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Commentary

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How does host biodiversity alter disease dynamics? This question has fuelled many empirical, experimental and modelling studies (Keesing & Ostfeld, 2015; Liu *et al.*, 2020; Rohr *et al.*, 2020), especially with regard to the current trends of biodiversity loss and emergence of infectious diseases. Two opposing hypotheses state that host biodiversity can modify disease incidence through either an amplification or a dilution effect. While these relationships have been investigated for a variety of host–parasite systems, questions about the effects of host diversity on the incidence of aboveground plant microorganisms are more scarce. These few studies have focused mainly on foliar fungal pathogens, and even fewer have addressed plant viruses (Pagán *et al.*, 2012; Lacroix *et al.*, 2014; Susi & Laine, 2021). The paper presented by Susi & Laine in this issue of *New Phytologist* (2021; pp. 2447–2458), describes the correlations between infection risk with the five most common viruses recently described in the wild plant *Plantago lanceolata* in the Åland islands (Finland), and the biodiversity and ecosystem characteristics of surrounding plant communities. This paper represents an important contribution to the literature on the relationships between plant diversity and disease incidence, and more generally to the still relatively overlooked field of plant virus dynamics in natural ecosystems (Malmstrom *et al.*, 2011), when compared with the vast literature on disease ecology and epidemiology in agricultural settings.

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Susi & Laine showed a negative correlation between plant diversity and the prevalence of the plant virus species examined (Plantago lanceolata latent virus (PlLV), Plantago latent caulimovirus, Plantago betapartitivirus, Plantago enamovirus and Plantago closterovirus). This result is in line with the dilution effect found in a variety of systems, including those involving plant and tree diseases (Liu *et al.*, 2020). The originality of this study resides not only in looking at the effect of plant diversity on virus prevalence, but also on virus richness. Theory predicts a positive relationship between plant and virus richness, as within-host microbiome and especially the assemblage of specialist pathogens, could differ across various host species. While this hypothesis has been verified empirically in some systems, this study showed that virus richness decreased as plant diversity increased in natural environments of wild *P. lanceolata* populations.

Plant diversity or richness *per se* might not be the best or the sole metric for assessing the relationships between host biodiversity and disease. The abundance of competent hosts, and its variation across the gradient of host richness, might matter more (Lacroix *et al.*, 2014; Johnson *et al.*, 2019). Nonrandom loss of noncompetent or poorly competent hosts has been shown to drive the increase in pathogen prevalence in species-poor communities in several systems. The same mechanism could also underlie the increase in virus richness. Host competence could be assessed under the lenses of both plant–virus, and plant–virus–vector interactions. Each host species from wild plant communities could be ranked with a qualitative measure of its ability to be infected with each virus species, and a quantitative evaluation of within-host virus multiplication, which is correlated with between-host transmission (Froissart *et al.*, 2010). As the average prevalence of each plant virus species varied greatly (0.8–46.8%) in *P. lanceolata* populations, it would be interesting to know whether the decrease in overall prevalence and in virus richness with increasing plant biodiversity is driven by a single (e.g. the most common Plantago latent caulimovirus) or several viruses. In addition, insect vectors such as aphids are known to vary in their feeding preference for different plant species, and in their ability and efficiency of virus transmission. A previous study revealed that *Dysaphis plantaginea*, a specialist aphid species of *P. lanceolata* and apple trees (*Malus domestica*), was moderately efficient at transmitting PlLV to *P. lanceolata* plants in controlled conditions (Susi *et al.*, 2019). Yet, the efficiency of transmission of the other viruses by this aphid species, or by other naturally occurring insect vectors, is unknown. Hence, biodiversity–disease relationships in this system could be further investigated with a survey of insect communities in wild plant populations, the identification of potential vectors, and an assessment of plant species competence for disease spread based on both plant–virus and plant–vectors interactions.

Another interesting result from Susi & Laine's work is that the relationship between host biodiversity and virus richness is affected by the level of human interference. Indeed, while virus richness decreased as plant biodiversity increased in natural *P. lanceolata* populations (>200 m from crop fields), no such relationship was found in plant populations that were in close proximity (within a 20-m distance radius) to agricultural fields. Furthermore, virus

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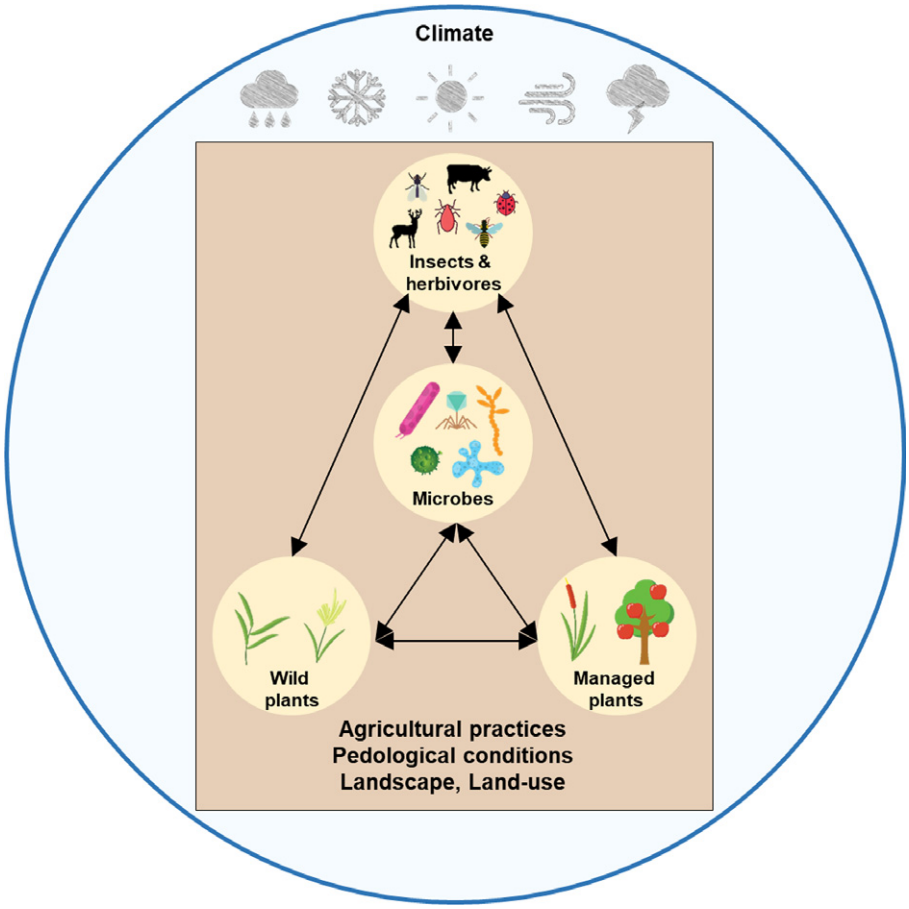

Fig. 1 Infection multifactorial network. The life cycle of microorganisms (e.g. viral, bacterial and fungal plant pathogens) can englobe a wide diversity of biotic interactions with: (1) cultivated and wild plant hosts, (2) microbial communities co-infecting each of these host environments, and (3) insect vectors that ensure between-host transmission. Plant disease dynamics can also be controlled by indirect effects of the community composition of insects (e.g. herbivores, pests, auxiliaries, parasitoids), and of vertebrate herbivores on the abundance and diversity of vector and plant communities, respectively. Furthermore, this network of biotic interactions is also affected by an array of abiotic and human-driven phenomena. Encounters between host plants and directly transmitted pathogens are controlled by precipitation, water and air mass movements, and plant material trade that drive dissemination over short to very long distances. Finally, the dynamics and severity of plant diseases is affected by an array of abiotic and biotic parameters such as those linked to climate, pedological (soil characteristic) conditions and agricultural practices, as well as by land-use and landscape characteristics. (Microbial, animal, plant, tree and weather icons were downloaded under a free license from www.vecteezy.com.)

richness, but not virus prevalence, was slightly higher in wild host populations that were close to agriculture than in natural populations that were located further away. This is in contrast with previous findings that showed that infection risk, measured as virus prevalence, was higher in crop-dominated landscapes (Pagán *et al.*, 2012; Claflin *et al.*, 2017a; Ingwell *et al.*, 2017), which could be partly due to changes in vector community composition (Claflin *et al.*, 2017b). Susi & Laine hypothesised that there were spillovers of viruses from crop fields to nearby wild plant populations to explain this context-dependent relationship between plant biodiversity and virus richness. Comparing both plant virus and vector community composition within cropped and wild plants could be informative to test the hypothetical spillover of viruses across the agro-ecological interface.

Biodiversity–disease relationships might also be affected by spatial patterns of transmission. In particular, host population connectivity could increase virus transmission, and therefore virus prevalence and richness. Contrary to expectations, Susi & Laine showed that virus prevalence, but not richness, decreased as connectivity among *P. lanceolata* populations increased. This pattern could be explained by higher rates of gene flow in well connected host populations that would lead to higher levels of host resistance to disease, as previously demonstrated in the case of fungal pathogens in the very same environments. Also, the most connected host populations could also be the most diverse; whereas the most fragmented ones, and perhaps the most disturbed because of human interference and changes in land use, could be the least diverse. Investigating these hypotheses leads back to examining the variation in the abundance of competent hosts across plant diversity gradients, as resistant hosts can be considered as non- or poor-competent hosts. This could also allow the identification of potential sources of resistance that could be interesting to introduce in crop plants to improve plant protection against various plant pathogens.

Overall, infectious disease dynamics have been thoroughly investigated in agronomical environments due to the negative

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impacts of plant pathogens on the quantity, sustainability and security of food production (FAO, http://www.fao.org, 2017). Nevertheless, this study provides another example of how prevalent and diverse plant viruses, and *more generally* plant-associated microorganisms, can be in wild plants. Indeed, 57% of tested plants were infected with at least one virus species, and co-infections were observed in 17.1% of infected plants, whether hosts showed symptoms of infection or not at the time of sampling.

As stated by Susi & Laine, the processes leading to infection and disease can be viewed as a multifactorial network of interactions where the biological component of the environment in the well known disease triangle and the impact of human activities are specified more explicitly (Fig. 1). Considering this network of interactions across natural and agronomical contexts, important avenues for research can be highlighted through several questions on: (1) the ecology of these microorganisms in natural environments and noncropped plants (Malmstrom *et al.*, 2011); (2) their impact on wild plant communities (Bradley *et al.*, 2008; Paseka *et al.*, 2020); and (3) the reciprocal influence of natural, and agronomical and human managed environments on disease dynamics. More specifically, Susi & Laine's work is a springboard for subsequent investigations such as: are the plant virus species examined in this study pathogens both for wild and cultivated plants? Are these virus species already found, or likely to emerge, on nearby crops? How important are these wild plant populations as reservoirs for crop plant epidemics? What are the factors that could lead to such an emergence? In addition to pathogen prevalence and richness, does host biodiversity alter rates of co-infection? Last, but not least, how plant pathogens that would have evolved in cropped plants could alter the composition and evolution of wild plant communities?

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