vs. reduced water availability or earlier snowmelt time), and (c) plant life form.

Predictor	Advance β	SE	N
Biome			
Alpine			153
Arctic tundra	**0.95***	0.419	39
Mediterranean	**0.70***	0.354	64
Temperate	**0.63***	0.252	211
Tropical/Subtropical	1.16	0.631	17
Climate variable			
Temperature			418
Snowmelt time	0.09	0.326	55
Water availability	**−2.31****	0.797	11
Life form			
Nonwoody			318
Woody	0.30	0.225	166

Note: Italicized names indicate reference categories used for each predictor. For life form, woody species include trees, shrubs, and lianas; nonwoody species include herbs, nonwoody vines, epiphytes, and succulents. β values in bold represent a significantly higher (+) or lower (−) likelihood of advanced phenologies in contrast to the "delay/no change" responses. Asterisks indicate statistical significance: $^*p \le 0.05$; $^{**}p \le 0.01$; $^{***}p \le 0.001$.
Abbreviations: N, number of responses analyzed; SE, standard error; β, regression coefficient.

phenologies (10%; Figure 4a,b). A significant association was found between species responses and the predictors pollinator group (Wald's $\chi^2 = 10.77$, $p = 0.005$) and biome (Wald's $\chi^2 = 41.53$, $p < 0.0001$). Under climate change variables, bees and flies were significantly more likely to advance their phenologies than butterflies (reference category; Table 3; Figure 4a). Animal phenologies were also more likely to advance in Alpine and Temperate biomes than in the Mediterranean reference biome (Table 3; Figure 4b).

For "other animal traits," we obtained 280 responses to climate change, encompassing bees, butterflies, flies, and a small number of vertebrates and wasps from Temperate (53%), Mediterranean (31%), Tropical (14%), and Alpine (2%) biomes. Warming and water limitation led to negative responses for 61% of species, while 16% of species exhibited positive responses and 23% remained unchanged. No significant association was found between species responses and pollinator group (Wald's $\chi^2 = 1.50$, $p = 0.472$) or biome (Wald's $\chi^2 = 0.93$, $p = 0.627$), but specific animal trait was a significant predictor of species responses (Wald's $\chi^2 = 23.23$, $p = 0.001$; Table 3, Figure 4c,d). Specifically, animal health, size, and physiological responses were more likely to decrease in response to climate change than species abundance (reference category). Decreased survival and life span responses to warming were also recorded for 11 tropical and one temperate fig-wasp species (not included in statistical analyses).

4 | Discussion

4.1 | Plant Reproductive Phenologies

This review revealed that flowering times are predominantly advancing with warming temperatures across most ecosystems (Figures 2 and 5); however, unchanged phenologies were particularly common in the Alpine biome (e.g., CaraDonna et al. 2014; Kudo 2020). The advancement of flowering times in response to climate change has been widely documented in arctic and temperate latitudes, where reproductive phenologies respond to changes in temperature, snowmelt time, and photoperiod (Byers 2017; Collins et al. 2021; Inouye 2020; Piao et al. 2019; Prather et al. 2023; Wolkovich et al. 2012). Many species require a period of chilling temperatures followed by warmer temperatures to break endodormancy and stimulate flowering (Kudo 2020; Tooke and Battey 2010; Wang et al. 2020). As a result, earlier springs lead to earlier flowering. Furthermore, evidence from community-level studies suggests that phenological advancement is more common for the onset or peak phases of the flowering cycle and for early flowering species. In contrast, flowering season length has more variable outcomes (Bock et al. 2014; Dunnell and Travers 2011; Park and Mazer 2019). All communities included species with contrasting phenological patterns, generally among the mid-season or late bloomers (Parmesan and Hanley 2015; Table S2). Moreover, some temperate communities show a higher frequency of delayed flowering phenologies, both in the Northern Hemisphere (Zu et al. 2024) and the Southern Hemisphere (Everingham et al. 2023). In the latter study, the prevalence of delayed phenologies in Australian plant species suggests that flowering patterns in the Southern Hemisphere may differ from those observed in northern temperate and Arctic regions (Everingham et al. 2023).

The current review suggests that low water availability may lead to delayed phenologies (Figure 2b). However, this proposal is not supported by phenological patterns from the Mediterranean biome. For example, flowering times have shifted an average of 22 days earlier over the past four decades in a plant community from Spain (Pareja-Bonilla et al. 2023). This result may be attributed to the rise in temperatures coupled with a reduction in precipitation in the Mediterranean; these factors appear to alter dormancy patterns, leading to earlier flowering, especially in winter and spring-flowering species (Gordo and Sanz 2010; Pareja-Bonilla et al. 2023; Peñuelas et al. 2002).

The unexpected advance in flowering phenologies observed in tropical/subtropical species is likely related to the fact that most surveyed species occur at mid-latitudes in China (e.g., Mo et al. 2017). A recent assessment of herbarium specimens over 200 years found significant shifts toward earlier and later flowering times in tropical plant species from both wet and dry forests (Graves et al. 2024). In the Tropical dry forests, grasslands, and shrublands biome, multiyear community-level studies indicate an important role of water availability on flowering phenology (e.g., Allen et al. 2017; Cortés-Flores et al. 2017, 2023). In less seasonal tropical habitats, where phenological cues have not been comprehensively assessed, plants are subject to more stable temperatures and water

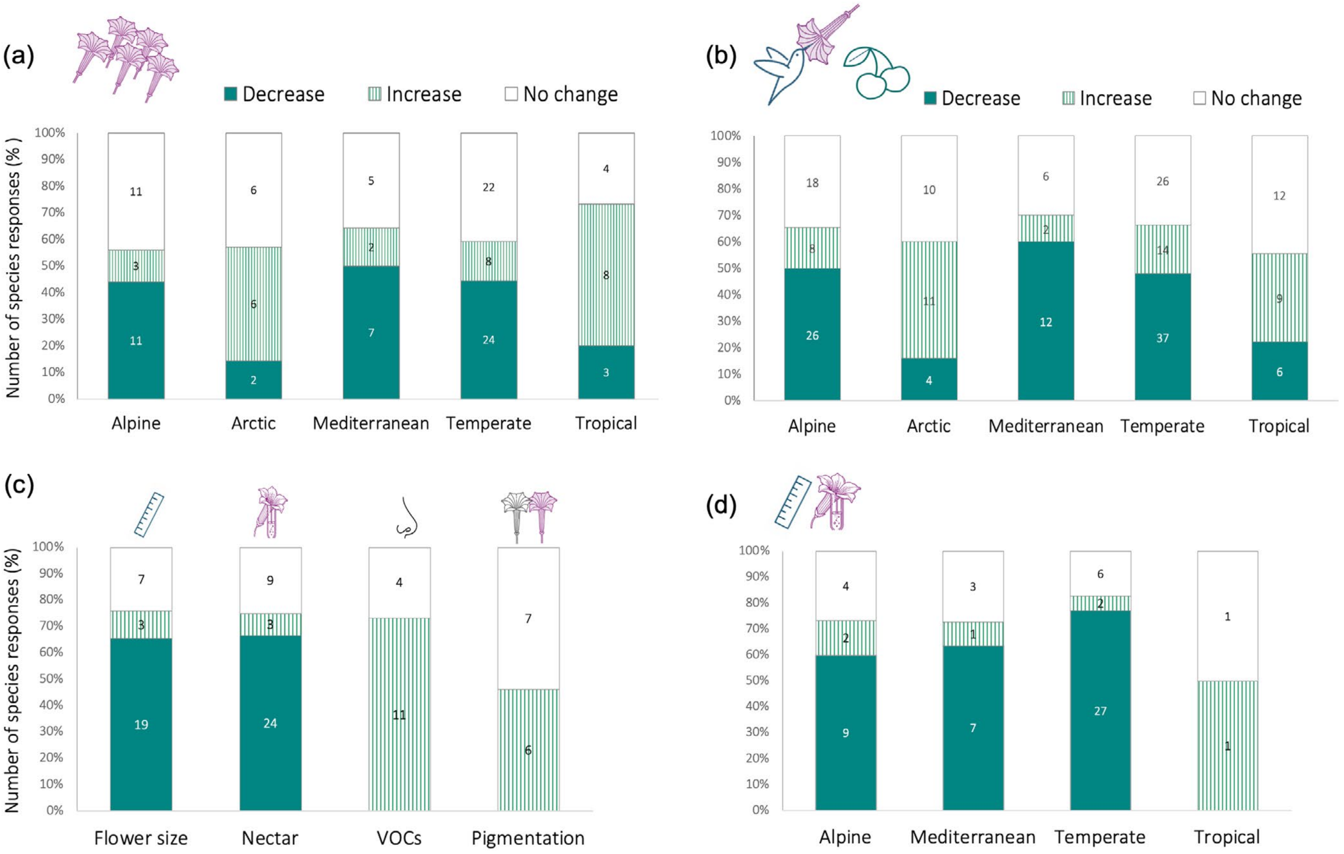


FIGURE 3 | Plant reproductive trait responses to climate change across biomes obtained in the literature review: (a) flower production, (b) pollinator visitation and reproductive success (fruit and seed production, pollen viability), (c) floral attraction and reward traits, and (d) flower size and nectar production. Comparisons were conducted among the following earth biomes: Alpine/subalpine montane biomes; Arctic tundra; Mediterranean ecosystems; Temperate forests, grasslands, and shrublands; and Tropical/Subtropical forests, shrublands, and grasslands. Numbers within bars represent the number of species responses per category. Flower images were generated by Image Generator Tool (version GPT-4), OpenAI, June 2024.

supplies, and often have multiple or extended flowering episodes (e.g., Marten and Quesada 2001; Newstrom et al. 1994; Sakai 2001; Fuchs et al. 2010). The available studies relate the flowering onset of tropical wet forest species to diverse factors, such as minimum temperatures, solar irradiance, precipitation, photoperiod, and extreme events (Cascante-Marín et al. 2017; Lobo-Segura 2019; Ramirez-Parada et al. 2020; Serna-González et al. 2021; Wright and Calderón 2018). Long-term community-level studies in tropical wet forests indicate that flowering intensity decreases with drought and changes in temperature and humidity (e.g., Dipterocarpaceae, Numata et al. 2022; Amazonian rainforest species; Vleminckx et al. 2024). Greater intensity and duration of flowering have also been associated with higher CO_2 levels in Panamanian tropical moist forests (Pau et al. 2018). However, the scarcity of long-term data sets that jointly evaluate climate and phenology limits our understanding of flowering responses to climate change in tropical regions (Davis et al. 2022).

In both temperate and tropical species, floral longevity or timing of anthesis have been associated with warming temperatures (e.g., temperate *Impatiens glandulifera* and *Oxalis compacta*, Arroyo et al. 2013; Descamps, Boubnan, et al. 2021; tropical *Stylosanthes capitata*, Alzate-Marin et al. 2021). Some insect species have short daily activity periods, particularly in more extreme (hot or cold) environments (e.g., Lobo 2021); therefore, shifts in the timing of anthesis could cause mismatches with pollinator foraging schedules (Murcia 1990). Although potentially important, the current evidence for shifts in flowering patterns at the flower and plant individual level is still limited.

4.2 | Flower Production, Plant Fecundity, and Pollinator Visitation

The analysis of population-level studies on flower production responses to climate change showed no significant trend or association with biome or climate variables. Species-specific responses to climate change variables were also reported within the same ecosystems (e.g., Mediterranean, del Cacho et al. 2013; Amazonia, Vleminckx et al. 2024). However, in the tropics, community-level studies show both increasing and declining trends in flower production. Higher flower production was associated with rising temperatures and CO_2 levels in the seasonal moist forest of Barro Colorado Island (Pau et al. 2013, 2018). In contrast, lower flower production was associated with warmer night temperatures and higher relative humidity in an Amazonian rainforest (Vleminckx et al. 2024). Variation in flower production has also been related to the indirect effects of climate through biotic factors such as herbivory (e.g., in *Gentiana formosa*, Liu et al. 2012). Unfortunately, the limited data available prevent further comparisons across world biomes.

TABLE 2 | Results from multinomial logistic regression testing for variation in reproductive plant responses to climate change across predictor variables: (a) biome, (b) climate variable driving response (warming vs. reduced water availability or earlier snowmelt time), (c) life form (woody vs. nonwoody), and (d) specific plant trait assessed (fecundity vs. pollinator visitation).

Predictor	Decrease β	SE	N
Biome			
Alpine			52
Arctic tundra	**−1.79****	0.664	25
Mediterranean	0.29	0.673	20
Temperate	−0.31	0.406	74
Tropical/Subtropical	**−1.36***	0.631	27
Climate variable			
Temperature			133
Snowmelt time	−0.66	0.547	44
Water availability	0.07	0.397	21
Life form			
Nonwoody			148
Woody	−0.24	0.449	50
Specific trait			
Fecundity			152
Pollinator visitation	−0.21	0.369	46

Note: Italicized names indicate reference categories used for each predictor. For life form, woody species include trees, shrubs, and lianas; nonwoody species include herbs, nonwoody vines, epiphytes, and succulents. β values in bold represent a significantly higher (+) or lower (−) likelihood of decreasing fecundity or pollinator visitation in contrast to the "increase/no change" responses. Asterisks indicate statistical significance: $^{*}p \leq 0.05$; $^{**}p \leq 0.01$; $^{***}p \leq 0.001$.
Abbreviations: N, number of responses evaluated in each category; SE, standard error; β, regression coefficient.

Plant reproductive success and pollinator visitation responses did not show a directional pattern; however, biome was a significant predictor of species responses. Specifically, Arctic and tropical species showed a greater proportion of *increase* or *no change* responses than other biomes. Higher reproductive success in Arctic tundra plants is not surprising, given that global warming has been associated with higher productivity and extended growing seasons in the Arctic biome (Berner et al. 2020). Studies of Arctic pollination networks suggest resilience of pollination interactions to climate change (Cirtwill et al. 2023) and population-level studies show higher, lower, or unchanged pollinator visitation in various plant species (e.g., Khorsand et al. 2024; Robinson and Henry 2018; Urbanowicz et al. 2018).

The limited data for tropical species showed an unexpected higher proportion of positive or neutral responses in plant reproductive success. Positive responses in flowering and fruiting intensity were mostly associated with "El Niño" events, as exemplified by a study of tropical lianas (Vogado et al. 2022). In tropical wet habitats, "El Niño" generates dry, sunny conditions that are thought to increase resources for plant reproduction, although these events are typically followed by years of low resource availability and reduced fruit production (e.g., Wright et al. 1999). Other climatic changes, such as greater cloud cover, higher precipitation, and warmer night temperatures, may instead decrease light availability, erode shallow soil nutrient-rich layers, or increase dark respiration (Alfaro-Sánchez et al. 2017; Vogado et al. 2022; Vleminckx et al. 2024), with little known consequences for plant fecundity in tropical wet environments.

For Alpine and Temperate biomes, plant reproductive success and visitation patterns mirrored those obtained for flower production, showing a combination of negative, neutral, and positive responses. A global meta-analysis of 164 predominantly temperate species subject to simulated warming experiments showed an overall decrease in fruit number, but not in flower production or seed number (Zi et al. 2023). These results indicate that, at least under experimental conditions, reproductive output tends to decrease with warming. Other factors, such as drought and the timing of snowmelt, are expected to negatively impact plant reproductive success. Earlier snowmelt may increase the risk of frost damage to plant reproductive structures (Pardee et al. 2019), whereas limited summer precipitation can lead to water stress later in the season (e.g., Harpold 2016; Powers et al. 2022). Our survey included studies conducted under natural and experimental conditions, which may partly explain the observed variation in reproductive success responses to warming, reduced water availability, and earlier snowmelt across ecosystems.

Male reproductive traits were also assessed in a small number of wild species from Temperate and Mediterranean biomes. These effects showed reduced pollen viability with higher ambient temperature (Mediterranean orchid species, Pellegrino et al. 2021), and changes in pollen protein production and pollen protein or lipid content (Centeno-Alvarado et al. 2022; Descamps, Jambrek, et al. 2021; Russo et al. 2020; Ziska et al. 2016). The effects of abiotic stress on male reproductive traits have been documented predominantly in economically important crops and model species (reviewed by Borghi et al. 2019). A recent meta-analysis also reported the negative effects of warming on pollen germination and viability in both crops and wild plants (Alquichire-Rojas et al. 2024), but comparisons across biomes are not yet possible.

4.3 | Floral Attraction and Reward Traits

Analysis of attraction and reward traits showed a general reduction in flower size and nectar production in response to warming and reduced water availability across Alpine, Temperate, and Mediterranean biomes (e.g., De Manincor et al. 2023; Descamps et al. 2018; Gallagher and Campbell 2017). These findings are consistent with previous reviews on the subject and have been attributed to the physiological responses of plants to extreme heat or water limitation, which affect flower physiology and development (Alquichire-Rojas et al. 2024; Borghi et al. 2019; Descamps, Quinet, et al. 2021; Scaven and Rafferty 2013). Nectar concentration, which was evaluated in some studies, mostly increased with warming, possibly due to higher evaporation rates (e.g., Bishop et al. 2023; Hall et al. 2018). In tropical regions, only three studies evaluated the effects of warming on nectar or pollen production (e.g.,

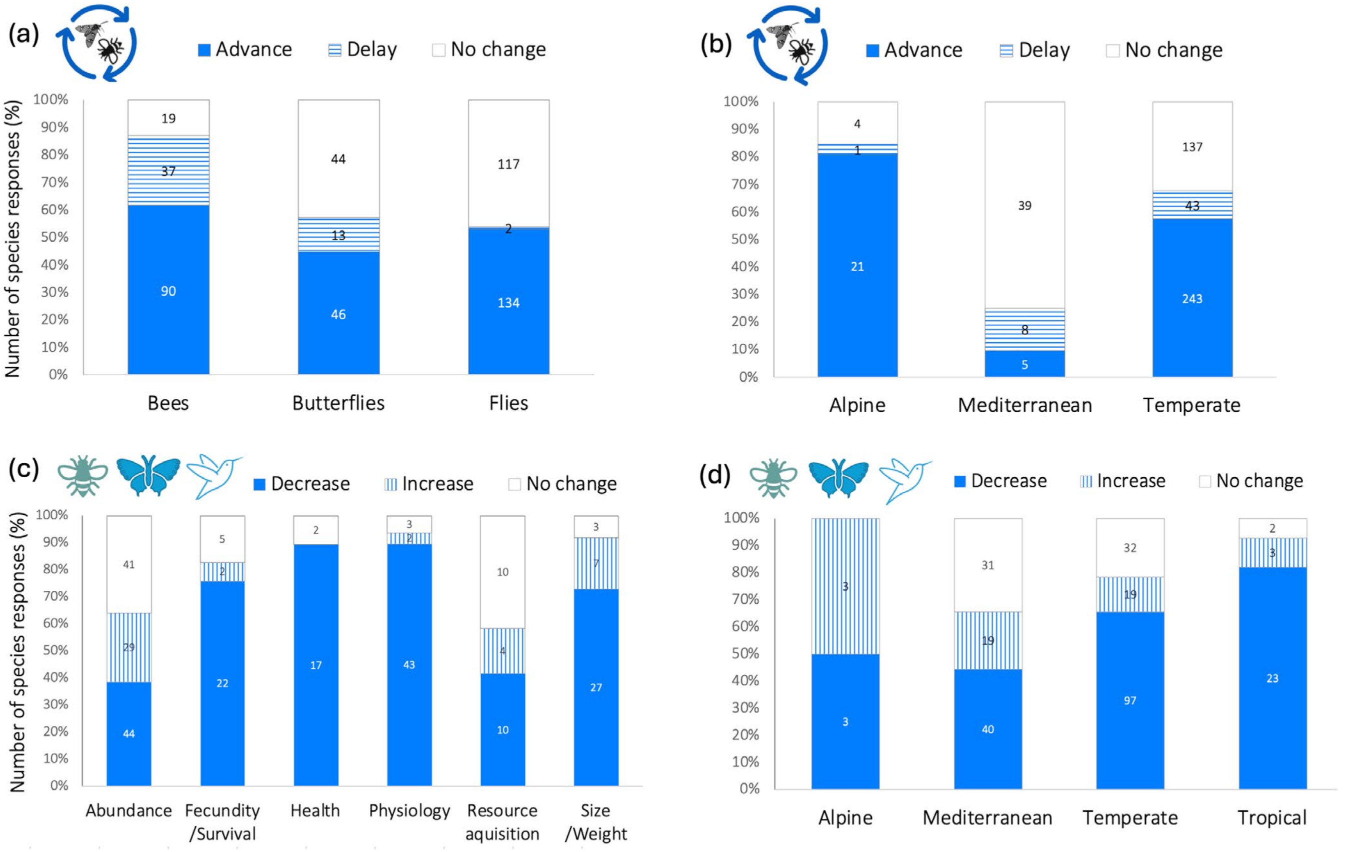


FIGURE 4 | Pollinator trait responses to climate change obtained in the literature review: (a) animal phenology (emergence, first or peak flight day) compared among pollinator groups; (b) animal phenology compared across earth biomes—Alpine/subalpine montane biomes, Mediterranean ecosystems, Temperate forests, grasslands, and shrublands; (c) responses compared across "other animal traits," including abundance, life-history, physiological, and behavioral traits; and (d) "other animal traits" responses compared across world biomes. Numbers within bars represent the number of species responses per category.

Centeno-Alvarado et al. 2022; Maluf et al. 2022); thus, the evidence is still limited for inference of broader geographical patterns.

Floral pigmentation and scents showed a trend for increased or neutral responses under warming temperatures (e.g., flower color: Brunet and Van Etten 2019; Sullivan and Koski 2021; scents: Farré-Armengol et al. 2014; Höfer et al. 2022, 2023). The higher production of floral scent has been attributed to the higher emission levels and volatility of VOCs (Borghi et al. 2019; Descamps, Quinet, et al. 2021; Yuan et al. 2009), but more studies are required to understand how these changes will affect pollinator visitation patterns. For instance, climate change may modify floral scent profiles (e.g., Jaworski et al. 2022) and cause recognition mismatches with pollinators (Gérard et al. 2020).

Climate change may influence pollinator visitation indirectly by affecting the aforementioned floral traits, or directly through its impact on the pollinators themselves (Corbet and Huang 2016; Johnson et al. 2023; Scaven and Rafferty 2013). For example, warming and water limitation generally lead to a reduction in flower size (e.g., De Manincor et al. 2023; Descamps et al. 2018), and pollinator visitation changed along with flower size in 10 out of 14 cases (e.g., Hemberger et al. 2023; Kuppler et al. 2021). Moreover, lower bee pollinator visitation rates were associated with higher temperatures and drought-driven reductions in nectar production in various plant species (e.g., De Manincor et al. 2023; Descamps et al. 2018; Gallagher and Campbell 2017; Hall et al. 2018). These examples suggest that the new set of floral morphologies, rewards, and attractants associated with global warming will likely influence future trajectories of floral evolution (Day Briggs and Anderson 2024).

4.4 | Pollinator Phenologies

The phenological responses of animal pollinators (emergence, flight dates, or peak abundances) were significantly predicted by pollinator group and biome. Advanced phenologies were more likely to occur in bees and flies than in butterflies, and they were more common in insects from Alpine and Temperate biomes than in those from Mediterranean ecosystems. Community-level studies and reviews support a predominance of advanced pollinator phenologies in temperate pollinators (Tables S1 and S4), with spring temperature as one of the key determinants of insect emergence time (Ellwood et al. 2012; Gordo and Sanz 2010; Høye and Forchhammer 2008). Advanced insect phenologies have been associated with earlier snowmelt and warming temperatures, particularly for early-emerging insects and those overwintering as adults (e.g., Gordo and Sanz 2006; Olliff-Yang and

TABLE 3 | Results from the multinomial logistic regressions (regression coefficients β and SE) testing for the association between animal pollinator responses to climate change recorded in the literature review and predictor variables biome, pollinator group, and specific animal trait.

Predictor	**Animal phenology**	**Advance β**	**SE**	***N***
Animal group	*Butterfly*			102
	Bee	**−1.23****	0.407	146
	Fly	**−1.28****	0.394	253
Biome	*Mediterranean*			52
	Alpine	**4.84*****	0.803	26
	Temperate	**3.86*****	0.641	423
Predictor	**Other traits**	**Decrease β**	**SE**	***N***
Animal group	*Butterfly*			112
	Bee	1.00	0.623	147
	Vertebrate	0.49	1.148	20
Biome	*Mediterranean*			92
	Temperate	−1.22	0.713	153
	Tropical	−1.41	1.060	28
Animal trait	*Abundance*			119
	Fecundity/ Survival	**1.69****	0.592	29
	Health	**3.22****	1.169	20
	Physiology	**2.73*****	0.625	48
	Resource acquisition	0.90	0.712	24
	Size/Weight	**1.47****	0.548	37

Note: Italicized names indicate reference categories used for each predictor. β values in bold represent a significantly higher (+) or lower likelihood (−) of the baseline response (advance or decrease) versus the alternative response. Asterisks indicate statistical significance: $^{*}p \leq 0.05$; $^{**}p \leq 0.01$; $^{***}p \leq 0.001$. Abbreviations: *N*, number of responses; SE, standard error; β, regression coefficient.

Mesler 2018; Stemkovski et al. 2020). Higher temperatures generally accelerate insect developmental rates, although other abiotic factors, such as rainfall, photoperiod, or a chilling period during wintertime, also influence species responses. These factors are often cues for physiological processes involving diapause development and termination (reviewed by Forrest 2016).

Butterflies and flies exhibited a relatively high proportion of species that did not alter their phenologies in response to climate change, although these results are based on one community-level study for each group (UK flies, Hassall et al. 2016, Mediterranean butterflies, Colom et al. 2022). The diversity of phenological responses is likely associated with variation in feeding habits, habitat use, and overwintering stages (Hassall et al. 2016). Organismal traits, such as nesting behavior (below or above ground), voltinism (one or multiple generations per season), and insect biological clocks (early vs. late emerging species), also influence phenological responses to climate. For instance, bees that nest above ground tend to have greater phenological sensitivity to snowmelt time and temperature than bees that nest below ground in montane ecosystems (e.g., Stemkovski et al. 2020). Moreover, insect emergence dates advanced more strongly than later phenophases, generally leading to longer flight seasons (e.g., Forrest 2016; Hassall et al. 2016).

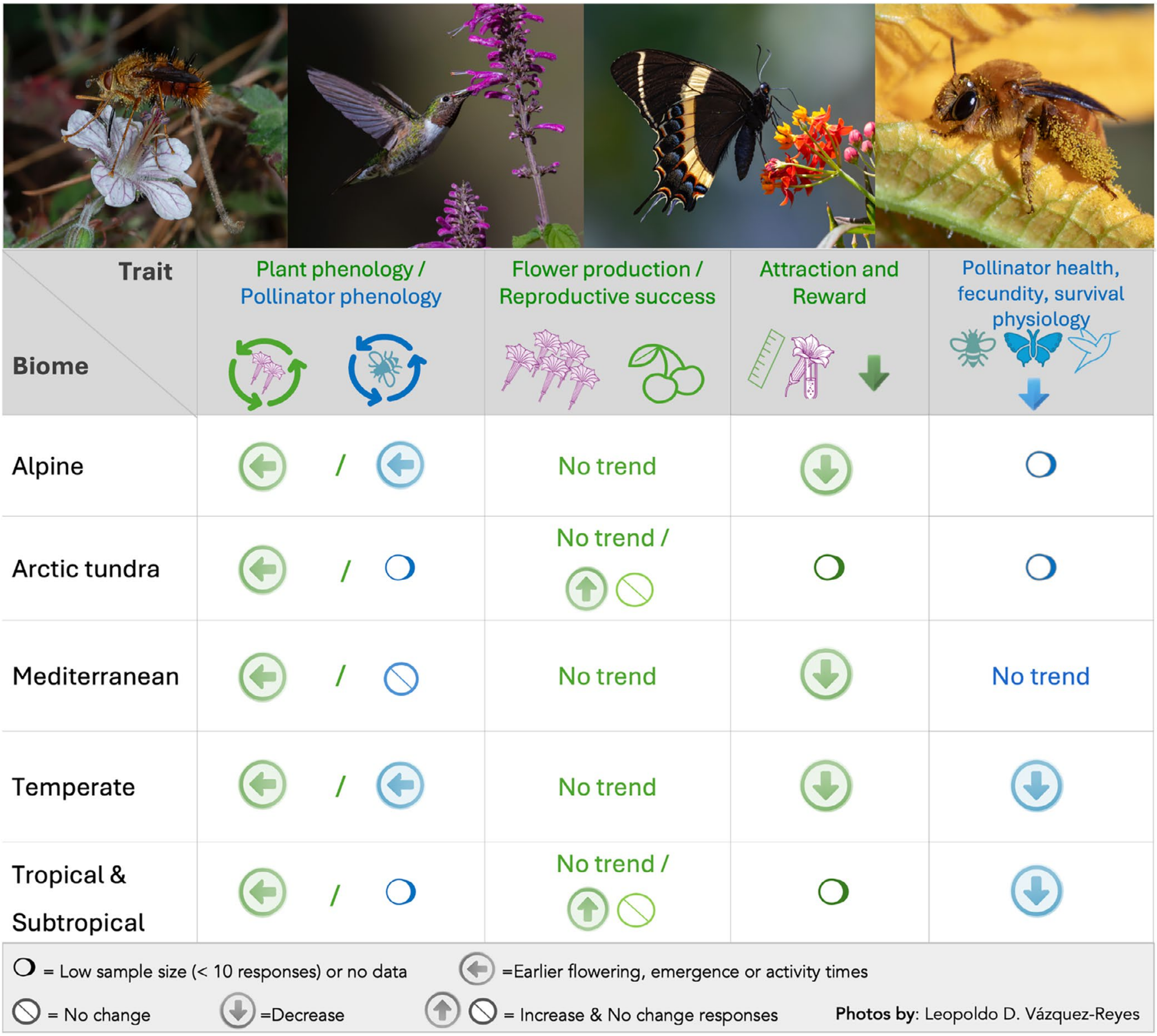
We did not obtain studies on pollinator phenology in response to climate change in tropical regions; however, many tropical insects undergo low metabolic activity and diapause during unfavorable weather conditions (Heithaus 1979). Shifts in precipitation patterns in the Tropical/Subtropical biomes will likely impact the abiotic cues insects use to emerge after diapause. For example, the desert bee *Perdita portalis* uses soil moisture as a signal for emergence, synchronized with the germination of its nectar plants (Danforth 1999). Tracking of plant phenologies may be common in insects from seasonal environments with erratic rainfall patterns or in species involved in specialized interactions.

4.5 | Other Pollinator Traits

Our initial prediction was that pollinators would be more negatively affected by climate change in Tropical/Subtropical biomes than their Temperate, Alpine, or Arctic counterparts, given the wider range of temperatures to which temperate insects are exposed over their lifetimes (Deutsch et al. 2008; Sutton et al. 2018). However, negative responses to climate change were predominant across all biomes and pollinator groups. These findings suggest that the seasonal variation in temperatures that animals in temperate latitudes and high mountains have experienced provides an advantage in terms of their low but not their high thermal limits (Addo-Bediako et al. 2000); however, this hypothesis requires further evaluation.

Pollinator responses were associated with specific traits, but not with pollinator taxon. There were clear trends for decreased reproduction and survival, size, and physiological or developmental responses to climate change (e.g., Becker et al. 2018; Slominski and Burkle 2019), but no specific trends for animal abundance or resource acquisition variables. Pollinator abundance reductions were often associated with changes in floral resource availability (Høye et al. 2013; Nürnberger et al. 2019; Ogilvie et al. 2017). However, neutral responses to climate change were common, particularly in Mediterranean butterflies, where abundance was associated with habitat specialization and voltinism (Colom et al. 2022). Determining the vulnerability of animal populations to climate change will require a large-scale assessment of these organismal traits.

In terms of health traits, climate warming increased parasite loads or disease infection in animal pollinators. Most analyzed cases showed increased levels of avian malaria in Hawaiian honeycreepers under warming temperatures, leading to actual or projected declines in bird populations (Atkinson et al. 2014; Benning et al. 2002; Freed et al. 2005; Judge et al. 2021; Liao



Trait / Biome	Plant phenology / Pollinator phenology	Flower production / Reproductive success	Attraction and Reward	Pollinator health, fecundity, survival physiology
Alpine	← / ←	No trend	↓	○
Arctic tundra	← / ○	No trend / ↑ ⊘	○	○
Mediterranean	← / ⊘	No trend	↓	No trend
Temperate	← / ←	No trend	↓	↓
Tropical & Subtropical	← / ○	No trend / ↑ ⊘	○	↓

○ = Low sample size (< 10 responses) or no data

← =Earlier flowering, emergence or activity times

⊘ = No change

↓ =Decrease

↑ ⊘ = Increase & No change responses

Photos by: Leopoldo D. Vázquez-Reyes

FIGURE 5 | Summary of climate change effects on plant (green) and animal (blue) phenologies, plant reproductive traits, and pollinator traits documented in the literature review across the most studied world biomes (based on Dinerstein et al. 2017). Main trends in response direction (> 50% of responses in one category) are indicated with arrows. Flower images were generated by Image Generator Tool (version GPT-4), OpenAI, June 2024.

et al. 2015). These examples highlight the importance of considering multitrophic interactions when assessing the effects of climate change on plant–pollinator interactions.

Extreme temperature is thought to affect tropical insects more than temperate ones (Deutsch et al. 2008; Sutton et al. 2018). However, our results indicate a predominant reduction in fecundity, longevity, and survival of insect pollinators associated with higher temperatures across latitudes (e.g., Becker et al. 2018; Slominski and Burkle 2019). For example, the lifespans of 11 tropical fig wasp species decreased under moderate warming (1°C–4°C) and extreme temperatures (Gigante et al. 2020; Jevanandam et al. 2013; van Kolfschoten et al. 2022), but only extreme temperatures affected longevity in the temperate wasp *Pleistodontes imperialis* (Sutton et al. 2018). Significantly shorter lifespans will likely threaten the specialized fig-wasp pollination mutualism, potentially affecting the survival of keystone fig species (Shanahan et al. 2001).

Consistent with previous findings (Johnson et al. 2023), warming generally had negative effects on the developmental and physiological processes of animal pollinators, particularly temperate bees. In addition, there was a trend for body size reductions under warming conditions. Size changes have been recognized as one of the major animal responses to climate change (Gardner et al. 2011), possibly related to thermoregulation processes in ectothermic insects. For instance, large bees stay warmer in cold environments but are more susceptible to overheating when temperatures rise above 30°C (Danforth et al. 2019). Reductions in the size of bumblebee proboscides have also been reported, leading to potential morphological mismatches with flowers and potentially impacting plant reproductive success (e.g., Miller-Struttmann et al. 2015).

4.6 | Mismatches in Plant–Pollinator Interactions

Temporal mismatches between blooming plants and pollinators are commonly predicted in the literature; however, unequivocal evidence for mismatches is still limited. In this survey, plant–pollinator mismatches in response to warming events were primarily studied in Temperate biomes. Most studies revealed changes in flowering time that were not mirrored by changes in pollinator phenologies (e.g., *Centaurea scabiosa* and its butterfly pollinator *Melanargia galathea* in the United Kingdom, Hindle et al. 2015; a US montane plant assemblage and its bumblebee pollinators, Pyke et al. 2016; *Pulsatilla vulgaris* and *Osmia* bee pollinators in Germany, Kehrberger and Holzschuh 2019). In a North American pollination network resampled after 120 years, Burkle et al. (2013) also recorded mean advanced plant and animal phenologies, and shorter bloom and flight periods; this study attributed 10% of interaction loss to temporal mismatch and 34% to species loss, while documenting 49% of novel interactions. Modeled and observed advanced phenologies in these historical and contemporary pollination networks (Memmott et al. 2007; Burkle et al. 2013; Revilla et al. 2015) found decreased species richness, with specialist species being the most affected. Additionally, mathematical modeling suggests that coevolution in pollination networks may slow the rate at which plant and pollinator species and interactions are lost under climate change-induced phenological shifts (Nuismer et al. 2018).

Temporal mismatches may also occur through changes in the timing of anthesis associated with warming (e.g., Murcia 1990), although pollinators may adjust their schedules to coincide with shifted floral anthesis (Alzate-Marin et al. 2021). Fitness reductions associated with temporal mismatches have been even less studied. However, Kudo and Cooper (2019) demonstrated a reduction in fruit set after an experimental mismatch in bumblebee-pollinated *Cordyalis ambiagua*. Slominski and Burkle (2021) also showed a negative effect on floral visitation and bee progeny weight after an experimental mismatch between *Osmia* bees and their floral resources. Fitness assessments will be critical to the understanding climate change effects on plants and their pollinators.

Plant–pollinator mismatches may also arise through a change in the migration time of certain animal pollinators (Forrest 2016; Moore 2011). This phenomenon has been observed in various hummingbird species, which are arriving either earlier or later at their breeding grounds, resulting in mismatches with their primary food resources (e.g., McKinney et al. 2012; Courter et al. 2013; Courter 2017). The monarch butterfly (*Danaus plexippus*) is another migratory pollinator that has been affected by climate change in terms of abundance (e.g., Agrawal and Inamine 2018; Rendón-Salinas et al. 2023; Zipkin et al. 2012), migration dates (Culbertson et al. 2022; Ethier and Mitchell 2023), and breeding ranges (Zylstra et al. 2022). Variation in climate change variables has the potential to alter other migratory pollinators and their floral resources.

Mismatches through non-coincident geographic range shifts of plants or their pollinators have also been reported (e.g., Gómez-Ruiz and Lacher, 2019; Remolina-Figueroa et al. 2022). However, being mobile, pollinators may be able to follow their shifting floral resources. For instance, modeling studies have predicted concurrent range contractions for *Lysimachia ciliata* and its rare oil-collecting bee pollinator (Buckner and Danforth 2022), as well as for Subtropical Andean Cactaceae and their vertebrate pollinators (Gorostiague et al. 2018). In the high mountains of Central Mexico, the upward shift in elevation of the alpine herb *Castilleja tolucensis* has not deterred its hummingbird pollinators, which ascend above 4400 m.a.s.l. during C. tolucensis flowering season (Arredondo-Amezcua et al. 2018). Moreover, spatial mismatches may also occur between a plant species and some, but not all of its pollinators (e.g., *Traunsteinera globosa*; Kolanowska 2021). Thus, although specialized pollination partners may be better adapted for synchronous shifts, generalized pollination systems might help buffer plants from geographical pollination mismatches. In contrast, modeling studies of mismatches in pollination networks have shown that specialist pollinators are more vulnerable to climate change (Schleuning et al. 2016). Other studies have shown geographic variation in the vulnerability of plant–pollinator networks to climate change (Bascompte et al. 2019; Sonne et al. 2022).

4.7 | Synergistic Effects of Climate Change With Other Anthropogenic Drivers

Understanding potential synergies among drivers of global change (e.g., climate change, land-use change, invasive species, pathogens, and xenobiotics) is crucial to comprehensively understand the future changes that plant and pollinator communities will experience. Land-use change, the primary threat to biodiversity, interacts with climate change resulting in detrimental effects on plant–pollinator interactions. For example, in Bavaria, Germany, where pollinator diversity was positively associated with reduced land-use intensity and high flowering plant diversity, lower diversity and homogenization of the interacting communities were predicted under scenarios of habitat loss and climate change (Ganuza et al. 2022). Similarly, conservation efforts in northwestern Costa Rica highlight the protective role of natural forests for certain insect groups. A study on the Euglossine bee community in the Guanacaste Conservation Area reported shifts in community composition but no significant changes in species richness over a 40-year period, attributed to the recovery of natural dry forest habitats (Bravo et al. 2022). However, insect declines have been reported in this region despite the recovery of forest habitats, possibly associated with longer dry seasons, extreme high temperatures, and lower cloud cover in mountain ecosystems adjacent to the lowland dry forests (Janzen and Hallwachs 2021). These studies highlight the preeminent importance of habitat conservation to the preservation of crucial ecological interactions, such as pollination, in the face of climate change.

4.8 | Study Limitations

The main limitations of our review derive from the sparse information available for most biomes, plant reproductive traits, and pollinator groups, which restricts our ability to generalize patterns across Earth's ecosystems and organismal groups. Moreover, the diverse approaches, methodologies, and response variables used in studies limit more complex statistical approaches without losing information from undersampled regions or groups. Nonetheless, our review provides a valuable synthesis of research that identifies consistent patterns across the most studied biomes, highlighting critical knowledge gaps.

5 | Future Directions

Our findings reveal that research on climate change effects on plant reproductive traits and pollinators is skewed toward Alpine and Temperate biomes, herbaceous plants, and some pollinator taxa (bees, butterflies, and flies). It should be noted, however, that even for the most well-researched biomes, life forms, and pollinators, the data are still very limited. Most earth ecosystems, plant lineages, and pollinator groups remain highly undersampled (Figures 1 and S1–S3). We need to identify the phenological cues and plant responses to climate change in Tropical and Subtropical biomes, as well as Temperate biomes from the Southern Hemisphere. We need to assess plant reproductive responses to different climate variables that are being modified by climate change in species with different life forms, pollination systems (e.g., different functional pollinator groups, specialized vs. generalized), and breeding or mating systems (e.g., self-fertile vs. self-incompatible species). Responses to climate change should also be contrasted among pollinators with different behavioral or life-history traits (oligolectic vs. polylectic feeders, below vs. above-ground nesting, univoltine vs. multivoltine, social vs. solitary habits) and across different developmental stages. Phenotypic plasticity should also be evaluated as it may facilitate adaptation to new environments. Finally, land-use change and synergistic interactions, such as multitrophic impacts of climate change, should be considered when assessing climate-driven plant and pollinator responses.

The reviewed articles include diverse methodologies that provide distinct insights into plant and pollinator responses to environmental change. Some studies evaluate species traits under current and historical conditions at specific sites, offering a comprehensive view of species' responses over time. Other studies involve short-term experiments addressing the effects of specific abiotic variables on plant or pollinator traits, capturing immediate responses within one or few reproductive cycles. Finally, some results come from simulation studies under climate change scenarios, which model potential changes in animal abundance, parasite loads, phenologies, and geographic distributions. Integrating long-term observational data with experimental and simulation approaches will provide a more comprehensive understanding of plant and pollinator responses to climate change.

6 | Conclusions

This review demonstrated significant impacts of climate change on plant reproduction, pollinator species, and plant–pollinator interactions; however, variation in species responses was evident across world biomes, organismal traits, and animal groups (Figure 5). Plant and animal phenologies are advancing in most world regions, but major gaps remain in our understanding of low and southern latitudes, woody plant species, and most pollinator taxa. The hypothesis that plant and pollinator traits would be more affected by climate change in tropical and Mediterranean ecosystems was not supported, as negative trait responses were common across biomes. However, we have limited knowledge of species biophysical thresholds and responses to climate for most world biomes. Significant variation in species responses was also documented for various traits (e.g., floral production, plant reproductive success, and animal abundance) and animal groups (butterflies and flies), sometimes showing more positive and neutral than negative outcomes. Differences in physiological processes, life histories, and reproductive strategies may underlie interspecific variation in species responses, highlighting the need for further research within and among organismal groups and ecosystems. Evaluating organismal responses to warming and other climate variables across underrepresented biomes and taxa will be essential for understanding the potential impacts of climate change on plant–pollinator interactions, the delicate threads that sustain much of Earth's biodiversity and human food security.

Author Contributions

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.14767689.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.