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Climate change alters plant–herbivore interactions

Author for correspondence:

Jill T. Anderson

Email: jta24@uga.edu

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Elena Hamann^{1,2} , **Cameron Blevins¹**, **Steven J. Franks²** ,
M. Inam Jameel¹  and **Jill T. Anderson¹** 

¹Department of Genetics and Odum School of Ecology, University of Georgia, Athens, GA 30602, USA; ²Department of Biological Sciences, Fordham University, Bronx, NY 10458, USA

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Summary

Plant–herbivore interactions have evolved in response to coevolutionary dynamics, along with selection driven by abiotic conditions. We examine how abiotic factors influence trait expression in both plants and herbivores to evaluate how climate change will alter this long-standing interaction. The paleontological record documents increased herbivory during periods of global warming in the deep past. In phylogenetically corrected meta-analyses, we find that elevated temperatures, CO₂ concentrations, drought stress and nutrient conditions directly and indirectly induce greater food consumption by herbivores. Additionally, elevated CO₂ delays herbivore development, but increased temperatures accelerate development. For annual plants, higher temperatures, CO₂ and drought stress increase foliar herbivory. Our meta-analysis also suggests that greater temperatures and drought may heighten florivory in perennials. Human actions are causing concurrent shifts in CO₂, temperature, precipitation regimes and nitrogen deposition, yet few studies evaluate interactions among these changing conditions. We call for additional multifactorial studies that simultaneously manipulate multiple climatic factors, which will enable us to generate more robust predictions of how climate change could disrupt plant–herbivore interactions. Finally, we consider how shifts in insect and plant phenology and distribution patterns could lead to ecological mismatches, and how these changes may drive future adaptation and coevolution between interacting species.

I. Introduction

Plant–herbivore interactions structure the ecology of natural communities and evolutionary trajectories of interacting species (Becerra, 2007). Herbivores first began to consume plant tissues in the late Silurian to early Devonian (e.g. Edwards *et al.*, 1995; Labandeira & Currano, 2013), shortly after land plants evolved *c.* 475 Ma (Wellman *et al.*, 2003). Since then, plants have evolved

complex mechanical and chemical defenses against herbivory (Gong & Zhang, 2014; Burkepile & Parker, 2017), and herbivores have evolved to circumvent these defenses (Karageorgi *et al.*, 2019). Coevolutionary dynamics can generate specialized interactions, resulting in a diversity of species, forms and functional traits (Jander, 2014; Karageorgi *et al.*, 2019). However, even intense and prolonged eco-evolutionary dynamics occur in the context of an abiotic environment that can change. Given that the abiotic

environment strongly influences trait expression of both plants and herbivores, changes in abiotic conditions can alter this ecologically important interaction. For example, during the intense planetary warming and increased CO₂ concentrations of the Paleocene-Eocene thermal maximum (55.8 Ma), fossilized plants show clear evidence of exposure to a greater degree and diversity of herbivory than in cooler times (Curran *et al.*, 2008; Pinheiro *et al.*, 2016).

In contemporary landscapes, natural populations are encountering novel suites of abiotic and biotic conditions as a result of rising atmospheric CO₂ concentrations, global temperatures, changing precipitation regimes, and increased nitrogen (N) deposition (Bellard *et al.*, 2012; IPCC, 2014). Shifts in plant–herbivore interactions mediated by climate change could reshape the ecological and evolutionary dynamics of entire communities (Rasman *et al.*, 2014; Becklin *et al.*, 2016). Insect herbivores have short generation times, high reproductive rates and extensive mobility (Menéndez, 2007). All of these traits could enable them to track favorable climates more readily than plants, through rapid migration, *in situ* population growth, and adaptation to novel conditions (Rasman *et al.*, 2014; Becklin *et al.*, 2016), which could lead to no-analog biotic assemblages (Parmesan, 2006). For these reasons, plant populations could experience increased amounts of herbivory under continued climate change.

Here, we synthesize existing literature and conduct meta-analyses to evaluate the extent to which rapid anthropogenic climate change disrupts plant–herbivore interactions. Specifically, we hypothesize that climate change will expose native plants to novel herbivore communities both in their home sites and expanded distributions, and heightened herbivory because of increased food consumption by resident and newly-established herbivores. We review the proximate mechanisms by which warming temperatures in concert with elevated CO₂, novel precipitation patterns and increased N deposition influence herbivore biology and plant damage from herbivory. We consider how multiple interacting climatic factors could result in additive, synergistic or antagonistic effects for plant–herbivore interactions. By reflecting on spatial and temporal shifts in plant–herbivore interactions, we explore whether natural plant populations will confront novel patterns of herbivory under future climates. Our review primarily focuses on arthropods (Hexapoda), which represent *c.* 62% of all *c.* 1.6 million described living species, as approximately half of all insects are herbivorous (Wiens *et al.*, 2015; Roskov *et al.*, 2019). Insects have received more attention in the context of plant–herbivore interactions under climate change, yet we draw on mammalian herbivore examples when possible.

To complement the qualitative literature review, we test whether climate change will alter herbivore biology and augment herbivory in natural and agricultural systems in a series of meta-analyses. To that end, we ask how abiotic factors associated with climate change affect herbivore performance and feeding rates. We consider whether climate change factors affect herbivores directly or indirectly via plant-mediated effects and examine potential differences across study systems. We then investigate herbivore damage records under simulated climate change to

evaluate how plant populations – adapted to historical amounts of herbivory – fare under novel herbivory associated with climate change.

Several earlier reviews and meta-analyses concentrated on the effects of elevated CO₂ on plant chemistry and functional traits, and herbivore performance (Bezemer & Jones, 1998; Zvereva & Kozlov, 2006; Stiling & Cornelissen, 2007; Robinson *et al.*, 2012). Additionally, Robinson *et al.* (2012) examined pairwise interactions between CO₂ and temperature, CO₂ and drought, and CO₂ and N for plant phenotypes, but they did not consider the effects of these interactions on insect performance or plant damage from herbivores. As changes in plant chemistry and phenotypes have been established in response to elevated CO₂ and temperature, we did not assess such responses. However, only 10 empirical studies included in previous meta-analyses examined herbivore damage to plants under climate change (Stiling & Cornelissen, 2007; Robinson *et al.*, 2012). Thus, we quantified herbivore responses and plant damage to multiple climate change factors across empirical studies. Moreover, while some previous studies considered the effects of feeding guilds or insect orders in their meta-analyses (Bezemer & Jones, 1998; Stiling & Cornelissen, 2007; Robinson *et al.*, 2012), previous efforts did not account for phylogenetic relatedness. Finally, we fill a gap in the literature by examining differences in climate change responses in native vs agricultural systems.

After evaluating how climate change factors influence plant–herbivore dynamics in the short term, we discuss how these proximate causes may ultimately alter plant–herbivore interactions longer-term by examining the potential for plants and their herbivores to adapt to novel abiotic and biotic pressures.

II. Literature review: proximate ecological responses of plants and herbivores to climate change

1. Elevated atmospheric CO₂

Atmospheric CO₂ concentrations have risen from 280 ppm during preindustrial times to the current 410 ppm, and are predicted to exceed 600 ppm by the end of the 21st century (NOAA, 2020). Although elevated CO₂ has little direct effect on insect herbivores (Kerr *et al.*, 2013), it can indirectly influence herbivores via changes in plant chemistry (Pincebourde *et al.*, 2017). Increased atmospheric CO₂ concentrations alter the carbon (C) and nitrogen (N) economy within the plant (increased C : N ratio), decreasing the N concentrations in plant tissue (Strain, 1987; Fajer, 1989; Johnson & Lincoln, 1990). As N is a limiting nutrient for insects (Mattson 1980), higher CO₂ concentrations diminish the nutritional quality of plant tissues by reducing concentrations of proteins and certain amino acids in leaves (Lincoln *et al.*, 1993; Docherty *et al.*, 1997). To compensate, insect herbivores can increase their food uptake (Johnson & Lincoln, 1990, 1991; Stiling & Cornelissen, 2007). Decreased foliar N content and increased defenses can reduce the conversion efficiency of ingested food (Fig. 1). The most extensive meta-analysis on herbivore responses to elevated CO₂ confirmed these patterns by examining 270 papers published between 1979 and 2009 (Robinson *et al.*, 2012). In response to a 19% increase in

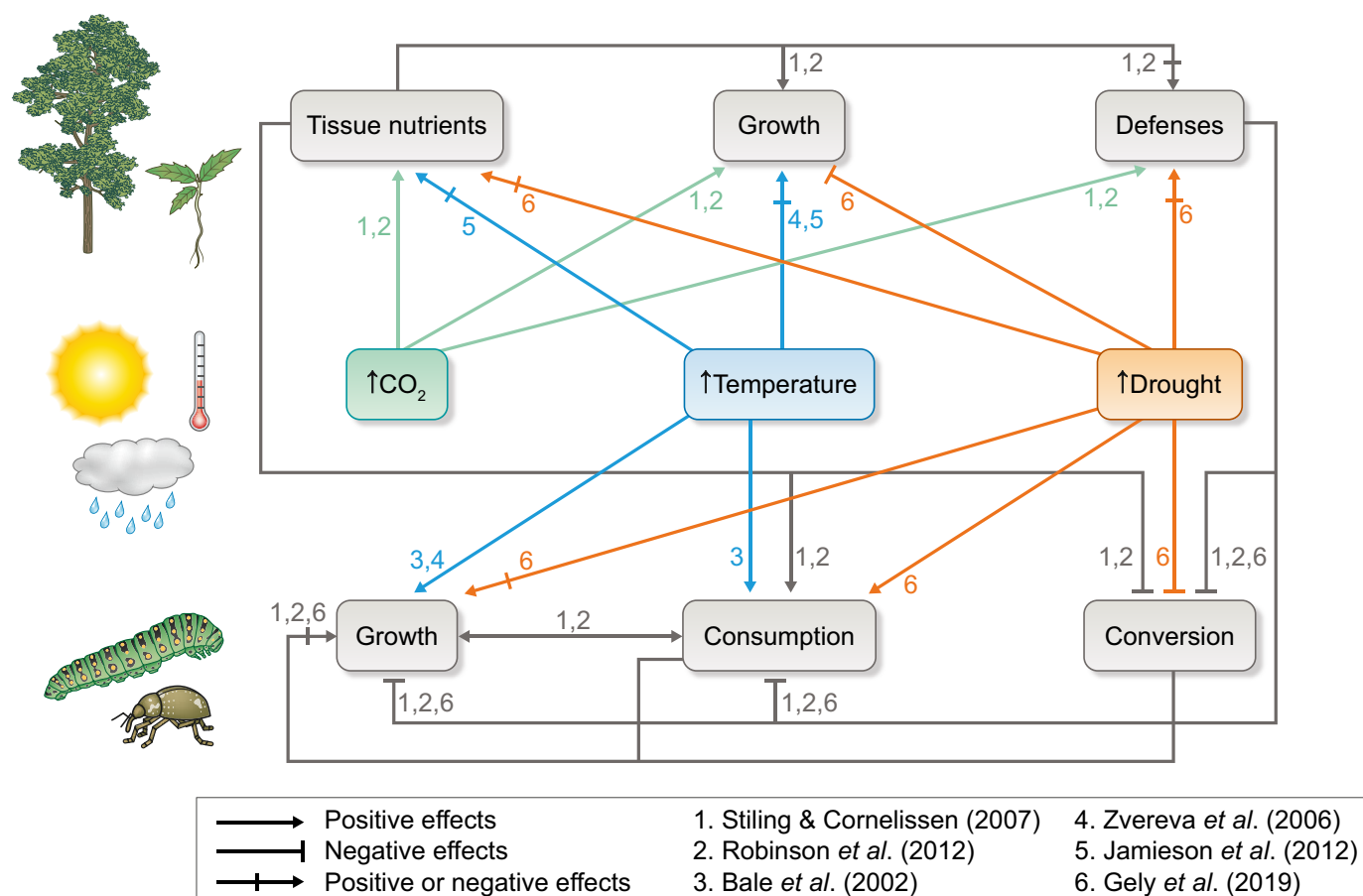


Fig. 1 Effects of single climate change factors (middle) on plant growth, tissue nutrients status and defenses (top), and insect growth, consumption and food conversion efficiency (bottom). Lines ending with arrowheads represent positive effects, lines ending in a vertical bar represent negative effects, and lines with both symbols represent either positive or negative effects. We supplemented the represented effects with references from reviews or quantitative meta-analyses (represented by numbers).

foliar C : N and a 10% decline in foliar proteins, insect herbivores increased their relative consumption rates by 14%, yet the conversion efficiency decreased by 15% under elevated CO_2 (Robinson *et al.*, 2012). However, in line with an earlier study showing that only leaf chewers significantly increased their food uptake in elevated CO_2 conditions (Bezemer & Jones, 1998), Robinson *et al.* (2012) found that consumption rates increased mainly in foliage feeders, particularly in Lepidoptera and Coleoptera. A taxonomic bias towards Lepidopteran herbivores (Bezemer & Jones, 1998; Stiling & Cornelissen, 2007) may drive the conclusion that herbivore consumption will increase under climate change, although this pattern may not hold across herbivore orders and feeding guilds.

Plants do not necessarily suffer more damage even when per-capita consumption rates increase, because plants can accumulate more biomass under elevated CO_2 (Hunter, 2001; Reddy *et al.*, 2010). Thus, enhanced plant growth from elevated CO_2 could compensate for increased leaf damage (Hughes & Bazzaz, 1997; Hall *et al.*, 2005). However, multiple climatic factors are changing simultaneously, and increased herbivore population growth rates induced by warming temperatures could compound the per-capita

consumption rates. Increased herbivory could impose strong selection on plant populations for constitutive and inducible defenses. Future studies can evaluate evolutionary responses by quantifying genetic variation in defenses within and across populations in conjunction with estimating gene flow rates, comparing patterns of selection on defenses under historical, contemporary and future climates, and taking resurrection approaches to test directly for adaptive responses to climate change and increased herbivory (see Section IV on evolutionary responses) (Agrawal *et al.*, 2006; Franks *et al.*, 2018a).

2. Rising temperatures

Greenhouse gas emissions have increased global temperatures by $1.0 \pm 0.2^\circ\text{C}$ since 1880, and temperatures are projected to rise $2\text{--}4^\circ\text{C}$ relative to preindustrial climates by 2100 under current rates of climate change (IPCC, 2018). Temperature regulates the metabolism and physiology of ectotherms and directly influences all components of the life history of arthropod herbivores (Bale *et al.*, 2002). Accelerated metabolic rates of herbivores under elevated temperature could lead to higher consumption, growth

and faster development (Fig. 1), which would increase population growth rates and reduce generation times (Cornelissen, 2011; Jamieson *et al.*, 2012). At the same time, warming temperatures could favor thermal plasticity (Rodrigues & Beldade, 2020). Furthermore, warmer winters and earlier springs associated with climate change could increase herbivore overwinter survival (Bale *et al.*, 2002). Warming could induce more frequent insect outbreaks (Coley, 1998). A particularly eruptive outbreak was documented for the mountain pine beetle (*Dendroctonus ponderosae*), an aggressive bark beetle that kills its host: under recent warming, *D. ponderosae* shifted from a semivoltine to a univoltine lifecycle, leading to outbreaks and increased damage to whitebark pine trees (*Pinus albicaulis*) in Yellowstone National Park (Logan *et al.*, 2010). These rapid changes in herbivore performance and life-history traits could render plant populations more vulnerable to herbivores.

While increased temperatures tend to have positive effects on insects (Bale *et al.*, 2002; Cornelissen, 2011), the biological impacts of rising temperatures depend on the magnitude of the change and on the herbivore's thermal sensitivity. Insect performance typically increases with temperature until reaching a maximum at an intermediate temperature and then rapidly decreasing (Kingsolver, 2009). The asymmetry in thermal performance curves could result in very different short-term responses to increased temperatures, depending on the current location along the curve (Fig. 2). Additionally, projected climate warming could augment insect performance at temperate and higher latitudes, where species have broader thermal tolerance, but warming could have deleterious consequences for tropical species with more narrow thermal tolerances where temperatures may already be close to optimal (Deutsch *et al.*, 2008; Angilletta *et al.*, 2010). In the longer term, rapid generation times and intraspecific genetic variation in heat resistance could result in rapid adaptation of thermal performance curves as temperatures continue to increase (Muñoz-Valencia *et al.*, 2016; Ranga *et al.*, 2017). We can turn to a non-herbivorous system as an example Carbonell & Stoks (2020) recently documented evolutionary changes in the thermal performance curves of the European damselfly (*Ischnura elegans*) during its range expansion toward warmer regions. Yet examples of the evolution of thermal performance curves under climate change are rare (Tüzün & Stoks, 2018), and more such studies are needed in herbivores, as it remains unclear whether standing genetic variation for heat resistance is adequate for sustained responses to selection (Kellermann *et al.*, 2012; Kellermann & van Heerwaarden, 2019).

Climate change can also affect the number of life cycles that can be completed in a single season (voltinism). Insect species typically respond to warmer temperatures with faster developmental rates and greater reproductive potential, which can increase both the number of generations within a season and the rate of population growth (Jönsson *et al.*, 2009; Altermatt, 2010; Fand *et al.*, 2014). These changes could intensify herbivory pressures and increase amounts of damage to plants, especially to long-lived species (DeLucia *et al.*, 2012; Forrest, 2016). Yet climate change will not induce advanced emergence or voltinism in all species (Grevstad & Coop, 2015), especially those that have obligate diapause with required chilling periods that may be disrupted under warmer

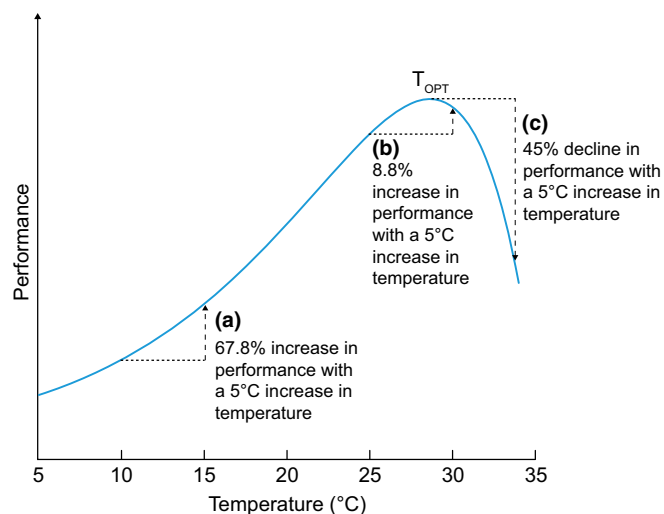


Fig. 2 A hypothetical thermal performance curve for an insect herbivore with optimal performance (T_{opt}) at 28.6°C. Owing to the asymmetry of the curve, an increase in temperature of 5°C leads to a much larger rise in performance at low temperatures (a) than when the temperature approaches the optimum (b). As temperatures rise above the optimum, insect performance declines precipitously (c), as shown by a 45% reduction in performance in temperatures that are 5°C greater than the optimum. We simulated this hypothetical curve using the R package *THERMPERF* (v.0.0.1) (Bruneaux, 2016).

winters (Harrington *et al.*, 1999; Forrest, 2016). Additionally, rapid development at higher temperatures is often accompanied by smaller size at maturity and reduced fecundity (Kingsolver & Huey, 2008). Yet, accelerated population growth rates increases the general abundance of insect herbivores, regardless of changes in voltinism and emergence times, and may increase herbivory on host plants.

Temperature directly influences plant growth and development (Grace, 1987). A moderate rise in temperature can increase plant productivity and production of secondary metabolites (Rustad *et al.*, 2001; Zvereva & Kozlov, 2006; Pincebourde *et al.*, 2017). However, severe drought could accompany heat waves associated with climate change and have adverse effects on plant productivity (Fig. 1). Plant populations located in regions that historically experienced low amounts of herbivory could be susceptible to decline if herbivore populations expand *in situ* and migrate into those areas. Biotic interactions, including herbivory, have historically been considered less intense in temperate and polar latitudes, where plants have, in turn, evolved fewer defense traits (Coley & Aide, 1991; but see Moles *et al.*, 2011); thus, plants could be particularly susceptible to increased herbivore pressures in those regions. It thus remains an open question whether plants will suffer greater damage if herbivore performance increases or generation times decrease with rising temperatures.

3. Drought

Under climate change, precipitation may increase in some parts of the world, but many other regions are projected to suffer more frequent and severe drought events (Knapp *et al.*, 2008; IPCC,

2014; Swain *et al.*, 2014). In combination with elevated temperatures and heat waves, drought is likely to affect many ecosystems (Jentsch *et al.*, 2007; Knapp *et al.*, 2008; Bloor *et al.*, 2010). Additionally, in snow-dominated ecosystems at high elevations and high latitudes, climate change is causing a reduction of winter snowpack (Fyfe *et al.*, 2017), which is critical as water availability to plants in the growing season can be determined by snowmelt (Jamieson *et al.*, 2012). In general, drought negatively affects plant productivity (Fig. 1) and alters plant chemical defenses as well as nutritional quality, digestibility and palatability (Jamieson *et al.*, 2017). Traditionally, herbivorous insects were thought to perform better on water-stressed plants (Huberty & Denno, 2004). During droughts, herbivore outbreaks could result from accumulations of N compounds in plant tissue, which enhance herbivore growth and reproduction (White, 1984). However, Huberty & Denno (2004) showed that prolonged water stress in plants negatively affects phloem and mesophyll feeders and other sap feeders, while the responses of leaf chewers differed between subguilds. Although foliar N concentrations generally increase during times of water deficit, decreased turgor and water availability can interfere with the herbivore's ability to access N, especially in continuously stressed plants (Huberty & Denno, 2004). Intermittent and moderate droughts may increase chemical defenses in plants, while prolonged and severe droughts could reduce these defenses; in both cases, limited access to nutritional compounds could depress herbivore performance (Gely *et al.*, 2019). The effect of drought stress on chemical defense production and nutritional quality has not yet been tested as rigorously as the effects of elevated temperature or CO₂.

4. Fertilization and N deposition

Fertilization is commonly used in agricultural systems, leading to agricultural runoff and increased N deposition in many parts of the world (Hattenschwiler & Schafellner, 1999; Driscoll *et al.*, 2003). Intensified N deposition can stimulate plant growth in the short term (Tamm, 1991; Hattenschwiler & Schafellner, 1999) and increase the nutritional value of plant tissues (Henn & Schopf, 2001). However, Hattenschwiler & Schafellner (1999) found that the stimulating effects of increased N deposition were lower in magnitude than the adverse effects of elevated CO₂, such that climate change may still impair herbivore growth and development. N deposition could allow plants to allocate more resources to herbivore defenses (plant vigor hypothesis) or could exacerbate herbivory because the stress caused by the pollution reduces investment in defense (plant stress hypothesis) (Mur *et al.*, 2017; Miles *et al.*, 2019). Moreover, drought severely limits the ability of plants to acquire soil nutrients (Bista *et al.*, 2018). Thus, it is important to consider fertilization at a regional level and in combination with other climate change factors.

5. Interactions between abiotic factors

Climate change is simultaneously altering key agents of selection, including CO₂, temperature, and precipitation patterns, while

increasing the frequency and severity of extreme weather (IPCC, 2014). In addition, habitat fragmentation restricts migration and could hinder adaptive responses to novel environments, as small fragmented populations often lack genetic variation (Young *et al.*, 1996; Leimu *et al.*, 2006). Global change factors interact in complex ways that could have additive, synergistic or antagonistic effects on plant–herbivore interactions (Jamieson *et al.*, 2017; Gely *et al.*, 2019). While elevated CO₂ is increasing at similar rates globally, changes in temperature and precipitation patterns vary regionally and interannually (Jentsch *et al.*, 2007; IPCC, 2014; Swain *et al.*, 2018). Yet, few empirical studies explore herbivore and plant performance under realistic, multifactorial scenarios (Zvereva & Kozlov, 2006; Cornelissen, 2011). By contrast, plant physiological responses to climate change have been relatively well-studied in a multifactorial framework (e.g. Veteli *et al.*, 2002; Williams *et al.*, 2003; Murray *et al.*, 2013). For example, elevated CO₂ and temperature significantly increased foliar C:N ratios in two *Eucalyptus* species (*E. robusta* and *E. tereticornis*), especially under ambient temperatures (Murray *et al.*, 2013; Gherlenda *et al.*, 2015). In other studies, N content decreased strongly under combined elevated CO₂ and temperature, while elevated temperatures alone had little effect (Williams *et al.*, 2000; Murray *et al.*, 2013; Gherlenda *et al.*, 2015). In a synthesis of 42 studies, Zvereva & Kozlov (2006) confirmed that the combined effects of elevated CO₂ and temperature on plant physiology and chemistry were often different from the effects of factors taken separately. Thus, multifactorial experiments can reveal unique biological responses to climate change that are not apparent from single factor studies (e.g. Zvereva & Kozlov, 2006; Robinson *et al.*, 2012).

Even less is known about interactive effects of climate change factors on herbivore performance than on plant physiology. In single-factor studies, insect performance declines under elevated CO₂ and increases under warmer temperatures, but when manipulated simultaneously, the effects often cancel each other out (Johns *et al.*, 2003; Johns & Hughes, 2002; Veteli *et al.*, 2002; Williams *et al.*, 2000, 2003; Chong *et al.*, 2004). More recently, Zhang *et al.* (2018) found that elevated CO₂ and temperature significantly decreased growth rates and conversion efficiency of consumed food in *Spodoptera litura*, but other studies detected no significant interactions between these climate change factors (Himanen *et al.*, 2009; Murray *et al.*, 2013; Niziolek *et al.*, 2013; Gherlenda *et al.*, 2015). The stimulating effects of temperature on insect performance may not ameliorate the negative plant-mediated effects of elevated CO₂. Yet, enhanced temperature and CO₂ could both increase foliar damage via increased insect abundance, growth and consumption (Niziolek *et al.*, 2013). We cannot make reliable predictions about plant–herbivore interactions under climate change until future studies explicitly evaluate the combined effects of climate change factors on herbivore performance, changes in host plant quality and plant damage.

6. Spatial and temporal mismatches between plants and herbivores

Climate governs the geographic distribution of many species (e.g. Sexton *et al.*, 2009), and climate change has already led to shifts in

the ranges of a diversity of species (Parmesan & Yohe, 2003; Root *et al.*, 2003; Thuiller, 2004; Pereira *et al.*, 2010). These distributional changes include expansions into new areas, especially towards the historically cooler, upper elevations and poles (leading edges), and local extinctions in areas that have become climatically unsuitable, especially at the warm lower elevational and latitudinal limits of species ranges (trailing edges) (Menéndez, 2007; Sheth & Angert, 2018). As a result, ecological communities may disassemble as individual species shift their ranges idiosyncratically, and new assemblages are likely to emerge (Thuiller, 2004; Leimu *et al.*, 2012; Maron *et al.*, 2019), which will probably influence plant–herbivore interactions (Harrington *et al.*, 1999; Menéndez, 2007).

Plant species could confront novel herbivore communities and novel amounts of herbivory both in their home sites and during distributional shifts. Herbivores may have greater migratory potential than plants, and fossil records show that many insect species tracked climate change via migration during geological periods of climate change (Coope, 1970; Lawton, 1995). As climates change, thermal limits may no longer constrain native herbivores to their historical ranges. For example, the mountain pine beetle (*D. ponderosae*), native to western North America, is currently expanding its range northeastwards, establishing on novel host trees, such as jack pines (*Pinus banksiana*), as it spreads through the boreal forest (Cullingham *et al.*, 2011; Rosenberger *et al.*, 2017). This example illustrates how the oligophagous or polyphagous diet of many insect herbivores may facilitate host shifts during range expansion, exposing many plant species to novel herbivory and driving host range evolution in insects (Agrawal, 2000).

Climate change is accelerating the timing of life-history events for many species (Parmesan & Yohe, 2003). Yet, the environmental cues that trigger phenological transitions, and their relative importance, often differ between plants and herbivores, resulting in phenological mismatches between interacting species and trophic levels (Choi *et al.*, 2019). In general, arthropod herbivores are advancing their phenology faster than plants, as they are more sensitive to temperature, while plants often have specific photoperiod thresholds (Visser & Christiaan, 2005; Menéndez, 2007; Körner & Basler, 2010; but see Forrest & Thomson, 2011). Asynchronous phenological shifts may generate temporal mismatches, which could amplify or dampen herbivore damage (Dewar & Watt, 1992; Diamond *et al.*, 2011; DeLucia *et al.*, 2012; Abarca & Lill, 2015; Ren *et al.*, 2020). Warm springs in temperate regions often induce earlier insect emergence and activity, especially for insects that overwinter as adults (Diamond *et al.*, 2011; Bell *et al.*, 2015). Consequently, herbivory could increase early in the season, and herbivores may have extended growing seasons (Forrest, 2016). In specialized interactions, phenological asynchrony may reduce herbivore growth and abundance if climate change causes larvae to emerge earlier than budburst of the host species (Visser & Holleman, 2001; Schwartzberg *et al.*, 2014). Yet, many generalist herbivore species may be resilient to phenological changes in host plants (Forrest & Thomson, 2011). For example, spring herbivore species have often evolved starvation tolerance, enabling them to survive when hatching occurs before budburst (Abarca & Lill, 2015; Kharouba *et al.*, 2018). Phenological shifts

can also remove temporal barriers (Kharouba *et al.*, 2018). For example, warming synchronized the hatching time of forest tent caterpillar (*Malacosoma disstria*) eggs and budburst of one tree host, but reduced synchrony with an alternate host (Visser & Holleman, 2001). Starvation endurance and broad dietary breadth may dampen the effects of altered plant phenology for herbivores, but shifting temporal dynamics could augment herbivore damage on plants.

III. Meta-analysis

1. Aims and hypotheses

We conducted phylogenetically corrected meta-analyses (Adams, 2008) to evaluate: the direct, indirect (i.e. plant-mediated), and total effects of climate change on arthropod herbivore performance and foraging biology; and the effects of climate change on plant damage, in natural and agricultural systems. We tested whether rapid contemporary climate change augments herbivory, similar to what occurred during periods of elevated atmospheric [CO₂] in the geological record (Currano *et al.*, 2008). We aimed to assess the interactive effects of climate change factors, but our statistical power was restricted by the low numbers of multifactorial studies (see Section III.3: Results and discussion).

2. Methods

In Supporting Information Methods S1, we describe study eligibility criteria and the literature search (illustrated in Fig. S1), data extraction, phylogeny reconstructions, data analysis and publication bias diagnostics (see Funnel plots in Figs S6, S9). In short, we used Web of Science to conduct literature searches from 1900 to 6 August 2020 on herbivore performance and herbivory in climate manipulation studies (we retained studies from 1989 to 2020 for the herbivore dataset, and from 1994 to 2020 for the plant dataset). We also extracted data from studies cited in previous meta-analyses (Stiling & Cornelissen, 2007; Robinson *et al.*, 2012) that measured herbivore performance and consumption rates in response to different CO₂ concentrations. Finally, we performed a forward search from Robinson *et al.* (2012) for publications that reported herbivore performance or herbivory in response to climate change. For herbivores, we concentrated on individual growth rates, development time and consumption rates, and population-level metrics, including abundance and population growth rates. For plants, we focused on measures of tissue damage caused by herbivore feeding, such as damaged leaf area, percentage tissue loss and feeding marks. We extracted data directly from tables, archived datasets or figures using WEBPLOT DIGITIZER (Rohatgi, 2019) for all papers fitting our eligibility criteria ($N = 62$ studies for herbivore performance, 26 of which had not been included in previous meta-analyses, and $N = 47$ for plant damage, 33 of which were unique to this meta-analysis; Figs S1, S4, S5, S7, S8; Tables S12, S13).

Studies in the herbivore dataset used three different experimental designs. Some studies evaluated the direct effects of climate change factors on herbivores by exposing individuals to experimental

manipulations while feeding them an artificial diet or leaves of plants grown under ambient conditions. Other studies assessed the indirect effects of climate change on herbivores mediated through plants by rearing herbivores under ambient conditions and feeding them tissue from plants exposed to climate change manipulations. Finally, the last set of studies tested the total effects of climate change by exposing both the plants and the herbivores to manipulations and monitoring herbivore responses. We present results from the full dataset and then dissect the direct, indirect and total effects of climate change through separate analyses of subsets of data.

Our datasets also included agricultural, biocontrol and native plant and herbivore species. To our knowledge, previous meta-analyses have not tested whether shifts in plant–herbivore interactions under climate change are consistent across wild and domesticated systems. However, a recent phylogenetically corrected meta-analysis showed that plant resistance to herbivores was lower in domesticated crops relative to their wild relatives (Whitehead *et al.*, 2017). We present results for the full herbivore and plant datasets, and then evaluate herbivore performance and plant damage under climate change factors in agricultural and biocontrol vs. native systems.

We constructed phylogenies (Figs S2, S3) based on publicly accessible data in the Open Tree of Life (Michonneau *et al.*, 2016) to include a phylogenetic correlation matrix in our models. We implemented multilevel mixed-effects meta-analysis in the R package METAFOR, using Hedges' g as our effect size metric (Viechtbauer, 2010). We computed effect sizes such that values < 0 indicated that treatments consistent with climate change projections (e.g. increased CO₂) depressed herbivore performance or leaf damage from herbivores, and effect sizes > 0 indicated that climatic manipulations augmented herbivore performance or leaf damage from herbivores. The final models included fixed effects (moderating factors) for climatic manipulations and herbivore or plant traits and other attributes of the studies (publication year, latitude, longitude, elevation, study setting, etc.), and random effects for publication (to account for multiple species or traits in a study) and the phylogenetic correlation matrix.

3. Results and discussion

Herbivore dataset Our analyses revealed significant effects of herbivore trait, climatic treatment and their interaction (Fig. 3; see Notes S1, Tables S1–S7). Across analyses, elevated CO₂, temperature, drought stress and fertilization increased herbivore consumption rates (Fig. 3), suggesting that herbivore pressures are intensifying under most climate change scenarios.

Elevated temperatures significantly accelerated herbivore developmental rates (Fig. 3). In analyses of the direct effects of climatic factors on herbivores, increased temperatures depressed growth rates and did not influence consumption (Fig. 3c). Yet, in analyses of the indirect effects of climate change (when only plants were exposed to climate change factors), elevated temperature augmented consumption and growth rates, and accelerated developmental time (Fig. 3d). While we did not examine effects of temperature on plant chemistry, Zvereva & Kozlov (2006) showed

that elevated temperature decreased carbohydrates and phenolics, increased terpenoids and had little effect on leaf C : N ratio. These changes in plant chemistry could reduce food conversion efficiency, prompting a compensatory feeding behavior in insects. Results of our meta-analysis suggest that consumption rates increase not only because of faster development and growth, but also to compensate for depressed host plant nutritional quality under higher temperature.

Our analyses detected increased consumption rates exclusively in agricultural systems and nonnative herbivore or plant food species, but not in native ecosystems (Fig. 4). Yet, in native systems, herbivores also had accelerated developmental times and increased growth rates (Fig. 4a). In diverse natural ecosystems, herbivores can feed selectively across hosts (Bernays *et al.*, 1994) and optimize foraging efficiency by regulating pre- and post-ingestive nutrient intake (Behmer, 2009). These mechanisms and the polyphagous nature of many herbivores may allow them to compensate for reductions in nutritional quality in certain host species in natural systems (Behmer, 2009). Additionally, reductions in plant nutritional quality may be more likely to arise in agricultural species, which have generally been subject to strong artificial selection for higher nutritional quality (Newell-McGloughlin, 2008; Whitehead *et al.*, 2017). Agricultural systems are typically species-poor, restricting the dietary options of herbivores; therefore, increased consumption rates may emerge more frequently in agricultural than in natural systems under climate change. By stimulating herbivore consumption in agricultural systems, and herbivore growth and development in natural systems, warmer climates could increase herbivore pressures on plants, as long as temperatures do not exceed performance thresholds (Angilletta *et al.*, 2010). We encourage additional empirical studies on native herbivore–plant systems to verify whether accelerated herbivore development and growth rates also increase consumption rates and plant damage.

Elevated CO₂ increased consumption rates despite delayed insect development and a tendency towards decreased population growth rates (Fig. 3) in both native and agricultural systems (Fig. 4). As we also identified these patterns in the analysis of plant-mediated indirect effects (Fig. 3d), we conclude that increased consumption rates are likely driven by decreased nutritional value of plant tissues (see also Stiling & Cornelissen, 2007; Robinson *et al.*, 2012). Across the six studies of the direct effects of climate change, elevated CO₂ also increased consumption rates and delayed development, yet accelerated population growth rates (Fig. 3c). However, in half of these studies of direct effects, herbivores were fed artificial diets (Xie *et al.*, 2015; Akbar *et al.*, 2016; Liu *et al.*, 2017), or examined in growth chamber feeding trials (Ipekdal & Caglar, 2012; Lemoine *et al.*, 2013, 2014), and may not be representative of natural field conditions. Effects of elevated CO₂ and other climatic factors on herbivore performance under field conditions should become a priority of future research. Taken together, our results strengthen the general conclusion that elevated CO₂ concentrations affect insect performance through plant-mediated mechanisms (Pincebourde *et al.*, 2017). However, herbivore compensatory feeding behavior does not seem sufficient to counteract declines in leaf nutrient quality,

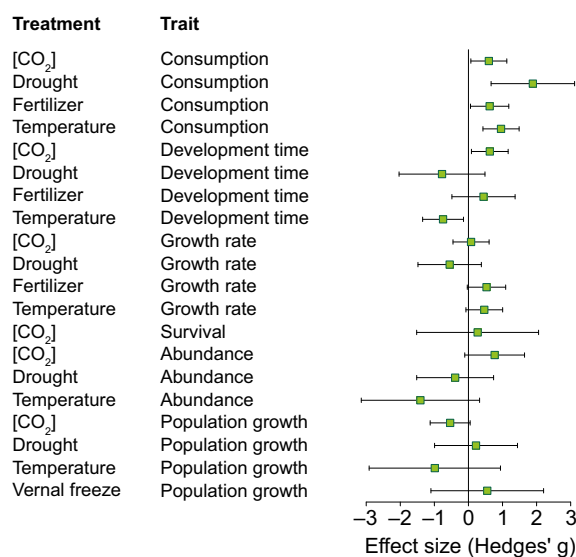
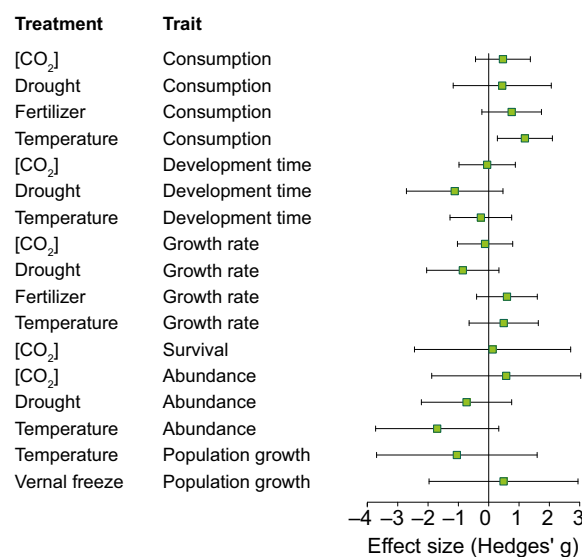
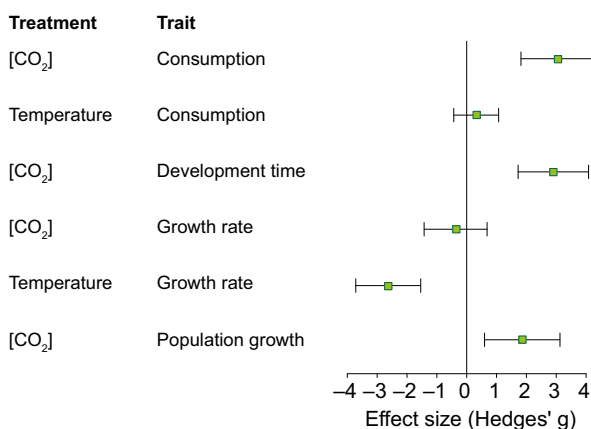
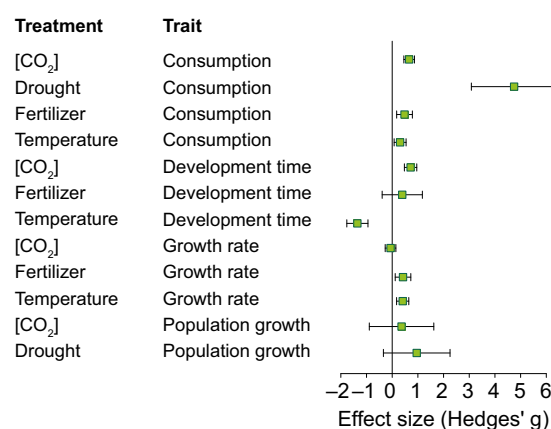
(a) Direct and indirect effects of climate change on herbivores (full dataset; 62 studies)**(b) Direct and indirect effects of climate change on herbivores (both plants and herbivores exposed to treatments; 24 studies)****(c) Direct effects of climate change on herbivores (herbivores exposed to treatments; 6 studies)****(d) Indirect effects of climate change on herbivores (plants exposed to treatments; 34 studies)**

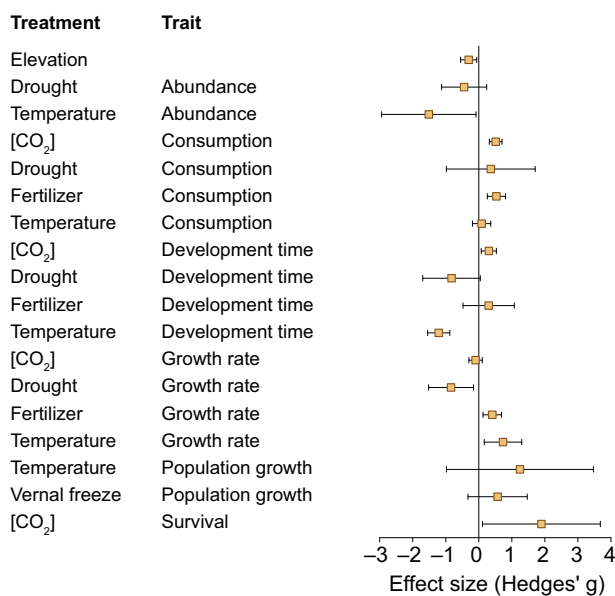
Fig. 3 Results of phylogenetically corrected meta-analysis of herbivore responses at the individual and population levels to climate change manipulations in the field and controlled conditions. Plotted are Hedges's *g* effect sizes and 95% confidence intervals. (a) The full dataset includes 61 studies that varied in experimental design. This panel represents the results of all studies combined. We also conducted meta-analyses of three subsets of data, representing: (b) studies that exposed both herbivores and plants to experimental treatments, documenting both direct and indirect effects of climate change on herbivores; (c) a small number of studies that exposed herbivores (but not plants) to elevated temperatures and atmospheric [CO₂], thus demonstrating the direct effects of climate change on herbivores; and (d) studies that exposed plants (but not herbivores) to experimental manipulations, revealing indirect effects of climate change on herbivores. Positive values with 95% confidence intervals > 0 indicate that climate change increases trait values (e.g. climate change factors increase food consumption in most analyses), and negative effect sizes indicate that climate change factors reduce trait values (e.g. temperature reduces developmental time in (a, d)). If the 95% confidence intervals span 0, the meta-analysis did not detect a significant effect of a treatment on a trait. Only one study manipulated springtime freezing conditions (vernal freeze), so this result must be treated with caution. Not all treatment × trait combinations are reflected in each of the subsets of data (b–d).

and insect performance and population growth rates may suffer under elevated CO₂.

Drought stress augmented herbivore consumption in agricultural – but not natural – systems (Figs 3, 4), but did not affect insect abundance, developmental time, growth rates or population growth rates in either agricultural or natural settings (Fig. 3). The effects of drought on insects depend on the length and severity of drought episodes and on the insect feeding guilds (Huberty & Denno, 2004; Gely *et al.*, 2019). Our meta-analysis

is dominated by Lepidoptera, mainly represented by leaf chewers. For these species, increased consumption rates under drought does not appear to translate into elevated individual or population growth rates. For instance, drought depressed larval growth rates in *Hyalophora cecropia* (Lepidoptera) (Scriber, 1977), and survival and fecundity in *Neodiprion gillettei* (Hymenoptera) (Mcmillin & Wagner, 1995). As for other feeding guilds, severe drought reduces plant turgor, which can restrict the availability of N-containing compounds, limiting performance of sap feeders (Gely

(a) Native systems



(b) Agricultural systems and non-native herbivores or plant food species

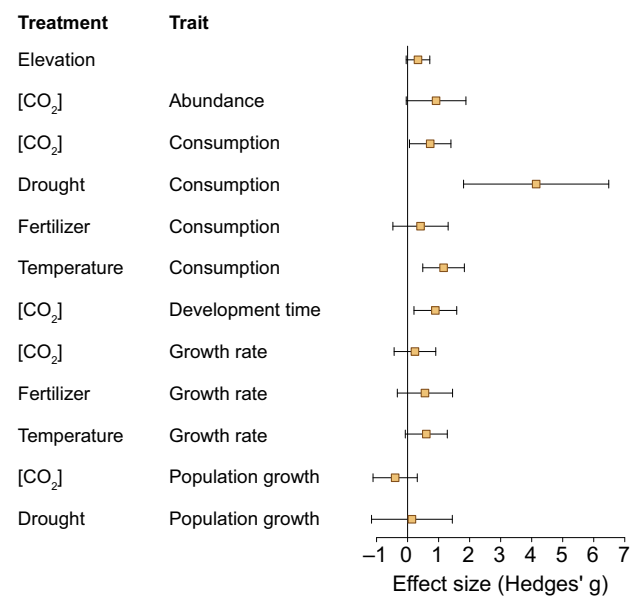


Fig. 4 Results of phylogenetically corrected meta-analysis of herbivore responses at the individual and population levels to climate change manipulations in the field and controlled conditions. Plotted are Hedges's *g* effect sizes and 95% confidence intervals. We conducted separate meta-analyses for studies conducted in native systems (42 studies) (a) or in agricultural systems and nonnative herbivores or plant food species (20 studies) (b).

et al., 2019). Additionally, drought can induce greater leaf toughness (Wright & Westoby, 2002), which could reduce palatability for herbivores, and can increase the concentrations of chemical defenses, which could deter herbivores (Gely *et al.*, 2019). In our meta-analysis, increased consumption rate under drought was entirely driven by studies that exposed plants but not herbivores to drought (Fig. 3d). Thus, it seems more likely that plants become less resistant to herbivores under drought conditions.

Nutrient fertilization increased consumption rates and tended to enhance herbivore growth rates (Fig. 3) in native but not agricultural systems (Fig. 4). Fertilization is already commonly used in agricultural systems. However, in natural systems, increasing N deposition has been accelerated in many parts of the world, which may change plant–herbivore interactions (Hattenschwiler & Schafellner, 1999). Under intensified N fertilization, plants have enhanced growth and increased protein concentrations in their tissue, which could increase susceptibility to herbivores (Henn & Schopf, 2001). Congruent with expectations, fertilization enhances insect performance via plant-mediated effects (Fig. 3d), but these indirect effects may be counteracted by elevated CO₂. For example, the negative CO₂ effects were greater than the positive N effects on *Lymantria monacha* larval performance (Hattenschwiler & Schafellner, 1999). Our results indicate that increased fertilization may enhance herbivore performance, particularly in natural systems where nutrient limitation may have been important historically.

Our analyses of interactive effects of climate change factors on herbivore performance and foraging behavior were restricted to 16 studies that evaluated interactions between CO₂ and drought (*n* = 2 studies), CO₂ and temperature (*n* = 8 studies), CO₂ and

fertilizer (*n* = 5 studies), and temperature and drought stress (*n* = 1 study) (Fig. S5). The overall meta-analysis captures additive effects of these climatic factors from these studies, but does not evaluate whether these factors interact to dampen or exaggerate herbivore responses. We conducted a complementary analysis to evaluate synergistic effects using multifactorial studies only (following Gurevitch *et al.*, 2000); however, we failed to detect interactive effects because of the limited numbers of studies and their highly species-specific results. For example, Zhang *et al.* (2018) showed that the combination of elevated temperatures and CO₂ decreased growth rate and food conversion efficiency for *S. litura*, an agricultural pest particularly destructive for soybean. However, studies conducted with multiple herbivore species, feeding on several host species, often reported contrasting results. Williams *et al.* (2000) detected no interactive effects of CO₂ and temperatures on gypsy moth (*Lymantria dispar*) performance fed on sugar maple (*Acer saccharum*), but the negative effects of elevated CO₂ for herbivore performance were slightly dampened under elevated temperatures when gypsy moth fed on red maple (*Acer rubrum*). Similarly, Johns *et al.* (2003) detected increased feeding under elevated CO₂ and temperatures in only one of two chrysomelid beetles. Finally, other studies failed to detect any interactive effects between climate change factors (Veteli *et al.*, 2002; Himanen *et al.*, 2009; Niziolek *et al.*, 2013; Gherlenda *et al.*, 2015). We suggest the differences in patterns observed by these empirical studies stem from varying experimental designs, where herbivores and/or plants were under climate factor manipulations, and differences in study systems or settings.

Plant dataset Our meta-analysis revealed that some plants may suffer more damage from herbivory under climate change (see

Notes S1; Tables S8–S11). For one, floral herbivory increased under elevated temperature and drought, yet this result is based on only two studies conducted on native perennial plants (Fig. 5a,b), and should be interpreted cautiously. We observed significantly increased leaf damage for annual plants under elevated CO₂, temperature and drought, which is probably driven by dynamics in natural – not agricultural – ecosystems (Fig. 5c). We observed no overall change in leaf damage for perennial plants under climate change factors. Annual plants reproduce during a single growing season, and the developmental switch from vegetative growth to reproductive growth occurs early in their life cycle. Therefore, annuals often have a higher investment in reproductive structures vs vegetative growth than do perennials (Bazzaz *et al.*, 1987) and may not be able to compensate for herbivore damage as effectively as perennials, which continuously invest in growth, even after reproduction. Additionally, perennials may allocate more resources to physical and chemical herbivore defenses than annuals (Bazzaz *et al.*, 1987). Additional studies on both perennial and annual native species are needed to evaluate how climate change factors influence above- and below-ground herbivory.

Our meta-analysis included only six studies that examined interactive effects of CO₂ and temperature ($n=2$ studies), temperature and drought ($n=2$ studies), temperature and N fertilization ($n=1$ study), and CO₂ and drought ($n=1$ study) (Fig. S8). Therefore, we were unable to analyze interactive effects of climate change factors on plant damage that extended beyond additive effects of each climate change factor. The two studies that simultaneously examined CO₂ and temperature found no interactive effect on feeding damage (Johns *et al.*, 2003; Himanen *et al.*, 2009). Yet, temperature and drought interacted to augment herbivore damage on St John's wort flowers (Fox *et al.*, 1999) and red oak leaves (Rodgers *et al.*, 2018). In addition, Lu *et al.* (2015) found greater rates of root galling under elevated temperature and N.

Taxonomic and geographic breadth of plant and herbivore datasets Our plant dataset included 71 angiosperm species, spanning 52 genera and 27 plant families, most represented by Fabaceae and Fagaceae (Fig. S7a). In our meta-analysis, 90% of the studies examined perennials, 54% examined herbaceous plants, and 90% of studies quantified foliar herbivory (Fig. S7b–d). Woody plants represent *c.* 45–48% of species globally (FitzJohn *et al.*, 2014) and perennials represent *c.* 60% of all seed plants and 40% of domesticated species (Miller & Gross, 2011; Miller, pers. comm.), illustrating that herbaceous and perennial species were probably overrepresented in our datasets. More studies should focus on plant–herbivore interactions with alternative life forms, especially shrubs, and other tissues, such as roots (Johnson *et al.*, 2016), and reproductive structures.

The taxonomic breadth of our herbivore dataset included 57 species, spanning 34 families and eight insect orders, most represented by Lepidopterans (Fig. S4a). This bias towards Lepidopterans and the leaf-chewing feeding guilds was also documented in earlier reviews (Bezemer & Jones, 1998; Stiling & Cornelissen, 2007). Are plant–herbivore studies taxonomically biased or is the dominance of Lepidopterans representative of insect herbivore

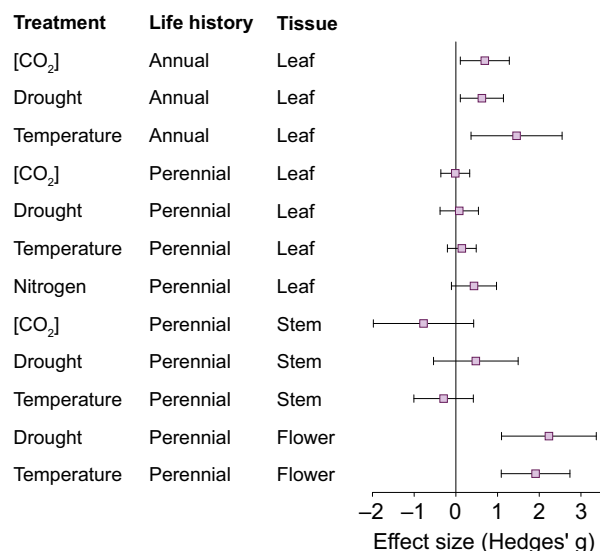
diversity? Lepidopterans are among the three most diverse insect orders (Goldstein, 2017). Although Coleoptera and Hymenoptera are more diverse insect orders, 100% of Lepidopterans are herbivorous species, while only 26% and 7% of Coleoptera and Hymenoptera are herbivores, respectively (Wiens *et al.*, 2015). Thus, empirical studies are probably not unduly biased toward Lepidopterans.

The most striking bias in both herbivore and plant datasets was that the vast majority of studies were conducted in the Global North. Only five studies examined plant damage and herbivore performance in southern latitudes, illustrating a clear underrepresentation of plant–insect interactions in the Global South. We call for funding to support future studies on the consequences of climate change for plant–insect interactions in the Global South, especially in tropical biodiversity hotspots.

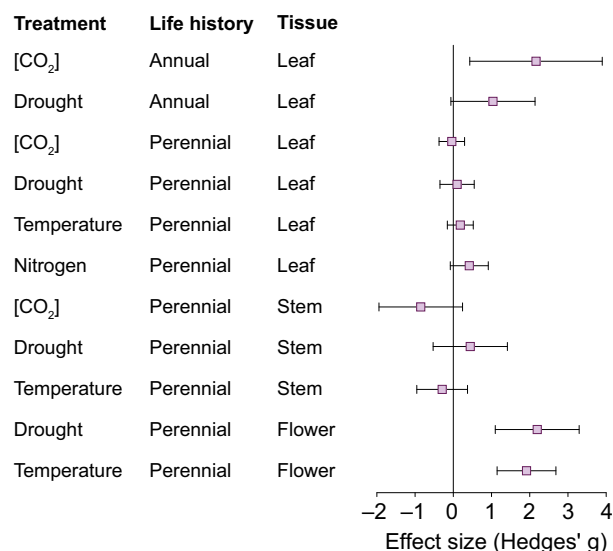
Future directions Our herbivore meta-analysis revealed that studies are not always performed with herbivores and plants both experiencing climate change manipulations. While having only plants or herbivores under manipulated climate change factors can help to disentangle direct and plant-mediated effects of climatic factors, we suggest that the most realistic results would come from exposing both plants and herbivores to changing environmental conditions.

More studies using multifactorial designs are urgently needed to achieve a realistic understanding of how current climate change influences plant–herbivore interactions. The joint effects of climate change factors probably depend on the magnitude of changes, on herbivore feeding guilds, and on species-specific interactions, and climate change factors may interact in complex ways (Jamieson *et al.*, 2017). For example, forest tent caterpillar (*Malacosoma disstria*) consumption increased on aspen under drought stress, regardless of CO₂ concentrations, but declined more strongly on drought-stressed maple leaves under elevated CO₂ (Roth *et al.*, 1997). Similarly, population growth rates of two-spotted spider mite (*Tetranychus urticae*) increased only when elevated CO₂ was combined with moderate drought stress (Sinaie *et al.*, 2019). Additionally, temperature affected the magnitude and the direction of plant and herbivore responses to elevated CO₂ in three chrysomelid beetle species and two plant species (Veteli *et al.*, 2002; Johns *et al.*, 2003). Furthermore, increasing temperature and CO₂ may have opposing effects on herbivore performance. We strongly encourage future multifactorial studies to evaluate plant and herbivore responses to the complex suite of climatic conditions that are changing simultaneously, ideally under field conditions that capture natural variation in numerous biotic and abiotic conditions simultaneously (Körner, 2003; Moles *et al.*, 2011; Rasmann *et al.*, 2014). While we are certainly not the first to call for multifactorial studies (Bale *et al.*, 2002; Massad & Dyer, 2010; Giron *et al.*, 2018; Hartley & Beale, 2019), our literature search revealed a dearth of multifactorial studies. Climate change factors could operate independently, synergistically or antagonistically, and multifactorial experiments are needed to generate robust predictions about plant–herbivore interactions under simultaneous changes in CO₂, temperature, precipitation and other variables.

(a) Overall analysis: 47 studies of 71 species



(b) Native systems: 36 studies of 64 species



(c) Biocontrol and agricultural systems: 11 studies of 7 species

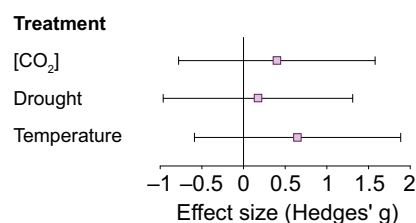


Fig. 5 Results of phylogenetically corrected meta-analysis of herbivore-induced plant damage to climate change manipulations in the field and controlled conditions. Plotted are Hedges's g effect sizes and 95% confidence intervals. We present the results for separate meta-analyses including the full dataset including all 47 studies (a), and studies conducted in native systems (b), or in biocontrol and agricultural systems (c). As studies differed in design, the treatments were not all applied to each life history or tissue type category. Positive values with 95% confidence intervals > 0 indicate that climate change increases trait values, and negative effect sizes indicate that climate change factors reduce trait values. If the 95% confidence intervals span 0, the meta-analysis did not detect a significant effect of a treatment on a trait. Only two studies examined floral herbivory, so these results must be treated with caution.

IV. Evolutionary consequences of climate change for plant–herbivore interactions

One fundamental question is whether species will be able to adapt fast enough to track rapid environmental change (Visser, 2008). Plants have evolved a variety of chemical and morphological traits that allow them to resist or tolerate herbivores, and insects have evolved traits that allow them to overcome many plant defenses (Ratzka *et al.*, 2002; Glauser *et al.*, 2011; Jander, 2014; War *et al.*, 2018). The evolution of plant and insect traits related to herbivory and defense can happen rapidly enough to influence ecological dynamics. For example, *Oenothera biennis* plants protected from herbivory evolved reduced resistance and increased competitive ability over the course of a 4 yr experiment (Agrawal *et al.*, 2012). Additionally *Brassica rapa* plants evolved rapidly in response to pollinators and foliar herbivores (Ramos & Schiestl, 2019). Furthermore, heterogeneity in herbivore abundance across the landscape can influence genetic variation in plant defenses. For example, geographic variation in the defense locus *GS-ELONG* in the model plant *Arabidopsis thaliana* is associated with aphid

abundance (Züst *et al.*, 2012). Insect species often have fast developmental rates, short generation times and high reproductive rates, which can lead to rapid evolution to novel conditions, like pesticides (Hawkins *et al.*, 2019) and introduced plant hosts (Carroll *et al.*, 2005). Evolutionary changes in herbivorous insects influence host preferences (Singer & Thomas, 1996; Thomas *et al.*, 2001) and herbivore distributional shifts (Haag *et al.*, 2005).

Adaptive responses to climate change depend on the magnitude of novel selection and the degree of genetic variation in functional traits. These quantitative genetic parameters are hard enough to quantify in response to changing abiotic conditions (Etterson & Shaw, 2001; Bemmels & Anderson, 2019; Torres-Martínez *et al.*, 2019). The situation becomes even more challenging when interacting species also impose strong selection on each other, and when one partner (often the insect herbivore) has a much faster generation time than the other (often the plant host). Is existing genetic variation within plant and herbivore populations sufficient to adapt to ongoing climate change? Will rapid contemporary evolution of arthropod herbivores further depress the fitness of native plant species? Could gene flow across plant populations

accelerate adaptation if gene flow occurs primarily from populations that evolved with a diverse and abundant herbivore community into populations that historically experienced a more depauperate community? Could adaptive responses to climate change in plants or herbivores be constrained by increased herbivory or defenses, respectively? Our meta-analysis suggests that climate change likely exerts strong selection on plant and herbivore traits, but we know very little about the longer-term evolutionary consequences of ongoing environmental change for plant–herbivore interactions.

Anthropogenic environmental changes such as climatic change, habitat fragmentation, pollution and urbanization probably interact to influence the coevolutionary dynamics of plants and herbivores (Leimu *et al.*, 2012; Miles *et al.*, 2019). Changes in temperature can influence plant chemistry and phenology, as well as insect growth and feeding rates (Bale *et al.*, 2002; Huberty & Denno, 2004; Zvereva & Kozlov, 2006). Because of the complex interactions involved, the long-term consequences of these environmental changes on community dynamics are likely to be difficult to predict. Our review has focused primarily on arthropod herbivores because fewer studies have evaluated changing plant–herbivore interactions under climate change for mammalian herbivores or other taxonomic groups (but see Brodie *et al.*, 2012; Choi *et al.*, 2019). Nevertheless, mammalian populations are declining globally (Collen *et al.*, 2008; Harris *et al.*, 2009; Ripple *et al.*, 2015), which could decrease plant damage from larger herbivores. Future studies using a variety of complementary approaches will be needed to predict how environmental changes will influence plant–herbivore eco-evolutionary dynamics.

Traditional approaches to investigating plant–herbivore coevolution have used techniques such as phylogenetic analysis (Ehrlich & Raven, 1964). However, plant–herbivore eco-evolutionary dynamics can occur rapidly and can also be studied via laboratory and field experiments (Agrawal *et al.*, 2012; Züst *et al.*, 2012; Ramos & Schiestl, 2019). Another promising technique is the resurrection approach of comparing ancestors and descendants under common conditions to directly examine evolutionary change (Franks *et al.*, 2018b). One study used ancestral and descendant seeds of *B. rapa* plants and showed that the evolutionary changes that occurred through artificial selection for rapid cycling resulted in changes to herbivore preference and performance (Franks *et al.*, 2018a). Resurrection studies may be more challenging to use for insects than plants, as seeds can often be stored long-term. However, for certain herbivore species, dormant eggs may be retrievable from the soil bank, or frozen and revived for comparison with contemporary generations (Kerfoot & Weider, 2004; Franks *et al.*, 2018b). Alternatively, laboratory colonies may be maintained over generations and serve as a link to the past (Cooper *et al.*, 2003). Similarly, in experimental evolution studies, colonies could be reared on artificial diets to eliminate selection by plant traits.

Resurrection studies and experimental or artificial selection experiments can be combined with genomics to study adaptation from standing genetic variation (Schlötterer *et al.*, 2015). Genomic studies can examine how spatially variable selection, mediated by plant–herbivore interactions, can maintain genetic variation within

natural populations of host plants and herbivores (Gloss *et al.*, 2013). For example, geographic variation in herbivory can drive adaptive evolution and maintenance of polymorphism in plant defense genes (Prasad *et al.*, 2012), while spatial mosaics of host plants may also maintain phenotypic variation in herbivores (Kant *et al.*, 2008). Experimental evolution studies (Ramos & Schiestl, 2019), studies using genome-wide sequencing (Gloss *et al.*, 2016), and studies that involve experimental manipulations of factors that are being altered with anthropogenic environmental change (Leimu *et al.*, 2012) will all be useful in helping to understand and predict changes in dynamic interactions between plants and herbivores.

V. Conclusions

Our meta-analysis revealed that climate change factors can increase herbivore consumption rates, probably leading to greater foliar damage to annual plants and floral damage to perennial plants. Furthermore, we found that increased CO₂ concentrations delayed the development of arthropod herbivores, whereas increased temperatures accelerated development. We hypothesize that some insect herbivores may shift from one to multiple generations per year under climate change. We caution that these results focus almost entirely on interactions between arthropod herbivores and foliar tissues in temperate systems, and that most studies manipulated a single climatic condition at a time. Funding for studies in the tropics and more broadly in the Global South will enable more robust generalizations to emerge while simultaneously enhancing our understanding of how climate change could alter plant–herbivore interactions in diverse ecosystems. We encourage future studies that evaluate additional plant–herbivore dynamics under climate change, including florivory and seed predation, both of which are tightly associated with plant fecundity (Parachnowitsch & Caruso, 2008). Future studies will reveal how climate change is likely to influence below-ground interactions and plant–soil feedback responses (Bezemer *et al.*, 2013; Lu *et al.*, 2015; Ourry *et al.*, 2018). Finally, several studies have evaluated mammalian herbivory under climate change (Brodie *et al.*, 2012), and future experiments that disentangle the contributions of multiple taxonomic groups to increased herbivory under climate change will increase our capacity to predict plant and herbivore population persistence. Given the strong immediate effects of climate change on plant and herbivore functional traits, novel conditions could impose strong selection and alter long-term evolutionary dynamics.


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Author contributions


EH conducted the literature search, extracted data and wrote the manuscript. CB contributed to data extractions and commented on the manuscript. SF contributed to manuscript writing and editing. IJ contributed to the introduction and commented on the manuscript. JTA developed the research framework, extracted data, conducted the meta-analyses, and wrote the manuscript.

ORCID

Jill T. Anderson  <https://orcid.org/0000-0002-3253-8142>

Steven J. Franks  <https://orcid.org/0000-0001-9681-3038>

Elena Hamann  <https://orcid.org/0000-0003-2888-6440>

M. Inam Jameel  <https://orcid.org/0000-0002-4973-3956>

Data availability

The data and R scripts for the meta-analyses have been uploaded to FigShare (doi:10.6084/m9.figshare.13070675).

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Supporting Information

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

Fig. S1 Flow diagram illustrating the literature search and eligibility criteria.

Fig. S2 Phylogenetic tree for the full herbivore dataset.

Fig. S3 Phylogenetic tree for the full plant dataset.

Fig. S4 Herbivore orders and performance traits represented in the herbivore dataset.

Fig. S5 Herbivore studies classified according to study settings and climate change factors.

Fig. S6 Funnel plot evaluating the publication bias in the herbivore dataset.

Fig. S7 Plant families, life strategies and damage types represented in the plant dataset.

Fig. S8 Plant studies classified according to study settings and climate change factors.

Fig. S9 Funnel plot evaluating the publication bias in the plant dataset.

Methods S1 Detailed methods description.

Notes S1 Detailed results description.

Table S1 Model results for herbivore responses to climate change manipulations.

Table S2 Effect sizes for herbivore responses (full dataset).

Table S3 Effect sizes for herbivore responses (direct vs indirect effects data subset).

Table S4 Effect sizes for herbivore responses (direct effects data subset).

Table S5 Effect sizes for herbivore responses (indirect effects data subset).

Table S6 Effect sizes for herbivore responses (native systems data subset).

Table S7 Effect sizes for herbivore responses (nonnative systems data subset).

Table S8 Model results for plant responses to climate change manipulations.

Table S9 Effect sizes for plant responses (full dataset).

Table S10 Effect sizes for plant responses (native systems data subset).

Table S11 Effect sizes for plant responses (nonnative systems data subset).

Table S12 List of studies included in the herbivore performance meta-analysis.

Table S13 List of studies included in the herbivore performance meta-analysis.

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