

Review Article



Refining Plant-Virus Interactions: Deciphering Host Range Evolution and Viral Emergence Dynamics

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Abstract | Plant viruses result from a complex interaction between genetic and ecological variables that affect the progression of the host spectrum. Recent studies on plant-pathogen dynamics are compiled in this review, with a focus on the contributions of intrinsic viral traits and extrinsic environmental factors. We investigate how a virus's capacity to infect a variety of host species is influenced by genetic uniqueness, adaptive trade-offs, and virus-vector interactions. This review also looks at how ecological factors, like species cohabitation and community interactions, affect the dynamics of viral transmission. Because environmental heterogeneity makes it difficult to extrapolate trends, the interaction of ecological and genetic models is essential to comprehending host range evolution. Plant viruses, which are mostly biotrophic diseases, cause large losses in agriculture since they depend on host cells for reproduction and spread. The review emphasizes the significance of taking into account both internal viral characteristics and external ecological impacts by examining genetic features and their adaptive implications. Predicting viral outbreaks and creating efficient disease management plans in agricultural settings requires an understanding of these dynamics. To improve our ability to forecast viral emergence and host range evolution, this review emphasizes the need for an integrated approach to the study of plant-virus interactions.

Received | December 14, 2024; **Accepted** | January 13, 2025; **Published** | January 22, 2024

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Citation | Khalid, B., M.U. Javed, T. Riaz, M.A. Ashraf, H.Z. Saeed, M. Shaheen, S. Nawaz, A.K. Korai, R. Riaz and M. Asim. 2025. Refining plant-virus interactions: deciphering host range evolution and viral emergence dynamics. *Hosts and Viruses*, 12: 47-61.

DOI | <https://dx.doi.org/10.17582/journal.hv/2025/12.47.61>

Keywords: Host range evolution, Virus emergence, Genetic specificity, Ecological factors, Adaptive trade-offs



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Introduction

Plant pathogens are biotrophic organisms that depend on their host cells to sustain their

replication and spread. In addition to several less-conserved proteins, the genomes of these viruses are usually small (between 2 and 20 kilobases) and contain DNA or RNA that contain the instructions

for several essential proteins, including the protective protein, movement protein, and replication-related enzymes (Koonin *et al.*, 2021). Plant diseases destroy about 15% of the world's agricultural yield, with viruses responsible for one-third of these losses on their own (Boualem *et al.*, 2016; Yadav and Chhibbar, 2018). According to Lefeuvre *et al.* (2019), the majority of viruses lead to severe symptoms that might result in a variety of physiological abnormalities in plants, endangering agricultural production and productivity. Current research often focuses on either intrinsic genetic factors or extrinsic ecological influences in isolation, making it challenging to predict viral emergence and develop effective disease management strategies. There is a need to emphasize the importance of integrating these perspectives to better understand host range dynamics and their implications for agricultural systems.

A variety of ecological and genetic variables combine to drive the complicated process of plant viral emergence, this results in the virus locating a new host adapting to it, and facilitating efficient transmission between individuals within the population of the new host (Elena *et al.*, 2014). Host range development plays a crucial role in the presence of plant viruses, which has recently attracted significant study attention. In theory, the host range number of host species that a disease use is a straightforward statistic that is essential to comprehending pathogen epidemiology and pathogenicity (Khaleeq *et al.*, 2024). However, as ecological variables like species abundance, distribution, and interaction define the spectrum of the potential host viruses that come into contact with them, this straightforward statistic shouldn't be viewed as an unchangeable characteristic (McLeish *et al.*, 2018).

Additionally, it is challenging to determine the virus's host range since it is nearly impossible to identify every non-host. Plant viruses may have notably little information on their host ranges, and research has mostly focused on those that infect crops, leaving interactions in natural environments largely unstudied (Roossinck and García-Arenal, 2015; Alexander *et al.*, 2014). The evolution of the Host range can lead to host shifts and the acquisition of new hosts, or the loss of existing ones (Elena *et al.*, 2014). This process is influenced by factors external to the virus, like its epidemiology and ecology, or internal factors, including genetic features that influence its adaptability

across various hosts. The historical perspective on the host range evolution primer is initially concentrated on the intrinsic gene factors, recently research has begun to explore the importance of extrinsic factors and the interplay between the intrinsic and extrinsic influences.

Virus-innate influences in the host range of evolution

Genetic specificity: Genetic specificity, where only particular viruses can infect and replicate within a specific host, and often only certain virus genotypes can infect and proliferate in a specific host genotype, is a crucial viral-intrinsic factor in determining host range. This specificity has been extensively studied using the matching-alleles (MA) and gene-for-gene (GFG) models of co-evolution (Agrawal and Lively, 2002). These models, originally developed to explain interactions between host and pathogen genotypes, have been broadly applied to examine the evolution of plant virus host ranges within the context of path systems (García-Arenal and Fraile, 2013). At the level of interspecies, an MA-like system facilitates shifts of the host, whereas a GFG-like system enables a range of host expansions. Studies analyzing the connection networks among a large number of sets of bacteriophage species and bacteria have shown either nested structures or modular structures (Latif *et al.*, 2019). It was proposed that modular infection networks would arise from the evolution of specialization driven by MA-like contacts and generalism represented by the layered structure driven by a GFG-like interaction (Flores *et al.*, 2013; Weitz *et al.*, 2013). The structure among the 37 viruses and 28 plant species infected with the matrix was recently uncovered (Moury *et al.*, 2017). While the entire network displayed a nested arrangement, it also contained significant modules aligning with viruses infecting specific plant families. This revealed two primary viral groups: Generalists (multiple hosts) and specialists (specific hosts) on distinct hosts.

Effects of virus infection on plants as an evolutionary result

Virus infection alters various plant traits, including those related to plant-insect interactions, and some of these traits enhance virus transmission, the impact of virus infection on plant-insect interactions is commonly referred to as virus manipulation (Mauck *et al.*, 2012; Zhang *et al.*, 2017; Carr *et al.*, 2018; Eigenbrode *et al.*, 2018). Plants are not passive spectators, though, since they are the most productive species on the planet

based on biomass. Rather, plants have evolved complex defense mechanisms against viruses and their vectors, including hormone-regulated immune-signaling networks (Pieterse *et al.*, 2012). Consequently, should the impacts of viral infection on interactions between plants and insects be regarded as the consequence of long-term plant adaptation to viruses, or should they be ascribed to virus manipulation? Defense responses against microbial pathogens, such as viruses or phytophagous insects, require the redistribution of carbon and nitrogen resources towards defense, along with the activation of defense phytohormone pathways that trigger the expression of numerous genes (Iqbal *et al.*, 2021). Because plants in agricultural ecosystems frequently have limited access to these resources, metabolic restructuring frequently results in the suppression of plant growth in the majority of cases, if not all of them. This is due to the interaction between growth-associated phytohormone pathways and defense pathways (Pieterse *et al.*, 2012; Vos *et al.*, 2013; Kliebenstein, 2016). When plants are attacked, they often employ complex regulatory mechanisms to balance growth and reproduction, which can lead to negative ecological consequences. In such cases, the resistance traits that are induced in response to one pathogen may interfere with resistance against other pathogens, as resources are reallocated away from defense mechanisms (Vos *et al.*, 2013). Two decades ago, the trade-off between herbivore and pathogen resistance was noted (Felton and Korth, 2000).

Adaptive trade-offs

The idea of adaptive trade-offs of different hosts stems from the variability in pathogen fitness across different hosts due to infection specificity. A virus may optimize its fitness in one or another closely relevant host but cannot maximize fitness in all potential hosts, as different fitness factors are host-specific (Shaheen *et al.*, 2024). When adapting to a single host comes at a cost to fitness in another host, it creates an adapted trade-off limiting host range expansion and promoting specialization over generalist (Wang *et al.*, 2024). Research into another host fitness trade-offs, which examines the fitness penalties incurred when adapting to a new host (often reflected in minimized fitness in the first host) has become an active area of study, providing substantial evidence of the trade-offs or their effects on transmitted across host species (Elena *et al.*, 2014; García-Arenal and Fraile, 2013).

Virus-vector interactions

It's interesting to note that there may be trade-offs between the two distinct hosts, such as the rice stripe virus's insect vector and plant host, where the virus has to reproduce to finish its life cycle (Zhao *et al.*, 2017). The pleiotropy of antagonistic of the host-range epistatic interactions and the mutations between them are two important mechanisms that have been thoroughly examined for creating host fitness across the trade-offs (Khaleeq *et al.*, 2024). Recently, studies examined the work of epistatic, antagonistic pleiotropy and complex interactions among adaptive mutations in the evolution of the host range (Whitlock, 1996; Ashby *et al.*, 2014; Bedhomme *et al.*, 2015).

Experimental evidence

The majority of the proof for cross-host fitness trade-offs comes from research that doesn't explore many virus-host interactions. For example, a viral genotype that has serially passed over to a new host is tested in both the original and new hosts. Experiments that look at more interactions produce more complicated results, which might make predictions about the development of the host range more difficult. A study on 20 different mutants of tobacco etches virus (TEV) across 8 random plant species revealed a host depended on the frequency distribution of the deleterious, natural, and beneficent mutations. These distributes were notably similar among taxonomically relevant hosts (Lalic *et al.*, 2011). A higher proportion of mutations proved advantageous in hosts from distant families, where the wild type of TEV genotype exhibited low fitness, whereas many mutations are detrimental in the first and closely relevant hosts. This shows that adapting to is new host can facilitate adapted to closely relevant hosts, promoting viral jumps to related species, and aligning with these observations (Longdon *et al.*, 2018).

Resistance-breaking mutations

In recent studies, resistance-breaking mutations have been extensively investigated in various crops, highlighting their significance in plant-virus interactions (Moreno-Pérez *et al.*, 2016). For instance, a study examined the effects of coat protein modifications in the pepper mild mottle virus (PMMoV) on overcoming resistance alleles in susceptible pepper genotypes. Similar investigations have been conducted on other crops (Rousseau *et al.*, 2018). In wheat, research has focused on the evolution of resistance-breaking mutations in the barley yellow

dwarf virus. In rice, studies have explored the genetic mechanisms by which the rice tungro spherical virus adapts to overcome host resistance. Additionally, in tomatoes, the interactions between the tomato yellow leaf curl virus and host resistance genes have been extensively studied (Wang *et al.*, 2024). These studies collectively underscore the importance of understanding resistance-breaking mutations across different plant-virus systems to develop robust disease management strategies.

Complexity of predictions

These findings demonstrate that it will be challenging to forecast host range development based on adaptive trade-offs in genetically diverse, vulnerable populations of the host, like those a virus may meet in the wild (Amin *et al.*, 2021). Because the fitness impacted by the mutations in the host range is influenced by extrinsic variables of the environment, predictions become challenging when other, different realistic scenes of host-range development are taken into account. For example, many viruses often infect plants in nature (Mascia and Gallitelli, 2016), and interactions between viruses during numerous infections may dictate the development of viral properties including virulence, host range, and within-host multiplication (Tollenaere *et al.*, 2016).

Co-infection may also impact the costs of expanding the host's range. Therefore, the different types like single or multiple types of infections and a mix of mutants affected the scenarios or severity of the pleiotropic effect of the resistant breaking mutations on viral growth when distinct PMMoV resistant breaking mutants are tested in co-infection (Moreno-Pérez *et al.*, 2016). The result is, that environmental factors, whether many or single infections, influenced across-host trade-offs.

Fitness components

Most studies on the across-host fitness trade-offs have focused on how host adaption mutations influence viral multiplication within the host or the reproductive system of viral fitness. Evolutionary constraints arise from competing trade-offs among other fitness components (Goldhill and Turner, 2014). These trade-offs could also shape host range evolution. Since host range changes often involve mutations in the coat protein gene, the reproduction-survival trade-off may play a crucial role in plant pathogens (García-Arenal and Fraile, 2013). For instance, in pepper mild mottle

virus (PMMoV), Selection for traits unrelated to the plant pathogen interaction, such as enhanced particle stability and survival, was found to be essential for expanding the host range (Fraile *et al.*, 2014).

An analysis of 9 coated proteins host adapted mutations showed pleiotropic on pathogen multiplied and particular stability. However, no correlation was found between viral multiplied and particular stability and between the traits and the host range breadth (Bera *et al.*, 2017). Although our findings refute a trade-off between reproduction and survival, they do suggest that environmental factors may influence across-host fitness tradeoffs (Saleem *et al.*, 2024).

Ecological factors

Gene models of host-virus co-evolution, which in corporate ecological components like asynchrony in host range and plant pathogen life cycle or spatial structuring of their populations, align with the limited experimental evidence on environmental influences on across-host trade-offs (Ashby *et al.*, 2014; Brown and Tellier, 2011). These models highlight the importance of considering ecological aspects in host range evolution, predicting that environmental heterogeneity can maintain poly-morphisms for the host-virus specialization even in the absence of fitness costs (Amin *et al.*, 2021).

Transmission of plant viruses

The fundamental stage of a virus to survive and proliferate is transmission. The majority of pathogens are limited to a specific kind of host (Clémence *et al.*, 2013), frequently result in the deaths of their hosts, or can spread from one plant to another plant mechanically or vegetatively in seeds, pollens, flies, insects, and pests, mites, nematodes, and other means (Pagán, 2022). The phylum arthropods, which spread plant viruses, comprise around 94% of all animal species (Singh *et al.*, 2020).

However, insects are the primary means by which viral infections are disseminated. When it comes to the economic significance of the illnesses in question as well as the transmission of the virus, insects constitute the most significant category of plant viral vectors (Manzoor *et al.*, 2019). A vector is an insect that spreads the illness. According to reports, insect vectors can spread more than 400 illnesses (Agrios, 2009). Different types of organisms like aphids, leaf-hoppers, white flies, thrips, and scale insects are

among the significant insect species that contribute significantly to the spread of plant viruses (Sarwar, 2020).

Because plant surfaces are protected by materials such as lignin or cuticles, plant viruses cannot penetrate them directly and must instead enter through wounds in the cells (Savatin *et al.*, 2014; Gergerich and Dolja, 2006). When insects feed on the diseased plant, it acquires the pathogen through their mouth, which can be used to bite and chew (beetles) or pierce and suck (hemipteran bugs and nematodes). This virus is inoculated in the healthy plant by feeding on the specific plant-like tissue, or young leaves (Smith, 1924; Gray and Banerjee, 1999). This incubation is the time frame during which the virus develops its infectivity within the vector (Louten, 2016).

Different viruses might take anything a few minutes and hours to many days to incubate. There is some connection between insect vectors and plant viruses. According to Whitfield *et al.* (2015), the majority of plant viruses that are spread by one set of vectors are not spread by another. For instance, the sugar beet mosaic virus is spread by the peach aphid (Laurent *et al.*, 2023), while it is not spread by leafhoppers that eat the same crop (Walkey, 1991).

Host range evolution

The fact that host range evolution depends on how animals interact with their surroundings is one of the primary reasons it is not well understood (Woolhouse and Gowtage-Sequeria, 2005; Jones, 2009). Numerous processes influenced by the patchiness of the interacting species lead to the formation of viruses and the spread of illness (Thrall and Burdon, 1997). Given this environmental variability, viruses are likely to develop different resource-use strategies and be exposed to a variety of possibilities to change their host range (Woolhouse and Gaunt, 2007; Hily *et al.*, 2016). Forming practical generalizations about the evolution of host range and its function in disease dynamics is significantly hampered by this variability (Poulin, 2007).

Resistance and susceptibility of host plant

Tomato plants are not exempt from the many plant illnesses brought on by viruses, which have a detrimental impact on plant quality and productivity (Moriones and Verdin, 2020). This is no cure for most viral diseases other than cultural and manual practices

like prevention, the use of inorganic sprays, and the adoption of gene resistance to lessen the damage caused by viral infections in plants (Arie *et al.*, 2007; Moriones and Verdin, 2020; Hanssen *et al.*, 2010). The viruses are known to hijack and use the genomes of their plant's host for benefit. The discovery or development of a host resistant to infections using genes and resources likely picked from land areas and wild areas is a crucial and ecologically friendly component of the sustainable management of disease systems due to the lack of antiviral medications (Ishaq *et al.*, 2024).

However, in various crops such as tomatoes, wheat, and rice, different resistance genes are often associated with undesirable traits that were lost during domestication and breeding processes (Lefebvre *et al.*, 2020; Hanssen *et al.*, 2010; Campos *et al.*, 2021; Qi *et al.*, 2021; Szymański *et al.*, 2020; Patil *et al.*, 2020). For instance, tomato viruses are challenging to control due to their high genetic diversity, characterized by rapid mutation rates and spread (Hanssen *et al.*, 2010; Huang, 2021). Similarly, wheat and rice face similar challenges with viruses like the barley yellow dwarf virus and rice tungro spherical virus, respectively (Table 1). To address these issues, it is crucial to identify and eliminate non-redundant proteins in the host based on the biological characteristics of the pathogens. Additionally, RNA interference technology offers a promising approach to combat pathogens in these crops (Ong *et al.*, 2020).

Furthermore, some weeds, such as those in the Solanaceae family, which includes tomatoes, act as reservoirs for tomato viruses, therefore effective weed control must be taken into account (Ong *et al.*, 2020; Rivarez *et al.*, 2023; Barreto *et al.*, 2013). Three factors—durability, effectiveness, and spectrum of resistance—are used to gauge host plant resistance. The host plant's disease resistance is evaluated using a straightforward biological experiment in a controlled environment (Lefebvre *et al.*, 2020). By either overriding the plant defense system or mimicking the avirulent component when detected by resistance protein, proteins effector modifies and change the cellular function of the host (Kanwal *et al.*, 2024). To create another and effective R genes against viruses, it is possible to identify, modify, and use the majority of conserved effectors from a variety of pathogen avirulent genes (Lefebvre *et al.*, 2020).

Species coexistence and virus interactions

Viruses interacting with closely related or co-existing host species are more frequent than those of unrelated hosts, and when significant host fitness or virus trade-offs are absent, species coexistence within a community relies on selective pressure and the ecological mechanisms of the community (Moury *et al.*, 2017; Cronin *et al.*, 2010; Seabloom *et al.*, 2015). Both perspectives agree that environmental variables and community interactions shape the evolution of organisms resource breadth (Latif *et al.*, 2019). In cases of minimal pathogen fitness trade-offs different available host species, factors such as stochastic changes in community composition (McLeish *et al.*, 2018), local extinctions, and virus movement ecology (e.g., vector behaviour) can drive host range evolution (Elena, 2017; Simpson *et al.*, 2012). Both chronic and emerging disease outbreaks include interactions between several species that are ingrained in local populations. Studies at the community level cover a wide range of sizes, from interactions at the landscape level to those that take place inside individual organisms. Connectivity between communities is linked to the landscape-scale process of disease onset (Yuen and Mila, 2015).

Importance of multiple infections

On a smaller scale, several infections in a single person might result in antagonistic or synergistic viral interactions, which can affect the dynamics of transmission (Mascia and Gallitelli, 2016). Disease epidemiology and host range evolution are made more difficult by the spectrum of species interactions involved in transmission (Jones, 2009). Species phenotypes, or traits, are commonly used to measure interactions in community-level ecology and pathology investigations. These traits can be extrapolated to higher levels of biological organization. By separating the interactions between species and traits, this method makes variables of interest community functions that are not species-specific (Barrett *et al.*, 2015).

Connectivity and its effects on biodiversity

Understanding ecological and evolutionary processes requires linking species interactions based on trait interdependencies (Bascompte, 2010). Connectivity between species may be used to quantify how the species interact, including such as predation, mutualism, competition, parasitism, and herbivory (Roossinck, 2015). The virus's ability to spread and change the host range may be impacted by this connection, which can fluctuate with biodiversity and

contact rates (Swei *et al.*, 2011).

Challenges in formulating generalisations

Characteristics such as host resistance and tolerant (Barrett *et al.*, 2015), susceptible (Susi *et al.*, 2015), pathogenicity of the pathogen (Susi *et al.*, 2015), and pathogen of the host specificity (Hillung *et al.*, 2014) are often measured in ecological and evolutionary investigations. Attempts to rationalize and generalize about the origins and transmission of illness are complicated by the non-linear interactions among these and other interacting elements (Sofonea *et al.*, 2017). The links between the factors thought to affect the spread of infections are depicted in Figure 1. This conceptual framework emphasizes how ecological (such as spatiotemporal, abiotic, and species interactions) and evolutionary (genetic) variables, such as viral host range, indirectly contribute to the transmission of illness.

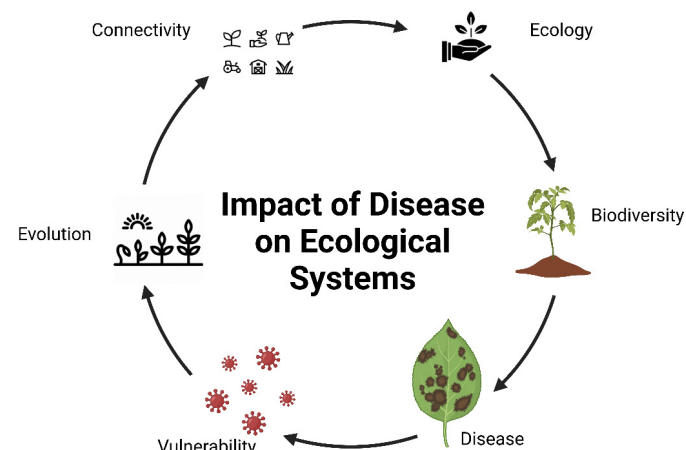


Figure 1: Impact of diseases on ecological system: A holistic approach.

Indirect interactions and their implications

Only a small number of the direct and indirect interactions that may contribute to the spread of illness are the subject of experimental research on the host-range evolution and risk of the diseases. Different ecological or evolutionary events that impact transmission through intricate channels give rise to indirect interactions between different viruses and animals (Raza *et al.*, 2024). For example, independent of the whitefly population, transmission frequency was dramatically impacted by the endosymbiotic type of bacteria *Hamiltonella* in the yellow leaf curl virus of tomato-carrying white fly *Bemisia tabaci* (Su *et al.*, 2013). In a similar vein, variations in mosquito vector feeding habits among populations caused variations in West Nile virus transmission patterns (Hamer *et al.*, 2011).

Table 1: *Impact of viral infection on crop health: Symptoms and affected species.*

S. No.	Name of virus	Symptoms of virus	Crops	References
1	Barley yellow dwarf virus	Leaf yellowing, inhibited growth, and decreased grain yield	Wheat	(Walls <i>et al.</i> , 2019)
2	Cassava mosaic virus	Patchy patterns, deformities, and diminished root yield	Cassava	(Eni <i>et al.</i> , 2021)
3	Maize dwarf mosaic virus	Irregular patterns, stunted growth, and streaks of yellow	Maize	(Kannan <i>et al.</i> , 2018)
4	Maize streak virus	Yellow streaking on leaves and inhibited growth	Maize	(Emeraghi <i>et al.</i> , 2021; Shepherd <i>et al.</i> , 2010)
5	Potato virus Y	Mosaic patterns on leaves, yellowing, and tissue death	Potato	(Gray <i>et al.</i> , 2010; Karasev <i>et al.</i> , 2013)
6	Rice tungro spherical virus	Inhibited growth, leaf yellowing, and lower grain yield	Rice	(Nihad <i>et al.</i> , 2021)
7	Southern rice black-streaked dwarf virus	Inhibited growth and black streaks on the leaves	Rice	(Zhou <i>et al.</i> , 2013)
8	Sugarcane mosaic virus	Mosaic patterns, yellow streaks, and stunted growth	Maize	(Jiao <i>et al.</i> , 2022)
9	Sweet potato chlorotic stunt virus	Leaf yellowing, growth inhibition, and deformation.	Sweet potato	(Clark <i>et al.</i> , 2012; Gutierrez <i>et al.</i> , 2003)
10	Tomato yellow leaf curl virus	Leaf yellowing, curling, and decreased fruit set	Tomato	(Diaz-Pendon <i>et al.</i> , 2010; Prasad <i>et al.</i> , 2020)

Community-specific mechanisms of host range evolution

Community-specific processes facilitate host range development through indirect, localized impacts. In four distinct plant communities, the frequency of eleven generalist viruses in 47 host species was analyzed (Shah *et al.*, 2021). The results showed that the viruses used specialized resources relevant to the community, indicating that exploitation techniques frequently include trade-offs with scarce resources (McLeish *et al.*, 2017). In every instance, connectivity- which was impacted by biodiversity and spatiotemporal variability necessary for viral interactions with hosts or other species. For example, the community composition of vector species was used to explain the temporal and geographical variability of numerous infections by communities of lute viruses and polioviruses (Seabloom *et al.*, 2009).

Diversity of the infection by determining factors

In another research on different infection diversification, the co-existence of 4 distinct B/CYDV organisms was primarily determined by their traits and the resources specific to particular regions (Seabloom *et al.*, 2009). Depending on temporal or geographical variables, biodiversity's indirect impacts may either raise or lower the risk of illness (Luis *et al.*, 2018). Eleven plant viruses' host ranges and host diversity within a habitat both have an impact

on prevalence-diversity interactions (McLeish *et al.*, 2017). Variations in realized host range across environments were consistent with facultative generalist criteria (Shipley *et al.*, 2009). The variety of characteristics (such as susceptible, resistant, and tolerant qualities) and accessible resources to different viruses varies throughout time and geography, much as species distribution and abundance are influenced by different sources of variation. Numerous factors have both reciprocal and non-reciprocal impacts, suggesting that the development of host range is a complex process influenced by both ecological systems and the genetic makeup of interacting species (Raza *et al.*, 2025).

Challenges in generalizing patterns

Because of environmental variability, processes that determine how a virus interacts with resources and characteristics that are essential to host-range development may spread from various geographical or temporal scales and include a wide variety of variables. According to the available data, it is very difficult to create broadly applicable ecological patterns that can account for the evolution of host range and transmission of diseases (Papale *et al.*, 2020). Comparison systems of pathogens, individuals with distinct eco-evo-devo traits, may lead to generalizations.

Conclusion and Recommendations

The majority of studies on the evolution of viruses in the plant host range have concentrated on aspects inherent to the virus, namely the genetic basis of host-specific fitness variations. That influences how resource utilization evolves toward specialization or generalism. Nonetheless, the most recent research discussed here shows that environmental variables affect viral fitness in different hosts, necessitating its inclusion in genetic models of host range development. Experiments may be used to investigate the interplay between intrinsic and extrinsic elements in host-range development, and we anticipate that additional work in this area will be undertaken soon. Understanding how ecological, non-deterministic variables affect the evolution host range is a most difficult task.

Analytical challenges involve multi-variate data sets with varying distributions, dependencies on regional or temporal scales, and taxonomy inconsistencies arising from the complexity of plant pathogen connection in the natural environment. Large datasets may be produced, for example, using high throughput techniques, which has led to the creation of techniques for integrating data to comprehend how the environment shapes species relationships. Although it is still in its infancy, the use of these methods to comprehend the development of the host range of viruses or different plant pathogens in particles yields insightful information. Importantly, to make generalizations about transmission patterns, infection in risk, host range development, and disease onset, intrinsic and extrinsic variables must be jointly considered, as well as the intricacy of their interactions.

Acknowledgements

We want to express our gratitude to the University of Agriculture, Faisalabad, Pakistan, and the Government College University, Faisalabad, Pakistan for providing the necessary resources and support throughout the preparation of this review paper.

Novelty Statement

The novelty of this article lies in its comprehensive integration of intrinsic viral traits and extrinsic ecological factors in understanding plant-virus interactions. By examining the interplay between genetic specificity, adaptive trade-offs, and

environmental influences, this review provides a fresh perspective on host range evolution and viral emergence dynamics. It emphasizes the need for an interdisciplinary approach to enhance predictions of viral outbreaks and inform effective disease management strategies in agriculture.

Author's Contribution

Burhan Khalid, Rabiya Riaz, Muhammad Asim and Hafiza Zara Saeed: Conceived and designed the review. **Muhammad Umer Javed, Amir Khan Korai, Talha Riaz and Musrat Shaheen:** Wrote the manuscript.

Muhammad Atiq Ashraf and Shumaila Nawaz: Critically revised it.

Funding

This study did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Availability of data and materials

Not applicable.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Conflict of interest

The authors have declared no conflict of interest.

References

- Agrawal, A. and Lively, C.M., 2002. Infection genetics: Gene-for-gene versus matching-alleles models and all points in between. *Evol. Ecol. Res.*, 4: 91-107.
- Agrios, G.N., 2009. Transmission of plant diseases by insects. University of Florida.
- Alexander, H.M., Mauck, K.E., Whitfield, A.E., Garrett, K.A. and Malmstrom, C.M., 2014. Plant-virus interactions and the agroecological interface. *Eur. J. Pl. Pathol.*, 138: 529-547. <https://doi.org/10.1007/s10658-013-0317-1>
- Alizon, S., de Roode, J.C. and Michalakakis, Y., 2013. Multiple infections and the evolution of virulence. *Ecol. Lett.*, 16: 556-567. <https://doi.org/10.1111/ele.12076>

- Amin, S.E., Qazi, Z.A., Karim, A., Masood, S., Soomro, M.B., Soomro, F., Bakhtawar, N., Anam, M., Gul, M., Ilyas, M.A., Yousaf, U., Riaz, T. and Haq, N., 2021. An insight on the importance of traceability and tracking in halal food industry in Pakistan. *Pak. J. Soc. Sci.*, 18(5): 85-91.
- Amin, S.E., Qazi, Z.A., Karim, A., Masood, S., Soomro, M.B., Soomro, F., Bakhtawar, N., Anam, M., Gul, M., Ilyas, M.A., Yousaf, U., Riaz, T., Shayan, M. and Haq, N.U., 2021. Identification of lab grown meat and its nutritional impacts on human health. *Vet. Res.*, 14(3): 34-39. Medwell Publications. <https://www.researchgate.net/publication/368996336>
- Arie, T., Takahashi, H., Kodama, M. and Teraoka, T., 2007. Tomato as a model plant for plant-pathogen interactions. *Plant Biotechnol.*, 24: 135-147. <https://doi.org/10.5511/plantbiotechnology.24.135>
- Ashby, B., Gupta, S. and Buckling, A., 2014. Effects of epistasis on infectivity range during host-parasite coevolution. *Evolution*, 68: 2972-2982. <https://doi.org/10.1111/evo.12479>
- Ashby, B., Gupta, S. and Buckling, A., 2014. Spatial structure mitigates fitness costs in host-parasite coevolution. *Am. Nat.*, 183: E64-E74. <https://doi.org/10.1086/674826>
- Barreto, S.S., Hallwass, M., Aquino, O.M. and Inoue-Nagata, A.K., 2013. A study of weeds as potential inoculum sources for a tomato-infecting begomovirus in central Brazil. *Phytopathology*, 103(5): 436-444. <https://doi.org/10.1094/PHYTO-07-12-0174-R>
- Barrett, L., Encinas-Viso, F., Thrall, P.H. and Burdon, J., 2015. Specialization for resistance in wild host-pathogen interaction networks. *Front. Plant Sci.*, 6: 761. <https://doi.org/10.3389/fpls.2015.00761>
- Bascompte, J., 2010. Structure and dynamics of ecological networks. *Science*, 329: 765-766. <https://doi.org/10.1126/science.1194255>
- Bedhomme, S., Hillung, J., Elena, S.F., 2015. Emerging viruses: Why they are not jacks of all trades? *Curr. Opin. Virol.*, 10: 1-6. <https://doi.org/10.1016/j.coviro.2014.10.006>
- Bera, S., Moreno-Pérez, M.G., Garcí'a-Figuera, S., Paga`n, I., Fraile, A., Pacios, L.F. and Garcí'a-Arenal, F., 2017. Pleiotropic effects of resistance-breaking mutations on particle stability provide insight into life history evolution of a plant RNA virus. *J. Virol.*, 91: e00435-17. <https://doi.org/10.1128/JVI.00435-17>
- Boualem, A., Dogimont, C. and Bendahmane, A., 2016. The battle for survival between viruses and their host plants. *Curr. Opin. Virol.*, 17: 32-38. <https://doi.org/10.1016/j.coviro.2015.12.001>
- Brown, J.K.M. and Tellier, A., 2011. Plant-parasite coevolution: bridging the gap between genetics and ecology. *Annu. Rev. Phytopathol.*, 49: 345-367. <https://doi.org/10.1146/annurev-phyto-072910-095301>
- Campos, M.D., Félix, M.D.R., Patanita, M., Materatski, P. and Varanda, C., 2021. High throughput sequencing unravels tomato-pathogen interactions towards a sustainable plant breeding. *Hortic. Res.*, 8: 171. <https://doi.org/10.1038/s41438-021-00607-x>
- Carr, J.P., Donnelly, R., Tungadi, T., Murphy, A.M., Jiang, S.J., Bravo-Cazar, A., Yoon, J., Cuniffe, N.J., Glover, B.J. and Gilligan, C.A., 2018. Viral manipulation of plant stress responses and host interactions with insects. *Adv. Virus Res.*, 102: 177-197. <https://doi.org/10.1016/bs.aivir.2018.06.004>
- Clark, C.A., Davis, J.A., Mukasa, S.B., Abad, J.A., Tugume, A.K., Cuellar, W.J., Fuentes, S., Kreuze, J.F., Tairo, F.D., Gibson, R.W., Mukasa, S.B., Tugume, A.K., Tairo, F.D. and Valkonen, J.P., 2012. Sweet potato viruses: 15 years of progress on understanding and managing complex diseases. *Plant Dis.*, 96: 168-185. <https://doi.org/10.1094/PDIS-07-11-0550>
- Clémence, H., Véronique, B., Véronique, Z.G. and Frédéric, R., 2013. Viral and cellular factors involved in phloem transport of plant viruses. *Front. Plant Sci.*, 4: 154. <https://doi.org/10.3389/fpls.2013.00154>
- Cronin, J.P., Welsh, M.E., Dekkers, M.G., Abercrombie, S.T. and Mitchell, C.E., 2010. Host physiological phenotype explains pathogen reservoir potential. *Ecol. Lett.*, 13: 1221-1232. <https://doi.org/10.1111/j.1461-0248.2010.01513.x>
- Dawson, W.O., Garnsey, S.M., Tatineni, S., Folimonova, S.Y., Harper, S.J. and Gowda, S., 2013. Citrus tristeza virus-host interactions. *Front. Microbiol.*, 4: 88. <https://doi.org/10.3389/fmicb.2013.00088>
- Diaz-Pendon, J.A., Canizares, M.C., Moriones, E., Bejarano, E.R., Czosnek, H. and Navas-Castillo, J., 2010. Tomato yellow leaf curl viruses:

- Menage a trois between the virus complex, the plant and the whitefly vector. *Mol. Plant Pathol.*, 11: 441–450. <https://doi.org/10.1111/j.1364-3703.2010.00618.x>
- Eigenbrode, S.D., Bosqueperez, N.A. and Davis, T.S., 2018. Insect-borne plant pathogens and their vectors: Ecology, evolution, and complex interactions. *Ann. Rev. Entomol.*, 63: 169–191. <https://doi.org/10.1146/annurev-ento-020117-043119>
- Elena, S.F., Fraile, A. and Garcí'a-Arenal, F., 2014. Evolution and the emergence of plant viruses. *Adv. Virus Res.*, 88: 161–191. <https://doi.org/10.1016/B978-0-12-800098-4.00003-9>
- Elena, S.F., 2017. Local adaptation of plant viruses: Lessons from experimental evolution. *Mol. Ecol.*, 26: 1711–1719. <https://doi.org/10.1111/mec.13836>
- Emeraghi, M., Achigan-Dako, E.G., Nwaoguala, C.N.C. and Oselebe, H., 2021. Maize streak virus research in Africa: An end or a crossroad. *Theor. Appl. Genet.*, 134: 3785–3803. <https://doi.org/10.1007/s00122-021-03914-y>
- Escriu, F., Fraile, A. and Garcí'a-Arenal, F., 2003. The evolution of virulence in a plant virus. *Evolution*, 57: 755–765. <https://doi.org/10.1111/j.0014-3820.2003.tb00287.x>
- Felton, G.W. and Korth, K.L., 2000. Trade-offs between pathogen and herbivore resistance. *Curr. Opin. Plant Biol.*, 3: 309–314. [https://doi.org/10.1016/S1369-5266\(00\)00086-8](https://doi.org/10.1016/S1369-5266(00)00086-8)
- Flores, C.O., Valverde, S. and Weitz, J.S., 2013. Multi-scale structure and geographic drivers of cross-infection within marine bacteria and phages. *ISME J.*, 7: 520–532. <https://doi.org/10.1038/ismej.2012.135>
- Fraile, A., Hily, J.M., Pagan, I., Pacios, L.F. and Garcí'a-Arenal, F., 2014. Host resistance selects for traits unrelated to resistance breaking that affect fitness in a plant virus. *Mol. Biol. Evol.*, 31: 928–939. <https://doi.org/10.1093/molbev/msu045>
- Garcia, J.A., Glasa, M., Cambra, M. and Candresse, T., 2014. Plum pox virus, and sharka: A model potyvirus and a major disease. *Mol. Plant Pathol.*, 15: 226–241. <https://doi.org/10.1111/mpp.12083>
- Gergerich, R.C. and Dolja, V.V., 2006. Introduction to plant viruses, the invisible foe. *The plant health instructor*. <https://doi.org/10.1094/PHI-I-2006-0414-01>
- Goldhill, D.H. and Turner, P.E., 2014. The evolution of life history trade-offs in viruses. *Curr. Opin. Virol.*, 8: 79–84. <https://doi.org/10.1016/j.coviro.2014.07.005>
- García-Arenal, F. and Fraile, A., 2013. Trade-offs in host range evolution of plant viruses. *Plant Pathol.*, 62: 2–9. <https://doi.org/10.1111/ppa.12104>
- Gray, S.M. and Banerjee, N., 1999. Mechanisms of arthropod transmission of plant and animal viruses. *Microbiol. Mol. Biol. Rev.*, 63(1): 128–148. <https://doi.org/10.1128/MMBR.63.1.128-148.1999>
- Gray, S., De Boer, S., Lorenzen, J., Karasev, A., Whitworth, J., Nolte, P., Singh, R., Boucher, A. and Xu, H.M., 2010. Potato virus Y: An evolving concern for potato crops in the United States and Canada. *Plant Dis.*, 94: 1384–1397. <https://doi.org/10.1094/PDIS-02-10-0124>
- Gutierrez, D.L., Fuentes, S. and Salazar, L.F., 2003. Sweet potato virus disease (SPVD): Distribution, incidence, and effect on sweet potato yield in Peru. *Plant Dis.*, 87: 297–302. <https://doi.org/10.1094/PDIS.2003.87.3.297>
- Hamer, G.L., Chaves, L.F., Anderson, T.K., Kitron, U.D., Brawn, J.D., Ruiz, M.O., Loss, S.R., Walker, E.D. and Goldberg, T.L., 2011. Fine-scale variation in vector host use and force of infection drive localized patterns of West Nile virus transmission. *PLoS One*, 6: e23767. <https://doi.org/10.1371/journal.pone.0023767>
- Hanssen, I.M., Lapidot, M. and Thomma, B.P.H.J., 2010. Emerging viral diseases of tomato crops. *MPMI*, 23(5): 539–548. <https://doi.org/10.1094/MPMI-23-5-0539>
- Hillung, J., Cuevas, J.M., Valverde, S. and Elena, S.F., 2014. Experimental evolution of an emerging plant virus in host genotypes that differ in their susceptibility to infection. *Evolution*, 68: 2467–2480. <https://doi.org/10.1111/evo.12458>
- Hily, J.M., Poulicard, N., Mora, M.A., Paga'n, I. and Garcí'a-Arenal, F., 2016. Environment and host genotype determine the outcome of a plant–virus interaction from antagonism to mutualism. *New Phytol.*, 209: 812–822. <https://doi.org/10.1111/nph.13631>
- Huang, C., 2021. From player to pawn: Viral avirulence factors involved in plant immunity. *Viruses*, 13: 688. <https://doi.org/10.3390/v13040688>
- Iqbal, Z., Iqbal, M.S., Hashem, A., Abd-Allah,

- E.F. and Ansari, M.I., 2021. Plant defense responses to biotic stress and its interplay with fluctuating dark/light conditions. *Front. Plant Sci.*, 12: 631810. <https://doi.org/10.3389/fpls.2021.631810>
- Ishaq, H., Nisar, K., Riaz, R., Murtaza, M.S., Shahbaz, M., Munir, T., Raza, A., Iqbal, D., Ahmad, M. and Riaz, T., 2024. Amini-review of medicinal uses and phytochemicals isolated from Himalayan plant *Delphinium brunonianum* royle. *Int. J. Adv. Eng. Manage.*, 6(10): 507-516. <https://doi.org/10.35629/5252-0610507516>
- Jiao, Z.Y., Tian, Y.Y., Wang, J., Ismail, R.G., Bondok, A. and Fan, Z.F., 2022. Advances in research on maize lethal necrosis, a devastating viral disease. *Phytopathol. Res.*, 4: 14. <https://doi.org/10.1186/s42483-022-00117-1>
- Johnson, P.T., De Roode, J.C. and Fenton, A., 2015. Why infectious disease research needs community ecology. *Science*, 349: 1259504. <https://doi.org/10.1126/science.1259504>
- Jones, R.A.C., 2009. Plant virus emergence and evolution: Origins, new encounter scenarios, factors driving emergence, effects of changing world conditions, and prospects for control. *Virus Res.*, 141: 113-130. <https://doi.org/10.1016/j.virusres.2008.07.028>
- Kannan, M., Ismail, I. and Bunawan, H., 2018. Maize dwarf mosaic virus: From genome to disease management. *Viruses*, 10: 492. <https://doi.org/10.3390/v10090492>
- Kanwal, R., Hafeez Ul Haq, M., Waseem, A., Riaz, T., Rehman, Z.U., Fazal, A., Javed, J., Ali, M.A., Ashfaq, S. and Saleem, H., 2024. Fungitoxic properties of essential oils to treat tinea. In: M.A. Zafar, R.Z. Abbas, M. Imran, S. Tahir and W. Qamar (Eds.). *Complement. Altern. Med. Essent. Oils* (pp. 81-89). Unique Scientific Publishers. <https://doi.org/10.47278/book.CAM/2024.192>
- Karasev, A.V. and Gray, S.M., 2013. Continuous and emerging challenges of potato virus Y in potato. *Annu. Rev. Phytopathol.*, 51: 571-586. <https://doi.org/10.1146/annurev-phyto-082712-102332>
- Kedem, H., Cohen, C., Messika, I., Einav, M., Pilosof, S. and Hawlena, H., 2014. Multiple effects of host-species diversity on coexisting host specific and host-opportunistic microbes. *Ecology*, 95: 1173-1183. <https://doi.org/10.1890/13-0678.1>
- Khaleeq, K., Akhundzada, K., Ehsan, Q., Behzad, M.A., Rathore, S.S., Samim, M. and Tamim, S.A., 2024. Optimization of crop establishment methods and phosphorus fertilizer levels on growth and economic efficiency of groundnut under semi-arid region of Afghanistan. *J. Res. Appl. Sci. Biotechnol.*, 3(2): 54-58. <https://doi.org/10.55544/jrasb.3.2.12>
- Khaleeq, K., Farkhari, Z., Amini, A.M., Ahmadi, A., Samim, M., Ashraf, M.A. and Frotan, S., 2024. Effects of nitrogen application on growth and yield of groundnut (*Arachis hypogaea* L.) in northeast agro-ecology of Afghanistan. *J. Res. Appl. Sci. Biotechnol.*, 3(2): 9-12. <https://doi.org/10.55544/jrasb.3.2.3>
- Kliebenstein, 2016. False idolatry of the mythical growth versus immunity tradeoff in molecular systems plant pathology. *Physiol. Mol. Plant Pathol.* 95: 55-59. <https://doi.org/10.1016/j.pmpp.2016.02.004>
- Koonin, E.V., Krupovic, M. and Agol, V.I., 2021. The Baltimore classification of viruses 50 years later: How does it stand in the light of virus evolution? *Microbiol. Mol. Biol. Rev.*, 85: e00053-e21. <https://doi.org/10.1128/MMBR.00053-21>
- Lalic, J., Cuevas, J.M. and Elena, S.F., 2011. Effect of host species on the distributions of mutational fitness effects for an RNA virus. *PLoS Genet.*, 7: e1002378. <https://doi.org/10.1371/journal.pgen.1002378>
- Latif, M.F., Aleem, M.T., Bakhsh, M., Sohail, A., Riaz, T. and Bilal, A., 2019. Extraction and utilization of pomegranate seed oil in cookies to alleviate hyperlipidemia in rats. *Int. J. Biol. Res.*, 2(1): 246-256.
- Latif, M.F., Naqvi, S.M.T., Shahzadi, N., Riaz, T. and Sohail, A., 2019. Effect of defatted wheat germ supplemented cookies on the protein quality parameters of rats. *Nat. Sci.*, 17(8): 110-116. <http://www.sciencepub.net/nature>
- Laurent, A., Favrot, A., Maupas, F., Royer, C. and Makowski, D., 2023. Assessment of non-neonicotinoid treatments against aphids on sugar beets. *Crop Prot.*, 164. <https://doi.org/10.1016/j.cropro.2022.106140>
- Lefebvre, V., Boissot, N. and Gallois, J.L., 2020. Host Plant resistance to pests and pathogens, the genetic leverage in integrated pest and disease management: Integrated pest and disease management in greenhouse crops. *Plant*

- pathology in the 21st Century, 2nd Edition. In: Gullino ML, Albajes R, Nicot PC, editors. Springer Nature, Switzerland AG. https://doi.org/10.1007/978-3-030-22304-5_9
- Lefeuvre, P., Martin, D.P., Elena, S.F., Shepherd, D.N., Roumagnac, P. and Varsani, A., 2019. Evolution and ecology of plant viruses. *Nat. Rev. Microbiol.*, 17(10): 632-644. <https://doi.org/10.1038/s41579-019-0232-3>
- Leventhal, G.E., Hill, A.L., Nowak, M.A. and Bonhoeffer, S., 2015. Evolution and the emergence of infectious diseases in theoretical and real-world networks. *Nat. Commun.*, 6: 6101. <https://doi.org/10.1038/ncomms7101>
- Longdon, B., Day, J.P., Alves, J.M., Smith, S.C.L., Houslay, T.M., McGonigle, J.E., Tagliaferri, L. and Jiggins, F.M., 2018. Host shifts result in parallel genetic changes when viruses evolve in closely related species. *PLoS Pathog.*, 14: e1006951. <https://doi.org/10.1371/journal.ppat.1006951>
- Louten, J., 2016. Virus transmission and epidemiology. *Essential Human Virology*, pp. 71-92. <https://doi.org/10.1016/B978-0-12-800947-5.00005-3>
- Luis, A.D., Kuenzi, A.J. and Mills, J.N., 2018. Species diversity concurrently dilutes and amplifies transmission in a zoonotic host-pathogen system through competing mechanisms. *Proc. Natl. Acad. Sci. U.S.A.*, 2018: 201807106. <https://doi.org/10.1073/pnas.1807106115>
- Malpica, J.M., Sacrista'n, S., Fraile, A., Garcí'a-Arenal, F., 2006. Association and host selectivity in multi-host pathogens. *PLoS One*, 1: e41. <https://doi.org/10.1371/journal.pone.0000041>
- Manzoor, E., Ghani, A., Khan, M.R., Sultana, M., Ishaque, A., Nasir, E., Latif, M.F., Riaz, T. and Sohail, A., 2019. Antioxidant potential of guava leaves extracts and their effects on hyperlipidemia. *Annal. Plant Sci.*, 8(5): 3553-3562.
- Mascia, T. and Gallitelli, D., 2016. Synergies and antagonisms in virus interactions. *Plant Sci.*, 252: 176-192. <https://doi.org/10.1016/j.plantsci.2016.07.015>
- Mauck, K.E., Bosque-Perez, N.A., Eigenbrode, S.D., De Moraes, C.M. and Mescher, M.C., 2012. Transmission mechanisms shape pathogen effects on host-vector interactions: Evidence from plant viruses. *Funct. Ecol.*, 26: 1162-1175. <https://doi.org/10.1111/j.1365-2435.2012.02026.x>
- McLeish, M., Fraile, A., Garcí'a-Arenal, F., 2018. Ecological complexity in plant virus host range evolution. *Adv. Virus Res.*, 101: 293-339. <https://doi.org/10.1016/bs.aivir.2018.02.009>
- McLeish, M., Sacrista'n, S., Fraile, A. and Garcí'a-Arenal, F., 2017. Scale dependencies and generalism in host use shape virus prevalence. *Proc. R. Soc. Lond. B Biol. Sci.*, 284: 20172066. <https://doi.org/10.1098/rspb.2017.2066>
- Mitchell, C.E., Blumenthal, D., Jaro9sı'k, V. and Puckett, E.E., 2010. Pysek 9 P: Controls on pathogen species richness in plants introduced and native ranges: roles of residence time, range size and host traits. *Ecol. Lett.*, 13: 1525-1535. <https://doi.org/10.1111/j.1461-0248.2010.01543.x>
- Moreno-Pe'rez, M.G., Garcí'a-Luque, I., Fraile, A. and Garcí'a-Arenal, F., 2016. Mutations that determine resistance breaking in a plant RNA virus have pleiotropic effects on its fitness that depend on the host environment and the type, single or mixed, of infection. *J. Virol.*, 90: 9128-9137. <https://doi.org/10.1128/JVI.00737-16>
- Moriones, E. and Verdin, E., 2020. Virus diseases. In: Integrated pest and disease management in greenhouse crops. *Plant Pathology in the 21st Century*, Volume 9, 2nd Edition. Gullino, M. L., Albajes, R. and Nicot, P. C. Springer Nature, Switzerland AG. 2020. pp. 3-31.
- Moury, B., Fabre, F., He'brard, E. and Froissart, R., 2017. Determinants of host species range in plant viruses. *J. Gen. Virol.*, 98: 862-873. <https://doi.org/10.1099/jgv.0.000742>
- Nihad, S.A.I., Manidas, A.C., Kamrul, H., Hasan, M.A.I., Omma, H. and Latif, M.A., 2021. Genetic variability, heritability, genetic advance and phylogenetic relationship between rice tungro virus resistant and susceptible genotypes revealed by morphological traits and SSR markers. *Curr. Plant Biol.*, 25: 100194. <https://doi.org/10.1016/j.cpb.2020.100194>
- Ong, S.N., Taheri, S., Othman, R.Y. and Teo, C.H., 2020. Viral disease of tomato crops (*Solanum lycopersicum* L.): An overview. *J. Plant Dis. Prot.*, 127: 725-739. <https://doi.org/10.1007/s41348-020-00330-0>
- Pagán, I., 2022. Transmission through seeds: The unknown life of plant viruses. *PLoS Pathog.*, 18(8): e1010707. <https://doi.org/10.1371/journal.ppat.1010707>

- Papale, F., Saget, J. and Bapteste, É., 2020. Networks consolidate the core concepts of evolution by natural selection. *Trends Microbiol.*, 28(4): 254-262. <https://doi.org/10.1016/j.tim.2019.11.006>
- Patil, B.L., Chakraborty, S., Czosnek, H., Fiallo-Olivé, E., Gilbertson, R.L., Legg, J., Mansoor, S., Navas-Castillo, J., Naqvi, R.Z., Rahman, S.U. and Zerbini, F.M., 2020. Plant resistance to geminiviruses: In *Encyclopedia of Virology*, 4th edition. Elsevier, 2020: 554–566. <https://doi.org/10.1016/B978-0-12-809633-8.21565-3>
- Pieterse, C.M., Van der Does, D., Zamioudis, C., Leon-Reyes, A. and Van Wees, S.C., 2012. Hormonal modulation of plant immunity. *Ann. Rev. Cell Dev. Biol.*, 28: 489–521. <https://doi.org/10.1146/annurev-cellbio-092910-154055>
- Poulin, R., 2007. Are there general laws in parasite ecology? *Parasitology*, 134: 763-776. <https://doi.org/10.1017/S0031182006002150>
- Prasad, A., Sharma, N., Hari-Gowthem, G., Muthamilarasan, M. and Prasad, M., 2020. Tomato yellow leaf curl virus: Impact, challenges, and management. *Trends Plant Sci.*, 25: 897–911. <https://doi.org/10.1016/j.tplants.2020.03.015>
- Qi, S., Zhang, S., Islam, M.M., El-Sappah, A.H., Zhang, F. and Liang, Y., 2021. Natural resources resistance to tomato spotted wilt virus (TSWV) in tomato (*Solanum lycopersicum*). *Int. J. Mol. Sci.*, 22: 10978. <https://doi.org/10.3390/ijms222010978>
- Raza, M., Ashraf, M.A., Ateeq, M., Rashid, S., Riaz, T., Khalid, B., Saleem, M.A., Usman, H.M., Shafquat, I., and Sajid, M., 2024. Assessing the impact of environmental variables on fruit growth dynamics and developmental physiology. *J. Surv. Fish. Sci.*, 11: 314-321.
- Raza, M., Hussain, Z., Abbas, F., Ashraf, M.A., Imene, H.H. and Riaz, T., 2025. Advanced strategies for detection and diagnosis of potato viruses: Harnessing molecular innovations and digital tools for precision agriculture. *Hosts Viruses*, 12: 39-46. <https://doi.org/10.17582/journal.hv/2025/12.39.46>
- Rivarez, M.P.S., Pecman, A., Bačnik, K., Maksimović, O., Vučurović, A., Seljak, G., Mehle, N., Gutiérrez-Aguirre, I., Maja and Kutnjak, D., 2023. In-depth study of tomato and weed viromes reveals undiscovered plant virus diversity in an agroecosystem. *Microbiome*, 11: 60. <https://doi.org/10.1186/s40168-023-01500-6>
- Roossinck, M.J. and Garcí'a-Arenal, F., 2015. Ecosystem simplification, biodiversity loss, and plant virus emergence. *Curr. Opin. Virol.*, 10: 56-62. <https://doi.org/10.1016/j.coviro.2015.01.005>
- Roossinck, M.J., 2015. Plants, viruses and the environment: Ecology and mutualism. *Virology*, 479: 271-277. <https://doi.org/10.1016/j.virol.2015.03.041>
- Rousseau, E., Tamisier, L., Fabre, F., Simon, V., Szadkowski, M., Bouchez, O., Zanchetta, C., Girardot, G., Mailleret, L., Grogard, F., Palloix, A. and Moury, B., 2018. Impact of genetic drift, selection and accumulation level on virus adaptation to its host plants. *Mol. Plant Pathol.*, 19: 2575-2589. <https://doi.org/10.1111/mpp.12730>
- Saleem, H., Naz, A., Sandhu, A.S., Fatima, M., Tahir, O., Zafar, M.J., Rusho, M.A., Iqbal, D., Riaz, T. and Kanwal, R., 2024. Pharmacological and therapeutic values of turmeric. In: A. Khan, M. Mohsin, A. M. Khan, and S. Aziz (Eds.), *Complementary and alternative medicine: Chinese/traditional medicine*. Unique Scientific Publishers. pp. 77-84. <https://doi.org/10.47278/book.CAM/2024.383>
- Sarwar, M., 2020. Insects as transport devices of plant viruses. In: *Applied plant virology*. Academic Press. pp. 381-402. <https://doi.org/10.1016/B978-0-12-818654-1.00027-X>
- Savatin, D.V., Gramegna, G., Modesti, V. and Cervone, F., 2014. Wounding in the plant tissue: the defense of a dangerous passage. *Front. Plant Sci.*, 5: 470. <https://doi.org/10.3389/fpls.2014.00470>
- Seabloom, E.W., Borer, E.T., Gross, K., Kendig, A.E., Lacroix, C., Mitchell, C.E., Mordecai, E.A., Power, A.G., 2015. The community ecology of pathogens: Coinfection, coexistence and community composition. *Ecol. Lett.*, 18: 401-415. <https://doi.org/10.1111/ele.12418>
- Seabloom, E.W., Borer, E.T., Mitchell, C.E., Power, A.G., 2010. Viral diversity and prevalence gradients in North American Pacific Coast grasslands. *Ecology*, 91: 721-732. <https://doi.org/10.1890/08-2170.1>
- Seabloom, E.W., Hosseini, P.R., Power, A.G., Borer, E.T., 2009. Diversity and composition of viral communities: Coinfection of barley and cereal yellow dwarf viruses in California

- grasslands. *Am. Nat.*, 173: E79-E98. <https://doi.org/10.1086/596529>
- Shah, A.A., Mahmood, M.A., Farooq, K., Qayyum, Z., Amjad, N., Nasib, M.U., Rizwan, B., Asif, H.S., Saeed, S., Riaz, T., Khan, M.M., Khan, A.S., Hamza, M., Aslam, M.A., Ijaz, R., Rafique, N., Niazi, M.K. and Zohra, B., 2021. Clinical practices of herbal antioxidant: A review. *J. Food Technol.*, 19(3): 32-37.
- Shaheen, C., Ahmad, I.A., Aslam, R., Naz, S., Mushtaq, S., Ahmed, S., Nawaz, A., Saeed, S., Qadir, M.F., Ashraf, M.A., Ahamed, M.S., Iqbal, D., Ansar, S., Riaz, R., Abubakar, M. and Riaz, T., 2024. A review of therapeutic and medicinal uses of fenugreek (*Trigonella foenum-graceum* L.). *J. Res. Appl. Sci. Biotechnol.*, 3(5): 39-50. <https://doi.org/10.55544/jrasb.3.5.8>
- Shepherd, D.N., Martin, D.P., van der Walt, E., Dent, K., Varsani, A. and Rybicki, E.P., 2010. Maize streak virus: An old and complex emerging pathogen. *Mol. Plant Pathol.*, 11: 1-12. <https://doi.org/10.1111/j.1364-3703.2009.00568.x>
- Shipley, L.A., Forbey, J.S. and Moore, B.D., 2009. Revisiting the dietary niche: When is a mammalian herbivore a specialist? *Integr. Comp. Biol.*, 49: 274-290. <https://doi.org/10.1093/icb/icp051>
- Simpson, J.E., Hurtado, P.J., Medlock, J., Molaei, G., Andreadis, T.G., Galvani, A.P., Diuk-Wasser, M.A., 2012. Vector host-feeding preferences drive transmission of multi-host pathogens: West Nile virus as a model system. *Proc. R Soc. Lond. B Biol. Sci.*, 279: 925-933. <https://doi.org/10.1098/rspb.2011.1282>
- Singh, S., Awasthi, L.P. and Jangre, A., 2020. Transmission of plant viruses in fields through various vectors. In *Appl. Plant Virol.*, Academic Press. pp. 313-334. <https://doi.org/10.1016/B978-0-12-818654-1.00024-4>
- Smith, C.E., 1924. Transmission of cowpea mosaic by the bean leaf-beetle. *Science*, 60(1551): 268-268. <https://doi.org/10.1126/science.60.1551.268>
- Sofonea, M.T., Alizon, S. and Michalakakis, Y., 2017. Exposing the diversity of multiple infection patterns. *J. Theor. Biol.*, 419: 278-289. <https://doi.org/10.1016/j.jtbi.2017.02.011>
- Su, Q., Pan, H., Liu, B., Chu, D., Xie, W., Wu, Q., Wang, S., Xu, B. and Zhang, Y., 2013. Insect symbiont facilitates vector acquisition, retention, and transmission of plant virus. *Sci. Rep.*, 3: 1367. <https://doi.org/10.1038/srep01367>
- Susi, H., Barre`s, B., Vale, P.F. and Laine, A.L., 2015. Co-infection alters population dynamics of infectious disease. *Nat. Commun.*, 6. <https://doi.org/10.1038/ncomms6975>
- Swei, A., Ostfeld, R.S., Lane, R.S. and Briggs, C.J., 2011. Impact of the experimental removal of lizards on Lyme disease risk. *Proc. R. Soc. Lond. B. Biol. Sci.*, 278: 2970-2978. <https://doi.org/10.1098/rspb.2010.2402>
- Szymański, J., Bocobza, S., Panda, S., Sonawane, P., Cárdenas, P.D., Lashbrooke, J., Kamble, A., Shahaf, N., Meir, S., Bovy, A., Beekwilder, J., Tikunov, Y., de la Fuente, I.R., Zamir, D., Rogachev, I., Aharoni, A., 2020. Analysis of wild tomato introgression lines elucidate the genetic basis of transcriptome and metabolome variation underlying fruit traits and pathogen response. *Nat. Genet.*, 52: 1111-1121. <https://doi.org/10.1038/s41588-020-0690-6>
- Thrall, P.H. and Burdon, J.J., 1997. Host-pathogen dynamics in a metapopulation context: The ecological and evolutionary consequences of being spatial. *J. Ecol.*, 85: 743-753. <https://doi.org/10.2307/2960598>
- Tollenaere, C., Susi, H. and Laine, A.L., 2016. Evolutionary and epidemiological implications of multiple infection in plants. *Trends Plant Sci.*, 21: 80-90. <https://doi.org/10.1016/j.tplants.2015.10.014>
- Vos, I.A., Pieterse, C.M.J. and Van Wees, S.C.M., 2013. Costs and benefits of hormone regulated plant defenses. *Plant Pathol.*, 62: 43-55. <https://doi.org/10.1111/ppa.12105>
- Walkey, D.G.A., 1991. *Applied plant virology* (2nd Edn). Springer, 171. <https://doi.org/10.1007/978-94-011-3090-5>
- Walls, J., Rajotte, E. and Rosa, C., 2019. The past, present, and future of barley yellow dwarf management. *Agriculture*, 9: 23. <https://doi.org/10.3390/agriculture9010023>
- Wang, X.M., Muller, J., McDowell, M. and Rasmussen, D.A., 2024. Quantifying the strength of viral fitness trade-offs between hosts: A meta-analysis of pleiotropic fitness effects. *Evol. Lett.*, 8(6): 851-865. <https://doi.org/10.1093/evlett/qrae038>
- Wang, X.M., Muller, J., McDowell, M. and Rasmussen, D.A., 2024. Quantifying the strength of viral fitness trade-offs between

- hosts: A meta-analysis of pleiotropic fitness effects. *Evol. Lett.*, 8(6): 851–865. <https://doi.org/10.1093/evlett/qrae038>
- Weitz, J.S., Poisot, T., Meyer, J.R., Flores, C.O., Valverde, S., Sullivan, M.B. and Hochberg, M.E., 2013. Phage-bacterial infection networks. *Trends Microbiol.*, 21: 82–91. <https://doi.org/10.1016/j.tim.2012.11.003>
- Whitfield, A.E., Falk, B.W. and Rotenberg, D., 2015. Insect vector-mediated transmission of plant viruses. *Virology*, 479–480: 278–289. <https://doi.org/10.1016/j.virol.2015.03.026>
- Whitlock, M.C., 1996. The Red Queen beats the jack-of-all-trades: The limitations on the evolution of phenotypic plasticity and niche breadth. *Am. Nat.*, 148: S65–S77. <https://doi.org/10.1086/285902>
- Woolhouse, M. and Gaunt, E., 2007. Ecological origins of novel human pathogens. *Crit. Rev. Microbiol.*, 33: 231–242. <https://doi.org/10.1080/10408410701647560>
- Woolhouse, M.E. and Gowtage-Sequeria, S., 2005. Host range and emerging and reemerging pathogens. *Emerg. Infect. Dis.*, 11: 1842–1847. <https://doi.org/10.3201/eid1112.050997>
- Yadav, S. and Chhibbar, A.K., 2018. Plant–virus interactions. *Molecular aspects of plant-pathogen interaction*. pp. 43–77. https://doi.org/10.1007/978-981-10-7371-7_3
- Yuen, J. and Mila, A., 2015. Landscape-scale disease risk quantification and prediction. *Annu. Rev. Phytopathol.*, 53: 471–484. <https://doi.org/10.1146/annurev-phyto-080614-120406>
- Zhang, L., Zhang, F., Melotto, M., Yao, J. and He, S.Y., 2017. Jasmonate signaling and manipulation by pathogens and insects. *J. Exp. Bot.*, 68: 1371–1385. <https://doi.org/10.1093/jxb/erw478>
- Zhao, W., Xu, Z., Zhang, X., Yang, M., Kang, L., Liu, R. and Cui, F., 2017. Genomic variations in the 30 termini of Rice stripe virus in the rotation between vector insect and host plant. *New Phytol.*, 219: 1085–1096. <https://doi.org/10.1111/nph.15246>
- Zhou, G., Xu, D., Xu, D. and Zhang, M., 2013. Southern rice black-streaked dwarf virus: A white-backed planthopper-transmitted filovirus threatening rice production in Asia. *Front. Microbiol.*, 4: 270. <https://doi.org/10.3389/fmicb.2013.00270>