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Perspective

Insect vectors as drivers of plant virus emergence

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All together, viruses account for 47% of emerging infectious diseases (EIDs) of plants [1]. Pathogen introduction is often regarded as the most important driver of plant EIDs, but most plant viruses have a vital dependence on their vectors for their survival and spread. Consequently, a pathogen accidentally introduced into a new area will never become emergent unless the appropriate vectors are present. Viruses transmitted by vectors are significantly much more likely to be designated as emerging threats than are non-vector transmitted viruses [2]. Among vectors, insects are by far the most important, transmitting more than 70% of all known plant viruses [3]. Plant viruses need their insect vectors to become emerging diseases either by increasing their incidence by jumping into a new host or causing severe epidemics in an existing host. From a genetic perspective, vectors impose strong bottlenecks between host-to-host transmissions, during which a large part of the standing variation is lost, thus vectors strongly influence the probability of successful emergence [4]. There are recent examples of emergence and re-emergence of insect-borne plant viruses that threaten food security causing instability of food supply. Understanding the causes that drive virus epidemics should provide means to reduce their impact on major crops around the world.

Insects as major drivers of emergence

It is not surprising that most emerging virus diseases are transmitted by hemipteroid insects (mainly aphids, whiteflies and thrips) as they have piercing–sucking mouthparts and are very well adapted to explore new

habitats (great dispersal capacity, high population growth rate and a wide host range). Insects drive the emergence of existing or new plant-pathogenic viruses under the following circumstances:

1. An insect species with higher vector propensity enters into a new region increasing the incidence and severity of a plant virus. Vector propensity, refers to the ability of a given insect species to transmit a plant pathogen under field conditions as opposed to its innate or potential capacity to transmit in the laboratory [5].

A good example is the closterovirus *Citrus tristeza virus* likely originated in Southeast Asia that was probably introduced into South America between 1927 and 1930. However, it was not until the introduction of the very efficient aphid vector, *Toxoptera citricida* that CTV was able to emerge as a destructive pathogen, causing the death of more than six million trees only in the State of Sao Paulo, Brazil [6]. Thus, the establishment and spread of an introduced virus may depend not only on the introduction itself but also on the presence of a vector species with a high propensity for virus transmission.

Another well-known example of an insect driven emerging disease is the explosion of begomoviruses and criniviruses epidemics in vegetable crops grown in the Mediterranean due to the displacement of the whitefly *Trialeurodes vaporariorum* by a much more efficient vector, *Bemisia tabaci*, which was restricted to outdoor crops but emerged into Mediterranean greenhouses in the early 1990s. The whitefly *B. tabaci* is nowadays considered a cryptic complex of several morphological indistinguishable species, being the MED species, formerly known as the Q biotype, the one of Mediterranean origin that is very well adapted to protected environments.

2. An insect species introduction with differential feeding habits than the existing vector population. An introduction of an efficient vector, with specific feeding habits, into a new region also caused devastating emerging epidemics not of a virus but of a bacterial pathogen, *Xylella fastidiosa*, the causal agent of Pierce Disease of grapevines. The introduction of the exotic glass-winged sharpshooter, *Homoladisca coagulata*, from southeastern USA into California grapevine-growing regions in the late 1990s became a significant threat to the \$35 billion wine and table grape industries [7]. This exotic insect species transmitted *X. fastidiosa* more efficiently than the existing sharpshooters vectors in the region because of its particular preference for feeding in overwintering woody parts

of vines. This exceptional feeding habit of *H. coagulata* increased the chances of polycyclic epidemics because several inoculations in summer and fall became successful after winter pruning [8]. The same bacterial pathogen has expanded recently in southern Italy causing severe epidemics and destroying already one million olive trees over a total of 40,000 ha [9]. The main causes why *X. fastidiosa* has emerged as a new devastating disease in Italy and the insect species transmitting and spreading the disease in olives groves are not yet known.

3. A vector species, better adapted to a wider host plant range expands into a new habitat enhancing virus spread. The MEAM1 species of the *B. tabaci* complex (previously known as the B biotype or *Bemisia argentifolii*) feeds on a very wide range of plants and has a very high dispersal capacity. Consequently, it has a higher probability to acquire, mix and deliver a diversity of begomovirus components into potential new hosts [10]. This insect species was able to adapt and feed readily on new host plants and also expand the host range of their vectored plant viruses. Until the mid 1980s, tomatoes were not colonized by native *B. tabaci* species in the Americas, but the introduction of the MEAM1 species that fed readily on tomatoes and other solanaceous crops led to an explosion of begomoviruses in the Western Hemisphere [11]. Thus, emerging virus diseases defined by pathogens that originate by jumping from one host species to another will depend on the plasticity of their vectors to adapt and colonize their shared host plant.

However, not always the MEAM1 species has been associated to virus emergence. In some rare cases, the displacement of a native vector by another whitefly species can result in virus extinction. This was the case of *Lettuce infectious yellow virus*, LIYV in the Imperial Valley, California. Unexpectedly, the incidence of LIYV, which was a very important emergent virus in the Imperial Valley in the late 1980s became extinct because of the displacement of the efficient native New World vector species (formerly known as the A biotype) by the much less efficient invasive MEAM1 species of *B. tabaci*. Thus, here is a rather unusual situation where introduction of an exotic insect has led to the reduction of an economically important emergent virus [10].

The expansion of *Tomato spotted wilt virus* (TSWV) epidemics across Europe in the 1980s has been attributed to a shift from the vector species *Thrips tabaci* to a much more polyphagous species *Frankliniella occidentalis*, which is very well adapted to a large range of host plants, many of them — at least 167 species — are also a host for the virus. The expansion of *F. occidentalis* from the Americas to other continents in the last 40 years is the major cause driving the re-emergence of TSWV and other tospovirus epidemics across Europe, Asia and Australia [12].

4. Exceptional weather conditions may facilitate long-distance migration and introductions of a vector species into new regions. *Tomato yellow leaf curl virus*-Is was accidentally introduced into the New World probably through tomato transplants that had been imported into the Dominican Republic from Israel in the early 1990s. This was the first report of the emergence of an Old World monopartite begomovirus in the New World [13]. After spreading through other Caribbean islands, TYLCV was first reported in the USA in 1999, hypothetically due to viruliferous whiteflies or infected plants that were introduced to Dade County in 1996–1997, the southernmost county in Florida [14]. The proximity — about 300 km — of Dade County to the Caribbean and the speed and facility with which TYLCV moved throughout Florida suggests that viruliferous *B. tabaci* would have been transported from the Caribbean across the ocean by strong winds. The appearance of *Bean golden mosaic virus* in Dade County in the fall of 1994 suggests that occasional long-distance air transport of viruliferous whiteflies could be one of the mechanisms by which begomoviruses can emerge.

An introduction of insect-vectored diseases by long-distance migration from mainland to neighbouring islands is also a perfectly plausible explanation for beetle-transmitted Sobemoviruses. A study using three sets of ORF4 sequences of virus isolates of *Rice yellow mottle virus* collected between 1966 and 2011 suggested that there was a single introduction to Madagascar, hundreds of kilometres from mainland Africa, as opposed to multiple introductions in the Zanzibar Archipelago, 40 km from the coast [15]. This recurrent introduction of RYMV to the Zanzibar Archipelago from mainland Tanzania is consistent with the recorded flight ability of Chrysomelidae vectors estimated to be of a few dozens kilometres [16].

Other smaller insects, such as cereal aphids are suspected to be transported much further by air currents reaching hundreds or even thousands of km during long distance migration [17]. Observations of sudden and dramatic outbreaks of *maize dwarf mosaic virus* (MDMV) epidemics suggest that viruliferous aphids were transported up to 1000 km under exceptional weather conditions from south to northern US States in about 12 h [18]. In fact, aphids can ascend after take-off into the planetary boundary layer (PBL), and then transported over long distances along with the horizontal air currents, also called low-level jet winds. These are fast moving ribbons of air currents in the low levels of the atmosphere that commonly occur in the Great Plains and Eastern USA [19]. They originate after dusk, and under mid latitudes when the earth's surface begins to cool and the PBL becomes compressed horizontally. Under such circumstances, aphids are trapped after sundown and overnight transport is common and can result in displacements of thousands of kilometres [20].

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