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RESEARCH ARTICLE

Meta-analysis reveals strong evidence for adaptive host and vector manipulation by plant viruses

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Abstract

1. Plant viruses often enhance their own transmission by modifying host phenotypes and vector behaviour, leading to the hypothesis that such effects are manipulations due to virus adaptations. However, few studies have linked putative manipulations with virus components, and the true frequency and magnitude of host and vector manipulation across virus taxa remain unknown.
2. We used meta-analysis to combine data from 215 studies to quantify convergence in virus effects on host plants that influence vector orientation and feeding behaviour and performance. We compared effects across taxonomic groups of viruses that share transmission mechanism traits and thereby may benefit from similar effects on vector behaviour and performance.
3. Our study considered virus transmission traits such as the infection location in the host (phloem vs. nonvascular tissue) and retention mechanism in vector arthropods to assess evidence for or against adaptive manipulation. We interpreted results in the context of virus taxonomic relationships, virus–vector relationships and host domestication status.
4. Overall, virus transmission traits strongly predicted the magnitude and nature of virus effects on vector preferences and performance. Consistent with predictions that increased vector–host contacts are beneficial, we found increased attractiveness to vectors is a host change common to all virus lineages. However, enhanced vector settling and feeding on infected plants is only apparent for phloem-restricted viruses that require vectors to engage in extended phloem feeding for acquisition. We also found that phloem-restricted viruses are associated with enhanced vector performance on infected hosts, but only for viruses that do not replicate in vectors. Across all analyses, plant viruses rarely elicited phenotypes that negatively affect vector transmission.

5. Our results confirm that host and vector manipulation are important aspects of plant virus ecology and evolution. However, limitations of existing studies include a focus on agriculturally important viruses and a bias toward studying virus effects in domesticated plants. Our synthesis emphasizes the need to incorporate more pathosystems and transmission traits in future studies.

KEYWORDS
phloem-limited viruses, plant virus ecology, vector behaviour, vector-host interactions, virus transmission

1 | INTRODUCTION

Arthropod-borne plant viruses establish systemic infections in both wild and crop plants that can result in disease conditions and major economic impacts (Jones, 2021; Sastry & Zitter, 2014). To reside in hosts, plant viruses have adaptations for managing host immunity, host resources and host vascular tissue to promote replication and movement (Patarroyo et al., 2012; Rojas et al., 2016; Yang & Li, 2018). Host changes that result (symptoms), and virus genes underlying symptoms, are often studied because of their effects on plant health. However, symptoms of infection can also indirectly affect interactions with vectors via changes in plant cues that mediate host seeking and feeding, such as visual traits, odour, palatability, defences and nutritional quality (Mauck et al., 2018; Ray & Casteel, 2022; Zhao et al., 2022). The reliance of many viruses on vectors for transmission has led to predictions that many viruses have evolved to elicit host phenotypes that increase transmission-conducive interactions.

There are now several hundred studies that test how one or more viruses affect hosts in ways that affect vector attraction, settling and feeding behaviour, or performance. A synthesis of these studies, which determines whether virus traits predictably mediate effects on host plants and vectors, could promote understanding of whether putative instances of vector manipulation by viruses are a result of adaptations or simply by-products of pathology (Thomas et al., 2005). If host manipulations stem from virus adaptations, viruses transmitted via the same mechanisms may exhibit convergence in effects on plant cues mediating vector–host interactions (Mauck et al., 2016, 2018; Thomas et al., 2005). Similar convergence in manipulation strategies is apparent in diverse lineages of animal-infecting parasites transmitted by blood-feeding vectors, suggesting such effects are adaptive (Lefèvre & Thomas, 2008; Thomas et al., 2005).

Plant viruses have diverse transmission mechanisms that may affect the elicitation of specific host phenotypes. One distinction is between phloem-limited viruses that require long feeding bouts by vectors for transmission and non-phloem-limited viruses transmitted with short feeding bouts (Hogenhout et al., 2008; Nault, 1997; Ng & Falk, 2006; Ng & Zhou, 2015). Both types of viruses are expected to alter hosts in ways that make infected plants more attractive than non-infected plants (Mauck et al., 2012, 2018). Yet, phloem-limited viruses are also expected to increase vector performance (the organism's ability to thrive and reproduce) and promote the long feeding bouts that are needed for acquisition, while non-phloem-limited viruses are expected to lower vector performance and promote rapid dispersal away from infected hosts after short feeding probes (Mauck et al., 2012, 2018). Despite a growing number of empirical studies testing these predictions, we currently lack a quantitative synthesis assessing whether viruses with similar characteristics have predictable and adaptive effects on host phenotypes, vector behaviour and vector performance.

To address whether plant viruses with different transmission mechanisms manipulate hosts and vectors in ways that reliably promote transmission, we conducted a global meta-analysis. Our analysis considered virus host infection location, vector behaviours required for transmission (Brault et al., 2010), and virus persistence in vectors as a framework to assess evidence for or against adaptive host manipulation (Figure 1). A glossary of terms for the virus traits and vector responses discussed is in Table S1 (Appendix S1). Phloem-limited viruses are restricted to host vascular tissue, whereby acquisition of sufficient virions for transmission depends on vectors sustaining phloem feeding for hours or even days (Brault et al., 2010; Hogenhout et al., 2008). Acquisition of phloem-limited viruses should be favoured when viruses increase host palatability (e.g. cues that stimulate increased feeding) or quality (e.g. increased nutrients) so vectors engage in extended feeding bouts (Mauck et al., 2012). Following acquisition, most phloem-limited viruses are retained in vectors for days (non-circulative-semi-persistent) or life (circulative-persistent) and can be inoculated to multiple hosts. Some circulative-persistent viruses traverse the gut and colonize the salivary glands (circulative-persistent-non-propagative), while others colonize and replicate in vectors (circulative-persistent-propagative; Hogenhout et al., 2008). For both circulative-persistent retention mechanisms, a single acquisition event can lead to multiple new infections.

In contrast, most non-phloem-limited viruses are transmitted following brief probes of nonvascular tissues such as epidermal or mesophyll cells (Martin et al., 1997; Ng & Falk, 2006). These non-circulative–non-persistent viruses account for ~40% of all known vector-borne plant viruses. Non-circulative–non-persistent viruses are rapidly lost from vector mouthparts and are retained for very short periods following acquisition, which limits inoculation

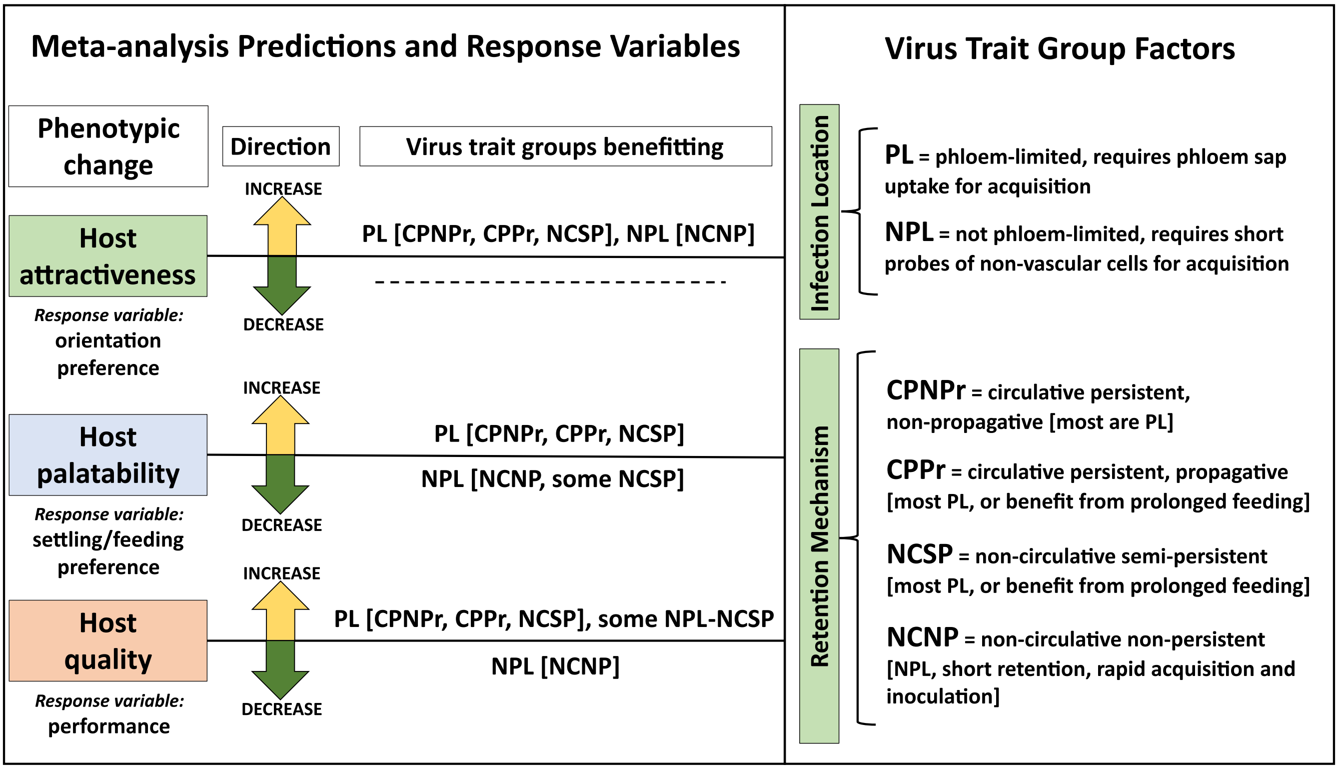

FIGURE 1 Predictions, response variables and factors included in the meta-analysis. For each predicted direction of the effect size, 'increase' means that virus infection enhances vector preferences for infected plants (host attractiveness, host palatability) or vector performance when living on infected plants (host quality).

potential for a vector to 1–2 plants (Hogenhout et al., 2008; Nault, 1997). As a result, the spread of most non-phloem-limited viruses is favoured by the rapid dispersal of vectors away from infected hosts (Hogenhout et al., 2008; Martin et al., 1997; Nault, 1997; Wang & Ghabrial, 2002).

By clearly defining host infection location: (i) phloem-limited (PL) vs. (ii) non-phloem-limited (NPL) and retention mechanism in vectors: (i) non-circulative-non-persistent (NCNP), (ii) non-circulative-semi-persistent (NCSP), (iii) circulative-persistent-non-propagative (CPNPr) or (iv) circulative-persistent-propagative (CPPr), we created a framework for testing the adaptive role of host and vector manipulation by viruses. We then quantified the effects of plant virus infection on three vector responses: (i) orientation preferences, (ii) settling/feeding behaviour and (iii) performance. We predicted viruses from all groups would induce host changes that promote vector orientation preferences for infected hosts over non-infected ones to increase vector contacts (Figure 1). We further predicted that increased vector settling/feeding and performance on infected compared to non-infected plants would only be apparent for virus taxa that require sustained phloem ingestion and vectors that are viruliferous (carrying the virus and capable of spreading it) for long time periods (Figure 1). We tested predictions using a meta-analysis of 215 published studies covering 72 viruses belonging to 14 families in association with hosts from 18 different families. Results were interpreted in the context of additional ecological dimensions known to affect virus transmission by insect vectors.

2 | MATERIALS AND METHODS

2.1 | Database assembly

We conducted an extensive literature search for studies of virus–host–vector interactions, using the ISI Web of Knowledge and Google Scholar (Mauck et al., 2012). We used terms including 'insect vector', 'non-persistent virus', 'persistent virus', 'plant virus', 'vector behaviour', 'vector performance' and 'virus–host–vector interactions', and specific family and species names of viruses and vectors to identify studies assessing effects of viruses on hosts and vectors. We also surveyed the references in review articles on virus–host–vector interactions (Bosque-Pérez & Eigenbrode, 2011; Eigenbrode et al., 2017; Eigenbrode & Bosque-Perez, 2016; Fereres & Moreno, 2009; Mauck et al., 2010, 2012, 2018). Articles were initially screened by scanning the titles and abstracts, which left ~500 studies that were assessed using three criteria: (i) the study included data on vector orientation behaviour, feeding/settling behaviour or performance for an infected and healthy plant, (ii) the study reported means, sample sizes and variances and (iii) the study reported data on a vector-borne virus. Our final database included 215 studies covering 89 virus × plant family combinations. A list of data sources used in the study are provided in the Data sources section of this manuscript. Appendices S2–S4 contain data tables with all factors listed, and all data and code are also available on the Data INRAE repository https://doi.org/10.57745/HF9NFG (Chesnais & Mauck, 2025). However, results were based on an inconsistent number of plant comparisons across hosts. Vector orientation data included 142 comparisons from 49 studies, vector settling/feeding data included 519 comparisons obtained from 124 studies, and vector performance data included 654 comparisons from 123 studies. We recorded multiple data points from a single study if it examined more than one relevant response or more than one host-vector combination. We also recorded virus traits related to transmission location and retention mechanism (Figure 1). For analyses by virus classification, we included families with at least three independent vector responses. Table 1 provides an overview of the modifiers we considered in our models (scale of inference) and levels within each modifier (scale applied).

2.2 | Effect size calculation

For each non-infected/infected plant comparison, we recorded the mean, standard deviation and sample size related to: (i) vector orientation preference, (ii) vector settling/feeding behaviour or (iii) vector performance. Data were obtained from tables or plots using Plot Digitizer (Huwaldt & Steinhorst, 2013). Orientation preference was any vector response to plant cues without host contact, including: (i) emigration and immigration rate (e.g. moving away from or toward an infected host), (ii) landing preference (where the vector would make contact based on cues perceived from a distance) or (iii) orientation preference (in a Y-tube olfactometer or near plant headspace). Settling/feeding preference was any vector response to plants that occurred following contact, including: (i) settling preference (e.g. selecting between adjacent leaves of infected and non-infected plants), (ii) retention time on hosts or time to dispersal (how long a vector remains after making a selection) or (iii) feeding behaviours that were measured by electrical penetration graph (e.g. navigation to vascular tissue, salivation in vascular tissue and uptake of vascular tissue). Vector performance was any response affecting (i) population growth (production of offspring by groups of vectors), (ii) fecundity (production of offspring by a single vector), (iii) development time (time to adulthood or maturity), (iv) longevity (total lifespan of the vector), (v) survival, (vi) weight or size. If studies had more than one measurement in a single category, we used two additional criteria. First, for studies that included repeated measures (e.g. retention behaviour after 1, 2, 24 h), we used measurements corresponding to the first and final time points because these correspond to the initial response to the host and the final choice. Second, for studies that included different points in disease progression, we reported all of the data (e.g. settling behaviour at 15, 20, 25, or 30 days) because virus-induced effects may change with the stage of the infection (Chesnais et al., 2022). To account for non-independence of these data points in statistical models, we included the study identifier as a random effect.

For each comparison, we calculated the virus effect size using the Hedges' g metric and its confidence interval (Hedges, 1981). Hedges g is calculated as $g = \left[\left(X_i - X_h \right) / s \right] \times J$, where X_i is the mean of the vector parameter on the infected plant, X_h is the mean of the vector parameter on the non-infected plant, s is the pooled standard deviation, and J is a correction factor for small sample size (Koricheva et al., 2013). Positive Hedges' g values indicate that the vector preferred or performed better on infected plants compared

TABLE 1 Replication statement.

Scale of inference	Scale at which factor of interest is applied	Number of replicates (experiments) at the appropriate scale
Virus infection location	Phloem-limited viruses	111
	Non-phloem-limited viruses	31
Virus retention mechanism in vectors	Circulative persistent, propagative	32
	Circulative persistent, non-propagative	68
	Non-circulative, semi-persistent	14
	Non-circulative, non-persistent	28
Virus classification (family)	Bromoviridae	15
	Caulimoviridae	2
	Closteroviridae	7
	Geminiviridae	15
	Nanoviridae	2
	Potyviridae	15
	Reoviridae	25
	Rhabdoviridae	2
	Secoviridae	3
	Solemoviridae	51
	Tospoviridae	5
Host domestication status	Domesticated	136
	Wild	5

to non-infected plants, whereas negative values indicate they preferred or performed better on non-infected plants. When necessary, we reversed the sign of the effect size, so a negative value of g always indicates a negative effect of virus infection; for example, decreased development time on infected plants represents increased performance. Hedges' g and its sampling variance were calculated using the '*escalc*' function in the '*metafor*' package in *R* 3.6.0 (Viechtbauer, 2010).

2.3 | Meta-analysis and meta-regression

We first calculated a mean effect size for each response across all studies to assess whether there was an overall effect of virus infection. We considered model-estimated effect sizes with 95% confidence intervals that did not cross zero as significant. We then tested how three moderators affected the magnitude and direction of effects using random-effects meta-regression: (i) infection location (phloem-limited, non-phloem-limited), (ii) retention mechanism (non-circulative-non-persistent, non-circulative-semi-persistent, circulative-persistent-non-propagative, circulative-persistent-propagative) and (iii) virus classification. We acknowledge that there is some collinearity among these moderators. For example, infection location and retention mechanism are mostly correlated (non-circulative non-persistent = non-phloem limited, and circulative categories = persistent), but non-circulative semi-persistent viruses can be both phloem-limited and non-phloem limited. Fitting separate models for each moderator allows us to assess if the effects of infection location differ when we consider nuances of vector retention mechanism. Within the virus classification moderator, each of the 11 virus families tends to be associated with one infection location and one transmission mechanism. However, fitting a separate model with the virus classification moderator enables us to see if families that share the same infection location and retention mechanism have similar effects. We fit the multilevel mixed effects models using the '*rma.mv*' function in the R package *metafor*, which weighted each effect size by the inverse of its sampling variance plus the residual heterogeneity not explained (Viechtbauer, 2010). To account for the non-independence of data from the same paper, we used study identity (the unique publication) as a random effect in all models. When significant moderator effects were detected, we carried out post hoc comparisons using the *multcomp* package in *R* (Hothorn et al., 2008). In addition to results detailed specifically below, we include a comprehensive set of tables and figures in the appendices that show virus effects sorted by infection location, retention mechanism and taxonomic classification (Appendix S1).

2.4 | Heterogeneity statistics and bias analysis

For models, we assessed residual heterogeneity using the QE statistic (Koricheva et al., 2013; Viechtbauer, 2010). To assess the potential for publication bias, we used funnel plots and meta-regression models with 'study year' and 'plant domestication' (wild or domesticated) as moderators (Koricheva et al., 2013). Fail-safe numbers for plant virus infection were also calculated for each response using the Rosenthal method, which indicate the number of nonsignificant unpublished or missing studies that would negate results, generally calculated as $5n + 10$, where n is the number of studies included in the meta-analysis (Rosenthal, 1979).

3 | RESULTS

3.1 | Effects of plant virus infection on vector behaviour and performance

Overall, plant virus infection had significant positive effects on host phenotypic traits mediating vector orientation (Figure 2; Tables S2 and S3), settling/feeding (Figure 3; Tables S2 and S4) and performance (Figure 4; Tables S2 and S5). There was a low probability that publication bias affected our results (Figures S1–S3), although the effect size for vector performance was higher on wild plants than cultivated ones ($p = 0.0003$, Table S2, Figure S3). Analysis of fail-safe numbers also indicated results were robust (Table S6). However, we found significant QE values for all models ($p < 0.0001$, Table S2), suggesting there were important moderators that we did not include in meta-regression analyses.

3.2 | Effects of virus transmission location in hosts on vector behaviour and performance

Effects of plant viruses on vector orientation varied with host transmission location ($Q_M = 27.4$, $p < 0.0001$; Figure 2; Table S2). Plants infected by phloem-limited viruses were more attractive to vectors than non-infected plants, but plants with non-phloem-limited viruses were similarly attractive as non-infected plants (Figure 2; Table S3). Effects of virus infection on vector settling and feeding also varied by host transmission location ($Q_M = 33.1$, $p < 0.0001$; Figure 3; Table S2). Both phloem-limited and non-phloem-limited viruses had greater vector settling and feeding compared to non-infected plants, but the effect was stronger for phloem-limited viruses (Figure 3; Table S4). Phloem-limited viruses also had stronger effects on vector performance than non-phloem-limited viruses ($Q_M = 39.1$, $p < 0.0001$; Figure 4; Table S2). Plants infected by a phloem-limited virus had greater vector performance than non-infected plants, but plants infected with non-phloem-limited viruses did not have altered vector performance (Figure 4; Table S5).

3.3 | Effects of virus retention mechanisms in vectors on vector behaviour and performance

Effects of plant viruses on vector orientation varied with retention mechanism in the vector ($Q_M = 90.6$, $p < 0.0001$; Figure 2; Table S2).

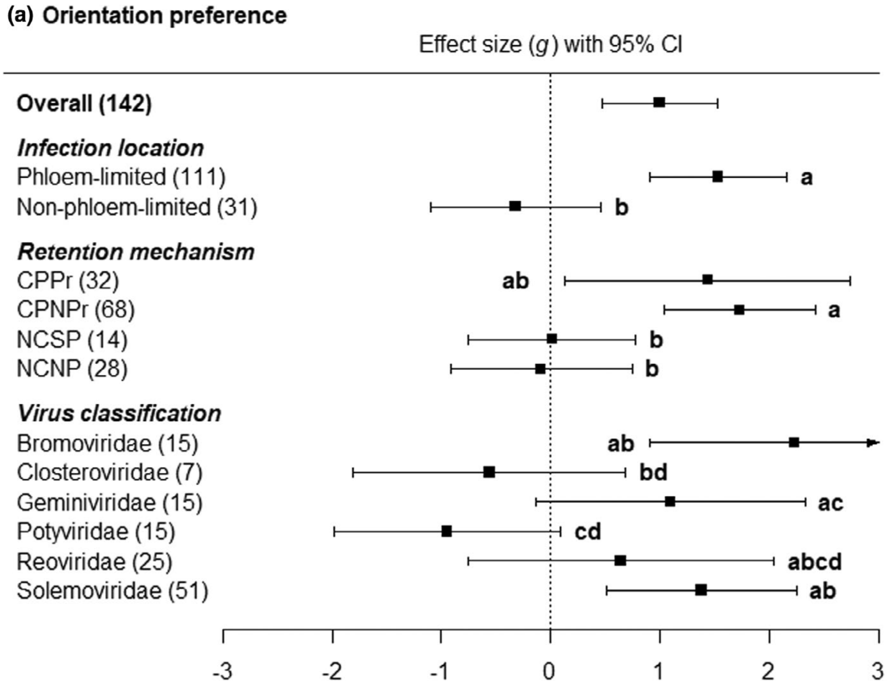

FIGURE 2 Effect size (Hedges' *g*) estimates and 95% CIs showing the effects of virus infections in plants on vector orientation preferences. Positive *g* values indicate a preference of vectors for infected compared to non-infected hosts. Arrows at the ends of error bars indicate 95% CIs that are outside the scale of the plotting region. Numbers in brackets indicate the number of studies each estimate. Different letters indicate significant differences among effect sizes within each grouping factor (infection location, retention mechanism and virus classification).

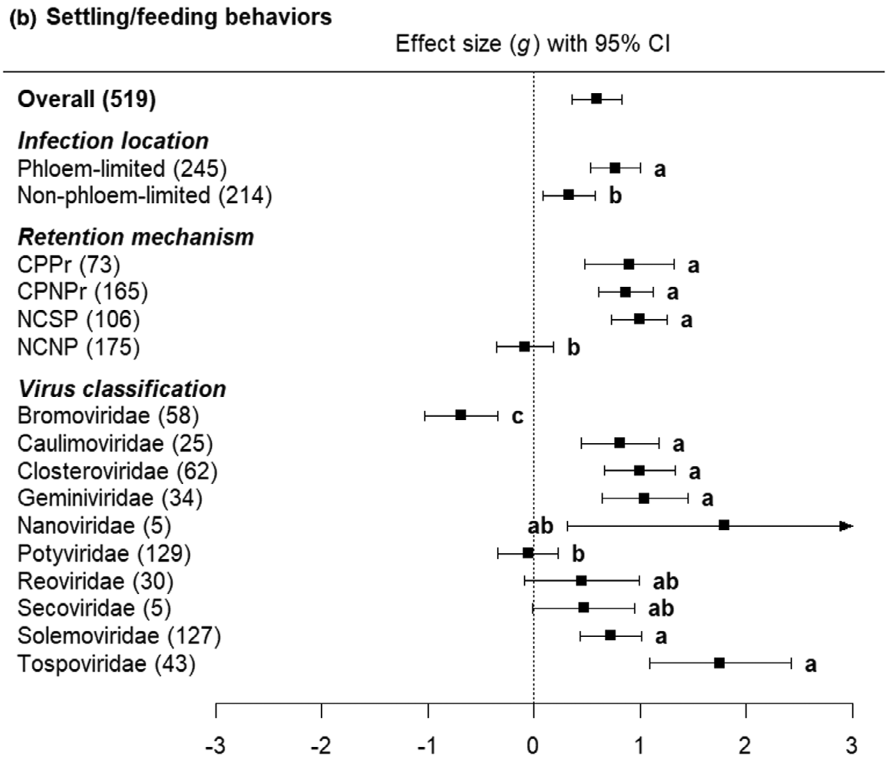

FIGURE 3 Effect size (Hedges' *g*) estimates and 95% CIs showing the effects of virus infections in plants on vector settling/feeding behaviour. Positive *g* values indicate a preference of vectors for infected compared to non-infected hosts. Arrows at the ends of error bars indicate 95% CIs that are outside the scale of the plotting region. Numbers in brackets indicate the number of studies each estimate. Different letters indicate significant differences among effect sizes within each grouping factor (infection location, retention mechanism, and virus classification).

Plants infected by circulative-persistent viruses were more attractive to vectors than non-infected plants but altered vector attraction was not seen in non-circulative viruses (Figure 2; Table S3). Effects of plant viruses on vector settling and feeding also varied with retention mechanism in the vector ($Q_M = 78.3$, $p < 0.0001$; Figure 3; Table S2). Plants with both circulative-persistent virus types, or non-circulative-semi-persistent viruses, altered hosts in ways that encouraged greater vector settling/feeding on infected plants compared to non-infected plants, but plants with non-circulative–non-persistent viruses did not (Figure 3; Table S4). Virus retention mechanism also affected vector performance ($Q_M = 40.8$, $p < 0.0001$; Figure 4; Table S2). However, only infection by circulative-persistent-non-propagative viruses increased vector performance on infected over non-infected hosts; infections by other virus types did not alter vector performance on infected relative to non-infected hosts (Figure 4; Table S5).

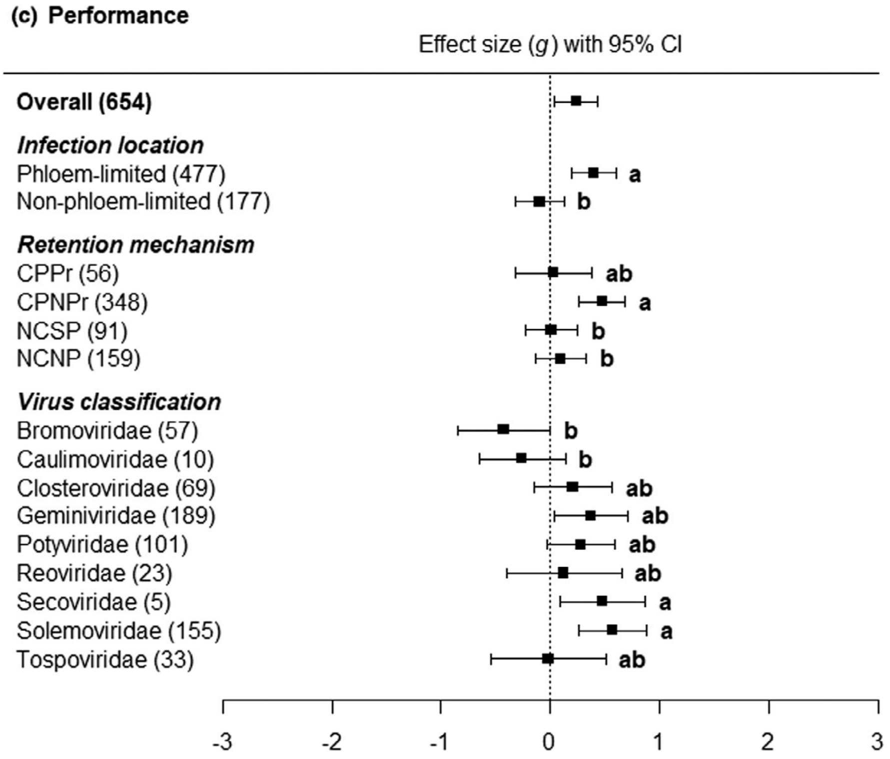

FIGURE 4 Effect size (Hedges' *g*) estimates and 95% CIs showing the effects of virus infections in plants on vector performance. Positive *g* values indicate higher performance of vectors on infected compared to non-infected hosts. Numbers in brackets indicate the number of studies each estimate. Different letters indicate significant differences among effect sizes within each grouping factor (infection location, retention mechanism and virus classification).

3.4 | Effects of virus classification on vector behaviour and performance

Effects of plant virus infection on vector orientation preference varied by virus family ($Q_M = 112.0$, $p < 0.0001$; Figure 2; Table S2). Of the six virus families with sufficient data, viruses in the *Bromoviridae* and *Solemoviridae* caused hosts to be more attractive than non-infected plants, but plants infected by members of *Closteroviridae*, *Geminiviridae*, *Potyviridae* and *Reoviridae* were not differentially attractive (Figure 2; Table S3). Effects of plant infection on vector settling and feeding also varied by virus family ($Q_M = 136.9$, $p < 0.0001$; Figure 3; Table S2), with ten families having sufficient representation for analysis. Infections by members of six different virus families tested increased vector settling/feeding relative to non-infected plants, infections by members of *Potyviridae*, *Reoviridae* and *Secoviridae* had no effect, and infections by *Bromoviridae* decreased vector settling and feeding (Figure 3; Table S4). Finally, effects of plant infection status on vector performance varied based on the virus family ($Q_M = 63.2$, $p < 0.0001$; Figure 4; Table S2), with nine virus families represented in the analysis. Infections by the *Geminiviridae*, *Secoviridae* and *Solemoviridae* increased vector performance on infected relative to non-infected plants, infections by *Bromoviridae* decreased vector performance, and infections by other virus families did not affect vector performance (Figure 4; Table S5).

4 | DISCUSSION

Our synthesis supported the prediction that enhanced vector settling, feeding and performance on infected plants would be more apparent for viruses that require long-term feeding bouts for transmission. Phloem-limited viruses elicited enhancements in settling and feeding preferences, and performance on infected hosts, while also increasing attractiveness to vectors. In contrast, non-phloem-limited viruses promoted settling and feeding on infected plants but did not alter host attractiveness or vector performance. Yet, a neutral effect of viruses on plant phenotypes mediating vector attraction, feeding or performance is still consistent with an adaptive explanation for virus effects, as has been found in animal parasite systems (Anderson et al., 1992; Poulin, 2010). For example, viruses could evolve traits that facilitate more rapid systemic infection in plant hosts, higher titres, or even an expanded host range (Elena, 2017). But if these traits also change plant phenotypes in ways that reduce transmission opportunities via interactions with vectors, the new virus genotype is less likely to spread to additional hosts. A lack of truly maladaptive effects in our meta-analysis suggests that there is selection against virus genotypes that elicit phenotypes with negative effects on vector–host interactions.

The vector settling and feeding response is arguably the most important vector trait that is manipulated by viruses, given that it is what determines the viruliferous status of the vector (Fereres & Moreno, 2009). Even if contact with infected hosts is not influenced by infection status, and infection does not impact vector performance, selection will favour virus adaptations that ensure vectors engage in probing and feeding behaviours needed for efficient transmission. We detected indirect evidence of adaptations producing positive effects on vector settling and feeding for all of the virus groups expected to benefit, especially phloem-limited viruses. We also found nuanced effects for non-phloem-limited viruses. In aggregate, non-phloem-limited viruses enhanced infected plant palatability, but this effect diverges sharply for the two transmission mechanisms that include non-phloem-limited species: non-circulative semi-persistent (NCSP) and non-circulative non-persistent (NCNP). The NCSP contains both phloem-limited and non-phloem-limited species, and generally, viruses with this transmission mode can benefit from sustained feeding by some vector species regardless of whether the virus is restricted to phloem. In contrast, the NCNP category contains only non-phloem-limited species that are transmitted when vectors rapidly disperse following acquisition. We did not find evidence that NCNP viruses enhance vector settling or feeding but did detect this effect for all other transmission mechanisms. Overall, for vector settling and feeding, the prediction of convergence in host phenotype effects based on shared virus traits was strongly supported.

We hypothesized virus effects on vector settling and feeding behaviour would be congruent with effects on vector performance, but this was not the case. Instead, while viruses had mostly strong positive effects on settling and feeding preferences, effects on performance were mostly neutral; these largely weak effects of viruses may reflect limitations imposed by other virus traits. For example, circulative-persistent-propagative viruses also use the vector as a host for replication, so a neutral effect may be evidence of adaptation, as the replicating virus does not have pathological effects on the vector, or that phenotypic host changes counteract these effects (Belliure et al., 2005). Direct effects of viruses on vector behaviour or performance may also occur as a result of acquiring and retaining virions and are apparent in some experimental circulative-persistent pathosystems (Ingwell et al., 2012; Mauck et al., 2018, 2019; Moreno-Delafuente et al., 2013; Rajabaskar et al., 2014; Roosien et al., 2013; Stafford et al., 2011). However, our meta-analysis only explored indirect effects on vectors that were mediated through alterations of host phenotypes by viruses, so we likely underestimated such direct effects.

Our meta-analysis focused on studies that often reduced pathosystems to one host and one vector species along with one virus isolate. However, the spread of many viruses is affected by interactions among numerous species. Phloem-limited viruses have co-evolved interactions with vectors that feed from the phloem of a virus's hosts (Hogenhout et al., 2008). Consistent with this, >80% of phloem-limited viruses in our study are transmitted by three or fewer vectors (Table S7, Figure S4). We predict that phloem-limited viruses generate transmission opportunities by interacting with few species that colonize hosts long enough to acquire virions. However, the opposite is true for non-phloem-limited viruses acquired by rapid probing and transmissible by vectors for which the infected host species is not suitable (Fereres, 2016; Ng & Falk, 2006). We found 50% of non-phloem-limited viruses included are transmissible by 15 or more vector species, and most (16/22) are transmissible by 5 or more (Table S7, Figure S4). Non-phloem-limited viruses generate transmission opportunities by interacting with many vectors that need not colonize a host to acquire virions (Bosque-Pérez & Eigenbrode, 2011).

While non-phloem-limited viruses have far more competent vector species than phloem-limited viruses, this reality is rarely considered in experiments or models of vector manipulation (Madden et al., 2000; Mauck et al., 2018; McElhany et al., 1995; Roosien et al., 2013; Shaw et al., 2017, 2019; Sisterson, 2008). Yet, transmission differences between virus groups may strongly affect fitness benefits of host manipulation. Plant viruses have limited coding capacity, and fixation of a mutation is dependent on a lack of epistatic interactions with other sites in the genome and pleiotropic effects (Bedhomme et al., 2012; Betancourt et al., 2013; Elena, 2017; García-Arenal & Fraile, 2013). For non-phloem-limited viruses, pleiotropic effects may manifest as reduced transmission opportunities, and mutations facilitating manipulation of one vector species may compromise transmission by other vectors. However, neutral effects on host phenotypes would increase the likelihood that most competent vector species will visit some infected plants and engage in behaviours required for transmission (rapid probing and dispersal) due to host plant incompatibility (Angelella et al., 2015; Mondal et al., 2016; Rydén et al., 1983; Sigvald, 1989). In contrast, phloem-limited viruses that rely on a few vector species for transmission may experience substantial gains by increasing the probability of transmission-conducive contacts with these highly specialized vector species. Our analysis supports this prediction with significantly positive effect sizes for phloem-limited viruses (and component transmission modes) in the categories of attraction, settling and feeding, and performance.

Host diversity is another factor that may shape the selection of manipulative traits, as suggested by our dataset on the effects of plant infection on the performance of vectors on wild and domesticated plants (Figure S3). However, current data are too unbalanced to reliably assess its importance or the biases it may introduce (e.g. 136 vs. 6 comparisons in vector orientation behaviour). Given the relevance of managing virus-induced manipulative effects in agriculture (Bak et al., 2019) and understanding their role in natural ecosystems (Alexander et al., 2014), future studies should prioritize a more balanced exploration of this factor. In this context, it will also be useful to understand how plant host and vector traits may enable or hinder the evolution of manipulative plant viruses. Regardless of domestication status, plant hosts likely vary in how susceptible they are to manipulation. Similar variation may exist for vector species, with some more likely to respond to virus manipulations than others. This variation could extend to the community level, with the distribution and abundance of manipulatable hosts or vectors shaping the evolution and persistence of manipulative viruses. Potential influences of plant and vector traits could be explored using theoretical models to generate testable hypothesis.

Transmission opportunities represent one ecological dimension affecting virus evolution, but other factors could shape selection for manipulative traits, including abiotic conditions, vector natural enemies and effects of host phenotype manipulations on resistance against non-vector pests and other pathogens (Chesnais et al., 2019; Davis et al., 2015; Jeger et al., 2011; Kersch-Becker & Thaler, 2013; Mauck et al., 2014, 2015). Virus genome type (e.g. RNA vs. DNA, single stranded vs. double stranded) may also influence the evolution of manipulative traits because RNA viruses tend to have higher mutation rates than DNA viruses, and single-stranded virus genomes have higher mutation rates than double-stranded genomes (Sanjuán & Domingo-Calap, 2016). We were equally likely to see manipulative effects from RNA vs. DNA viruses in our analysis by virus family. However, our dataset is not balanced regarding genome characteristics, leaving room for more work on understudied virus types (e.g. double-stranded DNA viruses). Even though we could not address some factors, our synthesis provides an important milestone by quantifying the magnitude and adaptive significance of virus effects on vectors. While the potential roles that virus manipulations of vectors play in pathogen spatiotemporal spread have been explored through mathematical models (Shaw et al., 2017, 2019; Zeilinger & Daugherty, 2014), the effects quantified in our synthesis provide opportunities for enhancing existing predictive theories of plant-pathogen dynamics. Incorporating new pathosystems and ecological dimensions is necessary to further understand the frequency and relevance of virus manipulation. Tackling these ambitious research directions requires integrative approaches informed by virology, ecology, entomology and plant biology.

AUTHOR CONTRIBUTIONS

All authors contributed to the scope and structure of the manuscript. Quentin Chesnais and Kerry E. Mauck assembled the database and worked with Christie A. Bahlai to perform the meta-analysis. All authors contributed to data interpretation. Quentin Chesnais and Kerry E. Mauck wrote the first draft of the manuscript and David W. Crowder, Nilsa A. Bosque-Pérez, Christie A. Bahlai and Angela Peace provided edits through an iterative revision process.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to disclose.

DATA AVAILABILITY STATEMENT

All extracted data that were used for the meta-analysis are accessible at:

https://doi.org/10.57745/HF9NFG (Chesnais et al. 2025).

STATEMENT ON INCLUSION

Our study was based on a meta-analysis of secondary data and did not include any new data collection. Our authorship team includes researchers ranging from early to late-career stages from multiple countries and was primarily led by an early career researcher (Quentin Chesnais). Authors engaged regularly through email and virtual discussions to ensure inclusion of relevant studies from a wide geographic distribution.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Glossary of terms used in the manuscript.

Table S2. Test statistics and variance components for models testing effects of virus infection on vector (a) orientation preference, (b) settling/feeding preference, and (c) performance. Values in bold were significant effects ($\alpha = 0.05$).

Table S3. Model estimated mean effect sizes, 95% confidence intervals, and sample sizes for how each value of (i) infection location, (ii) retention mechanism, and (iii) virus classification mediates the effect of virus infection on vector orientation preference. Retention mechanisms are: (i) CPP: circulative-persistent-propagative, (ii) CPNP: circulative-persistent-non-propagative, (iii) NCSP: non-circulative-semi-persistent, and (iv) NCNP: non-circulative-non-persistent. Values in bold were significant effects ($\alpha = 0.05$).

Table S4. Model estimated mean effect sizes, 95% confidence intervals, and sample sizes for how each value of (i) infection location, (ii) retention mechanism, and (iii) virus classification mediates the effect of virus infection on vector settling/feeding behavior. Retention mechanisms were: (i) CPP: circulative-persistent-propagative, (ii) CPNP: circulative-persistent-non-propagative, (iii) NCSP: non-circulative-semi-persistent, and (iv) NCNP: non-circulative-non-persistent. Values in bold were significant effects ($\alpha = 0.05$).

Table S5. Model estimated mean effect sizes, 95% confidence intervals, and sample sizes for how each value of (i) infection location, (ii) retention mechanism, and (iii) virus classification mediates the effect of virus infection on vector performance. Retention mechanisms are: (i) CPP: circulative-persistent-propagative, (ii) CPNP: circulative-persistent-non-propagative, (iii) NCSP: non-circulative-semi-persistent, and (iv) NCNP: non-circulative-non-persistent. Values in bold were significant effects ($\alpha = 0.05$).

Table S6. Fail safe numbers and the threshold to be considered robust against publication bias ($5n + 10$) for each of the three vector response variables. If the fail safe number is above the threshold, the meta-analysis is considered robust to publication bias.

Table S7. We determined how the number of competent vector species relates to virus effects. For all viruses in the meta-analysis, we surveyed the literature and recorded the number of competent vector species. We considered online databases such as Plant Virus Online (Brunt et al. 1997), The Universal Virus Database

(Buchen-Osmond 2006) and DPVweb (Adams & Antoniw 2006). When different numbers of competent vectors were shown, we kept the higher value. To complete our database, we also surveyed Edwardson & Christie (1991) which reviewed characteristics of viruses associated with legume crops, as well as specific articles for viruses characterized more recently and not reported in databases (Ghosh et al. 2016).

Figure S1. Funnel plots of effect sizes (Hedges' *g*) and the standard errors for vector (i) orientation preference, (b) vector settling/feeding preference, and (c) performance.

Figure S2. Plots showing the plant infection effect sizes (Hedges' *g*) for vector (a) orientation preference, (b) settling/feeding behavior, and (c) performance data as a function of study year. Model statistics test the significance of study year in mixed effects meta-regression models. Lines show the model predicted mean effect sizes and the 95% confidence intervals.

Figure S3. Effect sizes (Hedges' *g*) and 95% confidence intervals comparing the magnitude of differences in vector (a) orientation preference, (b) settling/feeding behavior and (c) performance in domesticated-wild plant comparison. Numbers in brackets indicate the number of studies used to inform each estimate (see Tables S2–S4 for complete sample size information). Different letters indicate significant differences among effect sizes within each type of analysis (orientation, settling/feeding, or performance).

Figure S4. Estimated number of competent vector species for each virus taxon in the meta-analysis database, delineated by site of virion acquisition in the host. Phloem-limited viruses are generally transmitted by fewer documented competent vector species than non-phloem-limited viruses. Of the phloem-limited viruses considered in our study, 82.3% (42/51) have three or fewer recorded competent vector species. In contrast, for non-phloem-limited viruses acquired and inoculated via rapid probes (22 viruses), all except MMWV and CPMMV are transmitted by at least three vectors, with 50% (11/22) being transmitted by 15 or more vector species.

Appendix S2. Data extracted from studies on the effects of plant virus infection in hosts on vector performance.

Appendix S3. Data extracted from studies on the effects of plant virus infection in hosts on vector settling behavior.

Appendix S4. Data extracted from studies on the effects of plant virus infection in hosts on vector orientation behavior.

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