Landscape composition is more important than local management for crop virus–insect vector interactions

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A B S T R A C T

Managing crop viruses is difficult due to complex interactions among vectors, reservoirs, and mediating factors such as land cover. Identifying the appropriate ecological neighborhood, or the spatial area in which the most influential interactions occur affecting virus epidemiology, would therefore be beneficial in exposing which of the many explanatory variables to target in the plant-pathogen system. We constructed partial least squares path models to find the neighborhood size for vectors of stylet-borne nonpersistent viruses infecting pumpkins, and compare the relative influence of within-field and extra-field land cover. Two economically important aphid-vectored viruses in the U.S. Midwest are included in these analyses: papaya ringspot virus (PRSV) and watermelon mosaic virus (WMV). In 2010 and 2011, we used commercial pumpkin fields to quantify virus infection, vector (aphid) alightment (i.e., landing rates), and within-field weed communities, and subsequently analyzed extra-field cover from 1 to 5 km concentric buffer zones within the surrounding landscape. Alightment rates of total noncolonizing vectors and the top three numerically dominant species (*Aphis craccivora* Koch, *Therioaphis trifolii* (Monell), and *Rhopalosiphum padi* [L.]) were included in individual path models. Overall, we found that extra-field landscape composition had a far stronger influence on vector alightment than within-field weed cover; this pattern was consistent for seven of eight statistical models. In one exception, weed cover influenced alightment of the putative PRSV vector, *A. craccivora,* while surrounding landscape had no effect. In this case, weed coverage and vector alightment were inversely related, demonstrating that aphids were less likely to land in weed-infested fields. However, weed cover did not predict alightment of *T. trifolii* or total noncolonizers. The neighborhood size scales for total noncolonizers' tended to be larger than for individual species (4–5 km), suggesting future studies of dispersal by multi-species aphid groups may benefit from an extended gradient. On balance, our results indicate that while surrounding land cover interactions are complex, they exert greater influence over vector dispersal than within-field weed cover, calling into question whether management of local weeds is an effective method of crop virus prevention in some systems.

1. Introduction

The abundance of agricultural pests and the damage they inflict on crops are shaped by some combination of management decisions made at the within-field scale (i.e., tillage regimes, irrigation, pesticide inputs) and extra-field factors (i.e., land use at a local or regional scale) that are typically beyond the control of individual farms. While this spatial delineation is implicitly recognized and many studies have tested the impacts of the two scales independently, few have integrated within-field and landscape-level factors into a single analysis (but see Kennedy et al., 1961, 2013; Scheper et al., 2015; Tamburini et al., 2016). For example, while there is evidence that insect-vectored crop viruses are mediated by both within-field weeds (e.g., Duffus, 1971; Ali et al., 2012; Smith et al., 2012; Srinivasan et al., 2013) and surrounding land cover (e.g., Fabre et al., 2005; Margosian et al., 2009; Carrière et al., 2014), there have not been direct comparisons of the relative strength of these two scales. Uncovering differences between spatial scales is important for crop protection because it reveals which management approaches may be more or less effective in combating pests. In the case of crop pathosystems – the subsystems concerning crop-vector-pathogen interactions – if the impact of local weed management affects vector dispersal, then

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growers could alter herbicide regimes to help manage virus transmission. However, if land use beyond the farm boundary is the critical factor driving vector movement patterns, then changing within-field decisions are unlikely to affect virus prevalence. In this study, we explore landscape-level interactions in a nonpersistent crop virus system, and implement a direct comparison of within-field versus surrounding landscape scales on virus epidemiology.

Nonpersistent viruses are a large and agriculturally-important group. For example, cucumber mosaic virus (CMV) is an economically important pathogen of cucurbits, celery, lettuce, pepper, banana, legumes and ornamentals (Tomlinson, 1987; Palukaitis et al., 1992; Flasinski et al., 1995; Jones, 2004): afflicted crops frequently experience loss rates of 10–20%, at times reaching 100% (Zitter and Murphy, 2009). Like CMV, the vast majority of nonpersistent viruses are transmissible by aphids (Gray and Banerjee, 1999; USAID et al., 2004). Nonpersistent virus epidemiology is challenging to study due to the combination of: a) rapid transmission time, b) the large number of aphid species capable of serving as vectors, and c) the broad host-plant range for many viruses, leading to numerous potential reservoirs in the landscape.

Because they are noncirculatory and only temporarily adhere to an aphid's stylet – until subsequent probing and salivation occurs – transmission occurs when susceptible plants are tested during exploratory probes (Wang et al., 1996; Martin et al., 1997). This induces rapid acquisition and inoculation: even a single probe of an aphid's stylet can transmit a virus. As a result, insecticides are either ineffective at preventing the spread of infection among plants or must be applied at rates which are not cost effective (e.g., Thackray et al., 2000). Instead, preventative measures primarily consist of growing resistant cultivars, using costly UV-reflectant mulches or row covers, and/or removing sources of virus and vectors in the farmscape (Lecoq and Katis, 2014).

Aphid-vectored viruses are also often transmissible by a large suite of species, including noncolonizers (i.e., those that do not feed and reproduce on a plant). In fact, several studies have documented the relative importance of noncolonizing aphid species' transient alightment (i.e., landing) within fields over that of colonizing species in virus epidemiology (e.g., Raccah et al., 1985; Summers et al., 1990; Fereres et al., 1992, 1993; Webb et al., 1994; Perez et al., 1995; Nebreda et al., 2004). Having a broad range of vectors with disparate host-plant preferences allows many types of land cover to function as potential vector population sources, and can lead to interspecific variation in vector dispersal ranges relative to spatial vegetation patterns within and near farm sites that cultivate susceptible crops.

Additionally, numerous factors simultaneously act on vector species' dispersal behavior and the likelihood of pathogen acquisition/inoculation. Within-field or surrounding land cover can mediate nonpersistent virus epidemiology in several ways. One is by provisioning vector natal habitat. Nonpersistent viruses often have large host-plant ranges: for example, over 800 species of plants are vulnerable to CMV infection (Zitter et al., 1996). Thus, both vector and virus reservoirs can lurk in the surrounding landscape or within fields, affecting the probability of virus infection within crop systems. Finally, the landscape can also mediate virus infection via aphid response to visual and structural variation present through windbreaks, and species-specific attraction to color and/or contrast (e.g., Moericke, 1955; Mayse and Price, 1978; Bottenberg and Irwin 1992).

Although the effects of within-field management on crop virus-vector interactions are fairly well-studied, landscape effects remained largely uninvestigated until very recently (Alexander et al., 2014; Carrière et al., 2014; Cunniffe et al., 2015). This is surprising because techniques from landscape ecology have increasingly been employed to model insect responses to agricultural land use, including herbivores, predators, parasitoids, and pollinators (Ricketts et al., 2008; Chaplin-Kramer et al., 2011; O'Rourke et al., 2011; Sivakoff et al., 2013). While numerous variables embedded in the landscape can influence nonpersistent plant virus epidemiology, the spatial scales within which these variables have the largest influence, or the ecological neighborhood (Addicott et al., 1987), in vector-virus dynamics is unknown. The migratory ability of vector species could play a role, as an ecological neighborhood may be largely determined by the movement of mobile organisms (reviewed in Addicott et al., 1987). However, there is a large range in recorded dispersal distances among aphids. At sufficiently low wind speeds aphids are capable of sustaining short intervals of directed flight for an estimated max. 200 m, losing directional control in winds above *ca.* $0.6\,\mathrm{m\,s^{-1}}$ (Haine, 1955; Loxdale et al., 1993; Parry, 2013). In contrast, long-distance migratory flights occurring via passive wind dispersal commonly cover ca. 20–50 km, but are thought to be much less frequent among aphid populations than localized movement (Loxdale et al., 1993).

To tackle the challenges of working within a nonpersistent pathosystem, which likely involves many vector-landscape interactions occurring at multiple spatial scales, we used partial least squares path models (PLS-PM). This is a 'soft-modeling' technique which takes a prediction-oriented approach to testing theoretical concepts. PLS-PM works by first creating an outer measurement model, which uses manifest variables (MVs or indicator variables), which are quantifiable observations, to generate a latent variable (LV), which can be a complex concept that is not directly observable. An inner structural model is then designed as a network of LVs with interconnections based on theoretical prediction, allowing one to test causal relationships among complex concepts. The path coefficients explain the residual variance of LVs, meaning that PLS-PM is better suited for predictive use rather than for statistically accurate estimates (Chin, 2010). It is especially useful for conducting exploratory analyses, building complex models, and utilizing data with small sample sizes, non-normal distributions, and multicollinearity (Tenenhaus et al., 2005; Chin, 2010; Bagozzi and Yi, 1988).

We studied a nonpersistent pathosystems in pumpkins, and used PLS-PM to identify the ecological neighborhood for vectors and corresponding virus infection in focal fields, a major goal of which was to determine whether interactions occurring within or surrounding fields mediate virus spread. To address the former, we quantified land cover components within concentric buffer zones surrounding focal sites (Brennan et al., 2002), and identified the spatial scales that best predict vector behavior and virus infection (Jackson and Fahrig, 2012). PLS-PM allowed us to quantify land cover to create a LV embodying the greater concept of 'landscape composition' within each concentric buffer zone relative to focal fields, and compare the predictive ability of surrounding landscapes at different scales with that of within-field weed cover on vector alightment and virus infection within fields (Fig. 1).

2. Methods

2.1. Aphid, virus quantification

Pumpkins host several aphid-vectored nonpersistent viruses (Zitter et al., 1996), and potential vectors and viruses in this system were recently described (Angelella et al., 2015).

Aphid species alightment and virus infection were quantified within Indiana pumpkin fields under varied management regimes in 2010 (n = 10) and 2011 (n = 15) (see Angelella et al., 2015 for further details). Field locations varied between years (Figs. A.1a,b). Aphid alightment (i.e., landing within pumpkin fields) was determined by identifying individuals landing in five pan traps