

Variable effects of temperature on insect herbivory

Rising temperatures can influence the top-down control of plant biomass by increasing herbivore metabolic demands. Unfortunately, we know relatively little about the effects of temperature on herbivory rates for most insect herbivores in a given community. Evolutionary history, adaptation to local environments, and dietary factors may lead to variable thermal response curves across different species. Here we characterized the effect of temperature on herbivory rates for 21 herbivore-plant pairs, encompassing 14 herbivore and 12 plant species. We show that overall consumption rates increase with temperature between 20 and 30° C but do not increase further with increasing temperature. However, there is substantial variation in thermal responses among individual herbivore-plant pairs at the highest temperatures. Over one third of the herbivore-plant pairs showed declining consumption rates at high temperatures, while an approximately equal number showed increasing consumption rates. Such variation existed even within herbivore species, as some species exhibited idiosyncratic thermal response curves on different host plants. Thus, rising temperatures, particularly with respect to climate change, may have highly variable effects on plant-herbivore interactions and, ultimately, top-down control of plant biomass.

1 **Variable effects of temperature on insect herbivory**

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9 Introduction

10 Environmental temperature drives a number of important ecological interactions,
11 including competition, predation, and herbivory, by determining the metabolic rates of
12 ectothermic organisms (Vassuer and McCann 2005, O'Connor et al. 2009, Vucic-Pestic et al.
13 2011). As metabolic demands increase exponentially with rising temperatures, consumers
14 generally either increase food intake or switch to higher quality diets to offset the rising costs of
15 metabolism (O'Connor 2009, Lemoine et al. 2013). As a result, predation and herbivory rates tend
16 to increase exponentially with increased temperature (Hillebrand et al. 2009, Vucic-Pestic et al.
17 2011). However, both consumption rates and fitness can decline precipitously once a species
18 encounters temperatures beyond its thermal optimum (Lemoine and Burkepile 2012). A suite of
19 adaptive and evolutionary factors determine these thermal optima, such that a given consumer
20 community may contain species with considerably different thermal response curves (Angilletta
21 et al. 2004). To date, however, few (if any) studies have examined variation in thermal response
22 curves for a community of co-occurring herbivores (Buckley et al. 2014).

23 Insect herbivores can be an important top-down force in terrestrial ecosystems,
24 controlling plant biomass (Carson and Root 2000), maintaining species diversity (Bagchi et al.
25 2014), reorganizing competitive hierarchies (Kim et al. 2013), and enhancing nutrient cycling
26 (Metcalf et al. 2014). Because insects are ectothermic, their physiological rates, including
27 consumption and growth rates, are directly tied to environmental temperature. By extension, top-
28 down control of plant biomass is also likely to be temperature dependent. Theoretical and
29 experimental studies suggest that herbivory rates should increase exponentially with rising
30 temperatures (O'Connor et al. 2011). One potential shortcoming of theoretical examinations of
31 temperature-driven herbivore-plant interactions is that they do not often incorporate variation in
32 thermal response curves within an assemblage of herbivore species. In part, this is because

33 thermal response curves for multiple herbivore species on a single host plant remain mostly
34 uncharacterized. Species are often examined singly, and ecologists have focused on a few readily
35 available model species like *Spodoptera* spp. (Stamp and Yang 1996) and *Manduca sexta*
36 (Kingsolver and Woods 1998). In contrast, the herbivore guild within a community, or even on a
37 single host plant, can vary from 1 – 100s of species, each with different life histories, climatic
38 niches, evolutionary histories, and dietary needs that may drive vastly different thermal response
39 curves (Buckley et al. 2014).

40 Multiple factors aside from evolutionary history and local adaptation can determine the
41 shape of a species' thermal response curve. For example, plant chemical defenses can become
42 more or less effective at high temperatures depending on the identity of the herbivore, plant, and
43 chemical compounds in question (Stamp and Osier 1998, Stamp et al. 1997). Similarly, different
44 insect species can become more or less nutrient-limited at higher temperatures, which is also
45 contingent on host plant quality (Kingsolver et al. 2006, Kingsolver and Woods 1998, Lemoine et
46 al. 2013). Thermal response curves therefore likely differ among herbivore species and within a
47 single herbivore species utilizing different hosts. Given the interest in predicting the effects of
48 climate change on trophic interactions and community structure (Singer et al. 2013, Urban et al.
49 2012), we sought to determine whether temperature influences herbivory in a predictable manner
50 based on a few easily measured variables of plant nutritional quality.

51 Here, we report thermal response curves of consumption rates for 21 herbivore-plant
52 pairs, encompassing 14 herbivores and 12 plant species (Table 1). We asked two specific
53 questions: (1) what is the extent of within- and among-species variation in thermal response
54 curves of consumption for insect herbivores? and (2) can plant nutritional quality explain
55 variation in thermal response curves? By working with multiple species of both herbivores and
56 plants, we demonstrate that thermal response curves vary substantially both among and within
57 herbivore species. However, we were unable to detect any influence of plant nutritional quality

58 on the overall shape of the thermal response curve across taxa, suggesting that thermal response
59 curves are idiosyncratic and highly variable among plant-herbivore pairs.

60 **Methods**

61 All experiments were conducted at the Smithsonian Environmental Research Center (SERC), in
62 Edgewater, MD, USA from June – August 2012. Using laboratory feeding assays, we evaluated
63 the feeding performance of 14 herbivore species from three Orders (Lepidoptera, Coleoptera,
64 Hymenoptera) on 12 plant species (Fig. 1, Table 1). Herbivores were collected by hand from host
65 plants in the forests and fields on the SERC premises throughout the summer. All herbivores were
66 kept in a cage and fed leaves from the plant species on which they were collected. Individuals
67 were used in feeding assays within 24 h of collection. No individual was used more than once. As
68 herbivores were opportunistically collected, the number of replicates per host plant/temperature
69 combination varied depending on the number of herbivores found (Table S1). Gregarious species
70 (*e.g. Hyphantria cuneata*) have higher replicate numbers than do rare, non-gregarious species
71 (*e.g. Danaus plexippus*). A single lepidopteran species could not be identified beyond the
72 Tortricidae family. We focused on folivorous individuals, using larvae from lepidopteran and
73 hymenopteran species and adults only from a single coleopteran species (*Chrysochus auratus*).

74 *Feeding Assays*

75 In no-choice assays, a single individual was weighed and placed in a single rearing cup with a
76 single, pre-weighed leaf from a potential host plant (see Table 1). Each rearing cup was randomly
77 assigned to one of four temperatures (20°, 25°, 30°, and 35° C, see Table S2 for temperature and
78 light data from each growth chamber) maintained in growth chambers on a 14:10 light:dark
79 cycle. Temperatures were selected to represent a realistic set of temperatures during the spring in

80 summer months. Data from a nearby NOAA weather station (Annapolis, MD) indicate that
81 temperatures can range from 20 – 35° during the summer months (June – July, Fig. S1). Leaf
82 petioles were placed in water-filled microcentrifuge tubes capped with cotton to prevent
83 desiccation, and we observed no obvious differences in leaf turgor during the assays. After 24
84 hours, herbivores and leaves were reweighed to estimate consumption rates. Feeding assays of
85 this duration have been used to assess herbivore performance and dietary preferences in
86 lepidopterans (Kingsolver and Woods 1998, Kingsolver and Woods 1997) and coleopterans
87 (Gange et al. 2012, Lemoine et al. 2013). We divided all consumption rates by the initial mass of
88 the individual used in the feeding assay to account for variation in body size among replicates.
89 Consumption rates are reported as grams consumed per gram body mass.

90 Control assays with no herbivores accounted for autogenic change in leaf weight over the
91 24 h period ($n = 5$ per plant species per temperature). Leaves of all plant species except *L.*
92 *styraciflua* gained mass over 24 h in the absence of herbivores. Larger leaves gained more mass
93 than did smaller leaves. We therefore used species-specific equations to correct for autogenic
94 change in leaf mass (Table S3) rather than using mean change in leaf mass across all autogenic
95 controls. Mass-specific autogenic changes, whether positive or negative, were added to leaf final
96 weights. Negative autogenic changes (*i.e.* plants lost mass in control assays) would therefore
97 lower estimates of consumption and vice versa. In total, we conducted 552 no-choice feeding
98 assays, resulting in 496 observations after removing individuals that died or molted overnight
99 (final replicate numbers for each herbivore/plant/temperature combination given in Table S1).

100 *Plant Traits*

101 To assess the mechanisms by which temperature affected herbivore performance among
102 plant species, we quantified nutritional characteristics of undamaged leaves ($n = 3-5$) of each
103 plant species, all collected from unique individuals. Prior to all nutrient content analyses, leaves

104 were weighed, dried to a constant mass at 60° C, and re-weighed to estimate water content. Dried
105 leaf material was ground to a fine powder for carbon (C), nitrogen (N), and phosphorus (P)
106 analyses. Percent C and N were estimated using an EAI CE-440 elemental analyzer (Exeter
107 Analytics, Coventry, UK). Phosphorus content was determined using dry oxidation-acid
108 hydrolysis extraction followed by colorimetric analysis on a microplate spectrophotometer
109 (PowerWave XS; Biotek, Winooski, VT).

110 *Statistical Analyses*

111 We used a Bayesian hierarchical model to determine thermal response curves of
112 consumption for each herbivore-plant pairing. This allowed us to estimate parameters for the
113 overall trend in consumption with increasing temperature, parameters for each herbivore-plant
114 pairing, and the impact of plant nutritional quality on these parameters. A multilevel model is
115 particularly appropriate for handling unbalanced data and small sample sizes for some herbivore-
116 plant pairings, but some of the predicted responses for less well-sampled taxa will be pulled
117 heavily towards the overall mean response (Gelman and Hill 2007). Although there could be a
118 phylogenetic signal in the patterns of thermal curves of different insect herbivores, we did not
119 have sufficient replication within genera or families to address this question. Most species were
120 in unique families (only three families had more than one species represented) and all but three
121 species were lepidopterans (Table 1). Thus, we did not incorporate the possibility of a
122 phylogenetic signal into our analyses.

123 Thermal reaction norms of consumption describe the influence of temperature on
124 consumption rates. Regardless of the specific equation used to model a reaction norm, all thermal
125 reaction norms are characterized by a thermal minimum below which consumption is zero, a
126 thermal optimum where consumption rate is maximized and beyond which consumption declines,
127 and a thermal maximum, above which consumption is zero. We modeled the thermal reaction

128 norm of consumption rates for each herbivore-plant pairing using a quadratic exponential (*i.e.*
 129 Gaussian) curve because such curves often describe thermal reaction norms (Angilletta 2006):

$$y_{ij} = \exp(a_j + b_j \text{Temp}_{ij} + c_j \text{Temp}_{ij}^2) + \varepsilon_{ij}$$

130 where y_{ij} is consumption of the i^{th} observation in the j^{th} herbivore-plant pair and ε_{ij} is residual
 131 error. We assumed that errors were normally distributed with a constant variance, but the variance
 132 was allowed to differ for each curve due to differing numbers of replicates among herbivore-plant
 133 pairings. Hereafter, parameters will be referred to as the intercept (a), exponential (b), and
 134 Gaussian (c) terms. The intercept a denotes mean consumption rate (since all predictor variables
 135 were standardized, see below), the exponential term b denotes the rate at which consumption
 136 initially increases with temperature, and the Gaussian term c denotes the extent to which
 137 consumption rates level off or decline at high temperatures.

138 Plant nutritional quality can affect the shape of the thermal response curve by influencing
 139 any one of the three parameters that determine the shape of the Gaussian curve. Therefore, each
 140 parameter (intercept, exponential, and Gaussian) was modeled as function of nitrogen,
 141 phosphorus, and water content of the given plant for each herbivore-plant thermal response curve.
 142 For example, the exponential term of the j^{th} curve was a linear function of plant quality:

$$b_j = \mu_b + \gamma_1 N_j + \gamma_2 P_j + \gamma_3 H_2O_j + \delta_j$$

143 where μ_b is the overall, community-level linear parameter, and γ_1 , γ_2 , and γ_3 represent the
 144 influence of nitrogen (%N), phosphorus (%P), and water content (%H₂O) respectively on the
 145 exponential parameter of the j^{th} thermal response curve. δ_j is a multivariate normal error term.
 146 Thus, mean consumption rate (a), the rate of increase with temperature (b), and the extent of
 147 curvature in the thermal response curve (c) were all modeled as linear functions of plant
 148 nutritional content. The random effects for each curve (*i.e.* parameters a_j , b_j , c_j) were assumed to

149 come from a multivariate normal distribution, allowing for covariance among parameter
150 estimates.

151 All predictor variables were standardized prior to analysis to speed chain convergence.
152 For all models, four MCMC chains were run for 5,000 ‘burn-in’ iterations to allow for chain
153 convergence. Posterior distributions of each parameter were simulated by saving the 20th sample
154 from an additional 5,000 posterior simulations, resulting in 1,000 independent estimates (250 per
155 chain, with four chains). Chain convergence and autocorrelation were assessed using trace plots
156 and density plots of posterior simulations. Each parameter was given a mildly uninformative
157 prior normal distribution ($N(0, 1)$); variance parameters were given uninformative prior uniform
158 distributions ($U(0, 100)$). Because predictors were standardized, the magnitude of parameter
159 estimates will be small, such that a standard normal distribution is relatively uninformative. For
160 each parameter, we calculated the 80% and 95% Bayesian credible interval (CI) from the
161 posterior simulations. Parameters whose 95% CI excluded zero were considered highly
162 significant, whereas parameters whose 80% CI excluded zero were considered marginally
163 significant. If the 80% CI included zero, we assumed that the parameter had a low probability of
164 being important. All assumptions of normality and homogenous variances were examined using
165 residual plots. All analyses were conducted using Python v2.7. Bayesian models were evaluated
166 using STAN v2.1 (Stan Development Team 2013), accessed via PySTAN. Python code for the
167 hierarchical model is available as Appendix 1. All code and raw data are available on the
168 corresponding author’s website¹ and will be uploaded to the Dryad database².

169 *Climate Change Simulations*

1 <http://www.natelemoine.com>

2 <http://datadryad.org/>

170 We sought to understand how potential variability in thermal response curves among
171 herbivores interacts with climate change to alter potential top-down control of plant biomass.
172 Thus, we next built a simple model utilizing observed feeding rates and temperatures to estimate
173 cumulative consumption first over one growing season, and then cumulative consumption given
174 two climate change scenarios, +3° and a +5°C increases in temperature, a moderate and severe
175 climate warming scenario, respectively (IPCC 2007). We obtained hourly temperature records for
176 June - August 2013 from the NOAA weather station in Annapolis, MD (Fig. S2). We then used
177 the 1000 posterior draws of observed feeding rates to estimate hourly consumption rates
178 (including parameter uncertainty) for each herbivore-plant combination across the observed
179 temperature range. Most hourly temperature readings were within the 20 – 35° C range used in
180 our experiments (Fig. S2). This yielded 1000 estimates of cumulative consumption for every
181 herbivore-plant pair. We then simulated climate change by adding 3° and 5° to hourly temperature
182 records and repeating the above calculations.

183 This method makes several important assumptions: 1) thermal effects of climate change
184 can be approximated by adding a constant increase in temperature to all hourly temperature
185 records, 2) that an individual feeds at a constant rate for the entire season with no variation as the
186 instar grows over time, and 3) that a single individual is responsible for feeding, or multiple non-
187 overlapping individuals immediately replace one another upon dying to maintain a constant
188 consumption rate across the growing season. These assumptions will often not hold true so our
189 method of assessing climate change is a relatively coarse picture of how climate change may
190 affect herbivory rates over the course of an entire season.

191 **Results**

192 The exponential parameter (b) of overall consumption rates was significantly greater than
193 zero, indicating that overall consumption rates did increase exponentially with temperature (Figs.
194 2, 3). However, the increase was restricted to temperatures between 20° and 30° C (Fig. 1). The
195 95% CI of the Gaussian parameter (c) narrowly included zero, but the bulk of the posterior
196 distribution for this parameter lay below zero, indicating that overall consumption rates began to
197 level off at temperatures above 30° C ($\text{Pr}(<0) = 0.96$, Fig. 3). Accordingly, our model predicts
198 relatively little change in overall consumption rates between 30° and 35° C (Fig. 2). Variance in
199 consumption rates among herbivore-plant pairs also increased substantially with rising
200 temperature. At 20°, variance among mean herbivore-plant consumption rates was 0.45, while at
201 35° this variance increased to 1.43. Thus, variability in consumption rates among herbivore-plant
202 pairs increased by over 300%. As a result, at 20° C the predicted mean community-level
203 consumption rates lie between 0.44 – 1.13 g per day (95% CI). Estimates of mean community-
204 level consumption were more uncertain at higher temperatures, lying between 0.93 – 2.13 g per
205 day (95% CI).

206 Uncertainty regarding overall consumption rates at higher temperatures stems from
207 idiosyncratic thermal response curves among herbivore-plant pairs (Figs. 4, 5). Six herbivore-
208 plant pairs (*Arge scapularis* – *Ulmus rubra*, *Chrysochus auratus* – *Apocynum cannabinum*,
209 *Hyphantria cunea* – *Acer negundo*, *H. cunea* – *Liquidambar styraciflua*, *Melanophia canadaria*
210 – *Lindera benzoin*, *Papilio troilus* – *S. albidum*) had Gaussian parameters (c) that were
211 moderately or significantly different from zero, indicating decreasing consumption rates at higher
212 temperatures (Figs. 4, 5). An additional eleven herbivore-plant pairs (*Atteva aurea* – *Ailanthus*
213 *altissima*, *Danaus plexippus* – *Asclepias syriaca*, *Epimecis hortaria* – *L. benzoin*, *E. hortaria* – *L.*
214 *albidum*, *Euchaetes egle* – *Asclepias syriaca*, *Malacosoma americanum* – *Prunus serotina*,
215 *Melanophia canadaria* – *Acer negundo*, *Nematus tibialis* – *Robinia pseudoacacia*, *P. troilus* – *L.*
216 *benzoin*, *Saucrobotys futilalis* – *A. cannabinum*, Unidentified Tortricid – *L. benzoin*) increased

217 consumption with warming throughout the entire temperature range, where the exponential
218 parameter (b) was significantly or moderately different from zero. In some cases the parameter
219 value was small enough that the fit was approximately linear (e.g. *Epimecis hortaria* – *Sassafras*
220 *albidum*, Figs. 4, 5). An additional four herbivore-plant combinations (*Danaus plexippus* – *A.*
221 *syriaca*, *E. hortaria* – *Liriodenron tulipifera*, *Euchaetes egle* – *Apocynum cannabinum*, *M.*
222 *canadaria* – *S. albidum*, *Papilio polyxense* – *Foeniculum vulgare*) showed no detectable change in
223 consumption rate with increasing temperature.

224 Even within herbivore species, thermal response curves varied considerably. For example,
225 *E. hortaria* consumption of *L. benzoin*, and to a lesser extent *S. albidum*, increased exponentially
226 with temperature (Fig. 4). However, *E. hortaria* consumption of *L. tulipifera* did not vary
227 significantly over the observed temperatures (Figs. 4, 5). Likewise, *P. troilus* increased
228 consumption of *L. benzoin* across temperatures, but consumption of *S. albidum* began to decline
229 at 35° (Fig. 4). We were not able to detect any effect of plant nutritional content on the shape of
230 thermal response curves among herbivore-plant pairs (Fig. 6).

231 High intra- and interspecific variability among thermal response curves for each
232 herbivore-plant pair led to variable effects of increasing temperatures on potential top-down
233 control of plant biomass (Fig. 7). For example, a 3° C increase in temperatures resulted in less
234 than a 20% increase in cumulative consumption for twelve herbivore-plant pairs compared to
235 what is predicted for current temperatures, while leading to a > 30% increase for four herbivore-
236 plant pairs (Fig. 7). A 5° C increase in temperature exacerbated this variability, as five herbivore-
237 plant pairs exhibited < 20% increase in cumulative consumption and four herbivore-plant pairs
238 exhibited a > 50% increase (Fig. 7). Further, increased warming from 3° to 5° C had highly
239 variable impacts on cumulative consumption rates among herbivore-plant pairs. For example,
240 *Atteva aurea* nearly doubled its estimated consumption of *Ailanthus altissima* as warming
241 increased from 3° to 5° C, whereas estimated consumption by *Melanophia canadaria* was

242 unaffected by temperature increases beyond 3° C (Fig. 7). Thus, high intra- and interspecific
243 variability in the herbivore-plant thermal response curves led to high variability in potential
244 climate change effects on top-down control of plant biomass over an entire growing season.

245 **Discussion**

246 Temperature influences herbivory rates via direct effects on insect herbivore physiology.
247 However, it is currently unclear how temperature affects top-down control of plant biomass at the
248 community or species level. Our data suggest that the influence of rising temperature on potential
249 top-down control of plant biomass via herbivory depends upon the identity of the herbivore-plant
250 pair under consideration. Such variability in the relationship between consumption rate and
251 temperature will make it difficult to predict the effects of temperature changes, *i.e.* climate
252 change, on top-down control of plant biomass.

253 Theory predicts that herbivory rates should increase exponentially with rising temperature
254 more quickly than primary production, reducing standing plant biomass at higher temperatures
255 (Gillooly et al. 2001, O'Connor et al. 2009, O'Connor et al. 2011). However, meta-analyses of
256 thermal response curves report substantial variability among species. Indeed, approximately 40%
257 of the thermal response curves examined by Dell et al. (2011) exhibited curvature, wherein the
258 thermal response curve began to decrease at high temperatures. In our study, 33% of the
259 herbivore-plant pairs exhibited substantial curvature, reducing consumption of plant biomass at
260 high temperatures, thereby contradicting theoretical predictions of exponential increases in top-
261 down control of plant biomass at high temperatures. Often, reduced consumption rates at high
262 temperatures result from metabolic demand exceeding energetic supply, such that energy
263 available for tasks beyond cellular maintenance, such as movement, feeding, or digestion,
264 decreases sharply at high temperature (Somero, 2011). This results in rapid decreases in

265 consumer fitness at temperatures beyond an organism's thermal optimum (Lemoine and
266 Burkepile 2012). We show that community-level herbivory rates display the same, albeit much
267 less pronounced, curvature as do some individual species. The slow decline at higher
268 temperatures, rather than a rapid drop-off beyond some threshold value, is a result of species-
269 specific variation in thermal response curves. Almost half (43%) of plant-herbivore pairings did
270 not show signs of decreased consumption at higher temperature, while one showed evidence of
271 declining consumption beyond 30° C, leading to no net change in overall consumption rates at
272 higher temperatures.

273 Such variation in thermal response curves makes predicting the effects of temperature
274 changes (*i.e.* microhabitat variation, seasonal effects, climate change) on herbivore-plant
275 interactions challenging in the absence of species-specific information. Indeed, a generalist
276 herbivore may have as many thermal response curves as host plants (Lemoine et al. 2013). We
277 report similar patterns here. For example, *Epimecis hortaria*, the tulip tree beauty moth, rapidly
278 increased consumption of both *Lindera benzoin* and *Sassafras albidum* with warming, but the
279 increased consumption of *S. albidum* was much slower. In contrast, *E. hortaria* showed no
280 relationship between consumption of *Liriodendron tulipifera* and temperature. Similarly, *Papilio*
281 *troilus* increased consumption of both *L. benzoin* and *S. albidum* with increasing temperature, but
282 consumption of *S. albidum* began to decrease at 35° C, and consumption of *L. benzoin* showed no
283 curvature.

284 Given the high variation in thermal response curves among herbivore-plant combinations,
285 predicting the effects of climate change on the top-down control of plant biomass remains
286 challenging. Some studies have ascribed a single thermal response curve to herbivore species,
287 demonstrating that plant biomass will decrease in a warming world as herbivory rates outpace
288 primary production (O'Connor et al. 2011). Our results suggest that using a single consumption-
289 temperature relationship for all herbivores can substantially overestimate the impact of climate

290 change on plant biomass. For example, between 20° and 30° C, both *Chrysochus auratus* and
291 *Saucrobotys futilalis* increased consumption of *Apocynum cannabinum*. However, at 35° C.
292 *auratus* decreased consumption while *S. futilalis* continued to increase consumption, resulting in
293 little change in overall consumption rates on *A. cannabinum* beyond 30° C.

294 When we integrated these changes in consumption over a full growing season, we showed
295 that top-down control on plant biomass is likely to increase with increasing temperature but the
296 magnitude of the increase depends on the herbivore-plant combination. Over the course of a
297 summer, simulated warming resulted in > 20% increase in cumulative consumption for 10
298 herbivore-plant pairs, just under half of the pairings examined. Conversely, simulated climate
299 change resulted in > 40% increase in cumulative consumption for five herbivore-plant pairs.
300 Overall, the change in consumption ranged from no change to an increase of over 60%. This
301 variability in consumption may explain why studies documenting significant effects of warming
302 on top-down control of plant biomass typically examine one herbivore species (Chase 1996,
303 Barton et al. 2009) while studies focusing on entire herbivore communities report weak or
304 negligible effects of warming (Richardson et al. 2002).

305 Surprisingly, we were unable to detect any influence of plant nutritional quality on the
306 shape of thermal response curves. Based on previous work (Lemoine et al. 2013), we expected
307 consumption rate to increase more rapidly on plants of higher nutritional quality. Conversely,
308 compensatory feeding predicts that consumption rates should increase more rapidly with
309 temperature for plants of low nutritional quality as herbivores attempt to fuel rising metabolic
310 demands (e.g. Williams et al. 1994). Our data suggest that plant nutritional content had little
311 effect on thermal response curves among herbivore species. However, prior work has found that
312 the relationship between temperature and consumption rates within a given species can vary with
313 dietary quality. For example, the Japanese beetle *Popillia japonica* increased growth and
314 consumption rates at high temperatures only on host plants with high nitrogen and carbon

315 concentrations (Lemoine et al. 2013). This may also be the case in our data. Within an herbivore
316 species, we can distinguish some patterns related to plant quality. For example, the generalist
317 herbivore *Epimecis hortaria* increased consumption rapidly with warming only on higher
318 nitrogen plant species. Within a plant species, however, patterns were less clear, as particular
319 herbivore species were equally likely to have unimodal or exponential curves when feeding on
320 the same plant. Thus, across all 21 plant-herbivore pairings, we were unable to detect an overall
321 pattern relating plant quality to multiple thermal reaction norms. Thus, dietary quality may be
322 more important for determining thermal response curves within herbivore species but cannot
323 predict the shape of consumption thermal response curves among herbivore and plant species.

324 We focused on examining herbivore response to increasing temperature while holding
325 plant phytochemistry constant, but rising temperatures might also affect plant phytochemistry.
326 Plant growth rates increase with rising temperatures (Veteli et al. 2002), which could alter
327 nutritional content or concentrations of defensive compounds as plants shuttle more resources
328 into growth (Coley et al. 1985). However, studies have shown that the effects of temperature on
329 plant secondary chemistry are highly idiosyncratic among species (Veteli et al. 2002, Zvereva and
330 Kozlov 2006). Furthermore, although variable temperature can alter nutritional quality within a
331 species, variation caused by temperature is substantially lower than inherent variation among
332 plant species (Aerts et al. 2009). However, the effects of rising temperature on plant chemistry
333 must be considered more completely before applying results such as ours in a climate change
334 context.

335 One potential caveat of our study is small sample size at many herbivore-plant-
336 temperature combinations. Given that we used field-collected organisms, sample size varied
337 considerably depending on the rarity of the species. Common and/or gregarious species, like *E.*
338 *hortaria*, *M. canadaria*, and *H. cunea*, have much higher sample sizes than rare or cryptic
339 species, like *D. plexippus* and *A. scapularis*. Thus, some herbivore-plant pairs show considerable

340 variability in the estimated thermal response curve and, in some cases, the prediction was heavily
341 influenced by the overall response. However, most work regarding the influence of temperature
342 on herbivory and its interaction with diet quality focus on a few readily available lepidopteran
343 herbivores (Kingsolver and Woods 1998, Kingsolver et al. 2006). The influence of temperature
344 on herbivory by the majority of the species reported here was heretofore unknown, and our
345 research adds considerably to the body of work documenting the importance of temperature on
346 rates of herbivory.

347 In summary, we show that herbivory, and therefore potential top-down control of plant
348 biomass, is highly contingent upon environmental temperature. While theoretical predictions
349 suggest that climate change might increase top-down control of plant biomass, our results
350 indicate that the effects of temperature on herbivory rates are highly variable. A single plant
351 species might experience more or less herbivory at higher temperatures, depending on the
352 identity of the herbivores present. Insects often control plant community structure (Carson and
353 Root 2000) and dominance hierarchies among plant species (Kim et al. 2013). Thus, studies
354 documenting the species-specific effects of temperature on insect herbivory levels will be crucial
355 to understanding how climate change might affect community composition in the plant-herbivore
356 assemblages of the future.

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Figure 1

Chrysochus auratus

Chrysochus auratus, the dogbane beetle, feeding on *Apocynum cannabinum*



Figure 2

Effect of temperature on overall consumption rates

Boxplot and predictions of overall consumption rates. Boxes depict the mean consumption rate of each herbivore-plant pair at that temperature ($n = 21$ per box). Shaded area represents the 80% (dark grey) and 95% (light grey) credible interval of the prediction. Line shows the median posterior prediction.

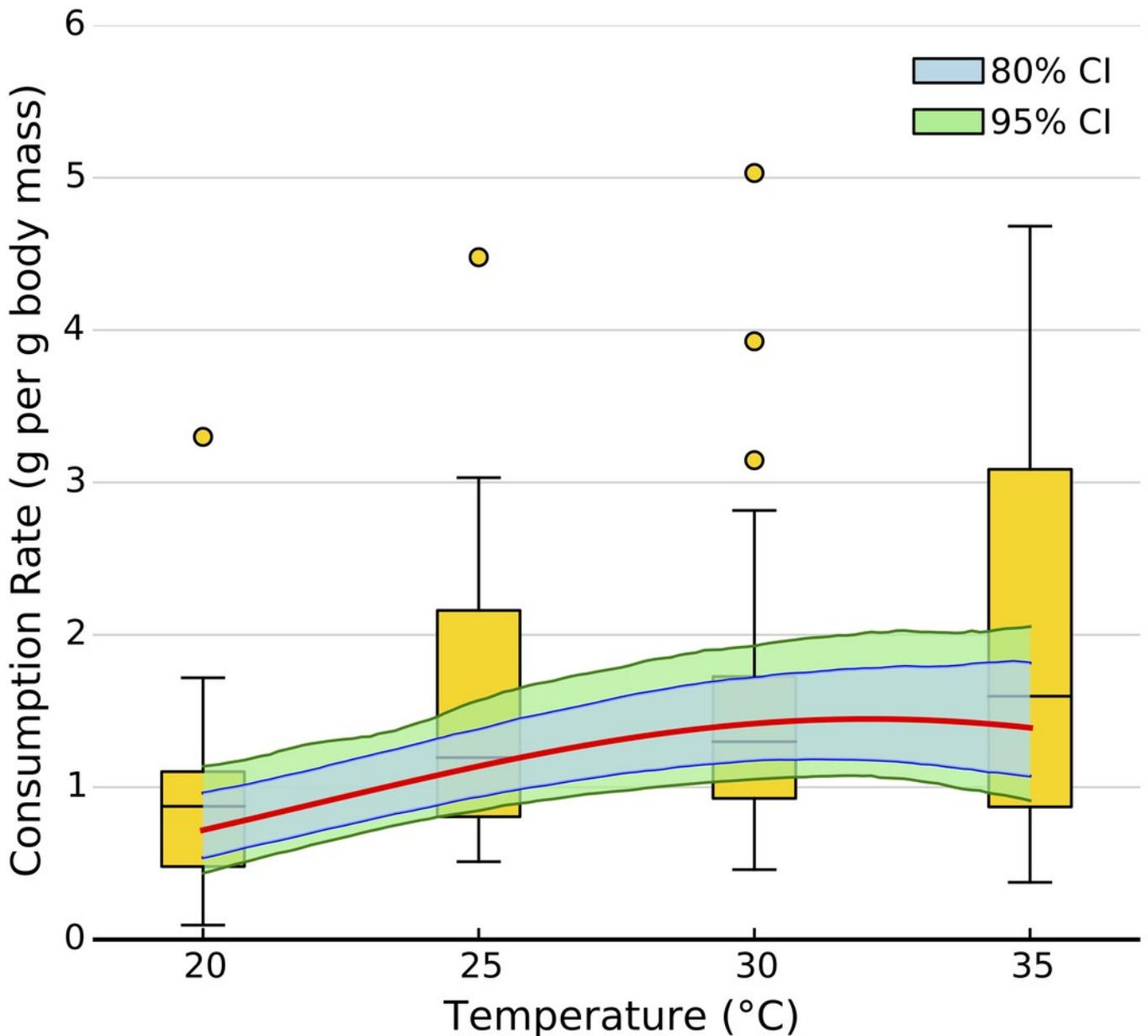


Figure 3

Parameter estimates of overall consumption rates

Posterior estimates of the parameters of community-level consumption rates. Points represent the median estimate, while lines show the 80% (thick line) and 95% (thin line) CI.

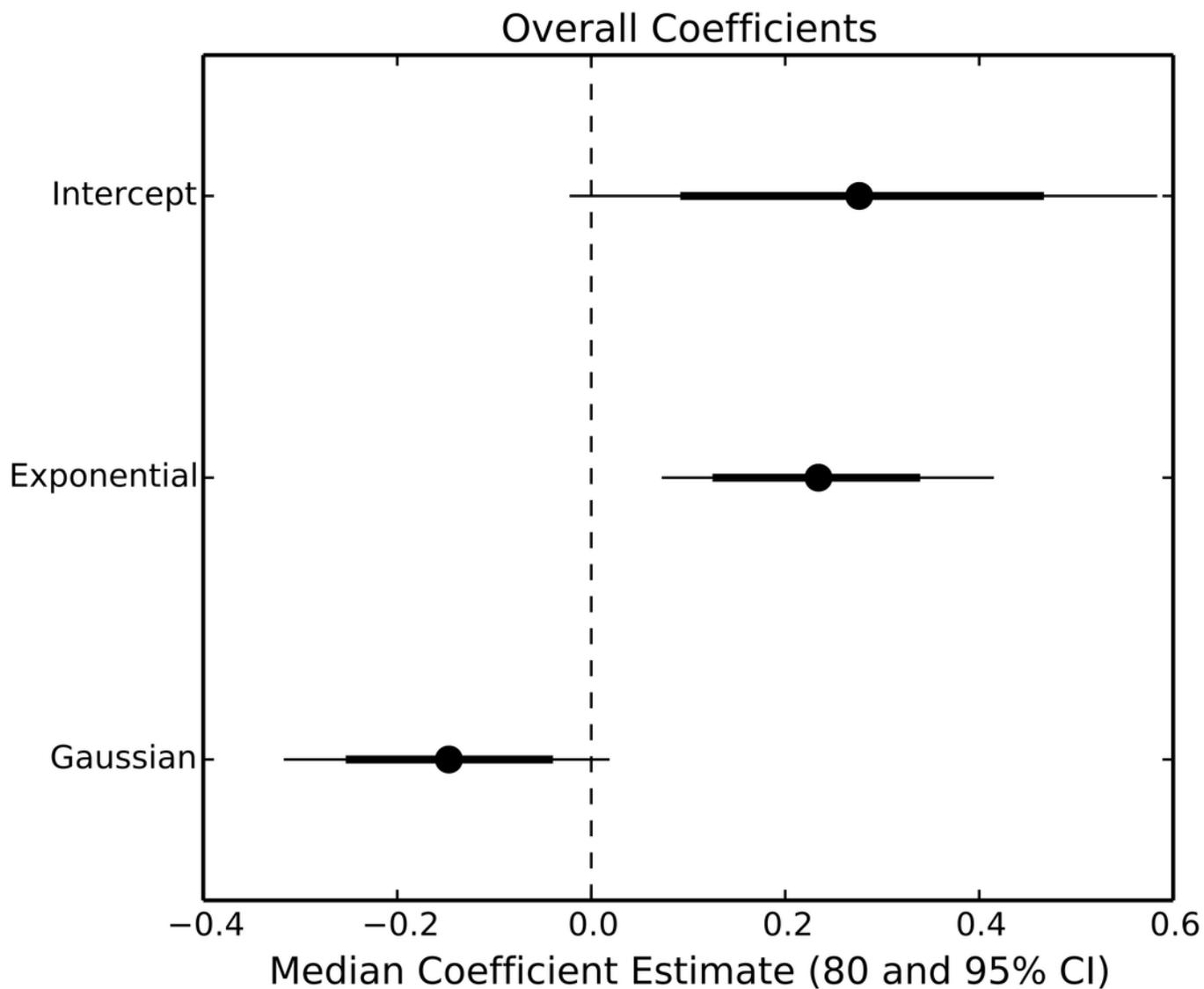


Figure 4

Effect of temperature on consumption rates for each herbivore-plant pair

Thermal response curves for each herbivore-plant pair. Thick line shows the median posterior estimate, shaded area shows the 95% confidence interval. Solid lines are significant at the 95% level, while dotted lines are significant at the 80% level. In some cases, a dotted line has a highly significant linear term but a moderately significant quadratic term (e.g. *Hyphantrea cunea* – *Liquidambar styraciflua*, see Figure 4). Points depict mean consumption rates (± 1 S.E.). Points are weighted by sample size, such that larger points contain more observations, to show how predictions for low sample sizes are pulled towards the overall response.

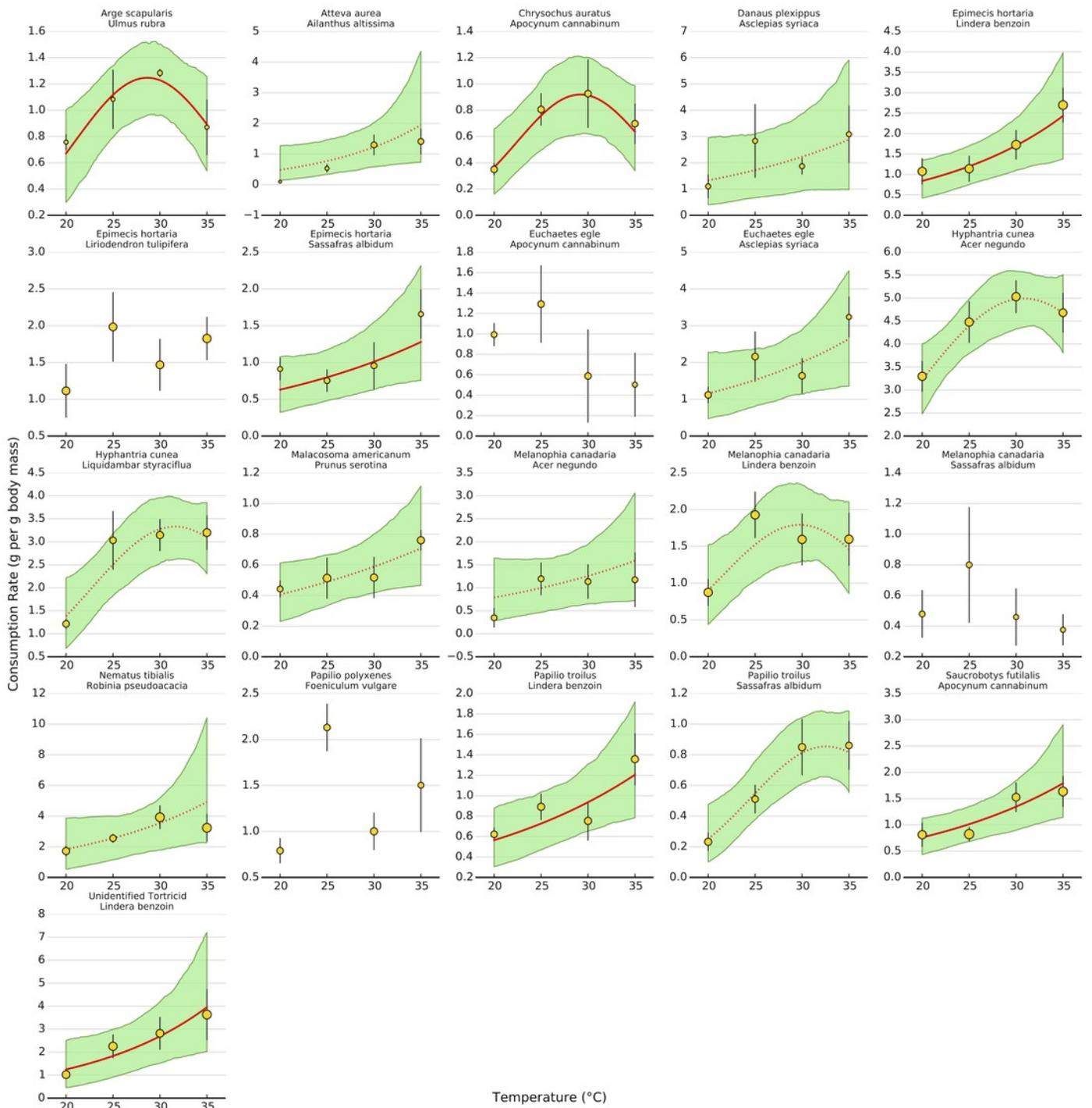


Figure 5

Parameter estimates for each herbivore-plant pair

Posterior estimates of the parameters of curve-level consumption rates. Points represent the median estimate, while lines show the 80% (thick line) and 95% (thin line) CI.

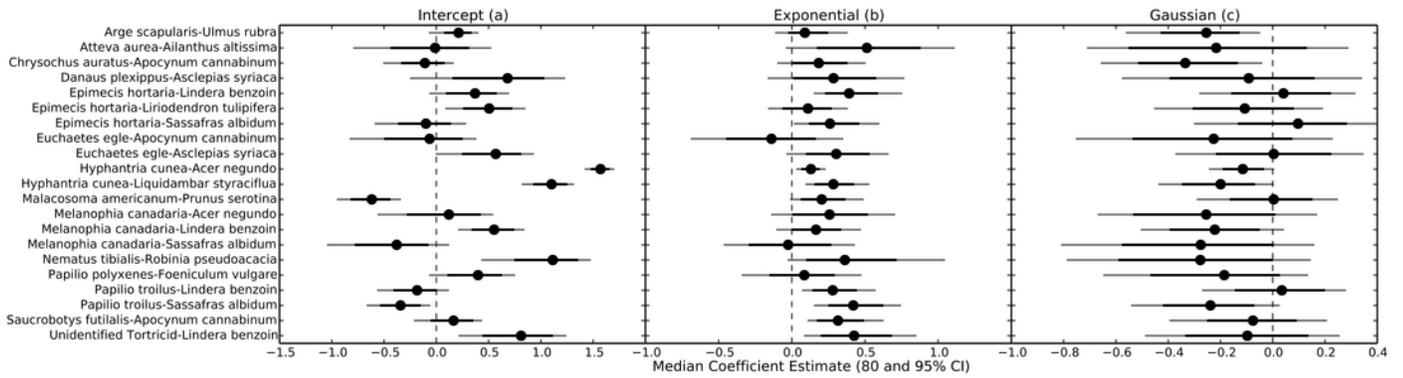


Figure 6

Parameter estimates for nutritional content effects on thermal response curves

Posterior estimates of the parameters of nutrient effects on the thermal response curves.

Points represent the median estimate, while lines show the 80% (thick line) and 95% CI.

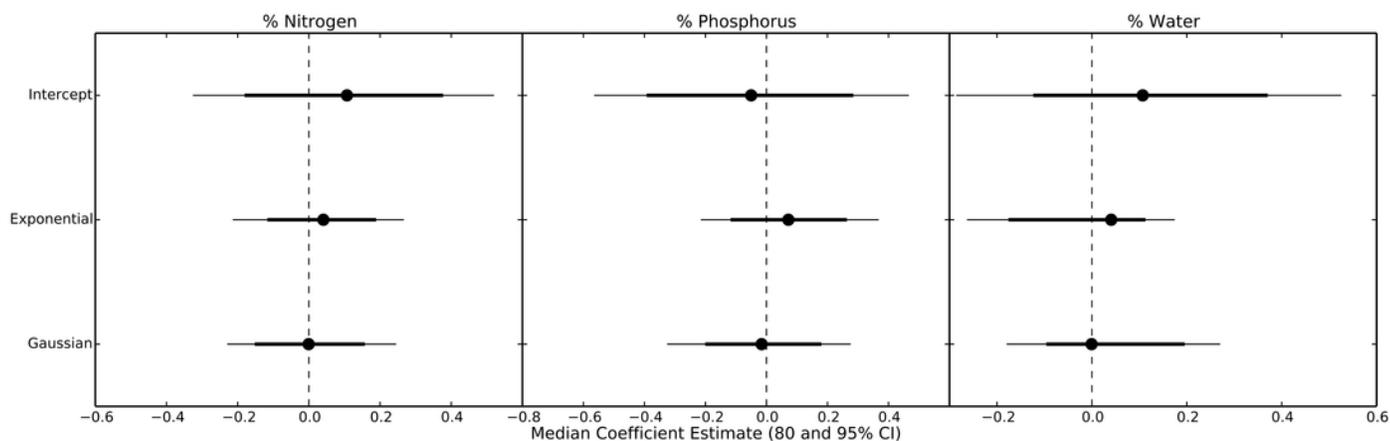


Figure 7

Change in cumulative consumption due to warming for each herbivore-plant pair

Percent change (± 1 S.E.) in cumulative consumption resulting from a 3° and 5° C increase in warming for all herbivore-plant pairs.

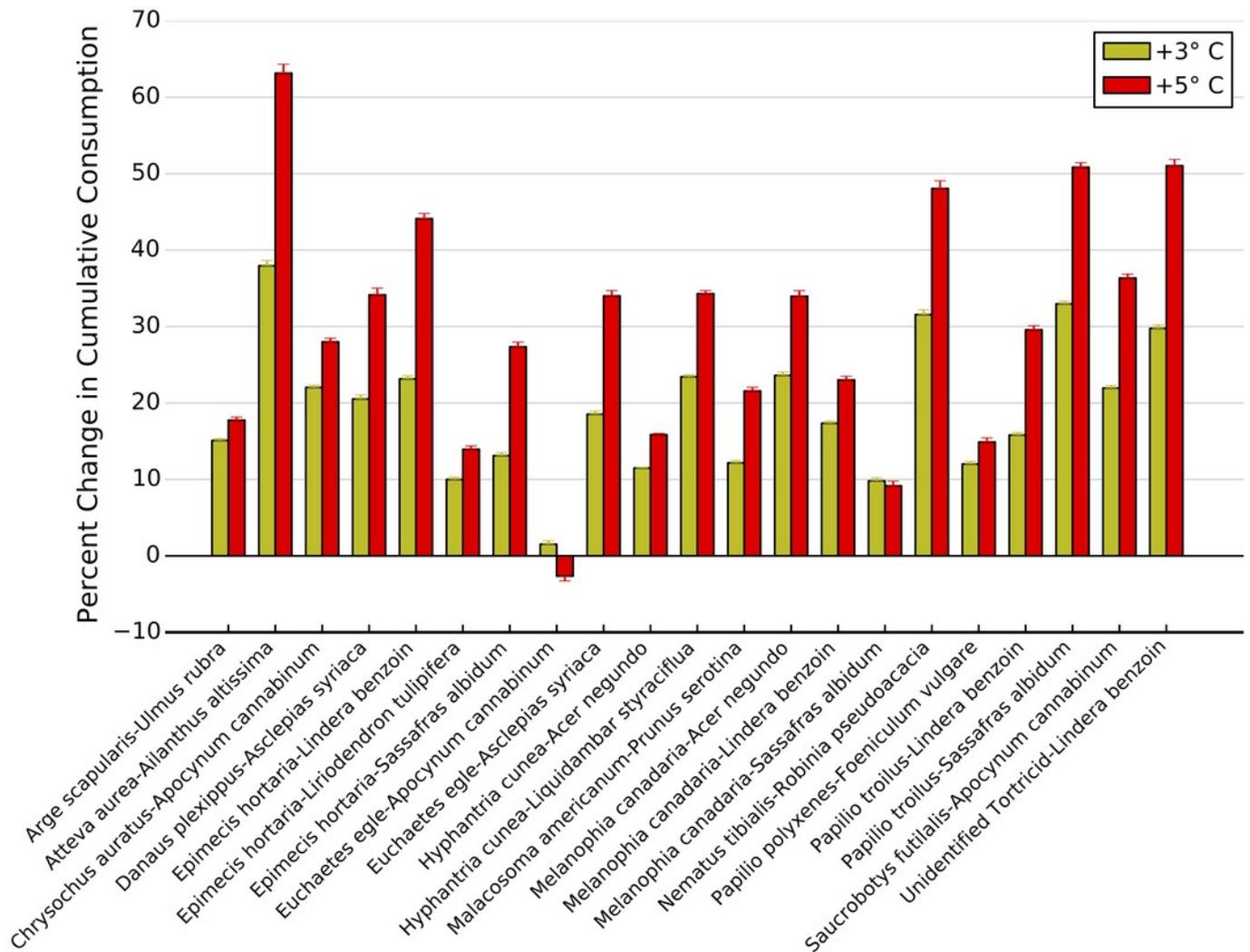


Table 1 (on next page)

Herbivores and plants used in this study

Herbivore – plant pairings used in feeding assays. Species marked with (I) are introduced species; common names are given in parentheses. Below each species name, we have listed the order and family of each species.

Herbivore Species	Herbivore Diet	Plant Species
Unidentified tortricid (Lepidoptera, tortricidae)	Specialist	<i>Lindera benzoin</i> (northern spicebush)
<i>Arge scapularis</i> (elm argid sawfly) (Hymenoptera, argidae)	Specialist	<i>Ulmus rubra</i> (slippery elm)
<i>Atteva aurea</i> (ailanthus webworm) (Lepidoptera, yponomeutidae)	Specialist	<i>Ailanthus altissima</i> (tree-of-heaven) (I)
<i>Chrysochus auratus</i> (dogbane beetle) (Coleoptera, chrysomelidae)	Specialist	<i>Apocynum cannabinum</i> (dogbane)
<i>Danaus plexippus</i> (monarch butterfly) (Lepidoptera, nymphalidae)	Specialist	<i>Asclepias syriaca</i> (common milkweed)
<i>Epimecis hortaria</i> (tulip tree beauty) (Lepidoptera, geometridae)	Generalist	<i>Lindera benzoin</i> (northern spicebush) <i>Liriodendron tulipifera</i> (tulip poplar)
<i>Euchaetes egle</i> (milkweed tussock moth) (Lepidoptera, arctiidae)	Specialist	<i>Sassafras albidum</i> (sassafras) <i>Apocynum cannabinum</i> (dogbane) <i>Asclepias syriaca</i> (common milkweed)
<i>Hyphantria cunea</i> (fall webworm) (Lepidoptera, arctiidae)	Generalist	<i>Acer negundo</i> (box elder) <i>Liquidambar styraciflua</i> (sweetgum)
<i>Malacosoma americanum</i> (eastern tent caterpillar) (Lepidoptera, lasiocampidae)	Generalist	<i>Prunus serotina</i> (black cherry) <i>Acer negundo</i> (box elder)
<i>Melanophia canadaria</i> (canadian melanophia) (Lepidoptera, geometridae)	Generalist	<i>Lindera benzoin</i> (northern spicebush) <i>Sassafras albidum</i> (sassafras)
<i>Nematus tibialis</i> (locust sawfly) (Hymenoptera, tenthredinidae)	Specialist	<i>Robinia pseudoacacia</i> (black locust)
<i>Papilio polyxenes</i> (black swallowtail) (Lepidoptera, papilionidae)	Specialist	<i>Foeniculum vulgare</i> (fennel)
<i>Papilio troilus</i> (spicebush swallowtail) (Lepidoptera, papilionidae)	Specialist	<i>Lindera benzoin</i> (northern spicebush) <i>Sassafras albidum</i> (sassafras)
<i>Saucrobotys futilalis</i> (dogbane webworm) (Lepidoptera, crambidae)	Specialist	<i>Apocynum cannabinum</i> (dogbane)