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Risk assessment for non-crop hosts of Pea Enation Mosaic Virus and the aphid vector Acyrthosiphon pisum

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Abstract:	Plant viruses carried by insects can have devastating impacts on agroecosystems. These vector-borne pathogens are often transmitted by generalist insects that move between non-crop (weedy) and crop hosts. Insect vectors can have wide diet breadths, but it is often unknown which hosts serve as pathogen reservoirs and whether vector abundance in non-crop hosts is predictive of outbreaks in crops. We addressed these issues by linking field surveys of an aphid vector and plant virus with statistical models to assess risks posted by non-crop, weedy legumes in habitats near farms. In the Pacific Northwest USA, the pea aphid (Acyrthosiphon pisum), is a key virus vector with a wide host range; in 2018 we completed a 65-site survey where aphids were surveyed in weedy legumes within and outside dry pea fields. We quantified the abundance of pea aphids on seventeen hosts, and plant tissue was tested for Pea enation mosaic virus (PEMV). High densities of pea aphids were associated with hairy vetch (Vicia villosa) along with the virus PEMV. Our results indicate that hairy vetch is an important alternative host for PEMV, and that pest management practices in this region should consider management of this weedy host in viral disease mitigation efforts.

Abstract

Viral insect-borne plant pathogens have devastating impacts in agroecosystems. Vector-borne pathogens are often transmitted by generalist insects that move between non-crop (weedy) and crop hosts. Insect vectors can have wide diet breadths, but it is often unknown which hosts serve as pathogen reservoirs and whether vector abundance in non-crop hosts is predictive of outbreaks in crops. We addressed these issues by linking field surveys of an aphid vector and plant virus with statistical models to develop risk assessments for legume crops. In the Pacific Northwest USA, the pea aphid (*Acyrthosiphon pisum*) is a key virus vector with a wide host range; in 2018 we completed a 65-site survey where aphids were surveyed in weedy legumes within and outside dry pea fields. We quantified the abundance of pea aphids on seventeen hosts, and plant tissue was tested for *Pea enation mosaic virus* (PEMV), a pathogen that causes considerable yield losses in certain years. High densities of *A. pisum* were found exclusively in habitats dominated by hairy vetch (*Vicia villosa*), which was the only legume other than cultivated pulses where PEMV was detected. Our results indicate that *V. villosa* is a key alternative host for PEMV, and that pest management practices in this region should consider the distribution and abundance of this weedy host in viral disease mitigation efforts for legume crops.

Keywords: Aphids, legumes, plant viruses, reservoirs, non-crop hosts

Introduction

Plant viruses cause an average 10% reduction in global agricultural productivity, which translates to global economic losses of more than US $30 billion annually (Strange & Scott 2005, Jones 2021). Most crop plant viruses require insects for transmission, especially phloem-feeding Hemipterans like aphids (Power 2000; Hogenhout et al. 2008). However, despite the importance of vector-borne plant viruses in agriculture, our ability to predict virus occurrence across time and space remains poor for most pathosystems. Many vectors are generalists with a broad host range that includes food and cover crops, agricultural weeds, and native plants (Mueller et al. 2012, Bommarco et al. 2007). Identifying host reservoirs is key to determine the source(s) of vector-borne pathogens that can outbreak in a crop system (Peterson 2018, Gobatto et al. 2019).

Like their vectors, many crop viruses occupy alternative hosts before infecting crop plants (Norris & Kogan 2005). Non-crop hosts have been established as reservoirs for insect vectors and vector-borne pathogens that infect annual crops such as wheat, corn, and rice (Rashidi et al. 2020, Wu et al. 2020). The replication and spread of a plant virus across multiple hosts depends on the compatibility and coordinated interactions of virus- and host-encoded proteins, and the severity of infection often differs among hosts (Heinlein 2015, Basu et al. 2018). Assessing whether certain hosts act as reservoirs of pathogens can be difficult, however, especially if alternative hosts do not show clear signs of infection because many viruses can exhibit slower replication in certain hosts by avoiding cellular damage (Lucas 2006, Takashi et al. 2019). Yet, management strategies for crop pathogens rely on identifying the potential for non-crop hosts to serve as pathogen reservoirs for vectors and pathogens using molecular diagnostics (Rageshwari et al. 2017). Understanding how pathogens and vectors move among distinct populations of hosts is also an important component of effective management of crop diseases.

When a non-crop host for pathogens or vectors is identified, integrated pest management (IPM) strategies suggest targeted removal to prevent crop infection (Catton et al. 2015, Macharia et al. 2016). For example, management of wheat stem rust relies on control of the pathogen's alternative host American barberry (*Berberis canadensis*), a strategy that dates back almost a century (Peterson 2018). Non-crop host removal can be difficult if these host plants are also weeds, however, particularly those that emerge early in seasons before crops are established (Norris & Kogan 2005). Consequently, some agricultural weeds and cover crops allow pest insect populations to increase before moving into crops, exacerbating outbreaks of herbivores themselves in crops. Colorado potato beetle is observed feeding on horse nettle before moving into potato (Mena-Covarrubias et al. 1996), and two spotted spider mites disperse from weeds to cotton (Wilson 1995, Norris & Kogan 2005).

Movement of generalist vectors between non-crop and crop hosts can mediate the spread of pathogens (Power et al. 1991; Davis et al. 2015; Srinivasan et al. 2008). Aphids that migrate over long distances often establish population in crops rapidly in the spring months as non-crop hosts senesce, which is often accompanied by high prevalence of virus-infected plants (Clement et al. 2010, Reynolds et al. 2006). Aphids with long-distance dispersal capability as alates can also complicate management efforts (Damgaard et al. 2020, Powell et al. 2006, Mueller et al. 2012). For these reasons, aphid-borne viruses are hard to track and outbreaks are often unpredictable, hampering pest management (Damgaard et al 2019). To address such challenges, identification of local sources of aphid-borne pathogens can be of great value in guiding optimal and cost-effective control strategies, such as removal of weedy reservoirs near crop fields. In turn, the goal of our study was to track and quantify potential non-crop hosts for a problematic pathogen and its vector in a single region (eastern Washington state and Northern Idaho, USA).

Methods

Study System

The pea aphid *Acyrthosiphon pisum* is a frequent pest of pulse crops that acts as the main vector for several pathogens, including Pea enation mosaic virus (PEMV) (Rashed et al. 2018; Chatzivassiliou 2021). Plants infected with PEMV produce a range of species-specific symptoms, with malformed pods ultimately reducing yield (Clement et al. 2010). Extreme outbreaks can lead to up to 40% yield loss in pulses (Elbakidze et al. 2011, Paudel et al. 2018). In addition to dry pea (*Pisum sativum*), PEMV infects crops and weeds like alfalfa (*Medicago sativa* L.), yellow sweet clover (*Melilotus officinalis* (L.), white sweet clover (*Melilotus albus* L.), wild white clover (*Trifolium repens* L.), common vetch (*Vicia sativa* L.), hairy vetch (*Vicia villosa* Roth), and broadbean (*Vicia faba* L.) (McEwen et al. 1957). Pea aphids acquire PEMV from a few perennial legume hosts and agricultural weeds (Hull 1981). However, *A. pisum* diet-breadth encompasses most of the Fabaceae (Peccoud et al. 2009), suggesting the diversity of PEMV-compatible hosts could be large.

Survey Design

We conducted field surveys from May to July 2018 during an outbreak season of *A. pisum*. Pea aphids and virus have been historically monitored in eastern Washington and Idaho by the University of Idaho using a long-term trapping network for 17 sequential growing seasons. In this trapping scheme, at least ten locations have three pan traps placed at field edges starting after spring peas are planted (May). Pan traps contain propylene glycol for capturing alate aphids, and these are sampling weekly or biweekly until dry peas in the region complete pod development.

Alate aphids are counted and tested for viral pathogens, including PEMV. In this trapping network, the 2018 season had the second highest alate arrival counts on a per-trap basis over this entire period (Fig. S1). This so-called "outbreak year" thus provided an opportunity to discover the non-crop hosts for *A. pisum* and PEMV in a season when aphids are widespread, thus we targeted sampling at areas with patches of weedy legumes in 60 locations. Plant and aphid communities were sampled in two climatic ecoregions: Palouse Prairie, a high-elevation grassland predominately converted to dryland wheat production (Looney and Eigenbrode, 2012) and shrub-steppe, a habitat found at lower elevations and warm slopes adjacent to the Palouse region (predominately along the Snake River in Washington and Idaho) (Knick & Rotenberry 1997). Both habitat types harbor a diverse community of herbaceous legumes and are purported sources of pea aphid outbreaks (Clement 2006). All non-agricultural sites were in either roadside edges, native prairie, or shrub-steppe. Agricultural sites were spring-planted pea fields on the lower Palouse in Whitman Co. Washington and Latah Co. Idaho between 47.46°N and 46.33°N (Fig. 1).

Aphid, plant, and virus surveys were conducted using a line-transect (Fig S2). At each of 60 sites sampled we ran 10 m line transects and quantified plant diversity (species identity) of all forbs touching the line transect; forb percent cover was calculated by measuring the length of the line transect (in cm) covered by plant material. At each transect we collected canopy arthropods using two 180° sweeps through the foliage; insects collected were stored in 95% ethanol until identification to species. Samples of aboveground terminal leaf tissue of legume species overlapping the meter-line transect were harvested, wrapped in aluminum foil, frozen in liquid N_2, and held on dry ice before storing at -80°C. These tissue samples were used to determine the presence of PEMV.

111

112 ***PEMV detection in plants***

113 To test all crop and non-crop legumes for PEMV, we used a two-stage protocol (Sint et al.
114 2016). First, we tested for PEMV by using reverse transcription-polymerase chain reaction (RT-
115 PCR) from pooled samples of all tissue collected from each transect (n = 65). Subsamples of
116 tissue from each plant, regardless of species, were pooled and ground into fine powder under
117 liquid N_2 by mortar and pestle into a transect-wide mix. Second, if PEMV was detected in the
118 pooled sample, the remaining tissue from all host plants was tested individually. This method
119 allows efficient scoring of each of plant in a sample for the presence PEMV while avoiding
120 unnecessary and costly sampling of individual plants if the entire population is free of the virus.
121 For detection of PEMV from plant tissue samples, 100 mg of homogenized tissue was run
122 through Promega SV total RNA isolation kits (Promega), producing cDNA from 1 µg of total
123 RNA using Bio-Rad iScript cDNA synthesis kits (Lee et al. 2021). Then RT-PCR was performed
124 using PEMV-1 coat protein specific primers (PEMV CP FP: 5' GTGGTGGCACCCTCTATG
125 3'; PEMV CP RP: 5' GTGTCCACATGGTAGGCTATG 3'). Primers were designed using the
126 IDT Primer Quest Tool for RT-PCR reaction (10 µl) containing 3 µl of ddH2O, 5 µl of dream
127 Taq mastermix (Thermo Scientific, Waltham, MA, usa), 1 µl of diluted primer mix (forward and
128 reverse [concentration 10µM]), and 1 µl of cDNA template. The RT-PCR program included an
129 initial denaturation for 5 min at 95°C followed by 21 cycles of denaturation at 95°C for 30 s,
130 annealing for 30 s at 56°C, and extension for 45 s at 72°C and final extension of 10 min at 72°C.
131 After PCR was complete, agarose gels (1%) were run at 90 v for 45 min, after which gel pictures
132 were taken in a documentation system (Bio-Rad, Hercules, CA). For one large population of
133 hairy vetch that contained PEMV (Fig. 1), we revisited the site later in the season and sampled a

living, adjacent hairy vetch population, validating that PEMV was indeed persistent in this location.

Statistical Analyses

All data analyses were completed using R version 4.1.2 (R Development Core Team 2021) using base functions unless otherwise specified. For analyses of plant and aphid data, we used GLMM (generalized linear mixed models) applying the 'lme4' package (Bates et al. 2015); model estimates and P-values were extracted using the 'car' package (Fox and Weisberg 2011). For plotting results and posthoc tests, we used the 'emmeans' package (Lenth 2016). Aphid counts, or cumulative abundance models used a negative-binomial link function appropriate for zero-inflated count data. These abundance data were then transformed for plotting by dividing abundance estimates by total host plant area (Fig. 2). Probability of aphid presence in transects was modeled as the ratio of presence and absence among sites (Fig. 4). Statistical analyses for line transects used site as a random effect. Analyses of pooled long-term monitoring data from https://www.legumevirusproject.org/ were completed using a GLMM with a negative binomial link function. These source data were comprised of samples from a minimum of 30 pan traps monitored weekly over 17-year survey period (Fig S1).

Results

We completed 118 transects at 65 sites, and opportunistically surveyed an additional five hairy vetch populations. We collected 15,289 pea aphids in total and assayed 1,076 candidate plant tissue samples for PEMV. In our transects we recorded 145 species of annual plants, of

156 which 23 were in the family Fabaceae. We observed significant variation in the percent coverage
157 of non-crop legumes (Fig. 2) and the abundance of aphids among host plant species (Fig. 3).
158 Hairy vetch had the highest abundance of pea aphids and was the most abundant non-crop,
159 weedy legume (Fig. 3). At the community level, increasing coverage of vetch in transects was
160 related to a greater likelihood of pea aphid presence (GLMMs, $\chi^2 = 15.02$, $P < 0.0001$, Fig. 4).
161 Notably, adjacent habitats also had high populations of hairy vetch colonized by pea aphids upon
162 subsequent revisit dates (Fig. S3). Finally, PEMV was only detected in hairy vetch (Fig. S4) and
163 crop (dry pea) sites colonized by pea aphids, but not in other hosts.
164
165 **Discussion**
166 Effective prediction of viral plant pathogen outbreaks requires a detailed understanding of
167 vector and pathogen movement from crop to non-crop hosts at the landscape scale (Srinivasan et
168 al. 2008). While our results are limited to a single field season, the first step in risk assessment is
169 evaluating potential alternative hosts during an outbreak (Holt et al. 2008). During an outbreak
170 year for pea aphids, hairy vetch plants were suitable and heavily occupied alternative hosts for
171 pea aphids and is a competent host for PEMV. While other alternative hosts may be found with
172 additional surveys, we found that hairy vetch has high densities in non-agricultural
173 environments, and it is conventionally used in the western U.S. as a cover crop (Luna et al.
174 2012). Our surveys of plant communities in habitats adjacent to pea fields suggest that there are
175 at least 23 potential hosts that can be resampled in future years, and the absence of aphids or
176 PEMV does not rule them out as compatible hosts for either.
177 Our understanding of pea aphid and PEMV outbreaks in the Palouse considers that pea
178 aphids likely colonize Palouse agroecosystems following wind currents from the Columbia Basin

and Willamette Valley, where milder winters allow aphids to overwinter on alfalfa and clover (Clement et al. 2010, Hampton 1983). Genetic data shows that the pea aphid biotype found on dry pea in the Palouse has shared markers with biotypes collected in these areas (Eigenbrode et al. 2016). Our study suggests two possibilities that align with this information. First, hairy vetch, which emerges early and in low elevation areas that warm up early in the growing season, is an effective "stopover" host for aphid alates dispersing from warmer western regions to the Palouse. Second, hairy vetch occurs in relatively warm microhabitats along the edge of the Palouse and in the lower elevations in the Columbia Basin, and aphids may overwinter in these areas. Vetch is a facultative biennial with an above-ground rosette during ideal climatic conditions (Pokorny et al. 2020, Mischler et al. 2010), and may have a small second generation in mesic habitats in the fall and winter (Clark personal observations). In either case, vetch may act as a short- (months) or long-term (years) reservoir for aphids and PEMV, playing an important role in this pathosystem at the landscape scale. In some years, PEMV-infected vetch may provide inoculum for arriving aphids, contributing to more injurious infections associated with early infection (Paudel 2018). In years when infectious aphids arrive later in the season, if they colonize vetch, the pathogen can gain a foothold for possible infection of legume crops in the following growing season.

Once non-crop hosts for specific plant pathogens are discovered, management implications arise. Removing non-crop host plants could reduce the incidence of that pathogen in crops (Peterson 2018, Strickland et al. 2020). In other systems, management of weeds may reduce pest populations in crops (Norris & Kogan 2005). However, in many cases removal of non-crop hosts may not be viable if they occur over large geographic regions or when movement of pests between hosts occurs over long distances, so local control would not prevent outbreaks. However, in our system it is unclear if a weed removal strategy is tenable. Hairy vetch is planted

as a cover crop for cattle forage (Golden et al. 2016), and this is why it persists at high abundance even as feral populations on dry hillsides. Hairy vetch also improves soil nitrogen, prevents erosion, and is not listed as a noxious weed (Pokorny et al. 2020, Mischler et al. 2010). Our results suggest that in this region, cover cropping of hairy vetch may increase PEMV outbreak risk in dry peas if in the same fields, but further work would be needed to verify this within-field spread occurs. For example, pathogen testing could be used to indicate if local infection risk and movement from vetch to pulse crops could occur at a single site.

The optimization of pathogen detection from field samples also depends on precision and specificity of the procedure to ensure efficient and accurate detection of true positive samples (Yazdkhasti et al. 2021). The use of more advanced molecular detection techniques, such as real time-PCR with much lower detection threshold can be used to detect pathogens with low titer (Rubio et al. 2020). Another key step toward improved pathogen detection is to maintain the quality and integrity of field samples by following proper collection technique in order to enhance detection of pathogens from field samples.

Hairy vetch emerges earlier and hosts pea aphids earlier in the season compared to cultivated legumes. The phenological difference between weeds and corps suggest that survey of PEMV in vetch may be available to predict seasonal prevalence of PEMV prior to crop emergence. Greenhouse work has demonstrated that pea aphid adults feeding on vetches with PEMV can then transmit these viral pathogens to dry pea (Clark et al. 2019). Sampling hairy vetch for aphids and PEMV may be a way to indicate if there are risks of large-scale, catastrophic outbreaks of PEMV likely to occur each year. While we only have one season of data reported here, PEMV and aphid populations go through large and difficult to predict population cycles. Consequently, it appears likely that if PEMV is found in April or early May in

many hairy vetch populations along the lower Palouse, it would portend an areawide impact of PEMV in the growing season for pulse farmers. Similar strategies could be employed in other non-crop and crop source-sink dynamics systems where the non-crop host is a perennial plant that emerges earlier in the growing season.

Conflict of Interest Statement

The authors declare no conflicts of interest.

Author Contribution

REC, DWC, and SDE and conceived project design. REC and ECO completed surveys and data analysis. REC and SB completed molecular assays. SDE provided long-term aphid trap data. All authors wrote, edited, and approved the final manuscript.

Data Availability Statement

Upon acceptance of this manuscript all data will be made available through a publicly available GitHub data and code repository by REC.

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Figure Legends

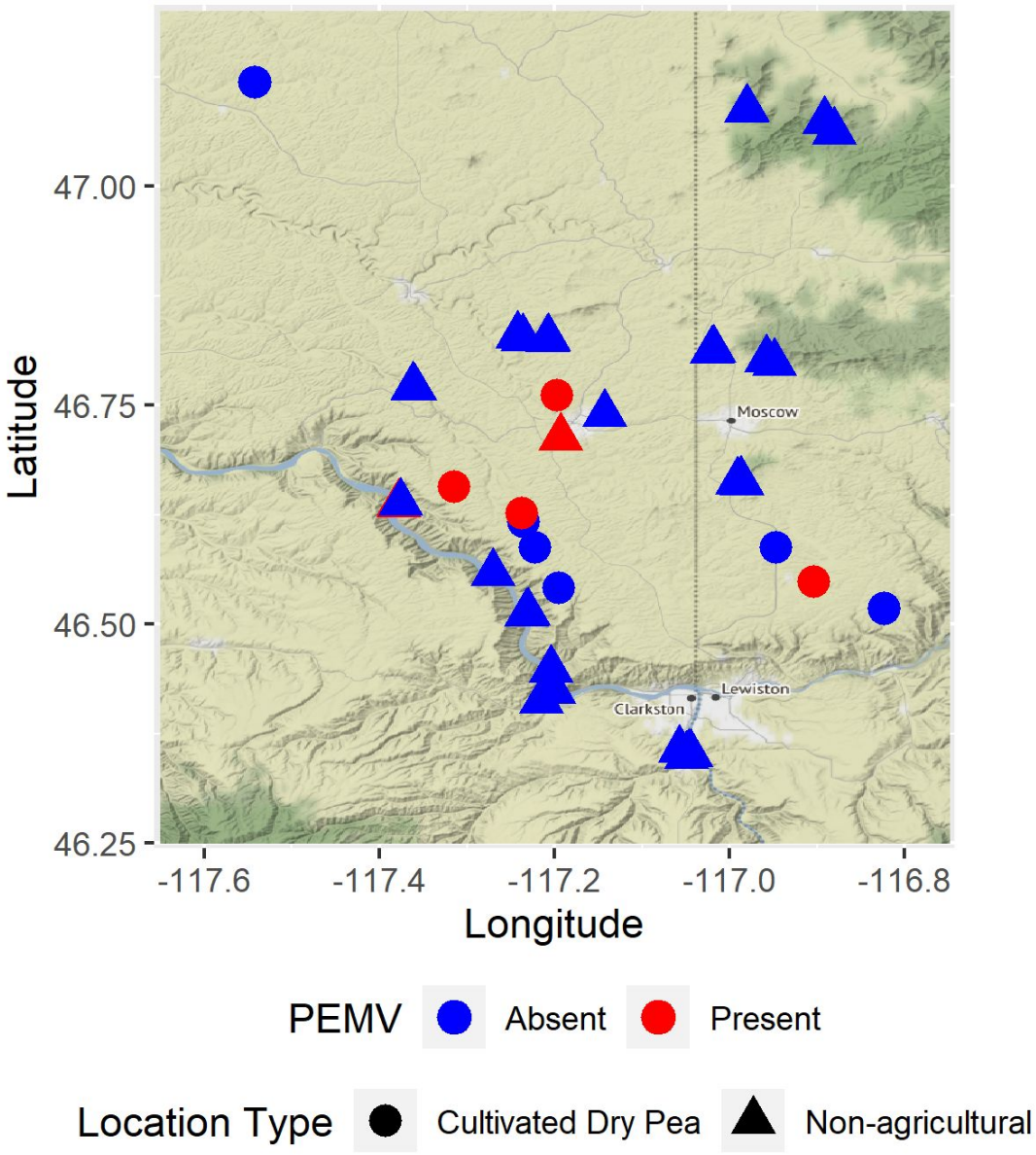
Fig. 1. Sampling locations for crop and non-crop transects. All cultivated dry pea fields were spring-planted fields in rotation with cereals. Non-agricultural sites included open public lands or lands that gave permission to sample. Color indicates presence or absence of PEMV at a given transect. The transects at Wawawai Canyon (westernmost non-agricultural site) yielded mixed populations of infected and non-infected plant hosts.

Fig 2. Cumulative aphid density (log transformed) for legume hosts found among all surveys. Bar colors indicate whether a host plant was discovered with PEMV RNA.

Fig. 3. Cumulative plant coverage for non-crop legumes found among all surveys; hairy vetch was the most common. Bar length indicates the cumulative coverage among our sites.

Fig 4. Probability predictions from GLMM (binomial fit) for pea aphid presence or absence in transects fitted to the abundance of non-crop host hairy vetch. The line indicates estimates means from GLMM, and the shaded area indicates the standard error of those model predictions. As hairy vetch coverage increased, aphids were more likely to be present in plant communities.

15 Fig. 1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46.50
46.25
Latitude
-117.6
-117.4
-117.2
-117.0
-116.8
Longitude
Moscow
Lewiston
Clarkston
PEMV
Absent
Present
Location Type
Cultivated Dry Pea
Non-agricultural

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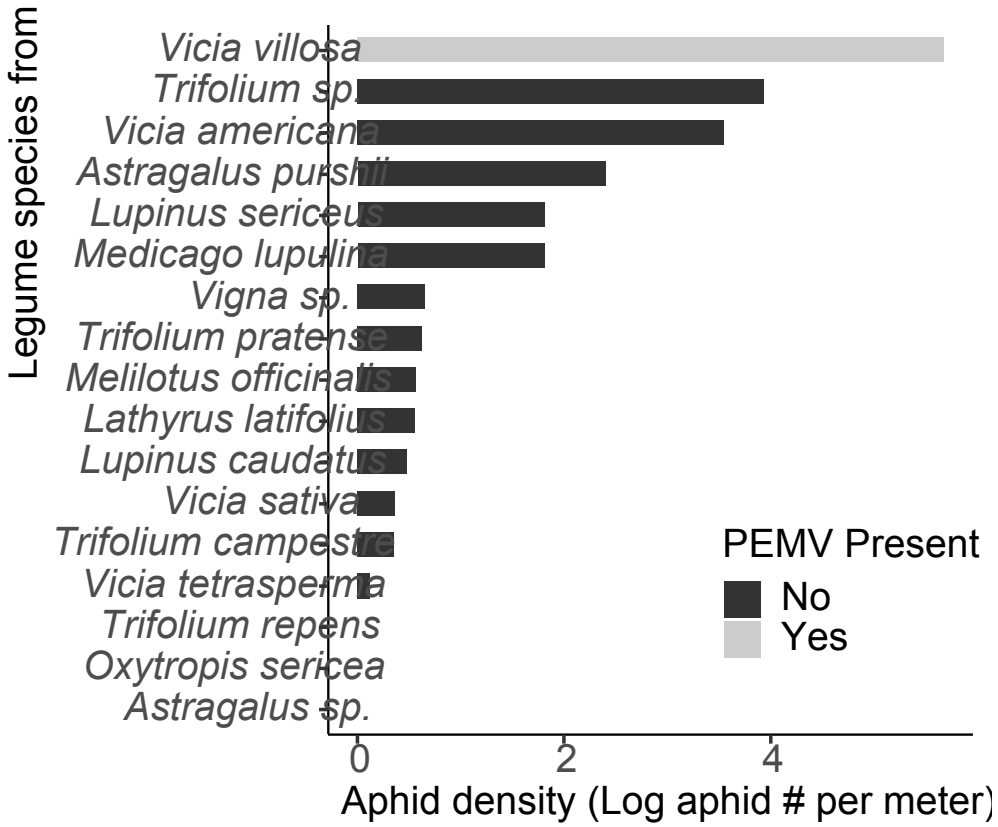
17 Fig. 2



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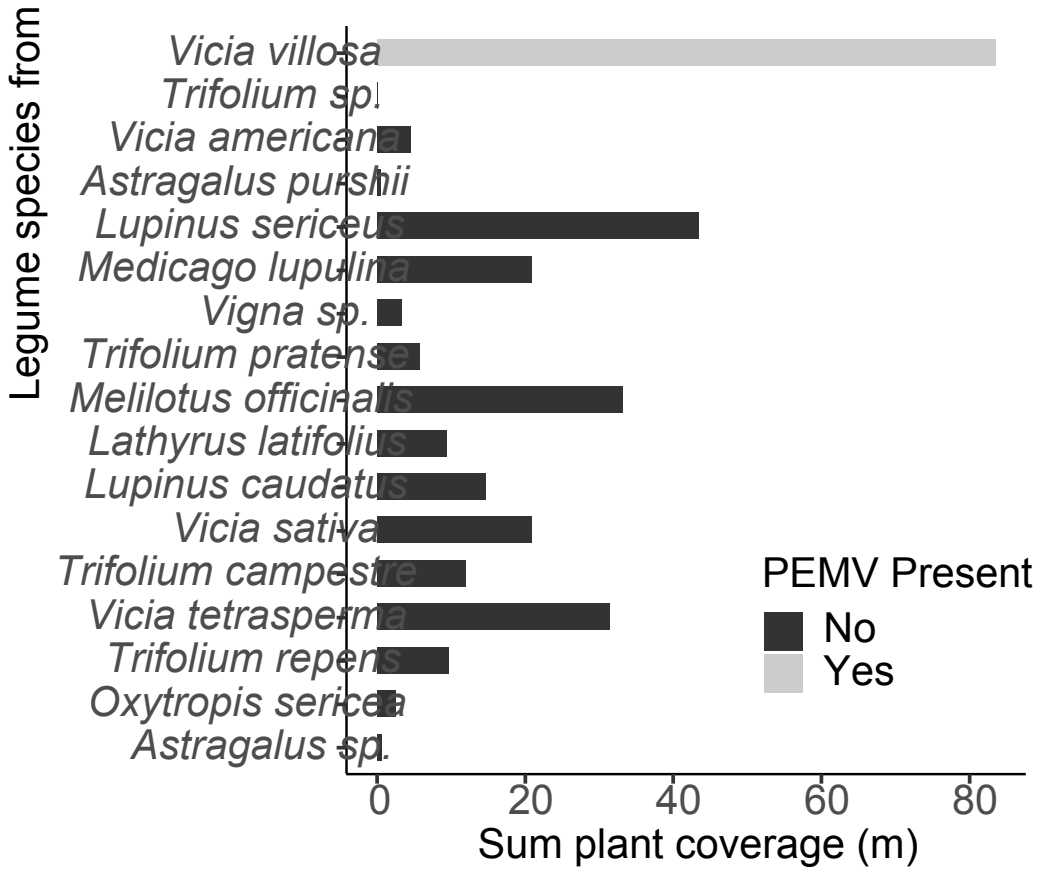

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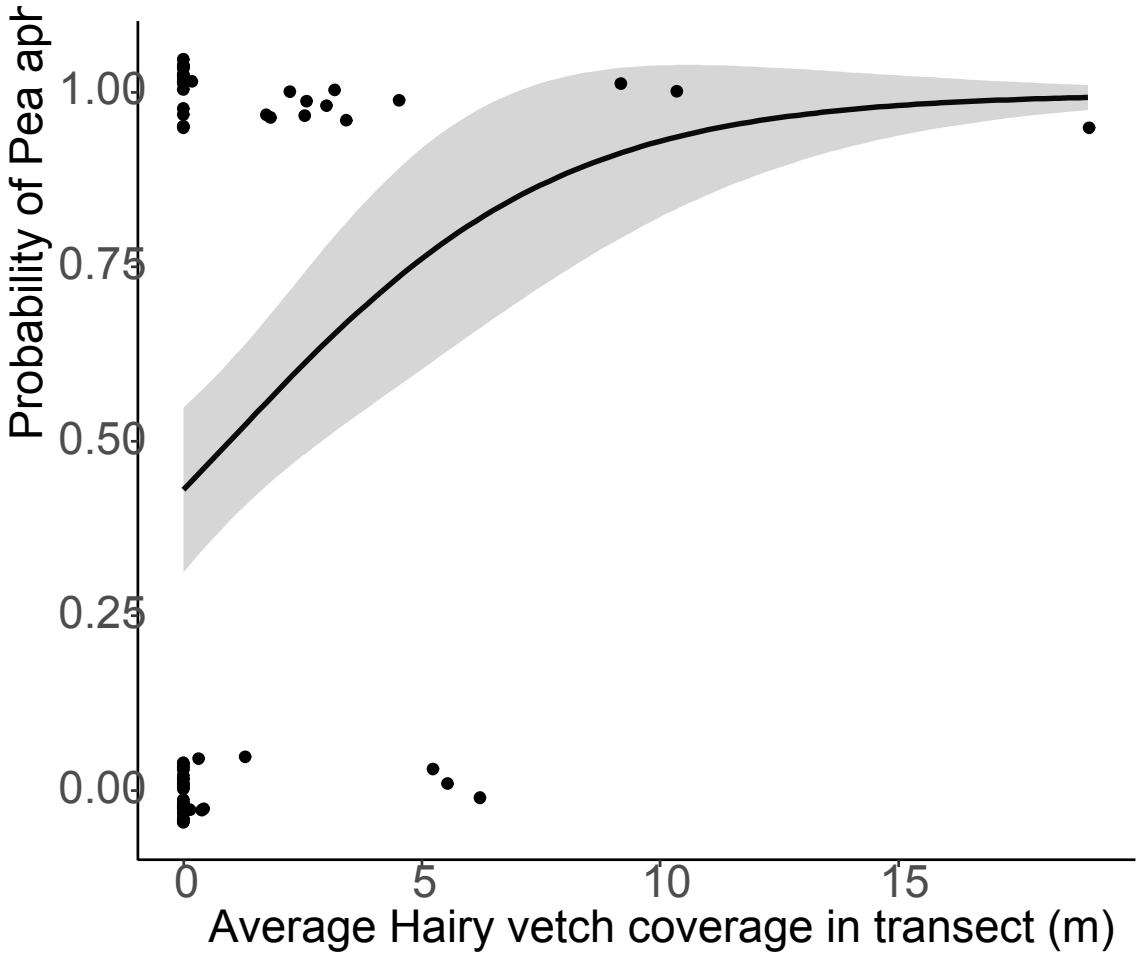

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