



# Vector-borne plant pathogens modify top-down and bottom-up effects on insect herbivores

Robert E. Clark<sup>1</sup> · David W. Crowder<sup>1</sup>

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## Abstract

Ecological theory predicts that host-plant traits affect herbivore population growth rates, which in turn modulates predator-prey interactions. However, while vector-borne plant pathogens often alter traits of both host plants and vectors, a few studies have assessed how pathogens may act as interaction modifiers within tri-trophic food webs. By applying a food web motif framework, we assessed how a vector-borne plant pathogen (*Pea-enation mosaic virus*, PEMV) modified both bottom-up (plant–herbivore) and top-down (predator–prey) interactions. Specifically, we assessed trophic interactions with PEMV-infectious *Acyrthosiphon pisum* (pea aphid) vectors compared to non-infectious aphids in a factorial experiment that manipulated predator and plant communities. We show that PEMV altered bi-trophic relationships, whereby on certain plant species, PEMV reduced vector performance but also increased their susceptibility to predators. However, on other plant species, PEMV weakened top-down control or increased vector performance. Our results suggest that vector-borne plant pathogens are important interaction modifiers for plant–herbivore–predator dynamics: host-plant response to viruses can decrease herbivore abundance by reducing herbivore performance, but also increase herbivore abundance by weakening top-down control. Broadly speaking, trophic interactions that regulate herbivore outbreaks appear to be modified for herbivores actively transmitting viruses to host plants. Consequently, management and monitoring of outbreaking herbivores should consider the infection status of focal populations.

**Keywords** Tri-trophic interactions · Vector biology · Aphids · Legumes · Plant viruses

## Introduction

Herbivore populations are regulated by combined effects of host-plant quality and predators (Gruner 2004; Hall et al. 2007; Mooney et al. 2010, 2012). For herbivores that transmit plant pathogens (vectors), it has been increasingly recognized that vector-borne pathogens can mediate such top-down and bottom-up effects by altering vector and plant traits (Wu et al. 2014; Clark et al. 2019; Crowder et al. 2019; Keissar et al. 2019). For example, vector-borne pathogens can alter selection of host plants by herbivores, increasing predation when herbivores move to plants associated with higher predation risk (Abdala-Roberts et al. 2014). In this

context, pathogens act as an ‘interaction modifier’, whereby pathogens alter the strength or direction of interactions between vectors and plants and predators (Wootton 1994; Hodge and Powell 2008; Golubski and Abrams 2011; Terry et al. 2017; Shoemaker et al. 2019).

Plant pathogens may affect vector–host–predator interactions through direct and indirect pathways, but it has proven difficult to predict how vector-borne pathogens may alter food webs as particular interactions may have complex additive or opposing effects. While pathogens that decrease host quality and vector fitness may weaken density-dependent top-down control (Denno et al. 2002; Han et al. 2020); for example, pathogens that promote vector fitness may strengthen density-dependent predation (Santolamazza-Carbone et al. 2014). Pathogens can also alter plant color and vector apparentness, altering predation risk (de Oliveira et al. 2014; Martini et al. 2014). Furthermore, pathogens often increase vector movement between infected and healthy hosts to promote transmission (Bosque-Perez and Eigenbrode 2011; Mauck et al. 2012), but increased vector

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✉ Robert E. Clark  
robert.e.clark@wsu.edu

<sup>1</sup> Department of Entomology, Washington State University, Pullman, WA 99164, USA

movement can increase apperency to natural enemies (Pearson 2009). However, given the complexity of multi-trophic interactions among host plants, their herbivores and pathogens, and predators, a few studies have been successful in untangling the multiple pathways by which pathogens might alter the trophic interactions of vector species.

We sought to determine the direct effects of host plants, predators, and PEMV on aphids over time, and then examined the outcomes to evaluate a suite of trophic hypotheses. We assessed multiple hypotheses regarding how a vector-borne pathogen could affect complex trophic interactions within a food web. We applied a ‘food web motif’ framework, where predictions are based on multiple bottom-up or top-down pathways acting as modifiable modules (Giling et al. 2019). For example, if pathogens weaken the ability of plants to defend themselves against herbivores, infection of host plants with a pathogen should increase vector fitness (mutualistic virus hypothesis) (Belluire et al. 2005; Davis et al. 2017), creating a modified plant–herbivore interaction. Conversely, pathogens may stunt plant growth and development, which typically lowers vector fitness (parasitic virus hypothesis) (Donaldson and Gratton 2007) (Table 1). Vector infection status may also alter predator suppression through density and trait-mediated mechanisms. For example, infectious herbivores are often more mobile (Chesnais et al. 2019), making it harder for predators to capture them (vector crypsis hypothesis) (Table 1). However, infectious herbivores may induce plant warning signals, which increases vector apperency (vector apperency hypothesis) (de Oliveira et al. 2014; Martini et al. 2014) (Table 1). Within this ‘food web motif’ framework, the overall effects of a pathogen might be predicted across multiple bi-trophic pathways and net outcome for tri-trophic interactions (Table 1).

Our model experimental system involved a vector, *Acyrthosiphon pisum*, which transmits a pathogen, *Pea-enation mosaic virus* (PEMV), to legume host plants. Within this pathosystem, we conducted a factorial experiment that manipulated top-down effects (*Hippodamia convergens*

predators present vs absent) and bottom-up effects (variation in host-plant quality). With this design, we were able to isolate how PEMV functions as an interaction modifier for bottom-up and top-down effects on vector fitness. Our study reveals that vector-borne pathogens can alter entire food webs by modifying the strength and direction of top-down and bottom-up effects.

## Materials and methods

### Study system

The pea aphid (*Acyrthosiphon pisum*) is a widely distributed phloem-feeding insect herbivore of legumes. In the Pacific Northwest US, *A. pisum* are outbreaking herbivores in pulse crops (Paudel et al. 2018), where they vector several viruses, including PEMV, to plant hosts including dry pea (*Pisum sativum*), lentil (*Lens* spp.), and fava bean (*Vicia faba*) (Clement 2006; Stokes et al. 2013). PEMV is a persistently transmitted pair of obligately mutualistic viruses (enamovirus and umbravirus) that can be rapidly taken up by *A. pisum* and spread by both adults and nymphs within hours of feeding (de Zoeten and Skaf 2001). Severe PEMV infection causes protuberance outgrowth on leaf tissue, discoloration, reduced growth of adult plants, and mortality in seedlings (de Zoeten and Skaf 2001). *A. pisum* populations are excellent vectors for PEMV as they have a wide host breadth in legumes. *A. pisum* facultatively feed and reproduce on weedy vetches (*Vicia* spp., such as *Vicia sativum* and *Vicia villosa*) and clovers (*Trifolium* spp.) adjacent to agricultural and urban habitats (McVean and Dixon 2002). Populations of *A. pisum* can be suppressed by native and introduced predator species such as the native convergent ladybeetle (*Hippodamia convergens*). *Hippodamia convergens* consumption of aphids in particular has been studied

**Table 1** Hypotheses and predictions for how PEMV modifies trophic interactions for pea aphids

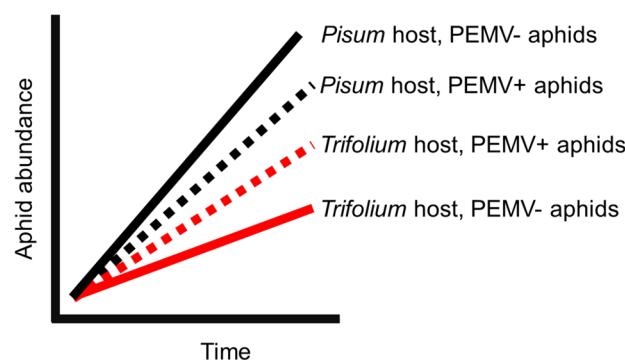
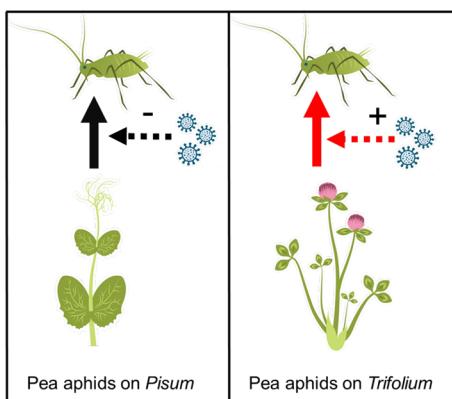
| Food web motif               | Hypothesis                         | Effect | Outcome for aphid vectors                       |
|------------------------------|------------------------------------|--------|-------------------------------------------------|
| Bi-trophic (plant–herbivore) | Mutualistic virus hypothesis (MVH) | (+, 0) | Higher performance for infective aphids         |
|                              | Parasitic virus hypothesis (PVH)   | (-, 0) | Lower performance for infective aphids          |
| Bi-trophic (predator–prey)   | Vector apperency hypothesis (VAH)  | (0, -) | Stronger predation for infective aphids         |
|                              | Vector crypsis hypothesis (VCH)    | (0, +) | Predation weaker for infective aphids           |
| Tri-trophic                  | MVH + VAH                          | (+, -) | Virus helps aphids compensate for depredation   |
|                              | PVH + VAH                          | (-, -) | Virus dramatically lowers aphid abundance       |
|                              | MVH + VCH                          | (+, +) | Virus dramatically increased aphid abundance    |
|                              | PVH + VCH                          | (-, +) | Avoidance compensates for reduced plant quality |

Predictions split into two levels of complexity (bi-trophic and tri-trophic), and effects column indicates effect on herbivore abundance (virus effect on plants, virus effects on predation) coded as + for strengthened, – for weakened, and 0 for not applicable

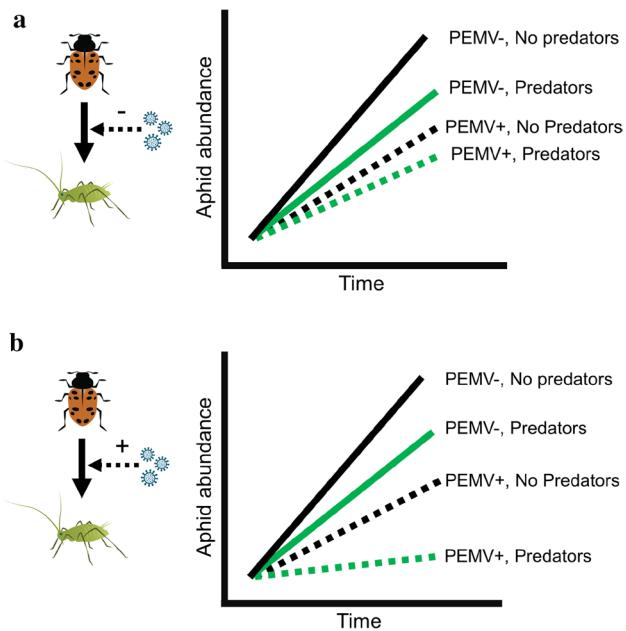
extensively as a model system for predator–prey interactions (Snyder 2009).

### System-specific food web predictions

The impact of vector-borne viral plant pathogens on direct, trophic interactions has been well documented for *Acyrthosiphon pisum*. Thus, we are able to make a priori, system-specific predictions based on hypotheses outlined in Table 1. First, *A. pisum* experiences a range of quality in potential hosts (Hopkins et al. 2017) and will experience higher growth rates on hosts like *P. sativum* compared to low-quality hosts like *Trifolium* spp. (Fig. 1). Importantly, PEMV can modify this relationship, decreasing the difference in host-plant quality experienced by *A. pisum* individuals (Fig. 1). Second, viruliferous *A. pisum* may experience weaker predator effects from *H. convergens* predators by making aphids less apparent to natural enemies due to host-plant selection and feeding behavior (Fig. 2a). Third, effects



**Fig. 1** Diagram of food web motifs for the parasitic virus hypothesis (PVH) and mutualistic virus hypothesis (MVH). Two host-plant species of different quality are shown as an example, *Pisum sativum* and *Trifolium pratense*. In this scenario, the PEMV pathogen has a negative effect on vector abundance on *Pisum sativum*, an outcome that would support the PVH. Conversely, performance is higher on red clover for aphids harboring PEMV, supporting the MVH. Arrows pointing to aphid–plant relationships illustrate ‘interaction modifications.’



**Fig. 2** **a** Diagram of food web motifs for the vector crypsis hypothesis (VCH). In this scenario, PEMV-infectious *A. pisum* could experience less predation relative to non-infectious aphids, supporting VCH. **b** Diagram of food web motifs for the vector apperancy hypothesis (VAH). In this scenario, PEMV-infectious *A. pisum* could experience less predation relative to non-infectious aphids, supporting the VAH. In both panels, viruses are assumed to directly reduce aphid fitness (PVH). Dotted lines indicate aphid populations modified by PEMV, while green lines represent predator presence. Arrows pointing to predator–aphid relationships illustrate ‘interaction modifications.’

of *H. convergens* on vectors may be stronger on viruliferous aphids, because they are more apparent to predators than non-viruliferous aphids (Fig. 2b).

### Greenhouse experiments

We ran a greenhouse mesocosm experiments manipulating predators and infection status of *A. pisum* in an arena of single and multiple host plants (Fig. S2). Our experiment involved a  $2 \times 2 \times 4$  factorial design that manipulated predators (present or absent), infection status of clonal *A. pisum* individuals (infectious or not), and four recipient host-plant species in separate cages (Fig. S3, no-choice assay). Seeds for all host plants were sown on the same date and *A. pisum* were added to plants 3 weeks after seeds were sown. After 1-week post-infestation, we added four *H. convergens* adults as a predator manipulation to each cage at approximately the time adult *A. pisum* would be producing new nymphs (e.g., Darby et al. 2003). *A. pisum* individuals were first established on *Vicia faba* (fava bean) to provide a common source plant among all treatments. Fava has a relatively high host quality for *A. pisum* and all *A. pisum* biotypes appear to perform well on this host (Losey and Eubanks 2000).

Both infectious and non-infectious *A. pisum* colonies were reared in separate greenhouses in cages containing mature *P. sativum* plants (Clark et al. 2019). For both colonies, plant tissue was repeatedly tested to ensure positive or negative PEMV infection status of populations. *Pisum sativum* was used as a host due to this plant species being the original source of the *A. pisum* populations. When *P. sativum* plants appear to be declining, *A. pisum* individuals are transferred to a clean cage with fresh plants. Both *A. pisum* populations only reproduce clonally and did not produce alates in any generations prior to this experiment. To ensure populations do not drift, non-viruliferous *A. pisum* are introduced to viruliferous colonies at least monthly.

For this assay, the goal was to track aphid population growth over 3 weeks on separate host plants with similar starting conditions. Each cage only contained one recipient host-plant species (common vetch, banner pea, red clover, and lentil) with *A. pisum* individuals starting on fava. Seeds were sown in the third week of December 2017 in a separate pathogen-free greenhouse, and the assay began with virus-free plants and *A. pisum* being placed into cages the second week of January 2018. There were six replicates for each plant species ( $n=24$ ), each replicate contained four hosts within a cage, for  $n=96$  plants in a repeated-measures design framework. We had two full replicates (time block 1 and time block 2), and a third incomplete replicate with pea, lentil, and clover—common vetch did not have a full third replication, because not enough viable seedlings germinated (included in time block 2 as this replicate occurred simultaneously). Ten adult *A. pisum* individuals were placed on fava immediately after the plant array was arranged, and the number of established adult and nymph *A. pisum* produced in the first 24 h were recorded. We then tracked aphid adult and nymph *A. pisum* abundance on each plant every 48 h, using a dental mirror to count individual aphids on the underside of leaves. Aphids were counted on the same days at these 48 h intervals across all treatments (predators, PEMV, and host plants).

## Statistical methods

We all Generalized Linear Mixed Models (GLMMs) using the glmmTMB package (Brooks et al. 2017) in R 3.6.2 (R Core Team 2020). Post hoc tests for all models were a priori contrasts examining differences in *A. pisum* abundance on days 8, 10, 12, 14, 16, 18, and 20. The emmeans package (Lenth 2016) was used to plot estimates of the mean and standard error based on the fitted GLMMs. Critical values and significance tests ( $P$  values) were estimated using analysis of deviance with the car package (Fox and Weisberg 2011). The number of *A. pisum* individuals on individual recipient plants was used as a response variable in all models. Since *A. pisum* counts per plant per day followed

a discontinuous Poisson distribution with peak abundances near zero (low density) and a second peak at higher densities, we fit GLMMs using the Tweedie distribution (Brooks et al. 2017). The glmmTMB package can effectively handle cases of extreme overdispersion observed in ecological studies modeling reproduction resulting from the same population containing individuals producing no offspring or very large numbers of offspring (Brooks et al. 2019).

Explanatory factors for the GLMM on aphid abundance included predator treatment (present, absent), PEMV status (infectious, control), recipient host-plant species (pea, vetch, clover, and lentil), and all accompanying first and second order terms. The fixed effects were nested within duration (days), with cage as a random effect. We also completed a single follow-up GLMM for aphids on the source plan, Fava (see Online Appendix 1, model specification). A ‘source aphids’ GLMM was intended to provide further insight into aphid movement over the course of the experiment without violating the autocorrelation assumptions of GLMM (i.e., by included ‘source aphids’ in the primary analysis). Overall, similar repeated-measures, mixed model approaches have been used to evaluate treatment effects on aphid population density over time (Alins et al. 2017). Further details on these linear models are found in Online Appendix 1: Model Specification for GLMMs.

## Results

### Direct effects of time, host plants, PEMV, and predators

The abundance of *A. pisum* individuals on recipient plants varied significantly over the course of the experiment, increasing over the 21-day assay (Table 2,  $P < 0.001$ ).

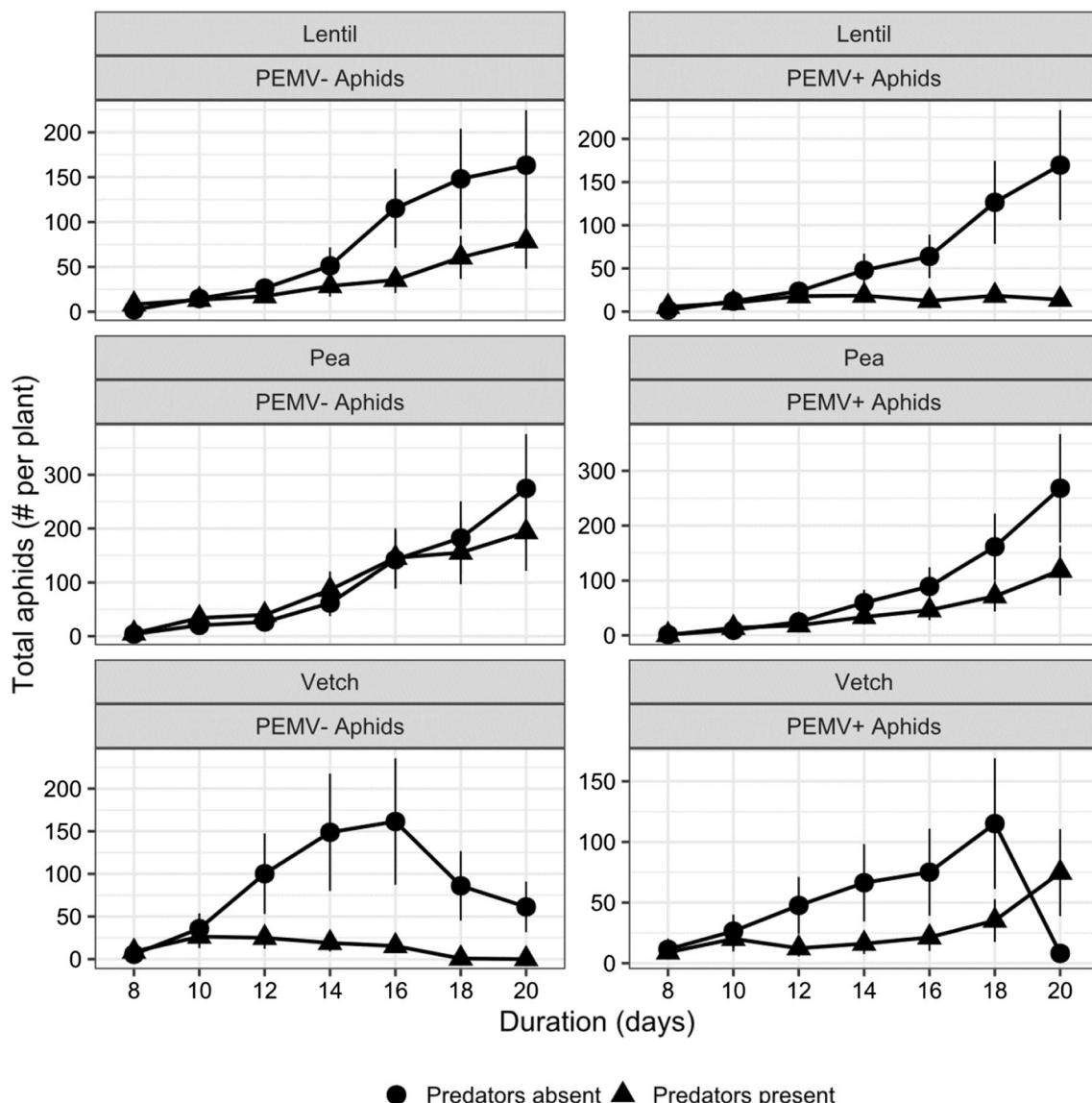
**Table 2** GLMM analysis of deviance tests for abundance of aphids on recipient plants

| Analysis of deviance table (type II Wald Chi-squared tests) |          |      |           |
|-------------------------------------------------------------|----------|------|-----------|
| Factor                                                      | $\chi^2$ | D.f. | $P$ value |
| Duration                                                    | 1153     | 7    | <0.001    |
| Duration (predators)                                        | 164.8    | 8    | <0.001    |
| Duration (host plant)                                       | 273.8    | 22   | <0.001    |
| Duration (PEMV)                                             | 13.60    | 7    | 0.0587    |
| Duration (predators $\times$ host plant)                    | 97.48    | 21   | <0.001    |
| Duration (predators $\times$ PEMV)                          | 5.417    | 7    | 0.6092    |
| Duration (host plant $\times$ PEMV)                         | 56.46    | 21   | <0.001    |
| Duration (predators $\times$ host plant $\times$ PEMV)      | 41.14    | 21   | 0.005     |

All treatment effects are nested within day (duration factor). Obs.=1232, dorms=44 (random effect), random effect variance=0.3579

Abundance of *A. pisum* also varied significantly among host-plant species (Table 2,  $P < 0.001$ ), with the highest abundance observed on lentil and pea, intermediate abundances on vetch, and the lowest abundance on clover (Fig. 3). Over the course of the 20-day assay, both host-plant species and PEMV interactively determined the abundance of *A. pisum* (Fig. 3; Table 2 host plant  $\times$  PEMV interaction,  $P < 0.001$ ), where PEMV modified the plant–herbivore interaction. Abundance of infectious *A. pisum* was significantly lower on *P. sativum* on day 16 (Fig. 3), while infectious *A. pisum* abundance was consistently lower on lentil after day 16. At

day 16, non-viruliferous *A. pisum* were significantly more abundant on *P. sativum*, while on day 18, viruliferous *A. pisum* were significantly more abundant on vetch (Fig. 3). However, on vetch, aphid populations became smaller on the final day (Fig. 3). Predators significantly reduced *A. pisum* abundance under certain conditions, depending on host-plant species and infection status (Fig. 3; Table 2, predator  $\times$  host plant  $\times$  PEMV,  $P = 0.005$ ). Predators suppressed infectious *A. pisum* on lentil and pea; however, predators did not reduce non-infectious *A. pisum* abundance on these two hosts. Predators suppressed *A. pisum* abundance on vetch for the third



**Fig. 3** Plot for change in *A. pisum* abundance over time in response to predators, host-plant species, and infection status. Each panel indicates a separate plant species with a *A. pisum* performance measured for PEMV-infectious and non-infectious aphids. Circle points indicate *A. pisum* populations without predators (control) and triangle points indicate predators present (ladybeetles added). Predators and PEMV

had no significant effect on *A. pisum* abundance for clover at any of the time points in this assay (not shown). Points indicate predicted marginal mean from GLMM and bars indicate error of the associate regression coefficient. Within each day, bars not overlapping are significantly different (planned contrasts)

week of the assay, but the strength of this effect weakened by the end of the assay at 20 days (Fig. 3). For source plants (Fava), we observed a significant negative effect of predators on source aphid abundance that peaked at day 16 and 18 of the assay (Fig. S4, GLMM,  $\chi^2=60.03$ ,  $P<0.001$ ).

### Support for PEMV modifying aphid trophic interactions

The effect of PEMV was predicted to vary among host-plant species with multiple competing hypotheses (Table 1). On lentil and pea, PEMV had a negative impact on *A. pisum* over time, supporting the parasitic virus hypothesis ('PVH'). Under some restricted scenarios, such as on vetch, *A. pisum* performance was higher for a short period when PEMV was present, providing weak support for the mutualistic virus hypothesis ('MVH'). We also observed predation effects of *A. pisum* differed for PEMV-infectious and non-infectious aphids, with predator effects being stronger for PEMV-infectious *A. pisum* on two host plants, pea and lentil, supporting the vector apparent hypothesis ('VAH'). In total, there were multiple lines of evidence showing the tri-trophic interactions of *A. pisum* was altered by PEMV, primarily due to the PVH and VAH (Table 1). Overall, PEMV generally had an overall negative impact on *A. pisum*, reducing their performance and increasing natural enemy risk. However, for weedy hosts, PVH and VCH were supported, because avoidance from predators compensated for reduced host-plant quality. We observed no support for either hypotheses for red clover, likely due to its exceptionally low quality in for *A. pisum* in all scenarios.

## Discussion

Ecologists have long-argued that examination of bi-trophic interactions in isolation is insufficient to understand variation in herbivore abundance (Bernays and Graham 1988; Janzen 1988; Dyer 1995). For example, herbivore performance on certain host plants is contingent on predators (Denno et al. 1990; Stamp 2001), but susceptibility to predators always occurs in the context of host-plant traits (Benrey and Denno 1997). Since most plant viruses are transmitted by insect herbivores (Hogenhout et al. 2008), we posited that a tri-trophic approach would generate new insights into host–vector interactions. Our results verify conclusions in which host-plant community composition mediates the spread of vector-borne pathogens, particularly in systems where many plant species are suitable virus hosts (Malmstrom et al. 2005). Results also suggest that viruliferous herbivores can have considerably different rates of predator suppression compared to non-viruliferous conspecifics (Martini et al. 2014). However, by manipulating

both host-plant species identity and predator presence, our work shows several emergent mechanisms by which plant pathogens can impact the tri-trophic interactions of vectors that otherwise would not be seen if studied from a bi-trophic perspective. For example, pea and lentil were the highest quality host plant for *A. pisum*, but when pathogens were present, *A. pisum* experienced the strongest predator effects. Consequently, if we had only observed plant–vector interactions (bi-trophic) we may conclude that high host quality can overcompensate for reduced vector fitness due to PEMV.

The effects of vector-borne pathogens on vector fitness and behavior are a key component of vector–virus interactions. Vector-borne pathogens exist on a continuum ranging from parasitism to mutualism, where some viruses consistently reduce vector fitness, increase suitability to predators (de Oliveira et al. 2014), or increase vector performance (Mauck et al. 2012). For two host-plant species, we found consistently negative effects of PEMV on *A. pisum*. However, for a short duration of time, this was not the case for one of our host-plant species: *Vicia sativa*. On this host, *A. pisum* performance was marginally higher at the end of the assay. In other systems, aphid-borne pathogens may be mutualistic if they facilitate predator avoidances through changes to herbivore vector behavior (Belluire et al. 2008). We suspect PEMV indirectly caused *A. pisum* to achieve some level of enemy-free space on the weedy host vetch (Stamp 2001; Williams et al. 2001). It is also likely that vetches have a low carrying capacity for *A. pisum* (Clark et al. 2019), and predators recruited to fava plants which had relatively higher aphid densities across the assay. Past work indicates that *A. pisum* disperse more evenly when host plants are infected by PEMV and that *Vicia* is a suitable *albeit* low-quality host for *A. pisum* (Clark et al. 2019). Due to lower density and larger dispersal radius on plants due to PEMV, *A. pisum* may be less likely to encounter predators.

Prior studies have pointed out the utility of drawing commonality between plant–herbivore and plant–pathogen interactions when discussing the host range of pathogens and herbivores, given that both co-evolve with hosts, and host-plant shifts are rare due to obligate associations (Raffa et al. 2020). For example, *A. pisum* populations are generally constrained to a narrow range of legume hosts, but ‘host races’ of *A. pisum* exhibit specialization on sub-groups of legumes (Caillaud and Via 2000; Frantz et al. 2006; Peccoud et al. 2009). This sympatric adaptation to host plants likely involves a combination of genetic specialization (Peccoud et al. 2009) and an ‘extended phenotype’ of bacterial endosymbionts that allow *A. pisum* to overcome plant defensive compounds (McLean et al. 2011). If PEMV functions similarly as an extended phenotype of *A. pisum*, this fits with the prediction that many aphid–virus

interactions may be a co-evolved mutualism (Hansen and Moran 2014; Lefevre et al. 2019). We did not find support for the hypothesis that vectored viruses are predominantly beneficial for vectors, nor did they alter *A. pisum* performance on one host-plant species (clover). However, we did demonstrate that viruses impact variation in *A. pisum* performance among host species. Consequently, pathogens like PEMV may be important to consider when trying to predict the host range of vectors.

One of the goals of tri-trophic interactions theory is to predict when herbivores are able to escape top-down or bottom-up control and outbreak (e.g. Kersch-Becker and Thaler 2015; Madahai et al. 2015; Nesbit et al. 2016; Mehrparvar et al. 2019). Not only is this important for understanding ecosystem function, because insect herbivores are dominant consumers in terrestrial food webs (Bernays and Chapman 1994), but also because insect herbivores are economically important pests in forestry and agriculture (Eberl et al. 2020; Strange and Scott 2005). Consequently, any ecological factor that can help explain the abundance or movement of herbivores has important ramifications for ecological communities. In our study, PEMV infection status fundamentally shifted the tri-trophic interactions of a dominant herbivore species. Other studies show that non-trophic interactions alter the trophic interactions of consumers in food webs (e.g., Bond and Lavers 2014). Many other insect herbivores beyond *A. pisum* frequently vector plant pathogens (i.e., are viruliferous), but this has rarely been considered when trying to understand how predators and host-plant variation impact herbivore abundance. We conclude that vector-borne pathogens play an underappreciated role in modifying top-down and bottom-up effects that regulate herbivore populations.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s00442-021-04987-8>.

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**Author contribution statement** REC conducted the experiments and analyses. Both authors designed the experiments and wrote the manuscript.

## Declarations

**Conflict of interest** The authors declare that they have no conflict of interest.

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