The influence of warming on the biogeographic and phylogenetic
dependence of herbivore–plant interactions

Mu, X., Xu, M., Ricciardi, A., Dick, J. T. A., Luo, D., Wei, H., Hu, Y., & Wei, Q. (2019). The influence of warming on the biogeographic and phylogenetic dependence of herbivore–plant interactions. Ecology and Evolution, 9(4), 2231-2241. https://doi.org/10.1002/ece3.4918

Published in:
Ecology and Evolution

Document Version:
Publisher's PDF, also known as Version of record

Queen's University Belfast - Research Portal:
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INTRODUCTION

Evolutionary experience is an important mediator of species interactions and thus commonly invoked to explain the success and impacts of biological invasions (Carthey & Banks, 2014; Ehrlich & Raven, 1964; Pearse & Altermatt, 2013; Saul & Jeschke, 2015; Verhoeven, Biere, Harvey, & Putten, 2009). A preference by generalist herbivores for novel plants (Agrawal & Kotanen, 2003; Fan, Yu, & Liu, 2013; Heard & Sax, 2013; Parker & Hay, 2005) could impose strong inhibitory effects on introduced species, consistent with the
biotic resistance hypothesis (Levine, Adler, & Yelenik, 2004). In contrast, if generalist herbivores prefer familiar plants (Agrawal et al., 2005; Liu & Stiling, 2006; Xiong, Dan, Wang, Liu, & Wang, 2008), plant invasion may be promoted by a suppression of native competitors, consistent with the enemy release hypothesis (Colautti, Ricciardi, Grigorovich, & Maclsaac, 2004; Keane & Crawley, 2002). A meta-analysis found that native generalist herbivores preferentially consumed exotic plants (Parker & Hay, 2005), whereas exotic herbivores preferentially consumed native plants (Parker, Burkepile, & Hay, 2006), conferring a competitive advantage to invading plants (Parker et al., 2006) through indirect facilitation (Simberloff & Von Holle, 1999). Such evolutionary mismatches render naïve plants particularly susceptible to herbivory (hereafter termed the “novel interaction hypothesis” (Buckley & Catford, 2016; Carthey & Banks, 2014; Saul & Jeschke, 2015; Verhoeven et al., 2009)). However, studies testing these patterns typically used only a dichotomic analysis (native vs. exotic species) while ignoring the specific biogeographic origins of the species involved; consequently, these studies did not test the effect of evolutionary exposure. Opportunities for such tests are provided when an exotic herbivore interacts with plants that have different biogeographic origins. If evolutionary exposure is important, the exotic herbivore should have different effects on the novel plants (native plants and exotic plants with different biogeographic origin) and on the familiar plants (exotic plants with the same biogeographic origin).

In addition to direct evolutionary exposure, herbivory damage may also be affected by plant phylogeny (Craft, Paul, & Setka, 2013; Hill & Kotanen, 2009; Ness, Rollinson, & Whitney, 2011; Pearse & Hipp, 2009). However, the direction and magnitude of the relationship between plant phylogeny and herbivory pressure are still highly debated. One might hypothesize that exotic plants closely related to natives are more likely to be recognized and attacked by native herbivores and thus encounter resistance to invasion (Levine et al., 2004). Alternatively, exotic plants closely related to natives may be preadapted to existing conditions of herbivory. On the other hand, a generalist herbivore may choose plants based on traits such as nutrition content, regardless of the phylogenetic relatedness between exotic and native plants (Pearse & Hipp, 2009). Testing the feeding efficiencies of exotic herbivores across a phylogenetic gradient of plants may help resolve these opposing hypotheses.

Increasing temperatures could influence consumer-resource interactions with respect to coevolutionary history (Diamond & Kingsolver, 2012). For example, Diamond and Kingsolver (2012) demonstrated that herbivore populations with different evolutionary exposures to host plants varied in their responses to these plants under different temperature. Studies have also linked altered temperature to the movement (Walther et al., 2009), establishment success (Chown et al., 2012), and spread (Stachowicz, Terwin, Whittlatch, & Osman, 2002) of species beyond their natural ranges. Recently, variation in temperature has been shown to influence competition, insect–plant, and predator–prey interactions involving native and exotic species (Fey & Cottingham, 2012; Fey & Herren, 2014; Lu, Siemann, Shao, Wei, & Ding, 2013). For example, Fey and Herren (2014) found that increasing temperature disproportionately benefited an exotic species compared to a native congener under threat from a shared native predator, resulting in a temperature-dependent enemy release. If increased temperature similarly shapes novel herbivore–plant interactions, it may mediate plant invasion and impact.

In this study, we conducted functional response (FR) experiments to examine how the biogeographic origin and phylogenetic relatedness of plants influence the feeding efficiency of an exotic herbivore under increasing temperatures. The main advantage of the FR method is its derivation of critical parameters of per capita feeding ability, including attack rate, handling time, and maximum feeding rate, rather than less informative “snapshot” measurements of feeding rates by arbitrarily setting one level of resource (Dick et al., 2014). Thus, specifically in this study, we use FRs to test (a) whether an invasive generalist herbivore prefers to feed on evolutionarily novel plants; (b) whether its feeding rate is related to the phylogenetic relatedness of the host plants; and (c) how increasing temperatures affect the effects of plant geography and phylogeny on herbivore feeding efficiency.

2 | MATERIALS AND METHODS

2.1 | Experimental organisms

The golden apple snail (Pomacea canaliculata; Gastropoda, Ampullariidae) is native to freshwater wetlands of South America and has been introduced widely into Asia since the 1980s (Hayes et al., 2015; Xu, Fang et al., 2016). In its introduced range, it has caused significant damage to agricultural production (Cowie, 2002), wetland plants (Fang, Wong, Lin, Lan, & Qiu, 2010), and ecosystem functioning (Carlsson, Brönmark, & Hansson, 2004) and is listed among the “Top 100” invasive species by the International Union for Conservation of Nature (Lowe, Browne, Boudjelas, & Poorter, 2000). It is an omnivorous species that feeds predominantly on aquatic and semi-aquatic macrophytes (Qiu & Kwong, 2009). The snails used for this study were cultured in ponds with recirculating water systems (5 m × 4 m × 1.5 m) at the Pearl River Fisheries Research Institute (23°04′9.42″N; 113°12′52.68″E) in Guangzhou City, China, in 2015, and fed with Carp food pellets (Composing of crude protein, amino acid, fat, calcium, and phosphorus; Zhongshan President Enterprises Co., Ltd, Zhongshan, China).

In the FR experiment, five plant species that share an evolutionary history with P. canaliculata were chosen as follows: Alternanthera philoxeroides (alligator weed), Eichhornia crassipes (water hyacinth), Ipomoea batatas (sweet potato), Myriophyllum aquaticum (parrot feather), and Pistia stratiotes (water lettuce). In addition, we chose the following five plant species with which P. canaliculata has had no evolutionary exposure: Apium graveolens (Chinese celery), Colocasia esculenta (taro), Ipomoea aquatica (water spinach), Hydrocotyle vulgaris (pennywort), and Lactuca sativa (lettuce) (Table 1). These plants are also phylogenetically diverse (Figure 1). Therefore, this set of host plants enables us to compare the FR of the snail on evolutionarily familiar and novel plant species.

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and across familiar plants of different phylogenetic distance from the novel plants (Figure 1).

We collected all host plant species on the day of the experiment to ensure their freshness. Each of these species is common in wetlands and agricultural areas of South China, and the snail was observed to consume all these plants to some degree in the laboratory. Cultivated plants may have higher nutrient content and thus higher palatability, which could potentially confound the effect of nutritional quality with that of the evolutionary novelty; therefore, we tested differences in nutritional quality across the host plant species. We found no evidence that major nutritional (total N) and physical (dry matter content) properties of evolutionarily novel plants differed from those of evolutionarily familiar plants (see Supporting Information).

### 2.2 Functional response experiment

The FR experiment was conducted in the summer of 2015 in three consecutive experimental blocks. For each block, the experimental units were allocated to five tanks (200 cm × 70 cm × 50 cm) using a split-plot design. The first block started at 08:00 on May 29 and ended at 20:00 on May 31 (60 hr); similarly, the second and third blocks started at 08:00 on June 4 and June 10, respectively, and ended at 20:00 on June 6 and June 12, respectively. Prior to the experiment, the snails were held without food for 24 hr to allow for standardization of hunger levels (Alexander, Dick, Weyl, Robinson, & Richardson, 2014; Xu, Mu et al., 2016). Snails with similar body size were used to minimize variation in the FR data due to body mass effects (mean body mass with shell: 13.04 ± 0.05 g). Fresh leaves of all 10 plants were picked, weighed, and allocated to experiment units. The natural air temperature range over the experimental duration was 22–26°C at nighttime and 26–32°C during daytime.

In the split-plot design, the tank with tap water was the whole-plot experimental unit and temperature was the whole-plot factor. We had five whole-plot units with water temperature controlled at 26, 28, 30, 32, and 34°C. To control the water temperature, we heated the tank using water tank heaters (mean temperatures during the experiment were 26.39 ± 0.21, 28.45 ± 0.19, 30.53 ± 0.18, 32.34 ± 0.20, and 34.38 ± 0.28°C, respectively). The tank water was maintained at 40 cm height. Within each tank, 70 boxes (12 cm × 10 cm × 6 cm) were used as subplot experimental units with plant species and plant biomass as subplot factors. These boxes consisted of 10 plant species, each having seven biomass gradients (wet weight 1, 2, 4, 6, 8, 10, and 12 g) and randomized with respect to position in tank. In each box, a golden apple snail was introduced. The experiment thus consisted of 1,050 (3 × 5 × 10 × 7) experimental units. At the end of the experiment, the leaves were removed from the boxes and allowed to dry in air for 3 hr to evaporate surface moisture before they were measured. Gross consumption by the snails was determined by subtracting final weight from initial weight. In order to characterize the potential variation of plant weights due to imbibition or air drying, we conducted a control experiment under

![Phylogenetic relationships of the plant species used for the laboratory experiment.](image)

**TABLE 1** Ten macrophytes used in the functional response experiments

| Plant species                  | Common names | Area of origin | Habitat     |
|--------------------------------|--------------|----------------|-------------|
| Alternanthera philoxeroides    | Alligator weed | South America | Aquatic     |
| Eichhornia crassipes           | Water hyacinth | South America | Aquatic     |
| Ipomoea batatas                | Sweet potato  | South America | Aquatic     |
| Myriophyllum aquaticum         | Parrot feather| South America | Aquatic     |
| Pistia stratiotes              | Water lettuce | South America | Aquatic     |
| Apium graveolens               | Celery        | Mediterranean | Semiaquatic |
| Colocasia esculenta            | Taro          | India          | Semiaquatic |
| Ipomoea aquatica               | Water spinach | China          | Aquatic     |
| Hydrocotyle vulgaris           | Pennywort     | Europe         | Aquatic     |
| Lactuca sativa                 | Lettuce       | Mediterranean  | Semiaquatic |

*References: Editorial-Board-of-Flora-of-China (1979) and Xu and Qiang (2011).
the same experimental conditions, where the same biomass gradients of each species were included in the boxes without snails. The experiment was replicated three times with 210 (10 × 7 × 3) experimental units. After 60 hr, the leaves were removed and allowed to dry in air for 3 hr, and the natural variation at each biomass gradient for each species was subsequently determined by subtracting final weight from initial weight. The mean natural variation across seven biomass gradients for *A. philoxeroides* (alligator weed), *E. crassipes* (water hyacinth), *I. batatas* (sweet potato), *M. aquaticum* (parrot feather), *P. stratiotes* (water lettuce), *A. graveolens* (Chinese celery), *C. esculenta* (taro), *I. aquatica* (water spinach), *H. vulgaris* (pennywort), and *L. sativa* (lettuce) was −0.076 ± 0.15, 0.171 ± 0.18, 0.895 ± 0.518, 1.179 ± 0.382, 0.200 ± 0.098, 0.376 ± 0.414, 0.481 ± 0.178, 0.781 ± 0.380, 0.014 ± 0.072, and 0.571 ± 0.562 (mean ± SD), respectively. The net consumption by snails at each biomass gradient for each plant species was determined by subtracting the natural variation from the gross consumption. Specifically, net consumption was get using this function: \[ \text{Net consumption} = (\text{Initial weight} - \text{final weight})_{\text{treatment}} - (\text{Initial weight} - \text{final weight})_{\text{control}}. \] Using the measured net consumptions across each biomass gradient, we conducted the FR analyses and estimated the per capita feeding parameters.

### 2.3 Functional response analyses

Functional responses are typically employed for analyzing predator-prey dynamics (Jeschke, Kopp, & Tollrian, 2002) and have been applied less often to mechanistically understand herbivore-plant interactions (Farnsworth & Illius, 1996; Spalinger & Hobbs, 1992). In a previous study, we successfully characterized the FRs of this herbivorous snail to derive its impacts on plant resources (Xu, Mu et al., 2016). In the context of herbivores, they may rarely suffer searching limitations, owing to concentrated and ubiquitous plant resources (Spalinger & Hobbs, 1992). Thus, herbivores are unlikely to experience the classic hypothesis of competition for time between searching and handling prey (Holling, 1959), rather, cropping and chewing have been viewed as the competing processes for herbivores (Spalinger & Hobbs, 1992). Based on this assumption, and accounting for the “digestive pause” (Holling, 1966), we can easily derive Type II FRs similar to the Holling’s disk function with respect to herbivores. Further, we used Rogers’ random predator equation (the integral of Holling’s function) to characterize FRs accounting for the nonreplacement of resource as it is consumed (Juliano, 2001):
To verify the phylogenetic structure of these species, for each of the five evolutionarily familiar and five novel plant species, gene sequences, which are commonly used in published plant phylogenies (Cadotte, 2013). We included a gymnosperm *Platycladus orientalis* as the out-group species. Sequences were aligned with ClustalW (Thompson, Gibson, & Higgins, 2003). The Bayesian phylogeny was reconstructed using BEAST version v1.8.2 (Drummond, Suchard, Xie, & Rambaut, 2012). The Bayesian MCMC chain was run for 1 million generations, and convergence was checked using Tracer version v1.6.0 (http://beast.bio.ed.ac.uk/Tracer). The maximum clade credibility tree was used to quantify phylogenetic pattern by TreeAnnotator version v1.8.2 (Drummond et al., 2012) (Figure 1).

### 2.5 Statistical analyses

Using a restricted maximum likelihood method in the "nlme" function of the "nlme" package, for the laboratory experiment, we fitted linear mixed models (LMMs) to the parameters of the FRs by log transformation (Pinheiro & Bates, 2006). In these models, temperature and the origin of species (evolutionarily familiar vs. novel) were used as fixed effects. We tested their main and interaction effects on three parameters derived from the Type II FRs as follows: attack rate, handling time, and estimated maximum feeding rate. The tank was used as a random effect to describe the error structure of a split-plot design. The notation of the model was as follows:

\[
y = \beta_0 + \beta_{\text{temp}}x_{\text{temp}} + \beta_{\text{origin}}x_{\text{origin}} + \beta_{\text{temporigin}}x_{\text{temp}}x_{\text{origin}} + b + \varepsilon,
\]

where \(y\) is the parameter derived from Type II FR model (\(a\), \(h\), or maximum feeding rate), \(\beta_0\) is the intercept, \(\beta_{\text{temp}}\) and \(\beta_{\text{origin}}\) are the coefficients associated with the fixed effect variable temperature and origin. \(\beta_{\text{temporigin}}\) characterizes the interaction between these two factors. \(b\) is random effect (tank) depicting the error structure of the split-plot design and \(\varepsilon\) is the remaining variance.

### Tables

| Models and variables | df treatment | df residual | Attack rate (a) | Handling time (h) | Maximum feeding rate (max) |
|----------------------|--------------|-------------|----------------|-------------------|---------------------------|
|                      |              |             | F  | P   | F  | P   | F  | P   |
| Temp × Origin        | 1            | 19          | 0.001 | 0.974 | 4.326 | 0.129 | 4.326 | 0.129 |
| Temp                 | 1            | 43          | 5.517 | 0.024 | 23.679 | <0.001 | 23.679 | <0.001 |
| Origin               | 1            | 18          | 1.151 | 0.289 | 4.952 | 0.031 | 4.952 | 0.031 |
| Temp:Origin          | 1            | 43          | 0.563 | 0.508 | 6.375 | 0.086 | 6.375 | 0.086 |
| Temp × Phylo         | 1            | 18          | 1.021 | 0.326 | 20.731 | <0.001 | 20.731 | <0.001 |
| Phylo                | 1            | 18          | 0.286 | 0.599 | 0.245 | 0.627 | 0.245 | 0.627 |
| Temp:Phylo           | 1            | 18          | 0.286 | 0.599 | 0.245 | 0.627 | 0.245 | 0.627 |
Then, in order to account for the possible effects of phylogenetic nonindependence among species on our analyses, we also conducted a PGLS (phylogenetic generalized least square regression) to examine the effect of origin and its interactions with temperature. As the PGLS required the data point must be equal to the number of tips in the phylogenetic tree (i.e., only one data point can be included for each species), we first performed the PGLS at each of the five temperature levels. Then, through averaging the data for a given species derived from different temperatures, we conducted another PGLS to test the mean effect of origin. These analyses were accomplished using the “gls” function in “nlme” package by hypothesizing a Brownian Motion model (Swenson, 2014).

Finally, based on the reconstructed phylogenetic tree, we calculated the mean phylogenetic distance of each familiar species to five novel species using the “cophenetic.phylo” function of the “ape” package. For example, the phylogenetic distance between the familiar species I. batatas and five novel species (A. graveolens, C. esculenta, I. aquatica, H. vulgaris, and L. sativa) was 0.236, 0.386, 0.012, 0.236, and 0.236, respectively, and then, we can obtain the mean phylogenetic distance 0.22. Using these phylogenetic distances, we fitted another LMMs to the FR parameters by log transformation. In these models, temperature and mean phylogenetic distance were fixed effects and tank was a random effect. Through these LMMs, we directly tested whether plant species closely related to novel species suffered more damage and how increasing temperature mediated the phylogenetic dependence.

All statistical analyses were performed in R, version 3.2.2 (R Core Team, 2018).

3 | RESULTS

Pomacea canaliculata had markedly different FRs when consuming the evolutionarily familiar plant species than when consuming the evolutionarily novel plants (Figure 2, Supporting Information Figure S1; lack of 95% CI overlap at all temperatures), with significantly lower attack rates (Table 2, Figure 3a), higher handling times, and lower maximum feeding rates (Table 2, Figure 3b,c). There was a significant interaction effect of temperature and plant origin for the handling time and maximum feeding rate (Table 2), with higher temperature enhancing the maximum feeding rate of the herbivore when consuming the evolutionarily familiar plants, but not when consuming the evolutionarily novel plants (Table 3, Figure 3b,c). This interaction effect and the main effect of temperature did not exist for the attack rate (Table 2, Figure 3a), indicating that temperature alters the handling efficiency, but not the attack ability, of the herbivore on evolutionarily familiar plants.

After accounting for the phylogeny nondependence, the results of PGLS were consistent with that of LMMs except for the attack rate. Across all temperature, the evolutionarily familiar plants yielded higher handling time ($t = 4.804, p = 0.001$) and lower maximum feeding rates ($t = 5.535, p = 0.001$) than the evolutionarily novel plants, but attack rate was not significantly different between the two origins ($t = 0.001, p = 0.999$) (Figure 4).

The mean phylogenetic distances of each familiar plant species to the five novel species significantly correlated with the handling time and maximum feeding rate of P. canaliculata toward these familiar species.
TABLE 3  Estimated effects of models predicting the log response of attack rate ($a$), handling time ($h$), and maximum feeding rate (max) derived from the Type II functional responses to plant origins × temperature and phylogenetic distance × temperature. “Origin” denotes whether plant species have same biogeographic origin (five familiar species) or different biogeographic origin (five novel species) with the herbivore. “Phylo” denotes the mean phylogenetic distance of each familiar species to five novel species.

| Models and variables | Attack rate ($a$) | Handling time ($h$) | Maximum feeding rate (max) |
|----------------------|-------------------|---------------------|---------------------------|
|                      | Estimate | t   | P    | Estimate | t   | P    | Estimate | t   | P    |
| Temp × Origin        |          |     |      |          |     |      |          |     |      |
| Familiar: Temp       | −0.041   | −0.733 | 0.467 | −0.129   | −3.044 | 0.004 | 0.129    | 3.044 | 0.004 |
| Novel: Temp          | 0.044    | 0.784   | 0.438 | 0.004  | 0.103   | 0.919 | −0.004  | −0.103 | 0.919 |
| Temp × Phylo         |          |     |      |          |     |      |          |     |      |
| 26: Phylo            | 1.741    | 0.215   | 0.833 | 12.051 | 2.350   | 0.033 | −12.051 | −2.350 | 0.033 |
| 28: Phylo            | −2.8438  | −0.350 | 0.731 | 10.930  | 2.132   | 0.050 | −10.930 | −2.132 | 0.050 |
| 30: Phylo            | −7.060   | −0.870 | 0.398 | 10.298  | 2.008   | 0.063 | −10.298 | −2.008 | 0.063 |
| 32: Phylo            | −4.684   | −0.577 | 0.572 | 4.734   | 0.923   | 0.371 | −4.734  | −0.923 | 0.371 |
| 34: Phylo            | −3.432   | −0.423 | 0.678 | 11.357  | 2.215   | 0.043 | −11.357 | −2.215 | 0.043 |

specifies (Table 2). Plant species more closely related to novel species yielded less handling time and more herbivory pressure (Table 3, Figure 5b,c). Increasing temperature did not significantly shift this relationship (Table 2, Figure 5b,c). The phylogenetic distance, temperature, and their interaction effect did not affect the attack rate of *P. canaliculata* (Table 2, Figure 5a).

4 | DISCUSSION

*Pomacea canaliculata* consumed evolutionarily novel plants to a greater degree than evolutionarily familiar plants, consistent with the novel interaction hypothesis (Morrison & Hay, 2011; Parker et al., 2006). Warming, however, increased the consumption rate on evolutionarily familiar plants and thus reduced the herbivory difference between evolutionarily novel and familiar plants. The feeding rate of *P. canaliculata* was higher for plant species more closely related to the palatable novel plants, and this trend was unaffected by warmer temperatures.

Our findings do not support the argument that the biogeographic origin of species has no bearing on its potential ecological impact (Davis et al., 2011; Valéry, Fritz, & Lefeuvre, 2013) and suggest that evolutionary novelty may benefit the herbivorous snail (Verhoeven et al., 2009). Five of the experimental host plants originate from South America, the same biogeographic region as *P. canaliculata*. A shared evolutionary history may have caused these plants to evolve some resistance to herbivory, whereas the plants that originated from other continents suffered higher consumption perhaps owing to lack of adaptation. Conversely, evolutionary novelty has paradoxically been cited to explain the release from natural enemies, by arguing that enemies have not been selected to counter the novel plant’s defenses (Callaway & Aschehoug, 2000; Cappuccino & Arnason, 2006). Distinguishing these two contrasting processes requires consideration of underlying mechanisms such as recognition-based and toxin-based defenses of novel plants (Verhoeven et al., 2009). Among the plants used in our study, perhaps those familiar with *P. canaliculata* have produced phytochemicals or developed physical traits to reduce the intensity of herbivory by this snail, whereas novel plants may lack such adaptations. We focused on how increased temperature mediates this novel interaction rather than the specific mechanisms underlying it, although the latter facet deserves further exploration.

Temperature reduced the handling time and increased the maximum feeding rate of *P. canaliculata* when consuming evolutionarily familiar plants but not novel plants. This finding, on the one hand, has implications for the management of exotic species...
in the context of global warming. Although introduced herbivores could facilitate the success of plant invaders by suppressing their competitors in the invaded region (Parker et al., 2006), our study suggests that this facilitation might break down with increasing temperature. By contrast, Fey and Herren (2014) found that increased temperature facilitated an invasive species by promoting greater consumption of a competing native congener by a native predator. A consistent result in our experiment was the enhanced suppression by *P. canaliculata* of evolutionarily familiar plants under increasing temperature. On the other hand, such altered feeding strategies with increasing temperature likely influence the consumer fitness and long-term population dynamics of herbivores (i.e., numerical response) (Lemoine & Burkepile, 2012; Rall, Vucic-Pestic, Ehnes, Emmerson, & Brose, 2010). When increasing temperature enhances the metabolic rate of a herbivore but not the feeding rate, those herbivores consuming novel plants may suffering lower population growth (Rall et al., 2010). For those herbivores consuming familiar plants, increasing temperature may enhance or reduce consumer population growth, depending on variation in feeding rate and the metabolic rate. Two possible mechanisms could drive this phenomenon as follows: (a) higher temperatures may reduce the amount of toxic phytochemicals released by evolutionarily familiar plants or reduce the resistance of their tissues to predation (Stamp, Temple, Traugott, & Wilkens, 1994); (b) higher temperatures may enhance bioenergetic demands of the herbivore, causing it to increase its consumption of less palatable exotic plants. We found that handling time, rather than attack rate, on evolutionarily familiar plants varied with temperature, suggesting that temperature principally mediated the snail’s efficiency of handling food rather than the attack behavior. However, an important caveat is that the attack rate was gained from the manipulated experiment with snail and plants being put in the small space. This would result in a higher value compared to that in the natural condition, in which a snail might spend more time to search for the plants. This might be a reason why we did not find the effect of temperature on this feeding parameter, given that they probably always had a “saturated” attack rate.

A significant phylogenetic dependence of diet was observed in our study. Not only did the invasive herbivore preferentially feed on evolutionarily novel native plants, it preferred the exotic plants closely related to the natives. Further, this relationship between plant phylogeny and herbivory was not influenced by the increasing temperature. When we consider novel interactions and the biogeographic origin of consumers, an intriguingly contrasting pattern may emerge in which native herbivores prefer novel plants and thus may reduce plant invasion success, whereas exotic herbivores prefer native plants and may increase plant invasion success. For example, Ricciardi and Ward (2006) found that native herbivores generally exerted stronger negative effects on the survival of exotic plants that were distantly related to native plants; whereas, in our study, an exotic herbivore had lower per capita effects on exotic plants that were distantly related to the natives. These patterns highlight the importance of considering both biogeographic context and the phylogenetic relationships of species involved in herbivore–plant interactions.

An impediment to assessing and comparing the ecological impacts of invasions is the lack of standardized methods for
measuring and interpreting per capita effects (Dick et al., 2014; Ricciardi, Hoopes, Marchetti, & Lockwood, 2013). By using FR experiments, we can better depict resource use and avoid the many pitfalls of “snapshot” assessments where resource levels are arbitrarily fixed (Dick et al., 2014; Xu, Mu et al., 2016). In our study, both handling time and maximum feeding rate varied with plant origin and phylogeny, and the effect of origin was mediated by increasing temperature. However, attack rate was only affected by origin, but not by plant phylogeny and temperature. To explain this result, it would be necessary to explore the feeding behavior of the herbivore and bioenergetic tradeoffs (Jeschke et al., 2002; Spalinger & Hobbs, 1992). These distinct responses may indicate that the invertebrate herbivore has not yet evolved the ability to identify and distinguish temperature-altered phytochemicals and therefore attacks plants without much discrimination while still exhibiting differential handling efficiencies. Alternatively, warming may enhance enzyme activity related to handling efficiency, but not attack behavior. In any case, the observed changes of handling time and maximum feeding rate indicate that plant origin and phylogenetic relationship can affect invasive herbivore–plant interactions, and such relationships are likely to be altered with increasing temperature.

ACKNOWLEDGMENTS

We thank Shaopeng Li, Xubing Liu, Nancai Pei, and Hongmei Song for help in phylogenetic analysis. This work was supported by Central Public-interest Scientific Institution Basal Research Fund, CAFS (NO. 2018SJ-ZH03) to M.X., the National Natural Science Foundation of China (31400487) to M.X., the Natural Science Foundation of Guangdong (2014A030313660) to X.D.M., and Agricultural Biological Resources Protection and Utilization Project of China (2130108) to Y.C.H.

CONFLICT OF INTEREST

None declared.

AUTHOR CONTRIBUTIONS

XDM and MX designed the experiments and wrote the first draft of the manuscript. XDM, MX, DL, and HW conducted the experiments and assembled the data. XDM, MX, AR, JTAD, YCH, and QWW performed data analysis and revised the manuscript.

DATA ACCESSIBILITY

Data files that support this study can be obtained from: https://doi. org/10.5061/dryad.8js8vp0

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How to cite this article: Mu X, Xu M, Ricciardi A, et al. The influence of warming on the biogeographic and phylogenetic dependence of herbivore–plant interactions. Ecol Evol. 2019;9:2231–2241. https://doi.org/10.1002/ece3.4918

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