



Changes in arthropod community but not plant quality benefit a specialist herbivore on plants under reduced water availability

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Abstract

Plants growing under reduced water availability can affect insect herbivores differently, in some instances benefitting them. However, the forces mediating these positive impacts remain mostly unclear. To identify how water availability impacts plant quality and multi-trophic interactions, we conducted manipulative field studies with two populations of the specialist herbivore *Pieris rapae*, and its host plant, *Rorippa indica*. We found that *P. rapae* larvae experienced higher survival on *R. indica* growing under low water availability compared with plants grown under high water availability. Higher survival of eggs and larvae was related to the reduced abundance of other herbivores and natural enemies. Water availability had differential impacts on other members of the herbivore community by altering plant quality. Low water availability decreased the quality of *R. indica* to most herbivores, as indicated by reduced abundance in the field and decreased relative growth rate in laboratory feeding assays. In contrast, *P. rapae* larval performance was not affected by sympatric *R. indica* grown under different water availability. These results indicate that local *P. rapae* populations possess physiological adaptations to overcome fluctuations in host quality. Our findings illustrate that reduced water availability is beneficial to a specialist herbivore but detrimental to most other herbivores. Our work highlights the complex effects of the arthropod communities associated with plants in determining the impacts of water availability on insect herbivores.

Keywords Drought · Environmental heterogeneity · Predation · Competition · Insect herbivore

Introduction

Water availability is an important factor influencing individuals, populations, and communities of plants (Bunker and Carson 2005; Schulze 1986) and ultimately heterotrophic organisms across trophic levels (Anderegg et al. 2013). The importance of water availability in affecting ecological interactions will likely increase in the future due to the predicted

increase in frequency and severity of drought under current models of climate change (National Research Council 2011). In addition to large-scale climatic factors, fine-scale topographic heterogeneity also influences water availability to individual plants, even when overall climatic conditions are similar (Murren et al. 2020). This is particularly the case for plants in urban and agricultural environments, because conditions, such as reduction in tree canopy coverage, increased in light intensity and temperature, and shallow soil depth contribute to high evaporation and low water availability (Dambros et al. 2013; Pickett et al. 2011). Given the many factors that influence plant water access, the variation in plant phenotypes due to changes in water availability are likely key factors influencing the performance and survival of associated insect herbivores.

The influence of water availability on insect herbivores has received much attention in past literature. A classic example is the relationship between drought and outbreaks of insect herbivores (Mattson and Haack 1987; White 1974, 1969). This observation has led to a fruitful area of research,

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and it is now clear that the impact of water availability on insect herbivores and plants is context-dependent and varies across different systems (Jamieson et al. 2012; White 2009). However, the main factors that contribute to the positive effect of low water availability on some insect herbivores remain unclear. A major limitation in past literature that contribute to this uncertainty was the emphasis on the direct interaction between plants and insects (English-Loeb et al. 1997). In contrast to a beneficial impact observed in natural conditions, low water availability generally elicits negative effects on plant quality (defined as a performance response of insect herbivores, see Awmack and Leather 2002) especially in herbaceous plants (Waring and Cobb 1992). Therefore, it is likely that beneficial impacts on herbivores are mediated by factors other than direct interactions between the focal herbivore and its host plants. Low water availability has been documented to reduce the arthropod abundance and alter the composition of arthropod communities associated with plants (Trotter et al. 2008), and drought-stressed plants have been shown to be less attractive to parasitoid wasps (Tariq et al. 2013). Thus, low water availability could affect the fitness of insect herbivores by altering the strength and direction of multi-species interactions. These influences could contribute more to the overall impacts of environmental changes than the effect of pairwise interactions between plants and insect herbivores (Ockendon et al. 2014). However, studies that incorporate multitrophic interactions remain scarce (Jamieson et al. 2012). Failure to do so may greatly undermine the ultimate impact of plant water availability of insect herbivores.

In this study, we aimed to evaluate how water availability alters the performance of a focal insect species through direct effects on plant quality and indirect effects mediated by changes in other arthropods. We hypothesized that water stress in plants can affect herbivore performance directly via plant quality or indirectly by altering community interactions. To quantify these effects and their interactions, we conducted a manipulative field study using a wild host, *Rorippa indica* (L.) Hiern, of the specialist herbivore cabbage white butterfly (*Pieris rapae*). To compare the generality of the responses and to investigate the potential role of local adaptations in shaping these responses, we conducted experiments on two populations of *P. rapae* in Taiwan and Japan that have distinct climatic conditions and fauna/flora. *R. indica* is a perennial glabrous herb that is commonly found in highly disturbed areas, such as roadsides, gardens, and field margins throughout the main island of Taiwan (Huang 1996), and also during May to September in most parts of Japan (Jisaburō Ōi and Walker 1965). *R. indica* individuals with different phenotypes due to water availability are commonly observed in the field. By manipulating water status of *R. indica* in the field, in combination with laboratory feeding assays, we aimed to determine (1)

the responses (i.e., preference and performance) of insect herbivores to *R. indica* of different water status, and (2) the factors (i.e., plant quality and species interactions) that contribute to these responses.

Materials and methods

Insects and plants

Cabbage white butterflies (*Pieris rapae*) were collected in the experimental field of National Taiwan University (NTU, Taipei, Taiwan) and the University of Tsukuba (UT, Ibaraki, Japan), and kept at 25–27 °C with a 14:10 light:dark cycle on cabbage (*Brassica oleracea* var. capitata) and komatsuna (*B. rapa* var. Perviridis), respectively. North American *P. rapae* were collected on campus at the Pennsylvania State University (PSU; University Park, PA, USA) and maintained on kale (*B. oleracea* var. sabellica). Cabbage looper (*Trichoplusia ni*), corn earworm (*Helioverpa zea*), and fall armyworm (*Spodoptera frugiperda*) were purchased from Benzon Research (Carlisle, PA, USA) and reared on artificial diet (Peiffer and Felton 2005). All insects were kept under the same conditions as described above. Seeds of *Rorippa indica* were collected in the experimental fields. Plants were maintained in a semi-closed greenhouse and grown in 3-in. pots (400 mL) with a 3:1 mixture of peat moss (Kekkila, Finland): perlite (2–8 mm) and supplied with Osmocote Plus fertilizer (Everris, Netherland). The water-holding capacity of peat moss was estimated as 195 mL (65% of volume) based on information provided by Kekkila.

Water treatment and water status quantification

Plants with 7–8 fully expanded leaves were subjected to one of two water treatments: (1) high water availability (200 mL day⁻¹ pot⁻¹), or (2) low water availability (10 mL day⁻¹ pot⁻¹). The water levels were chosen on the basis of morphological comparisons of plants growing in different water availabilities (10, 30, 50, 100, and 200 mL day⁻¹ pot⁻¹) to plants growing in the field in moist and dry areas. Water was applied daily at 9 a.m. for 7 days. To quantify the water status of plants (Jones 2007), we measured shoot biomass, root biomass, shoot water content, and volumetric water content of soil (θ_v). For shoot biomass and water content, the entire aboveground tissue was collected, weighed, dr; (70 °C; 48 h), and weighed again. For root biomass, below ground tissue was collected after the above ground tissue, and the roots were washed, and dried (70 °C; 48 h), and weighed to obtain dry mass. For soil water content, 100 cm³ of soil sample was collected from each pot avoiding root tissues. Soil was weighed, dried (70 °C, 48 h), and weighed again. The water content was calculated using

the following formula: $\left(\frac{\text{mass of water}_{(g)}}{\text{density of soil}_{(g\text{ cm}^{-3})}} \right)^{-1}$ $\left(\frac{\text{mass of soil}_{(g)}}{\text{density of water}_{(g\text{ cm}^{-3})}} \right)^{-1}$. All samples were collected 3 h after daily water application. For field experiments, water status of *R. indica* was maintained by the same procedure, accompanied with daily observations at 12, 2, and 4 p.m. When signs of low turgor were observed, 10 mL of water was added. This procedure prevented irreversible tissue damage in most leaves. Loss of turgor was not observed in plants growing under high water availability. The high and low water availability phenotypes were maintained as consistently as possible throughout the field experiment (Appendix 1).

Oviposition preference, survival, and relative growth rate of insect herbivores

All field experiments were conducted in Taiwan and Japan. Individual *R. indica* grown under different water statuses (in pots) were placed in the experimental field at 7 a.m. Plants were arranged 3 m apart in a square grid (Appendix 2). *P. rapae* ovipositional preferences were determined by recording the number of eggs laid after the first 72 h. Individual plants were kept in the field for an additional 7 days before *P. rapae* larvae were collected. Only larvae older than second instar were collected to ensure that the collected caterpillars came from the recorded eggs. Because *P. rapae* larvae rarely move away from their host, even when the host plant is stressed (based on our rearing observations), and experienced high levels of egg predation, the survival of *P. rapae* was defined and calculated as: $(\text{caterpillar number}) / (\text{egg number})^{-1}$. See “Methods: Arthropod community” for additional details on field experiments.

We analyzed the relative growth rate (RGR) of larvae to determine the quality of *R. indica* under different water treatments. *P. rapae* larvae from Taiwan and Japan were each fed with *R. indica* from a sympatric population. Third instar larvae of *P. rapae* were weighed and placed in 30 mL plastic cups with a thin layer of 1% agar (5 mL). The larvae were fed with detached mature leaves of plants grown under high (200 mL day⁻¹), low (10 mL day⁻¹), or intermediate water level: 50 mL day⁻¹). Leaves were replaced daily to minimize the potential changes in plant quality caused by excision. Larvae were weighed after 3 days. The start and end weights were used to calculate RGR using the following equation: $(\text{end weight} - \text{start weight}) / (\text{end weight} + \text{start weight})^{-1} \text{ days}^{-1}$ (Felton et al. 1989). This set of experiments was conducted at NTU and UT.

To test the impacts of host plant quality on insects without co-evolutionary history, we conducted another set of common garden experiments at PSU with *R. indica* from Taiwan and Japan. Plants were grown in a greenhouse with a 16:8

light:dark cycle at 25 °C. Leaves were collected from two different water treatments (200 mL day⁻¹ and 10 mL day⁻¹) from both populations of *R. indica* and fed to third instar lepidopteran larvae from North America: *P. rapae* (specialist), *Trichoplusia ni* (semi-specialist), *Helicoverpa zea* (generalist), and *Spodoptera frugiperda* (generalist) following the methods described above.

Arthropod community

Insect communities associated with *R. indica* were determined by visual observation after the plants were placed in the field for 72 h. All arthropods on each plant during 7 a.m.–12 p.m. were recorded. Morphospecies observed in the field are listed in Appendix 3. Field experiments took place in Taiwan during April–June 2018, and in Japan during July–September 2018. The experiment was replicated three times in both locations, with one trial in each month, defined as early, middle, and late season. The experimental fields were located within the campuses of NTU (25°00′55.9″N 121°32′25.0″E) and UT (36°06′51.7″N 140°05′59.7″E). Both fields were of a similar size (900 m²). The natural community of plants in the experimental fields was allowed to grow undisturbed. Each trial contained 20–25 individual *R. indica* from each water treatment (total of 40–50 plants). The timing of field experiments was determined according to governmental weather forecasts in Taiwan and Japan. The experiments were conducted during the 10-day-period that had the lowest probability of rain in each season. Incidences of rain were rare: on average, there were 0–1 rainy days per field experiment. In cases of rain, plants were covered with transparent plastic bins until it had stopped raining. In addition, plants were placed on a round plastic trays to prevent them absorbing moisture from the soil. To determine parasitism incidence, field-collected *P. rapae* larvae were reared individually on *Brassica oleracea* var. capitata and *Brassica rapa* var. Perviridis as food in Taiwan and Japan, respectively, until pupation or parasitoid emergence. If the caterpillar died before pupation, the carcass was dissected to determine presence of parasitoids.

Statistical analyses

All statistical analyses were conducted in R version 3.5.3 (R Core Team 2017). Univariate response variables were modeled with generalized linear models (GLM) with treatment, population, season and their interactions as fixed effects. We analyzed all count data (eggs, caterpillars, herbivores, and natural enemies) with negative binomial GLMs (package: MASS) (Venables and Ripley 2013) with plant biomass as an offset variable. Survival probabilities of *P. rapae* were modeled with a binomial GLM as the odds ratio between alive

(caterpillar count) and dead (egg count—caterpillar count). We excluded samples with no eggs observed. Dispersion, zero-inflation, residual normality, and homoscedasticity of all model fits were evaluated with simulation-based residual plots (package: *DHARMa*) (Hartig 2017). Significance of model parameters was tested by Type II rather than Type III Wald's Chi-squared test (package: *car*) (Fox and Weisberg 2018) to account for unequal sample sizes among treatments (Langsrud 2003).

To examine whether *P. rapae* survival could be attributed to abundance of other arthropods, we pooled samples between treatments and fitted binomial generalized linear mixed-effect models (GLMM, package: *glmmTMB*) (Brooks et al. 2017) with an observation-level random effect to improve residuals. Abundances of trophic guilds (herbivores and natural enemies; Fig. 4), and the abundances of individual species (Table 2) were used as fixed effect predictors. An individual GLMM was fitted for each season in each location. We implemented backwards model selection (likelihood ratio tests) until all terms were significant (Zuur et al. 2009). Other model diagnostics were performed as described above. Continuous variables, such as water content, biomass, and relative growth rate, were analyzed using ANOVA, followed by Tukey HSD. Diagnostic plots were used to check for model assumptions, such as equal variance and normality (Zuur et al. 2010). Indicator species analysis was conducted to ascertain whether specific species were associated with a particular water treatment in a particular season (packages: *indicspecies* and *vegan*) (Cáceres and Legendre 2009; Oksanen et al. 2010). We conducted indicator species analysis on presence/absence data to partially remove the effects of the difference in absolute abundance among species because we were more interested in whether each individual species showed any association towards a particular treatment-season combination. A permutation test (with 999 permutations) was used to assess the significance of associations between species and treatment-season combinations. In addition, we applied a PCA on $\log(x+1)$ -transformed (to improve skew of species abundance distributions) and z -standardized (to put equal weights on each species) species abundances independently for herbivores and natural enemies to help visualize the changes in species composition between treatments and seasons.

Results

Water status quantification

Different water treatments led to observable changes in plant phenotypes (Fig. 1a). Leaf number and shape were not affected by water availability (Fig. 1b); however, leaf shape differed between the Taiwanese and Japanese

populations (Fig. 1c; $F_{1,29} = 13.03$, $P = 0.001$). The fresh weight of shoots of individuals was reduced under low water availability (Fig. 1d; $F_{1,29} = 65.29$, $P < 0.001$) and higher in the Taiwanese population compared to the Japanese population ($F_{1,29} = 22.59$, $P < 0.001$). The dry weight of shoot was also reduced under low water availability (Fig. 1e; $F_{1,29} = 17.05$, $P < 0.001$) and higher in the Taiwanese population ($F_{1,29} = 8.5$, $P = 0.007$). Water content of shoots was reduced under low water availability (Fig. 1f; $F_{1,28} = 105.02$, $P < 0.001$), and higher in the Taiwanese population ($F_{1,28} = 5.48$, $P = 0.027$). However, the effect of population on shoot water content was only significant under low water availability, indicated by a significant interaction between water and population ($F_{1,28} = 5.48$, $P = 0.027$). The root biomass was not affected by water treatments. However, the root biomass was higher in the Taiwanese population (Fig. 1g; $F_{1,28} = 8.605$, $P = 0.007$). The root: shoot ratio was increased under low water availability (Fig. 1h; $F_{1,28} = 88.17$, $P < 0.001$). The volumetric water content (θ_v) of the soil was 0.53–0.55 for high water availability and 0.09 for low water availability (Fig. 1i; $F_{1,29} = 2238.65$, $P < 0.001$).

Oviposition preference, caterpillar number, and survival (field experiment)

More eggs were observed on *R. indica* under high water availability (Fig. 2a; GLM, water: 200 mL day⁻¹, estimate = 1.04, $Z = 4.79$, $P < 0.001$). The number of eggs on *R. indica* was higher in Taiwan than in Japan (GLM, region: Taiwan, estimate = 2.2, $Z = 10.21$, $P < 0.001$). In addition, the number of eggs was lower during late season in Taiwan (GLM, season \times region: late \times Taiwan, estimate = -1.74, $Z = -7.11$, $P < 0.001$), but this pattern was not observed in Japan.

The number of *P. rapae* caterpillars on *R. indica* was greater overall in Taiwan compared with Japan (Fig. 2b; GLM, region: Taiwan, estimate = 1.25, $Z = 3.57$, $P < 0.001$), but the number of caterpillars was lower in Taiwan on *R. indica* under high water availability (GLM, water \times region: 20 mL day⁻¹ \times Taiwan, estimate = -0.94, $Z = -2.66$, $P = 0.008$). The number of caterpillars was lower during late season (GLM, season: late, estimate = -1.72, $Z = -4.19$, $P < 0.001$), and was not affected by the water treatment in general.

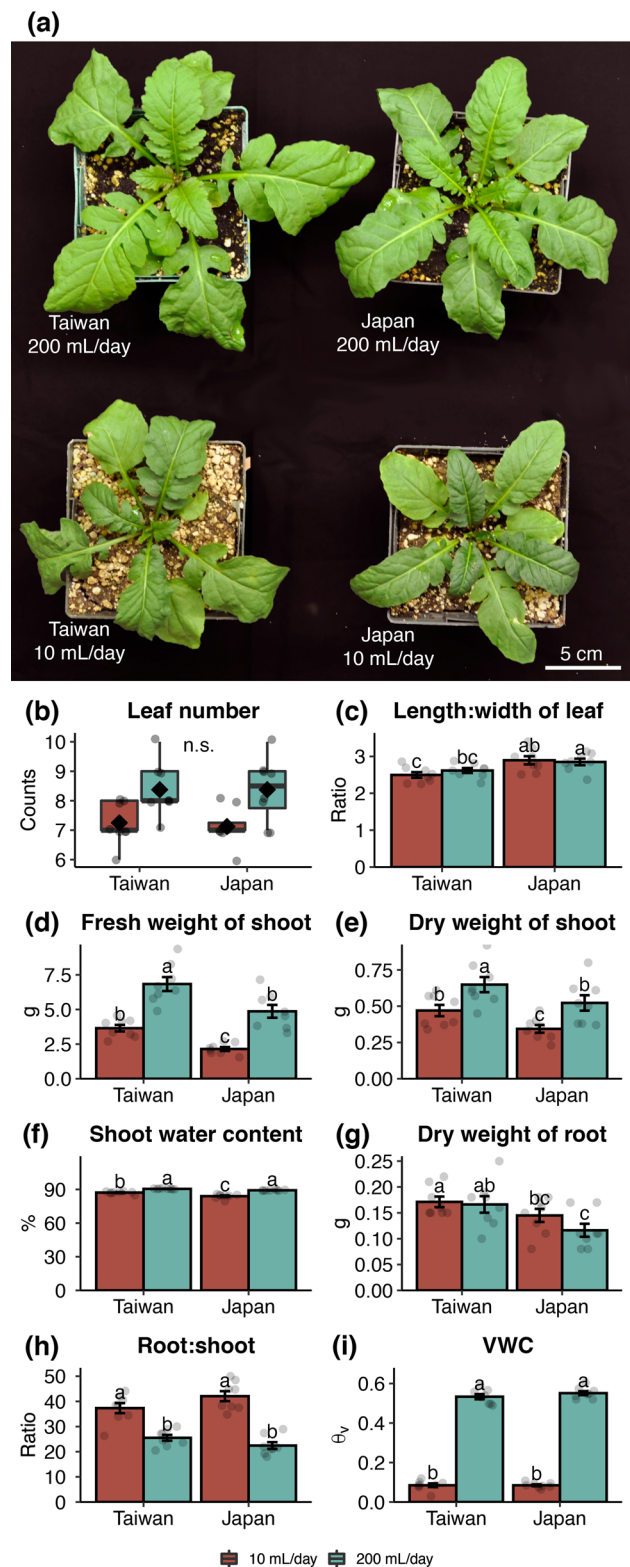
Survival of *P. rapae* was lower on *R. indica* under high water availability (Fig. 2c; GLM, water: 200 mL day⁻¹, estimate = -2.15, $Z = -8.79$, $P < 0.001$), and in the middle, and late seasons (GLM, season: middle, estimate = -0.63, $Z = -2.58$, $P = 0.01$; season: late, estimate = -3.96, $Z = -14.95$, $P < 0.001$). However, this pattern was influenced by several interacting factors. For example, Although the survival of *P. rapae* was overall lower on *R. indica* under high water availability, the survival on *R. indica*

Fig. 1 Quantification of water status on *Rorippa indica*. **a** Phenotypes after water treatment in a common garden experiment (2 h after daily water application). **b** Box plot of leaf number ($N=8$, GLM, Poisson). **c** Ratio of length and width of mature leaves ($N=8$). **d** Fresh weight of shoots ($N=8$). **e** Dry weight of shoots ($N=8$). **f** Shoot water content ($N=8$). **g** Dry mass of roots ($N=8$). **h** Root: shoot ratio (g g^{-1} , dry mass) ($N=8$). **i** Soil volumetric water content (θ_v) ($N=8$). Dots indicate individual observations. Values indicate mean \pm SE. Different letters indicate significant differences between means (ANOVA, Tukey HSD)

under high water availability was slightly increased in middle and late season in both Taiwan and Japan (GLM, water \times season: $200 \text{ mL day}^{-1} \times$ middle, estimate = 1.57, $Z=10.1$, $P<0.001$; water \times season: $200 \text{ mL day}^{-1} \times$ late, estimate = 1.31, $Z=6.52$, $P<0.001$). Although the survival of *P. rapae* was overall lower in Taiwan (GLM, location: Taiwan, estimate = -2.74 , $Z=-10.81$, $P<0.001$), the survival was significantly higher during the late season (GLM, season \times location: late \times Taiwan, estimate = 4.2, $Z=17.49$, $P<0.001$) and lower in the middle season (GLM, season \times location: middle \times Taiwan, estimate = -0.53 , $Z=-2.34$, $P=0.019$). We also observed an overall lower *P. rapae* survival on *R. indica* under high water availability in Taiwan compared to Japan (GLM, water \times region: $200 \text{ mL day}^{-1} \times$ Taiwan, estimate = -0.53 , $Z=-2.34$, $P=0.019$).

Relative growth rate of caterpillars (laboratory experiment)

The relative growth rates (RGR) of *P. rapae* larvae from Taiwan and Japan were not affected by the water status of *R. indica* from the same geographic origin (Fig. 3a, b). In contrast, populations of *R. indica* from Taiwan and Japan growing under low water availability led to significant decreases in the RGR of *P. rapae* from North America (Fig. 3c; $F_{1,141}=12.96$, $P<0.001$). *R. indica* growing under low water availability also decreased the RGR of generalist caterpillars. The RGR of *H. zea* larvae was lower on *R. indica* growing under low water availability (Fig. 3d; $F_{1,147}=25.41$, $P<0.001$). RGR of *T. ni* larvae was overall lower on *R. indica* growing under low water availability (Fig. 3e, $F_{1,128}=8.76$, $P=0.004$) and *R. indica* from Taiwan ($F_{1,128}=8.62$, $P=0.004$). However, the negative impacts of low water availability were only significant when *T. ni* larvae fed on *R. indica* from Taiwan ($F_{1,128}=5.2$, $P=0.024$). *S. frugiperda* completely rejected *R. indica* from Taiwan as a food source, and we observed a small amount of feeding on *R. indica* from Japan. The mortality of *S. frugiperda* larvae was significantly lower when *R. indica* from Taiwan was provided as food (Fig. 3f; GLM, 200 mL day^{-1} : estimate = -1.81 , $P<0.001$).



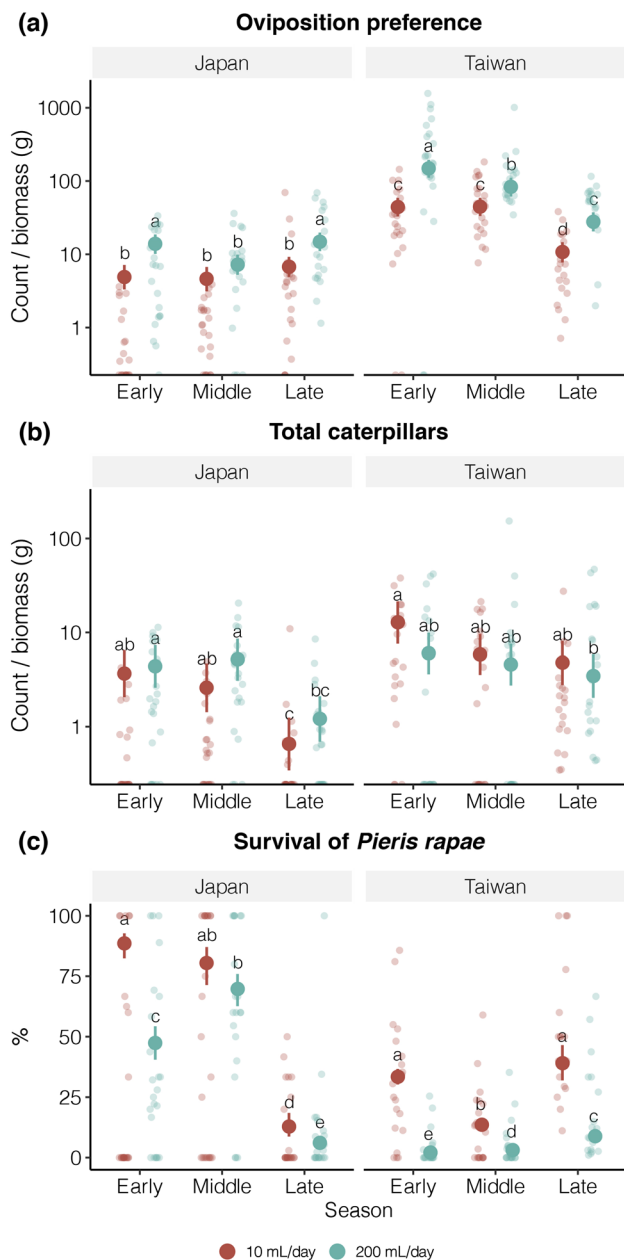


Fig. 2 Influence of *Rorippa indica* water status, population, and season on *Pieris rapae*. **a** Ovipositional preferences. **b** Total caterpillars at the end of field experiment, **c** survival of *P. rapae* on *R. indica*. Count data were offset by biomass of *R. indica*. Due to high values of egg, caterpillar, and herbivore counts, data were plotted at the log scale. Transparent points indicate individual observations; opaque points and error bars indicate mean \pm 95% CI

Abundance and composition of herbivores and natural enemies

Herbivore abundance in Japan and Taiwan (Fig. 4a, i) on *R. indica* was higher on *R. indica* growing under high water availability (GLM, water: 200 mL day⁻¹, estimate = 1.43, $Z = 4.32$, $P < 0.001$) and lower in the late season (GLM,

season: late, estimate = - 2.61, $Z = - 6.54$, $P < 0.001$). The negative influence of the late season on herbivore abundance was stronger on *R. indica* growing under high water availability (GLM, water \times season: 200 mL day⁻¹ \times late, estimate = - 1.45, $Z = - 3.39$, $P < 0.001$). However, the influence of the late season changed from negative to positive in Taiwan (GLM, season \times location: late \times Taiwan, estimate = 2.69, $Z = 6.23$, $P < 0.001$).

Natural enemy abundance in Taiwan and Japan (Fig. 4e, m) was higher on *R. indica* growing under high water availability (GLM, water: 200 mL day⁻¹, estimate = 1.98, $Z = 4.21$, $P < 0.001$), but lower during the middle and late seasons (GLM, season: middle, estimate = - 1.54, $Z = - 2.28$, $P = 0.022$; season: late, estimate = - 2.04, $Z = - 3.26$, $P = 0.001$). Natural enemy abundance was overall lower in Taiwan compared to Japan (GLM, region: Taiwan, estimate = - 1.84, $Z = - 3.24$, $P = 0.001$) but increased drastically in the middle and late seasons in Taiwan (GLM, season \times location: middle \times Taiwan, estimate = 2.51, $Z = 5.04$, $P < 0.001$; season \times location: late \times Taiwan, estimate = 4.49, $Z = 8.61$, $P < 0.001$).

The composition of invertebrate herbivores and natural enemies associated with *R. indica* changed as a result of water availability and season. In Taiwan, there was a clear separation of herbivore communities on *R. indica* growing under high and low water availability (Fig. 5a). Indicator species analysis revealed that several specialist herbivores associated significantly with *R. indica* growing under high water availability (Table 1). In contrast, generalist herbivores had a weaker association with *R. indica* growing under high water availability. Grasshoppers (Catantopidae) were the only generalist that associated significantly with *R. indica* growing under high water availability in Japan. The only morphospecies associated with *R. indica* growing under low water availability was spider mites (Tetranychidae) in Taiwan (Table 1). The composition of herbivores also changed across seasons in Taiwan. Both the PCA (Fig. 5b) and indicator species analysis (Table 1) indicated no strong association between *R. indica* and natural enemies under low water availability. The association between natural enemies and *R. indica* was stronger in later seasons in Taiwan under high water availability (Table 1). Many of the natural enemies we observed attacked *P. rapae*. Based on field observations, predators, such as ants (Formicidae), predatory stink bug (*Eocanthecona concinna*), ladybugs (Coccinellidae), and spiders (Araneae), were observed to cause high mortality of *P. rapae* eggs and larvae. A surprising finding in Taiwan was that the parasitism rate of *P. rapae* larvae on *R. indica* by the specialist parasitoid wasp *Cotesia glomerata* was less than 1%. In comparison, parasitism of *P. rapae* larvae in nearby cabbage fields was regularly observed.

In Japan, the separation of herbivore composition between *R. indica* growing under different water availability was

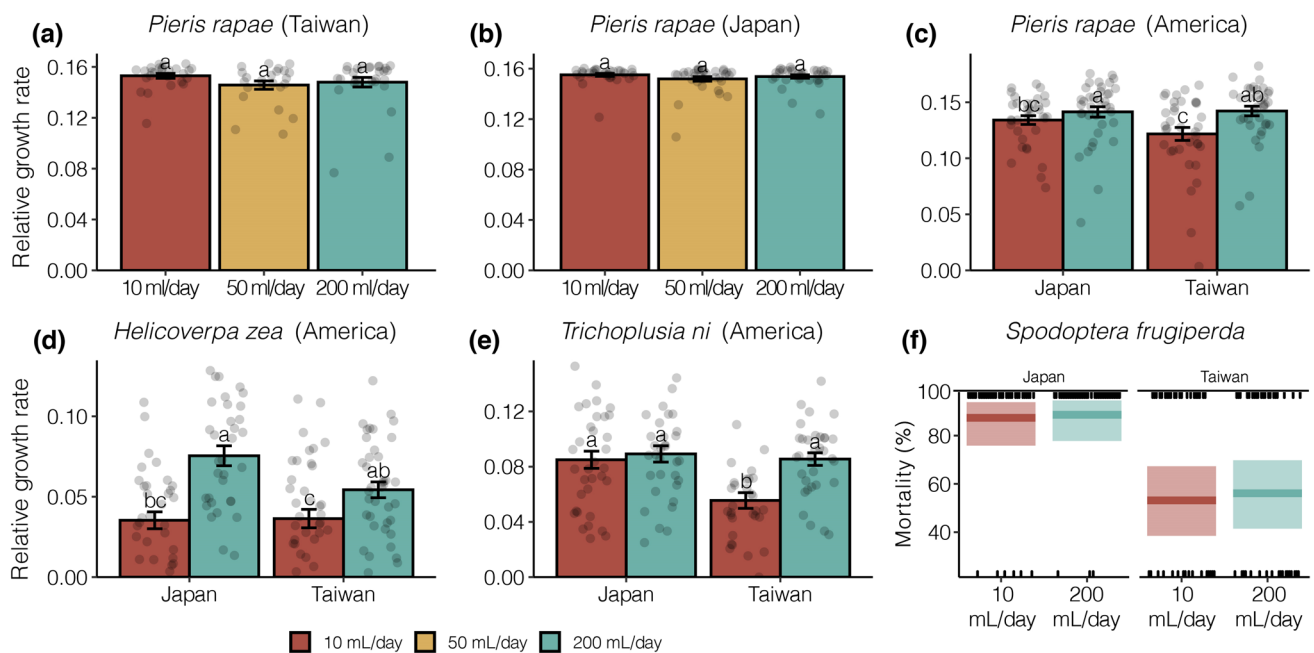


Fig. 3 Relative growth rates of lepidopteran larvae feeding on leaves of *Rorippa indica*. **a** *Pieris rapae* (Taiwan) and *R. indica* (Taiwan) ($N=30$). **b** *P. rapae* (Japan) and *R. indica* (Japan) ($N=35$). **c** *P. rapae* (North America) and *R. indica* (Taiwan and Japan) ($N=40$). **d** *Helicoverpa zea* (North America) and *R. indica* (Taiwan and Japan) ($N=40$). **e** *Trichoplusia ni* (North America) and *R. indica* (Taiwan

and Japan) ($N=40$). Values represent means \pm SE. Different letters indicate significant differences between means (ANOVA, Tukey HSD). **f** *Spodoptera frugiperda* (North America) and *R. indica* from both location (Taiwan and Japan) ($N=40$). 100=dead, 0=alive. Bars indicated means and boxes represent 95% CI (GLM, binomial)

less apparent (Fig. 5c). Based on indicator species analysis, most herbivores were significantly associated with *R. indica* growing under high water availability (Table 1). Season also influenced the composition of herbivores on *R. indica*. Only scarlet shieldbug (*Eurydema dominulus*) and grasshoppers (Catantopidae) sometimes caused noticeable damage, but the level of herbivory in the field was much lower than the level of herbivory in Taiwan. For natural enemy compositions, there were no observable differences between natural enemies associated with *R. indica* growing under different water availability (Fig. 5d). According to indicator species analysis, some natural enemies were significantly associated with *R. indica* growing under high water availability in the early season (Table 1). However, we did not observe any predation on *P. rapae* throughout all field experiments.

Survival of *Pieris rapae* and arthropod communities

We found significant negative associations between the abundance of herbivores and natural enemies with the survival of *P. rapae* during several seasons in both locations (Fig. 4). In Taiwan, herbivore abundance was negatively associated with the survival of *P. rapae* during the early (Fig. 4b; GLMM, estimate = -1.75 , $Z = -5.7$, $P < 0.001$) and middle seasons (Fig. 4c; GLMM, estimate = -0.12 , $Z = -2.41$, $P = 0.016$). Natural enemy abundance was negatively associated with

survival of *P. rapae* during the early (Fig. 4f; GLMM, estimate = -3.64 , $Z = -10.11$, $P < 0.001$) and late seasons (Fig. 4h; GLMM, estimate = -0.24 , $Z = -4.05$, $P < 0.001$).

Most of the herbivores observed on *R. indica* showed negative associations with *R. indica* survival (Table 2). For instance, flea beetles (*Phyllotreta striolata*) that heavily attacked well-watered *R. indica* were negatively associated with survival of *P. rapae* during the early season in Taiwan (GLMM, estimate = -6.50 , $P = 0.04$). Scarlet shieldbugs (*E. dominulus*) and Cicadellidae were positively associated with survival of *P. rapae* in Taiwan during the middle and late seasons, respectively (GLMM, estimate = 0.99 , $P = 0.08$; GLMM, estimate = 1.31 , $P < 0.001$). However, the scarlet shieldbug (*E. dominulus*) had contrasting associations with the survival of *P. rapae* in different seasons (negative association during the late season, GLMM, estimate = -0.95 , $P < 0.001$), likely due to the difference in abundance between seasons (individual plant $^{-1}$: middle = 0.136 ; late = 0.275). The analysis of morphospecies in Japan revealed some unexpected associations; for example, Lauxaniidae, a parasitic mite of aphids, and Syrphidae (during early season, GLMM, estimate = -0.95 , $P = 0.021$; estimate = 0.50 , $P = 0.001$; estimate = -0.31 , $P = 0.041$).

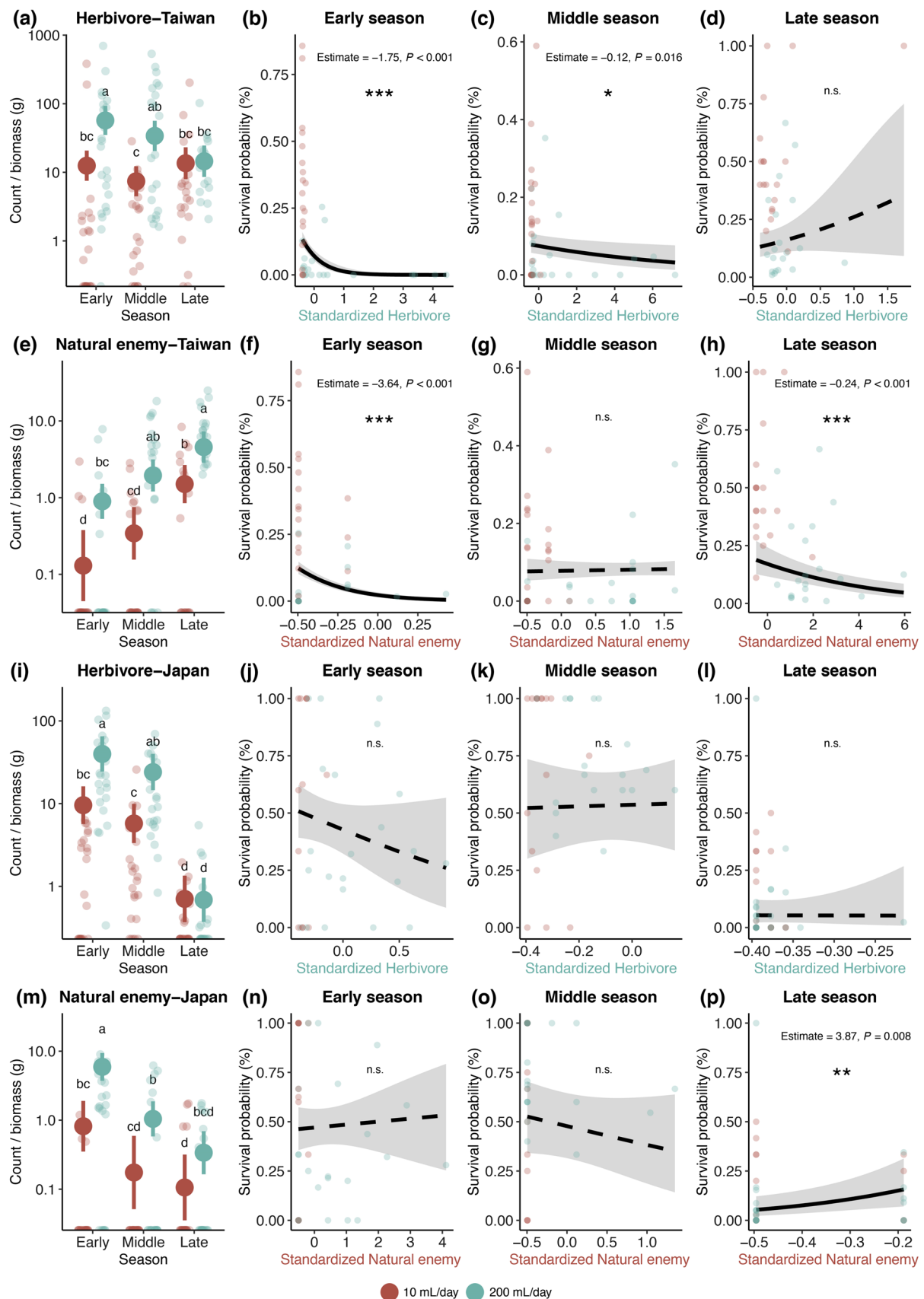


Fig. 4 Abundance of herbivores and natural enemies and associations with water status of *Rorippa indica* and survival of *Pieris rapae*. **a** Abundance of herbivores in Taiwan. **b–d** Associations between herbivore abundance and survival of *P. rapae* in Taiwan during early, middle, and late seasons. **e** Abundance of natural enemies in Taiwan. **f–h** Associations between natural enemy abundance and survival of *P. rapae* in Taiwan during early, middle, and late seasons. **i** Abundance of herbivores in Japan. **j–l** Associations between herbivore abundance and survival of *P. rapae* in Japan during early, middle, and late seasons. **m** Abundance of natural enemies in Japan. **n–p** Associations between natural enemy abundance and survival of *P. rapae* in Japan during early, middle, and late seasons. Lines represent model predictions (solid: significant; dashed: non-significant). Grey areas indicate 95% CI. For abundance plots, values indicate estimated means with 95% CI. All dots indicate individual observations. Letters indicate significant difference between means (Tukey HSD). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Discussion

As spatial and temporal variation in plant access to water increases in the future (National Research Council 2011), understanding the impacts of water availability on plants and associated heterotrophs is important to identify the complex effects of water availability on community interactions. By evaluating interactions across multitrophic levels, we show that plant water availability differentially impacts specific herbivores and has overall effects on arthropod community composition. Low water availability reduces overall arthropod abundance associated with plants, and this negative impact is linked with a decrease in plant quality, indicated by reduction in caterpillar performances. These findings are similar to the common observation that low water availability negatively affects insect herbivores on herbaceous plants (Waring and Cobb 1992). Notably, we observed that a specialist herbivore was capable of coping with fluctuations in host plant quality that are driven by water availability. The performance of *P. rapae* from Taiwan and Japan revealed a potential case of local adaptation, where local *P. rapae* performed equally well on sympatric *R. indica* of different water status. The ability of *P. rapae* to cope with variation in host quality, suggests that host variations could shape the evolution of *P. rapae* physiological adaptations. Similar local specialization caused by regional effects and host plants was also documented in another butterfly species, such as *Melitaea cinxia* (Kuussaari et al. 2000).

Even with the physiological capacity to overcome variations in host plant quality, *P. rapae* still displayed a preference toward *R. indica* growing under high water availability. The preference-performance hypothesis (PPH) predicts that oviposition of females should match the performance of their offspring (Gripengberg et al. 2010; Thompson 1988). Based on the observed decrease in oviposition on *R. indica* growing under low water availability in both populations, the preference-performance relationship predicted by PPH was not observed. It has been shown that temporal variation

in resource quality hinders the evolution of female preference (Cronin et al. 2001; Gripengberg et al. 2007), and thus resulted in failure to evolve a proper mechanism to perceive these changes in host quality for their offspring. Alternatively, lower preference toward plants under low water availability could also be a passive response of female *P. rapae* to changes in attractiveness due to size or chemical cues of plants. For example, changes in volatile emission patterns alter the attractiveness of plants to insects (Orre et al. 2010; Pichersky and Gershenzon 2002), and water availability can affect volatile emissions (Copolovici et al. 2014; Scott et al. 2018). It is also likely that the stability of plant resources (Garssen et al. 2014) and the preference of the insects to feed on plant tissues with higher water content also contribute to the evolution of preference for plants growing under high water availability.

Given the capacity of *P. rapae* to use host plants of variable water status, the reduction in other herbivores and natural enemies on *R. indica* growing under low water availability is likely to explain the increased survival of *P. rapae* observed on these plants. Although we did not explicitly evaluate the level of predation and competition, the drastic changes in abundance of herbivores and natural enemies provide a strong basis in shifting in competition and predation. Several morphospecies that were either consistently observed to prey on *P. rapae* or cause large amounts of damage to *R. indica* in Taiwan, were linked to observable changes in *P. rapae* abundance. In addition, the overall low abundance of both herbivores and natural enemies, and species from these groups that directly interact with *P. rapae* in Japan, is likely a reason for the lack of overall association between arthropod abundance and *P. rapae* survival. This result further supports our conclusion that multitrophic interactions are an important reason that *P. rapae* benefits from *R. indica* grown under low water availability.

A surprising finding that appeared was the positive associations between *P. rapae* survival and two piercing-sucking herbivores in Taiwan. Although this observation contradicted our overall conclusion that stronger competition reduced the survival of *P. rapae* on *R. indica* growing under high water availability, it reveals potential divergent defense responses elicited by herbivores in different feeding guilds. For example, plant defenses induced by piercing-sucking hemipterans are often salicylic acid-dependent, in contrast to jasmonic acid-dependent defenses induced by chewing herbivores. Because of the antagonistic relationship between these defenses, induction of salicylic acid defenses has been frequently shown to benefit chewing herbivores (De Vos et al. 2005; Kroes et al. 2015; Li et al. 2014; Pieterse et al. 2012; Soler et al. 2012). We speculate that the positive associations between *P. rapae* survival and the two piercing-sucking herbivores were likely mediated by a similar mechanism described above. One study found that

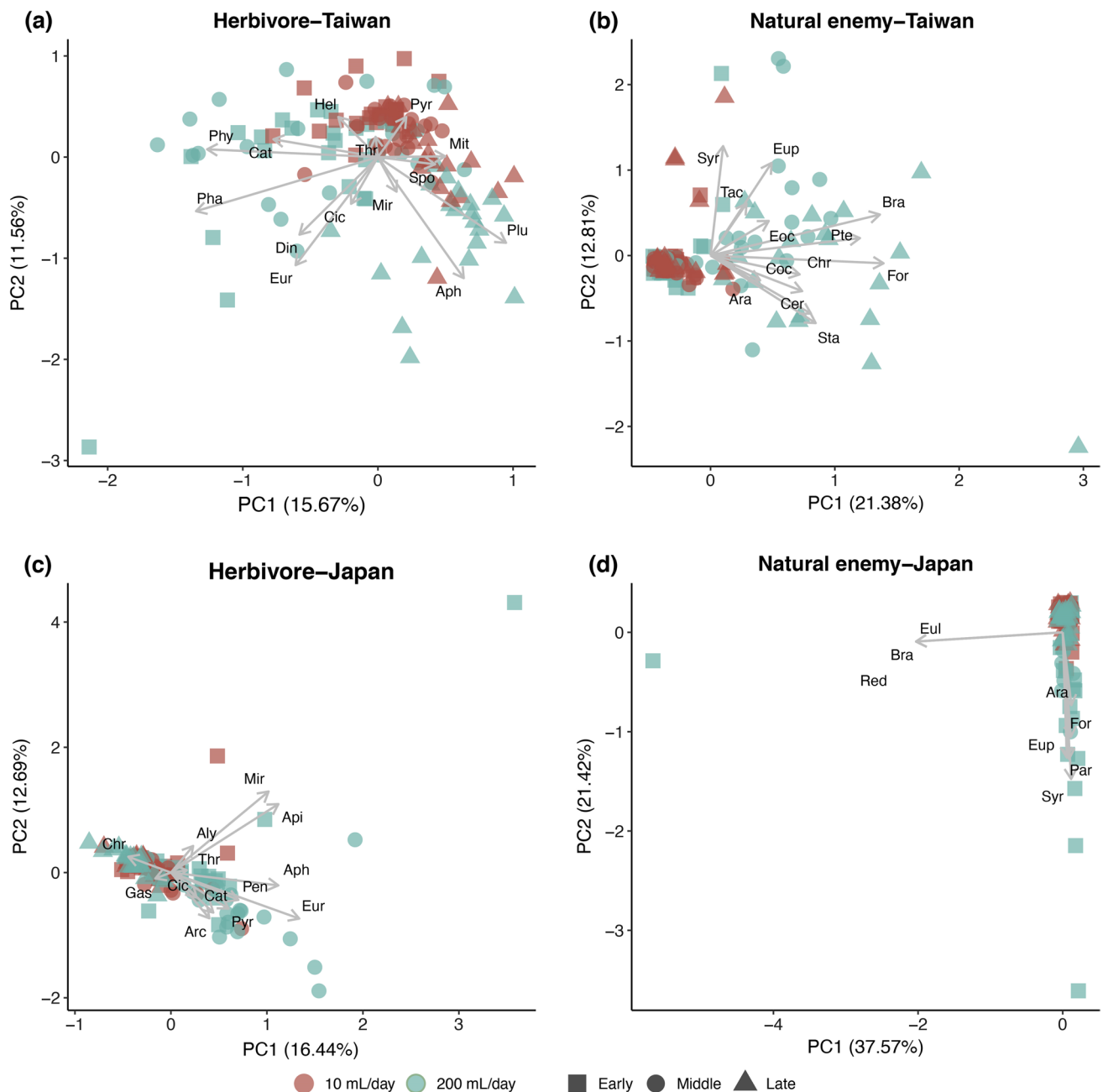


Fig. 5 Herbivore and natural enemy composition on *Rorippa indica* with different water status across seasons. **a** Herbivore composition in Taiwan. **b** Natural enemy composition in Taiwan. **c** Herbivore composition in Japan. **d** Natural enemy composition in Japan. For methods please see Appendix 6. Abbreviations for herbivores: Aph=Aphididae, Api=Apidae, Acr=Acridae, Aly=Alydidae, Cat=Catantopidae, Cic=Cicadellidae, Chy=Chrysomelidae, Din=Dinidoridae, Eur=*Eurydema dominulus*, Gas=Gastropoda, Hel=*Helicoverpa armigera*, Mir=Miridae, Mit=Tetranychidae,

Pen=Pentatomidae, Pha=*Phaedon brassicae*, Phy=*Phyllotreta striolata*, Plu=*Plutella xylostella*, Pyr=Pyrgomorphidae, Spo=*Sporoptera litura*, Thr=Thripidae. Abbreviations for natural enemies: Ara=Araneae, Bra=Braconidae, Cer=Ceraphronidae, Chr=Chrysopidae, Coc=Coccinellidae, Eoc=*Eocanthecona concinna*, Eup=Eupelmidae, Eul=Eulophidae, For=Formicidae, Pte=Pteromalidae, Syr=Syrphidae, Tac=Tachinidae, Tro=Trombididae, Red=Reduviidae

these positive impacts took place only under low density of piercing-sucking herbivores (Kroes et al. 2015), which may explain the switch in association between survival of *P. rapae* and *E. dominulus* from positive to negative as the

density of *E. dominulus* doubled. Further exploration into the mechanisms and associated tradeoffs of these interactions are needed.

Table 1 Indicator species of water availability in different seasons

Species	Treatment (mL day ⁻¹)	Ind. val	P value
Herbivore			
Japan (early)			
Thripidae	200	0.486	< 0.001
Japan (middle)			
Aphididae	200	0.555	< 0.001
Eurydema	200	0.675	< 0.001
Catantopidae	200	0.369	0.004
Pyrgomorphidae	200	0.505	< 0.001
Pentatomidae	200	0.340	0.019
Japan (late)			
Chrysomelidae	200	0.340	0.034
Taiwan (early)			
Phaedon	200	0.551	< 0.001
Taiwan (middle)			
Phyllotreta	200	0.559	< 0.001
Eurydema	200	0.363	0.023
Catantopidae	200	0.447	0.001
Taiwan (late)			
Plutella	200	0.589	< 0.001
Aphididae	200	0.555	< 0.001
Tetranychidae	10	0.345	0.03
Natural enemy			
Japan (early)			
Formicidae	200	0.481	< 0.001
Syrphidae	200	0.437	0.002
Trombidiidae	200	0.510	< 0.001
Taiwan (middle)			
Eupelmidae	200	0.364	0.017
Taiwan (late)			
Formicidae	200	0.693	< 0.001
Braconidae	200	0.539	< 0.001
Eocanthecona	200	0.359	0.019
Coccinellidae	200	0.544	< 0.001
Araneae	200	0.366	0.009
Pteromalidae	200	0.456	0.001
Ceraphronidae	200	0.316	0.046
Others			
Japan (middle)			
Diptera	200	0.429	0.001
Taiwan (middle)			
Lauxaniidae	200	0.392	0.017
Taiwan (late)			
Staphylinidae	200	0.337	0.022

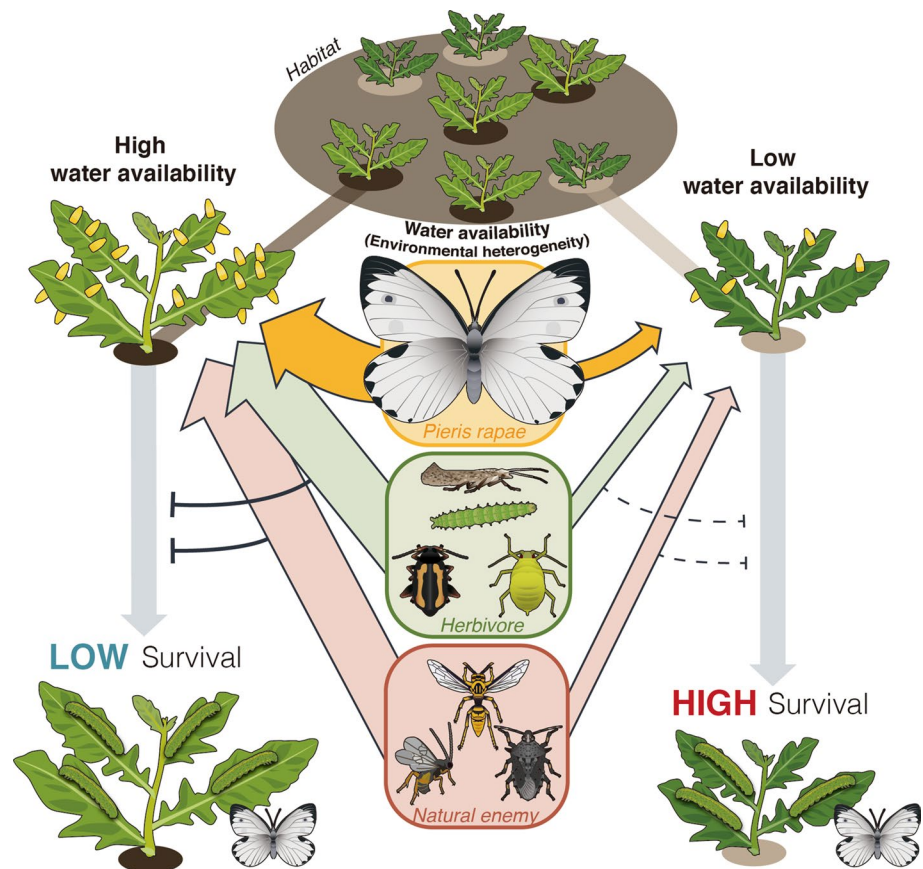
There are some caveats to our study. First, while we generated plants of different water status that were morphologically comparable to field individuals, our methods for quantifying water status are mostly indirect measures of water

Table 2 Model summaries of associations between survival of *Pieris rapae* and morphospecies

Term	Estimate	SE	Z value	P value
Taiwan (early)				
Intercept	− 5.215	1.236	− 4.221	< 0.001
Phyllotreta	− 6.500	3.151	− 2.063	0.04
Taiwan (middle)				
Intercept	− 3.544	0.33	− 10.729	< 0.001
Phyllotreta	− 1.049	0.334	− 3.141	0.002
Eurydema	0.988	0.374	2.643	0.008
Braconidae	− 1.675	0.419	− 3.994	< 0.001
Tetranychidae	− 0.789	0.376	− 2.095	0.036
Taiwan (late)				
Intercept	− 1.283	0.171	− 7.506	< 0.001
Eurydema	− 0.953	0.272	− 3.503	< 0.001
Cicadellidae	1.31	0.29	4.516	< 0.001
Eupelmidae	− 0.6	0.178	− 3.382	0.001
Eocanthecona	− 0.441	0.186	− 2.371	0.018
Japan (early)				
Intercept	− 0.639	0.194	− 3.298	0.001
Lauxaniidae	− 0.953	0.412	− 2.315	0.021
Trombidiidae	0.499	0.15	3.326	0.001
Japan (middle)				
Intercept	0.873	0.206	4.238	< 0.001
Syrphidae	− 0.31	0.151	− 2.048	0.041
Japan (late)				
NA	NA	NA	NA	NA

stress rather than detailed physiological characterizations of plant stress (Jones 2007). Although they are valuable in detecting plant responses to water limitation, they are not useful for studies investigating changes in physiological/molecular processes associated with droughts (Jones 2007). Second, although using detached leaves in caterpillar RGR bioassay is a commonly used method to detect chemical changes in leaves (Chung et al. 2013; Wang et al. 2017), the detachment procedure itself may alter leaf chemistry (Schmelz et al. 2001), and lowers plant defenses (Huang et al. 2003). While this method enables us to identify changes in the host plant quality, it may not fully reflect herbivores performance under natural feeding conditions. Third, since we only recorded the abundance of herbivores and natural enemies once in each field experiment, it is possible that arthropod abundance and species richness are underestimated. Finally, the time period of the field experiment was shorter than the larval stage of *P. rapae*. As a result, we do not know whether *R. indica* can support the number of larvae observed in field. However, the likelihood of complete defoliation seems low due to the ability of plants to regrow and the presence of natural enemies under high water availability, and the low quality of plants to other herbivores

Fig. 6 Graphical summary of the relationship between water availability, plant, and insect herbivore. Female *Pieris rapae* showed ovipositional preferences toward *Rorippa indica* growing under high water availability. *R. indica* growing under low water availability was associated with lower overall abundance of arthropods. The changes in species interactions may contribute to the higher survival of *P. rapae* larvae on *R. indica* growing under low water availability



under low water availability. The majority of the plants still maintained approximately 50–70% of their biomass after the 10-day field experiment.

The observation that *P. rapae* was unaffected by the reduction in host quality suggests that addressing focal herbivores without incorporating the natural insect community can alter interpretations of herbivore success. It can be misleading to focus on few selected insect species and groups of defense responses because changes in plants under low water availability might have differential impacts to community members. For example, some insect herbivores might have better ability to cope with changes in plant quality than others. Future studies should aim to include more focal species and aspects of plant–insect interactions to capture a broader scope of how insect and plant communities respond to environmental changes.

In summary, the present study provides insight to the ongoing discussion on how water availability influences insect herbivores (Jamieson et al. 2012; Mattson and Haack 1987; White 2009). By studying impacts of water availability in the context of arthropod communities in addition to the direct interactions between plants and insect herbivores, we revealed that plants growing under low water availability can be beneficial to some insects but detrimental to

others (Fig. 6). The contradicting impact of water availability on different arthropod species highlights the complexity and context dependency of these interactions. The findings also raise the question of how variation caused by environmental heterogeneity, including heterogeneity in water availability and other factors, affects the ecology and evolution of interactions between plants and insect herbivores.

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Author contribution statement PAL, KN, CKH, WPC, and GWF conceived the ideas, and designed the methodology. PAL and JAO analyzed the data. PAL, CML, and CHS collected the data. PAL, CML, JAO, KN, CKH, WPC, and GWF wrote the manuscript.


Data availability statement Data in this manuscript are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.g1jwstqq0>.

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