

Unpredictable effects of temperature on insect herbivory

Temperature can influence the top-down control of plant biomass by increasing herbivore metabolic demands. However, we know relatively little about the effects of temperature on herbivory rates for most insect herbivores in a given community. However, 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 unpredictable effects on plant-herbivore interactions and, ultimately, top-down control of plant biomass.

1 **Introduction**

2 Environmental temperature drives a number of important ecological interactions, including
3 competition, predation, and herbivory, by determining the metabolic rates of ectothermic
4 organisms (Vassuer and McCann 2005, O'Connor et al. 2009, Vucic-Pestic et al. 2011). As
5 metabolic demands increase exponentially with temperature, consumers generally either increase
6 food intake or switch to higher quality diets to offset the rising costs of metabolism (O'Connor
7 2009, Lemoine et al. 2013). As a result, predation and herbivory rates tend to increase
8 exponentially with temperature (Hillebrand et al. 2009, Vucic-Pestic et al. 2011). However, both
9 consumption rates and fitness can decline precipitously once a species encounters temperatures
10 beyond its thermal optimum (Lemoine and Burkepile 2012). A suite of adaptive and evolutionary
11 factors determine these thermal optima, such that a given consumer community may contain
12 species with considerably different thermal response curves (Angilletta et al. 2004). To date,
13 however, few (if any) studies have examined variation in thermal response curves for a
14 community of co-occurring herbivores (Buckley et al. 2014).

15 Insect herbivores can be an important top-down force in terrestrial ecosystems,
16 controlling plant biomass (Carson and Root 2000), maintaining species diversity (Bagchi et al.
17 2014), reorganizing competitive hierarchies (Kim et al. 2013), and enhancing nutrient cycling
18 (Metcalf et al. 2014). Because insects are ectothermic, their physiological rates, including
19 consumption and growth rates, are directly tied to environmental temperature. By extension, top-
20 down control of plant biomass is also likely to be temperature dependent. Limited theoretical and
21 experimental studies suggest that herbivory rates should increase exponentially with rising
22 temperatures (O'Connor et al. 2011). One potential shortcoming of theoretical examinations of
23 temperature-driven herbivore-plant interactions is that they do not often incorporate variation in
24 thermal response curves within an assemblage of herbivore species. In part, this is because
25 thermal response curves for multiple herbivore species on a single host plant remain mostly

26 uncharacterized. Species are often examined singly, and ecologists have focused on a few readily
27 available model species like *Spodoptera* spp. (Stamp and Yang 1996) and *Manduca sexta*
28 (Kingsolver and Woods 1998). In contrast, the herbivore guild within a community, or even on a
29 single host plant, can vary from 1 – 100s of species, each with different life histories, climatic
30 ranges, and dietary needs that may drive vastly different thermal response curves (Buckley et al.
31 2014).

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

43 Here, we report thermal response curves of consumption rates for 21 herbivore-plant
44 pairs, encompassing 14 herbivores and 12 plant species (Table 1). We asked two specific
45 questions: (1) what is the extent of within- and among-species variation in thermal response
46 curves of consumption for insect herbivores? and (2) can plant nutritional quality explain
47 variation in thermal response curves? By working with multiple species of both herbivores and
48 plants, we demonstrate that thermal response curves vary substantially both among and within
49 herbivore species. However, we were unable to detect any influence of plant nutritional quality
50 on the overall shape of the thermal response curve across taxa, suggesting that thermal response

51 curves are idiosyncratic and generally unpredictable among plant-herbivore pairs.

52 **Methods**

53 All experiments were conducted at the Smithsonian Environmental Research Center (SERC), in
54 Edgewater, MD, USA from June – August 2012. Using laboratory feeding assays, we evaluated
55 the feeding performance of 14 herbivore species from three Orders (Lepidoptera, Coleoptera,
56 Hymenoptera) on 12 plant species (Fig. 1, Table 1). Herbivores were collected by hand from host
57 plants in the forests and fields on the SERC premises throughout the summer. All herbivores were
58 kept in a cage and fed leaves from the plant species on which they were collected. Individuals
59 were used in feeding assays within 24 h of collection. No individual was used more than once. As
60 herbivores were opportunistically collected, the number of replicates per host plant/temperature
61 combination varied depending on the number of herbivores found (Table S1). Gregarious species
62 (*e.g. Hyphantrea cuneata*) have higher replicate numbers than do rare, non-gregarious species
63 (*e.g. Danaus plexippus*). A single lepidopteran species could not be identified beyond the
64 Tortricidae family.

65 *Feeding Assays*

66 In no-choice assays, a single individual was weighed and placed in a single rearing cup with a
67 single, pre-weighed leaf from a potential host plant (see Table 1). Each rearing cup was randomly
68 assigned to one of four temperatures (20°, 25°, 30°, and 35° C, see Table S2 for temperature and
69 light data from each growth chamber) maintained in growth chambers on a 14:10 light:dark
70 cycle. Temperatures were selected to represent a realistic set of temperatures during the spring in
71 summer months. Data from a nearby NOAA weather station (Annapolis, MD) indicate that
72 temperatures can range from 20 – 35° during the summer months (June – July, Fig. S1). Leaf

73 petioles were placed in water-filled microcentrifuge tubes capped with cotton to prevent
74 desiccation, and we observed no obvious differences in leaf turgor during the assays. After 24
75 hours, herbivores and leaves were reweighed to estimate consumption rates. Feeding assays of
76 this duration have been used to assess herbivore performance and dietary preferences in
77 lepidopterans (Kingsolver and Woods 1998, Kingsolver and Woods 1997) and coleopterans
78 (Gange et al. 2012, Lemoine et al. 2013).

79 Control assays with no herbivores accounted for autogenic change in leaf weight over the
80 24 h period ($n = 5$ per plant species per temperature). Leaves of all plant species except *L.*
81 *styraciflua* gained mass over 24 h in the absence of herbivores. Larger leaves gained more mass
82 than did smaller leaves. We therefore used species-specific equations to correct for autogenic
83 change in leaf mass (Table S3) rather than using mean change in leaf mass across all autogenic
84 controls. Mass-specific autogenic changes, whether positive or negative, were added to leaf final
85 weights. Negative autogenic changes (*i.e.* plants lost mass in control assays) would therefore
86 lower estimates of consumption and vice versa. In total, we conducted 552 no-choice feeding
87 assays, resulting in 496 observations after removing individuals that died or molted overnight
88 (final replicate numbers for each herbivore/plant/temperature combination given in Table S1).

89 *Plant Traits*

90 To assess the mechanisms by which temperature affected herbivore performance among
91 plant species, we quantified nutritional characteristics of undamaged leaves ($n = 3-5$) of each
92 plant species. Prior to all nutrient content analyses, leaves were weighed, dried to a constant mass
93 at 60° C, and re-weighed to estimate water content. Dried leaf material was ground to a fine
94 powder for carbon (C), nitrogen (N), and phosphorus (P) analyses. Percent C and N were
95 estimated using an EAI CE-440 elemental analyzer (Exeter Analytics, Coventry, UK).
96 Phosphorus content was determined using dry oxidation-acid hydrolysis extraction followed by

97 colorimetric analysis on a microplate spectrophotometer (PowerWave XS; Biotek, Winooski,
98 VT).

99 *Statistical Analyses*

100 We used a Bayesian hierarchical model to determine thermal response curves of
101 consumption for each herbivore-plant pairing. This allowed us to estimate parameters for the
102 overall trend in consumption with increasing temperature, parameters for each herbivore-plant
103 pairing, and the impact of plant nutritional quality on these parameters. A multilevel model is
104 particularly appropriate for handling unbalanced data and small sample sizes for some herbivore-
105 plant pairings, but some of the predicted responses for less well-sampled taxa will be pulled
106 heavily towards the overall mean response (Gelman and Hill 2007).

107 Consumption rates for each herbivore-plant pairing was modeled using a quadratic
108 exponential (*i.e.* Gaussian) curve because such curves often describe thermal reaction norms
109 (Angilletta 2006):

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

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

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

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

123 where μ_b is the overall, community-level linear parameter, and γ_1 , γ_2 , and γ_3 represent the
124 influence of nitrogen (%N), phosphorus (%P), and water content (%H₂O) respectively on the
125 exponential parameter of the j^{th} thermal response curve. δ_j is a multivariate normal error term.
126 Thus, mean consumption rate (a), the rate of increase with temperature (b), and the extent of
127 curvature in the thermal response curve (c) were all modeled as linear functions of plant
128 nutritional content. The random effects for each curve (*i.e.* parameters a_j , b_j , c_j) were assumed to
129 come from a multivariate normal distribution, allowing for covariance among parameter
130 estimates.

131 All predictor variables were standardized prior to analysis to speed chain convergence.
132 For all models, four MCMC chains were run for 5,000 ‘burn-in’ iterations to allow for chain
133 convergence. Posterior distributions of each parameter were simulated by saving the 20th sample
134 from an additional 5,000 posterior simulations, resulting in 1,000 independent estimates (250 per
135 chain, with four chains). Chain convergence and autocorrelation were assessed using trace plots
136 and density plots of posterior simulations. Each parameter was given a mildly uninformative
137 prior normal distribution ($N(0, 1)$); variance parameters were given uninformative prior uniform
138 distributions ($U(0, 100)$). Because predictors were standardized, the magnitude of parameter
139 estimates will be small, such that a standard normal distribution is relatively uninformative. For
140 each parameter, we calculated the 80% and 95% Bayesian credible interval (CI) from the
141 posterior simulations. All assumptions of normality and homogenous variances were examined

142 using residual plots. All analyses were conducted using Python v2.7. Bayesian models were
143 evaluated using STAN v2.1 (Stan Development Team 2013), accessed via PySTAN. Python code
144 for the hierarchical model is available as Appendix 1. All code and raw data are available on the
145 corresponding author's website¹ and will be uploaded to the Dryad database.

146 **Results**

147 The exponential parameter (b) of overall consumption rates was significantly greater than
148 zero, indicating that overall consumption rates did increase exponentially with temperature (Figs.
149 2, 3). However, the increase was restricted to temperatures between 20° and 30° C (Fig. 1). The
150 95% CI of the Gaussian parameter (c) narrowly included zero, but the bulk of the posterior
151 distribution for this parameter lay below zero, indicating that overall consumption rates began to
152 level off at temperatures above 30° C ($\text{Pr}(<0) = 0.96$, Fig. 3). Accordingly, our model predicts
153 relatively little change in overall consumption rates between 30° and 35° C (Fig. 2). Variance in
154 consumption rates among herbivore-plant pairs also increased substantially with rising
155 temperature. At 20°, variance among mean herbivore-plant consumption rates was 0.45, while at
156 35° this variance increased to 1.43. Thus, variability in consumption rates among herbivore-plant
157 pairs increased by over 300%. As a result, at 20° C the predicted mean community-level
158 consumption rate lie between 0.44 – 1.13 g per day (95% CI). Estimates of mean community-
159 level consumption were more uncertain at higher temperatures, lying between 0.93 – 2.13 g per
160 day (95% CI).

161 Uncertainty regarding overall consumption rates at higher temperatures stems from
162 idiosyncratic thermal response curves among herbivore-plant pairs (Figs. 4, 5). Seven herbivore-
163 plant pairs (*Arge scapularis* – *Ulmus rubra*, *Chrysocus auratus* – *Apocynum cannabinum*,
164 *Hyphantrea cunea* – *Acer negundo*, *H. cunea* – *Liquidambar styraciflua*, *Melanophia canadaria*

1 ¹ www.natelemoine.com

165 – *Lindera benzoin*, *M. canadaria* – *Sassafras albidum*, *Papilio troilus* – *S. albidum*) had Gaussian
166 parameters (c) that were moderately or significantly different from zero, indicating decreasing
167 consumption rates at higher temperatures (Figs. 4, 5). An additional nine herbivore-plant pairs
168 (*Atteva aurea* – *Ailanthus altissima*, *Epimecis hortaria* – *L. benzoin*, *E. hortaria* – *S. albidum*,
169 *Euchaetes egle* – *Asclepias syriaca*, *Malacosoma americanum* – *Prunus serotina*, *Nematus*
170 *tibialis* – *Robinia pseudoacacia*, *P. troilus* – *L. benzoin*, *Saucrobotys futilalis* – *A. cannibinum*,
171 Unidentified Tortricid – *L. benzoin*) increased consumption with warming throughout the entire
172 temperature range, where the exponential parameter (b) was significantly or moderately different
173 from zero. In some cases the parameter value was small enough that the fit was approximately
174 linear (e.g. *Epimecis hortaria* – *Sassafras albidum*, Figs. 4, 5). An additional five herbivore-plant
175 combinations (*Danaus plexippus* – *Asclepias syriaca*, *E. hortaria* – *Liriodendron tulipifera*,
176 *Euchaetes egle* – *Apocynum cannibinum*, *M. canadaria* – *A. negundo*, *Papilio polyxense* –
177 *Foeniculum vulgare*) showed no detectable change in consumption rate with increasing
178 temperature.

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

186 Discussion

187 Temperature influences herbivory rates via direct effects on insect herbivore physiology.
188 However, it is currently unclear how temperature affects top-down control of plant biomass at the
189 community or species level. Our data suggest that the influence of rising temperature on potential
190 top-down control of plant biomass via herbivory depends upon the identity of the herbivore-plant
191 pair under consideration. Such unpredictability in the relationship between consumption rate and
192 temperature will make predicting the effects of temperature changes, *i.e.* climate change, on top-
193 down control of plant biomass difficult.

194 Theory predicts that herbivory rates should increase exponentially with temperature more
195 quickly than primary production, reducing standing plant biomass at higher temperatures
196 (Gillooly et al. 2001, O'Connor et al. 2009, O'Connor et al. 2011). However, meta-analyses of
197 thermal response curves report substantial variability among species. Indeed, approximately 40%
198 of the thermal response curves examined by Dell et al. (2011) exhibited curvature, wherein the
199 thermal response curve began to decrease at high temperatures. In our study, 33% of the
200 herbivore-plant pairs exhibited substantial curvature, reducing consumption of plant biomass at
201 high temperatures, thereby contradicting theoretical predictions of exponential increases in top-
202 down control of plant biomass at high temperatures. Often, reduced consumption rates at high
203 temperatures result from metabolic demand exceeding energetic supply, such that energy
204 available for tasks beyond cellular maintenance, such as movement, feeding, or digestion,
205 decreases sharply at high temperature (Somero, 2011). This results in rapid decreases in
206 consumer fitness at temperatures beyond an organism's thermal optimum (Lemoine and
207 Burkepile 2012). We show that community-level herbivory rates display the same, albeit much
208 less pronounced, curvature as do some individual species. The slow decline at higher
209 temperatures, rather than a rapid drop-off beyond some threshold value, is a result of species-
210 specific variation in thermal response curves. Some (43%) plant-herbivore pairings did not show

211 any sign of decreased consumption at higher temperature, while one showed evidence of
212 declining consumption beyond 30° C, leading to no net change in overall consumption rates at
213 higher temperatures.

214 Such variation in thermal response curves makes predicting the effects of temperature
215 changes (*i.e.* microhabitat variation, seasonal effects, climate change) on herbivore-plant
216 interactions difficult in the absence of species-specific information. Indeed, a generalist herbivore
217 can have as many thermal response curves as host plants (Lemoine et al. 2013). We report similar
218 patterns here. For example, *Epimecis hortaria*, the tulip tree beauty moth, rapidly increased
219 consumption of both *Lindera benzoin* and *Sassafras albidum* with warming, but the increased
220 consumption of *Sassafras albidum* was much slower. In contrast, *E. hortaria* showed no
221 relationship between consumption of *Liriodendron tulipifera* and temperature. Similarly, *Papilio*
222 *troilus* increased consumption of both *L. benzoin* and *S. albidum* with increasing temperature, but
223 consumption of *S. albidum* began to decrease at 35° C, and consumption of *L. benzoin* showed no
224 curvature.

225 Given the high variation in thermal response curves among herbivore-plant combinations,
226 predicting the effects of climate change on the top-down control of plant biomass remains
227 challenging. Some studies have ascribed a single thermal response curve to herbivore species,
228 demonstrating that plant biomass will decrease in a warming world as herbivory rates outpace
229 primary production (O'Connor et al. 2011). Our results suggest that using a single consumption-
230 temperature relationship for all herbivores can substantially overestimate the impact of climate
231 change on plant biomass. For example, between 20° and 30° C, both *Chrysocus auratus* and
232 *Saucrobotys futilalis* increased consumption of *Apocynum cannabinum*. However, at 35° C.
233 *auratus* decreased consumption while *S. futilalis* continued to increase consumption, resulting in
234 little change in overall consumption rates on *A. cannabinum* beyond 30° C. Indeed, our results
235 indicate that variability in thermal response curves results in no overall change in consumption

236 rates, and therefore plant biomass, at high temperatures. This may explain why studies
237 documenting significant changes in top-down control of plant biomass under warming scenarios
238 focus on one herbivore species (Chase 1996, Barton et al. 2009) or show highly idiosyncratic
239 responses among plant species (Richardson et al. 2002).

240 Surprisingly, we were unable to detect any influence of plant nutritional quality on the
241 shape of thermal response curves. Based on previous work (Lemoine et al. 2013), we expected
242 consumption rate to increase more rapidly on plants of higher nutritional quality. Conversely,
243 compensatory feeding predicts that consumption rates should increase more rapidly with
244 temperature for plants of low nutritional quality as herbivores attempt to fuel rising metabolic
245 demands (e.g. Williams et al. 1994). Our data suggest that plant nutritional content has little
246 effect on thermal response curves among herbivore species. However, prior work has found that
247 the relationship between temperature and consumption rates within a given species can vary with
248 dietary quality. For example, the Japanese beetle *Popillia japonica* increased growth and
249 consumption rates at high temperatures only on host plants with high nitrogen and carbon
250 concentrations (Lemoine et al. 2013). This may also be the case in our data. Within an herbivore
251 species, we can distinguish some patterns related to plant quality. For example, the generalist
252 *Epimecis hortaria* increased consumption rapidly with warming only on higher nitrogen plant
253 species. Within a plant species, however, patterns were less clear, as particular herbivore species
254 were equally likely to have unimodel or exponential curves when feeding on the same plant.
255 Thus, across all 21 plant-herbivore pairings, we were unable to detect an overall pattern relating
256 plant quality to multiple thermal reaction norms. Thus, dietary quality may be more important for
257 determining thermal response curves within herbivore species but provide little information on
258 the shape of thermal response curves among particular herbivore-plant pairings, which might be
259 influenced more by the thermal environment experienced over the course of an herbivore's
260 evolutionary history (Angilletta 2009).

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

272 One potential caveat of our study is small sample size at many herbivore-plant-
273 temperature combinations. Given that we used field-collected organisms, sample size varied
274 considerably depending on the rarity of the species. Common and/or gregarious species, like *E.*
275 *hortaria*, *M. canadaria*, and *H. cunea*, have much higher sample sizes than rare or cryptic
276 species, like *D. plexippus* and *A. scapularis*. Thus, some herbivore-plant pairs show considerable
277 variability in the estimated thermal response curve and, in some cases, the prediction was heavily
278 influenced by the overall response. However, most work regarding the influence of temperature
279 on herbivory and its interaction with diet quality focus on a few readily available lepidopteran
280 herbivores (Kingsolver and Woods 1998, Kingsolver et al. 2006). The influence of temperature
281 on herbivory by the majority of the species reported here was heretofore unknown, and our
282 research adds considerably to the body of work documenting the importance of temperature on
283 rates of herbivory.

284 In summary, we show that herbivory, and therefore potential top-down control of plant
285 biomass, is highly contingent upon environmental temperature. While theoretical predictions

286 suggest that climate change might increase top-down control of plant biomass, our results
287 indicate that the effects of temperature on herbivory rates are unpredictable. A single plant
288 species might experience more or less herbivory at higher temperatures, depending on the
289 identity of the herbivores present. As insects often control plant community structure (Carson and
290 Root 2000) and dominance hierarchies among plant species (Kim et al. 2013), studies
291 documenting the species-specific effects of temperature on insect herbivory levels will be crucial
292 to understanding how climate change might affect community composition in the plant-herbivore
293 assemblages of the future.

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Table 1 (on next page)

Herbivore – plant pairings used in feeding assays

Herbivore – plant pairings used in feeding assays. Species marked with (I) are *introduced species*; common names are given in parentheses.

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

Figure 1

Chrysocus auratus

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



Figure 2

Temperature effects 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.

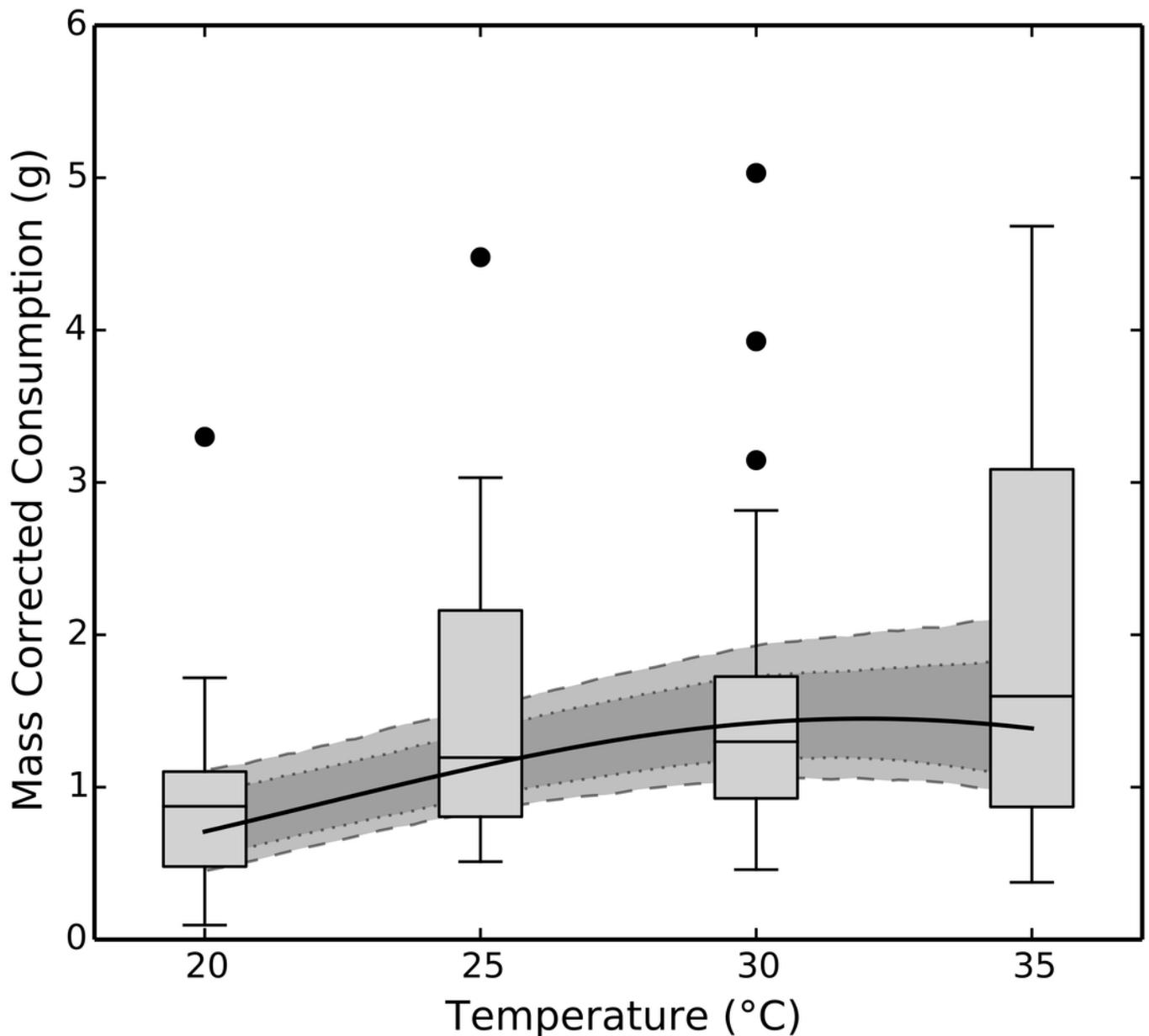


Figure 3

Parameter estimates for 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.

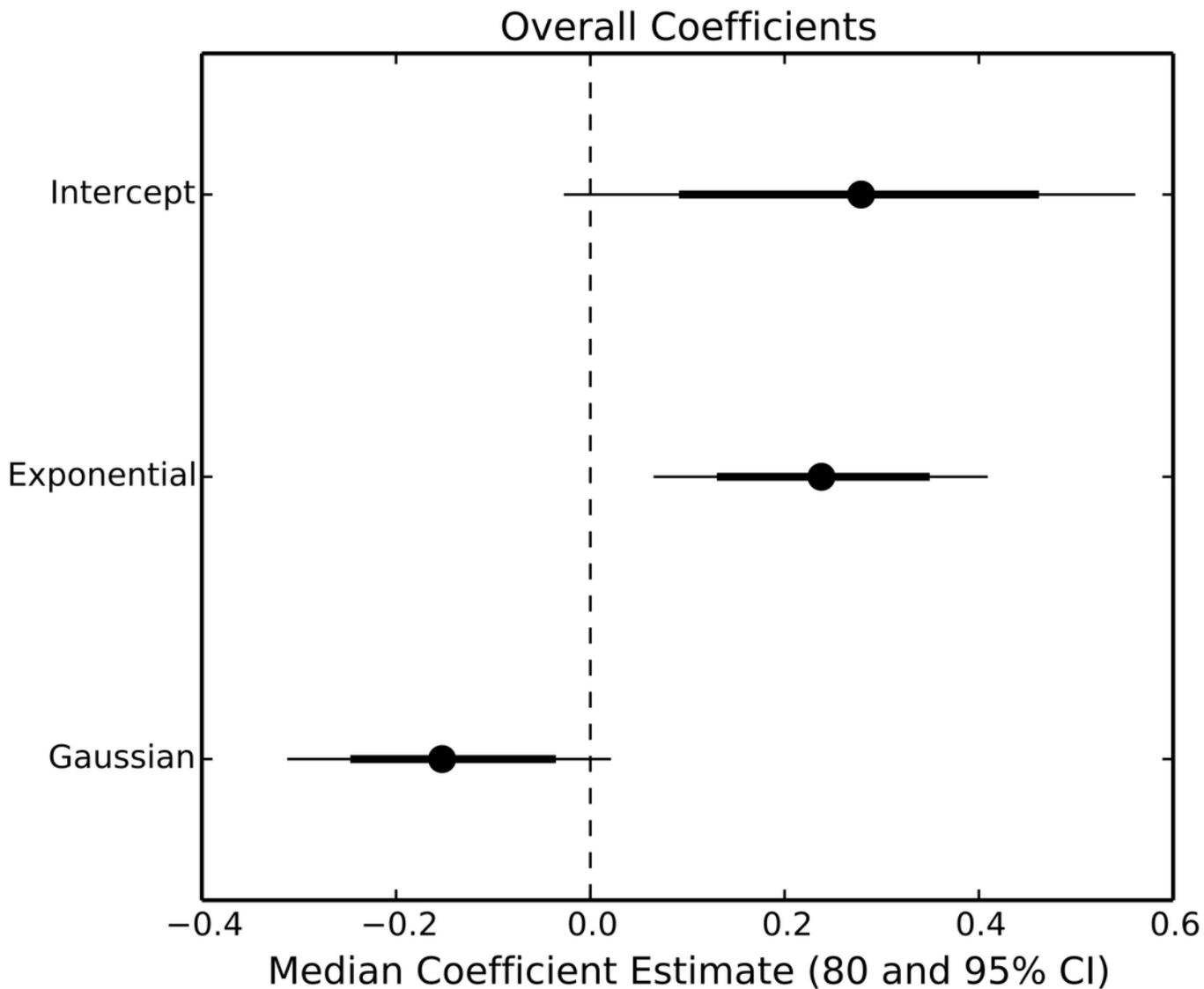


Figure 4

Effects of temperature on consumption 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.

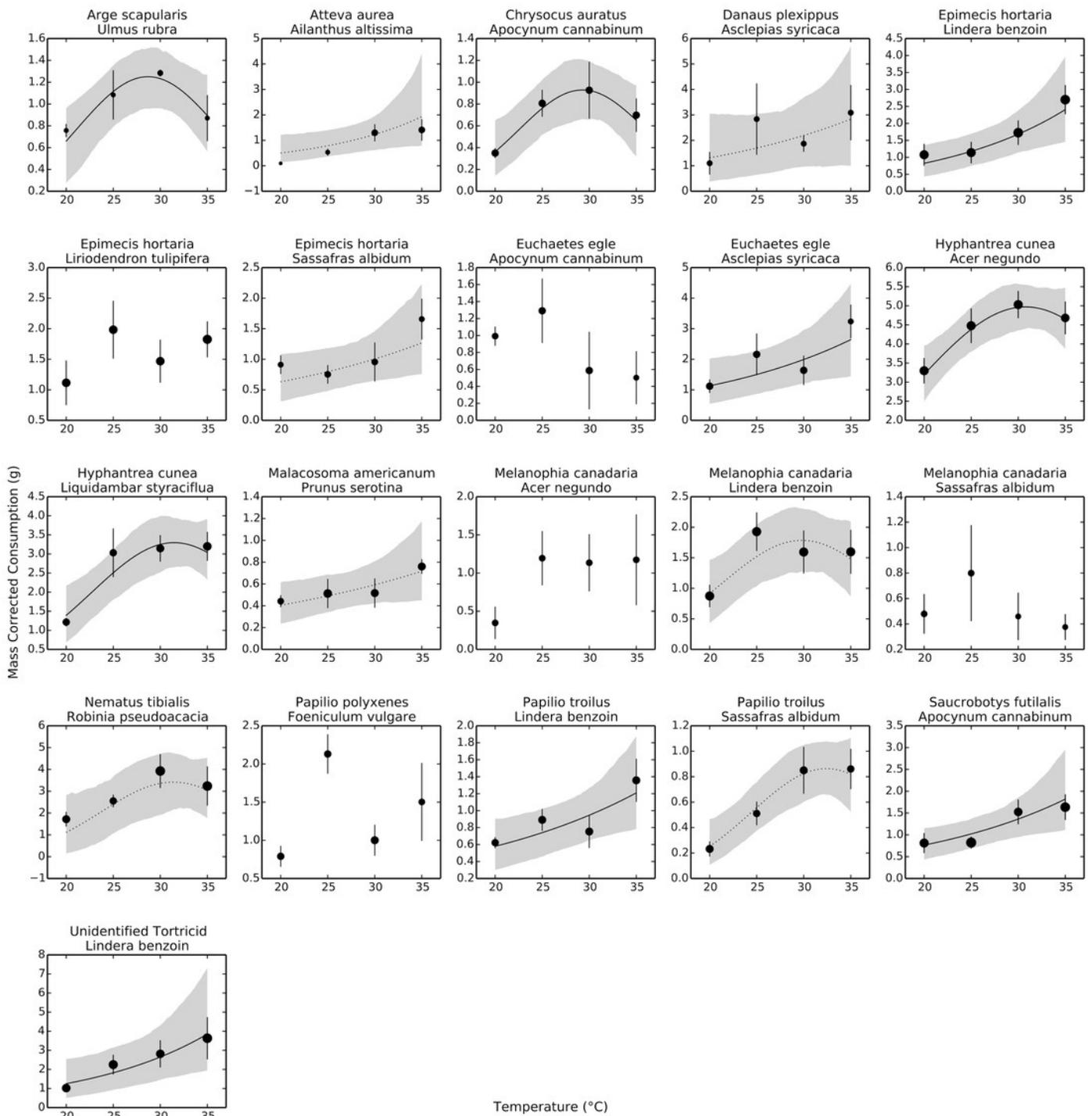


Figure 5

Parameter estimates for each herbivore:plant thermal response curve

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.

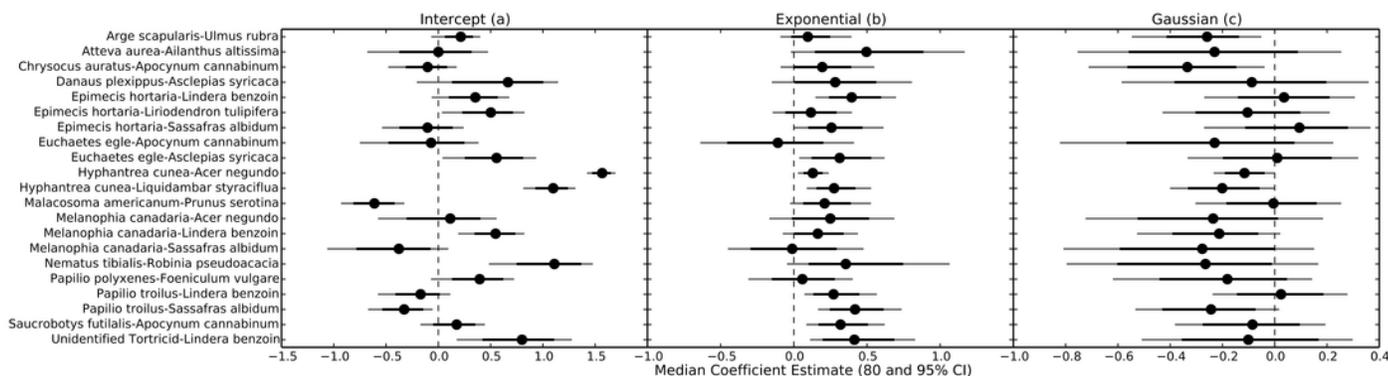


Figure 6

Effects of plant quality on thermal response curve shape

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.

