Virus invasions of the New Zealand flora

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Abstract More than 200 plant viruses and many of their invertebrate vectors have invaded New Zealand (NZ) in the last two centuries. All of these invaders are associated with introduced agricultural, horticultural and/or weed species. At least 16 of the viruses have invaded the native flora, including some rare and critically endangered species. Patterns are emerging: aphid transmitted viruses which are able to infect species from a number of families are prominent. For example, cucumber mosaic virus infects native species from seven families. There are also examples of viruses with more restricted host ranges invading individual families, particularly the native grasses. The yellow dwarf viruses have escaped from cereals and pasture into native grasses. Some of the species are also native to Australia and the Pacific Islands and the review and its literature should be of interest to those working further afield. Prospects for controlling or mitigating the effects of the viruses in agricultural systems have limited application in the native flora but they are relevant to propagation and rescue strategies. Biosecurity measures are not only the first line of defence against threats to agriculture but also to the conservation estate. The protection of native floras from virus invasion is another justification for the control measures and legislative procedures already in place to protect agriculture. High throughput sequencing to detect all viruses at the border, and genetic engineering and RNAi technologies to mitigate the effects of invasions are promising developments for the protection of the native flora.

Keywords Virus invasions · Aphids · Native floras · Plant protection

Introduction

As the simplest obligate parasites, viruses need to replicate in the living cells of a susceptible host, avoid host defences and be acquired by a vector, usually an invertebrate, which transfers infectious particles to the next susceptible individual. Some viruses are transmitted vertically in seed and other propagules to the next generation of their host. Although New Zealand (NZ) is small and remote, a significant number of plant viruses, and other plant pathogens, have been recorded here. Over the past century the number of plant viruses recorded in NZ rose steadily to over 100
by 1990 and to more than 180 by 2005 (Pearson et al. 2006). Since that time the number increased by 18% to 220 (Veerakone et al. 2015) and this increase continues (e.g. Tang et al. 2017; Veerakone et al. 2021).

Mostly these records centred on economically important species and weed reservoirs that impact on crop, pasture and horticultural species, however there is an emerging understanding that these pathogens are invading the NZ flora. Endemic viruses are now being detected in the native flora (Rabbidge et al. 2021) and integrated plant retrovirus (badnavirus) sequences occur in many taxa (Lytte et al. 2011); the potential for them to be activated is unknown.

Each year, newly arrived invertebrates establish viable populations in NZ (Martin and Paynter 2014). Many of these are herbivores and some of these feed on the native flora. Forty percent (Veerakone et al. 2015) of the introduced viruses are transmitted by introduced aphids with most belonging to three groups: the carlaviruses, the luteoviruses and the potyviruses. The most significant invaders of the NZ flora are aphid transmitted. Aphids are most diverse in the temperate northern hemisphere, with only a few lineages native to the southern hemisphere; of the 12 endemic species, none are reported to transmit plant viruses (von Dohlen and Teulon 2003).

The NZ flora has many indigenous species but few indigenous genera (Dansereau 1964; Wilson and Lee 2012). Since human settlement, around 2100 gymnosperms and angiosperms have arrived compared to approximately 1900 native species (Wilton and Breitwieser 2000). Despite Dansereau’s (1964) assertion that the “competing power of exotics is overwhelming” not all of NZ habitats have been invaded (Wilson and Lee 2012) but many have, and this has implications for reservoirs of virus disease. The most specious families are the Asteraceae and the Poaceae followed by the Scrophulariaceae and Cyperaceae: both in terms of exotic and native species, however, as can be seen from Table 1, our understanding of

| Family* | Total* spp | Indig spp* | Virus invaders | Virus acronyms |
|---------|------------|------------|----------------|----------------|
| Top 10 families by Number of species | | | | |
| Asteraceae | 520 | 287 | 1 | CMV |
| Poaceae | 460 | 185 | 3 | BYDV, CYDV, CoMV |
| Plantaginaceae | 217 | 160 | 1 | AGLV |
| Cyperaceae | 213 | 170 | | |
| Fabaceae | 142 | 30 | 1 | TRSV |
| Rosaceae | 139 | 29 | | |
| Apiaceae | 131 | 98 | | |
| Brassicaceae | 105 | 29 | 3 | CaMV, TuMV, TYV |
| Orchidaceae | 100 | 99 | | |
| Ranunculaceae | 84 | 54 | 1 | CMV |
| Other families | | | | |
| Boraginaceae | 35 | 1 | | CMV |
| Liliaceae | 26 | 2 | CMV, TuMV |
| Haloragaceae | 22 | 1 | TSWV |
| With Indigenous species hosting viruses | | | | |
| Cornaceae | 5 | 1 | ToMV |
| Piperaceae | 3 | 1 | CMV** |
| Solanaceae | 2 | 5 | CMV, PVX, PVY, TMV, TSWV |
| Corynocarpaceae | 1 | 1 | CMV, RMV |
| Cucurbitaceae | 1 | 3 | CMV, WMV, ZYMV |

*After Wilton & Breitwieser (2000) AGLV: Ageratum latent virus, BYDV: Barley yellow dwarf virus, CYDV: Cereal yellow dwarf virus, CoMV: Cocksfoot mottle virus, CMV: Cucumber mosaic virus, PVX: Potato Virus X, PVY: Potato Virus Y, RMV: Ribgrass mosaic virus, TMV: Tobacco mosaic virus, TRSV: Tobacco ringspot virus, TSWV: Tomato spotted wilt virus, TuMV: Turnip mosaic virus, TuYV: Turnip yellows virus, ToMV: Tomato mosaic virus, WMV: Watermelon mosaic virus, ZYMV: Zucchini yellow mosaic virus

**Online record (PPIN 19,943) (see https://www.mpi.govt.nz/resources-and-formsregisters-and-lists/ plant-pest-information-netwerk/)

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Virus invasions is very patchy. Some species from families with few representatives in NZ harbour more viruses than those from the larger families. This seems unlikely. This probably reflects the bias of researchers’ focus rather than the actual pattern of virus invasions.

The only NZ native species recruited by agriculture is Solanum laciniatum which was used briefly for the production of the alkaloid solasodine (Thomson 1976). NZ flax (Phormium tenax) was used as a fibre crop until its demise after WWII when it was replaced by synthetic fibres (Ushiyama et al. 1969, Wehi and Clarkson 2007). NZ flax and Cabbage Tree (Cordyline australis) are popular in gardens and NZ spinach (Tetragonia tetragonoides) is grown in home vegetable gardens in NZ and around the world (Haase 1990).

Native solanums (Solanum spp.)

Although a widespread genus with over 1500 species only two Solanum spp occur naturally in NZ. Solanum aviculare and S. laciniatum (poro poro) occur in coastal and forest margins throughout NZ and also in eastern Australia (Allan 1961). S. aviculare also occurs in the highlands of Papua New Guinea (Poczai et al. 2011). S. laciniatum was grown in Europe, India and in NZ for the production of the steroid alkaloid solasodine. In Czechoslovakia virus infection reduced solasodine production by 50–70% (Neubauer 1960). Commercial crops were grown in NZ during the 1960’s and 1970’s. Virus surveys (Thomson 1976) revealed that infection by aphid transmitted viruses was common (cucumber mosaic virus: CMV, 25% range 0–70%; potato virus Y: PVY, 27% range 0–48%). Mechanically transmitted viruses (potato virus X: PVX, tobacco mosaic virus: TMV) were only observed in single crops at Tauranga (PVX, 77%) and New Plymouth (TMV, 17%). A single plant growing in a nature reserve in Christchurch was infected with tomato spotted wilt virus (TSWV, Thomson 1976). CMV caused the most severe symptoms, including mottling and narrowing of leaf lamina. The other viruses induced mild mottling of the leaves. There are no records of S. aviculare infection in NZ, however Neubauer (1960) reported that virus infection of S. aviculare in Europe caused varying degrees of mottling and leaf distortion. There are no published surveys of viruses in wild populations of S. aviculare (Papua New Guinea, Australia, NZ) or S. laciniatum (Australia, NZ) but small-scale surveys in NZ (e.g. Guy 2011) have found very low incidence of infection. The high incidences found by Thomson (1976) may be a consequence of cultivation.

Other viruses are established in solanaceous crops and weeds in NZ (Veerakone et al. 2015) but to date have not invaded the native flora.

Native cucurbits (Sicyos spp)

Sicyos is an herbaceous climber or scrambling herb native to eastern Australia, Tasmania, New Zealand and some of their associated and more distant islands including the Kermadec Islands. Sicyos is believed to be extinct on Lord Howe and Norfolk islands (Telford et al. 2012). Sicyos australis was considered NZ’s only native cucurbit, however after the study by Delmiglio and Pearson (2006) was completed, it was determined that the NZ populations represent two species: Sicyos australis and S. mawhai (Telford et al. 2012). S. mawhai is endemic to NZ while S. australis has the wider distribution outlined above. Both are considered threatened species due to habitat loss and population decline. For the purposes of this review the effects of virus infection will be attributed to Sicyos.

Because Sicyos is rare and endangered and has been declining over the last 50 years it was suspected that viruses introduced to NZ cucurbit crops were infecting and affecting this species. Experimental infections with CMV isolates caused severe symptoms which developed 2–3 weeks after inoculation (Fig. 1). Symptoms included mosaic, vein chlorosis, reduced leaf size and leaf distortion and a general reduction in growth of 65–72%. While infection with zucchini yellow mosaic virus (ZYMV) resulted in milder symptoms and caused no significant reduction in growth, unexpectedly, all infected plants died when exposed to high temperature (30 °C) in the glasshouse suggesting that ZYMV infection may predispose Sicyos to heat stress (Delmiglio and Pearson 2002, 2006).

Field surveys of 14 remnant populations detected ZYMV and watermelon mosaic virus (WMV) at 5 and 3 sites respectively while CMV was detected only once from an urban mainland site. All three viruses
are transmitted by aphids introduced from the Northern Hemisphere. Because Sicyos is mostly found on offshore islands the chance of aphid-borne infection from mainland crops and gardens is reduced. However, collections made during this study did confirm the presence of aphids (Myzus spp) on two islands and studies have shown (e.g. Hullé et al. 2003) that aphids have spread as far as the remote sub-Antarctic Islands.

Delmiglio and Pearson (2006) also found that ZYMV was seed transmitted in Sicyos. Seed production is required for the continued presence of this species in small, isolated populations. Reduced seed supply and seed quality could reduce plant numbers to a level beyond recovery. As ZYMV is transmitted via seed it is likely to perpetuate in populations through successive generations through seedlings.

**Native cresses (Lepidium spp.)**

Cook’s scurvy grass originally classified as *Lepidium oleraceum*, is now known to be a collection of related species (including *L. aegrum*, *L. castellanum*, *L. crassum*, *L. juvencum*, *L. oleraceum*). They are critically endangered species of native brassicas. These cresses occur in small populations scattered along NZ’s coastline and on offshore islands. In some places, populations are reduced to a single plant (Amey et al. 2007; de Lange et al. 2013) and there are a number of efforts underway to bolster and protect these species. At some sites attempts have been made, with varying success, to re-establish these species (Norton and de Lange 1999).

Plants collected from a newly discovered population (*L. aegrum*) at Island Rock (Fletcher et al. 2009) were propagated in a glasshouse for restoration planting. Cuttings and seedlings from these plants were used for a re-establishment program at Stony Bay where they were examined and found to have mosaic and mottling symptoms typical of virus infection. These plants were infected with turnip mosaic virus (TuMV), a virus with a wide host range which includes more than 20 species in NZ (Veerakone et al. 2015). Most of the plants infected with TuMV were either glasshouse grown research specimens or plants temporarily maintained under glass where aphid infestations are frequently a problem. Other potential hosts of TuMV were growing in the glasshouse and in the surrounding countryside (Fletcher et al. 2011).

van Vianen et al. (2013) surveyed the known remaining wild populations of Cook’s scurvy grass on the southern South Island (*L. crassum*, *L. juvencum*) and one population of *L. tenuicaule* (shore cress) for TuMV and two other viruses which commonly infect brassicas: cauliflower mosaic virus (CaMV) (Fig. 2) and turnip yellows virus (TuYV). These surveys showed that virus infection was widespread in these native cress populations although the one population of *L. tenuicaule* was free of these two viruses. Of the 6 populations of Cook’s scurvy grass surveyed, 5 were infected with viruses. CaMV was present at all 5 of those sites, while TuMV and TuYV infected plants...
at 4 and 1 site respectively. The incidence of infection at each site ranged 8–75%. Mixed infections with CaMV and TuMV were common. At some sites virus symptoms were conspicuous while at others, although plants appeared healthy, there was a high incidence of infection. van Vianen et al. (2013) conclude that this may be due to the interaction of various genetic and environmental factors.

In a further study van Vianen et al. (2015) explored the consequences of interspecific hybridisation and TuMV infection on the growth and fecundity of three *Lepidium* spp. Two of the three species were successfully selfed and interspecific hybrids were generated to examine hybrid fitness and inbreeding depression. These were inoculated with the TuMV isolate from *L. aegrum*. They showed that interspecific hybrids of the three species outperformed the original species in terms of total biomass and the numbers of flowering stems and seeds produced. Infected hybrids also showed reduced virus susceptibility compared to the original three species.

**Native grasses (Poaceae)**

More than 185 species of grasses (Poaceae) are native to NZ with a high degree of endemism (157 species: Edgar and Connor 2000; Wilton and Breitwieser 2000). Ten of these grasses are of conservation interest and are considered vulnerable to critically endangered. None of these species have been tested for virus infection in NZ, however, one species...
Deschampsia cespitosa which is also native to Australia was infected with barley yellow dwarf virus (BYDV) and cereal yellow dwarf virus (CYDV) (Guy et al. 1987) in Tasmania.

NZ native grasses have been invaded by BYDV and CYDV both of which are transmitted by aphids and cocksfoot mottle virus (CoMV) which is transmitted by contact. In the Northern Hemisphere CoMV is also transmitted by a beetle which has not been introduced into NZ. Other coleopterans present in the country have been tested and some of these transmit CoMV at a very low rate (Smales et al. 1995). Infection by these three viruses has been detected throughout the country (Delmiglio et al. 2010).

A distinctive feature of the NZ flora is the prevalence of tussock grassland dominated by Chionochloa spp. These perennial species are very long lived and reproduce erratically. They produce an unusually large biomass and provide a range of ecological services including gathering precipitation from fog in the drier part of the country (Edgar and Connor 2000).

Davis and Guy (2001) reported BYDV infection of the type species Chionochloa rigid on the South Island and that aphids could transmit BYDV to C. beddlei and C. conspicua in glasshouse studies. Delmiglio et al. (2010) did not detect BYDV in C. rubra but detected a low incidence of CoMV in this species on the North and South Island. Davis and Guy (2001) did not detect CoMV in this species. It is uncertain whether CoMV has recently invaded this native species or is just present at a low level. Another Danthonoid grass Rytidosperma setifolium was also infected with low levels of BYDV (Davis and Guy 2001).

There are very few native Bambusoid, Chloroid and Panicoid grasses in NZ. The Bambusoid grass Microlaena stipoides is infected with CYDV and BYDV (Delmiglio et al. 2010) and aphids transmitted BYDV to M. avenacea in glasshouse studies but no infection was detected at 16 sites across the country. M. avenacea occurs in shaded forest on the North and South Island (Edgar and Connor 2000) which is not the preferred habitat for the aphids which transmit these viruses (Davis and Guy 2001).

Most of NZ native grasses are Pooids with species occurring in open habitats near sea level to high into the alpine zone. The highest incidence of infection was detected in Festuca novae-zelandiae (CoMV: 50%) which grows from near sea level into sub-alpine grasslands. This species was also infected with BYDV (Delmiglio et al. 2010). Another common species Poa cita, which is also used as a landscaping species, was infected with CoMV (19%) and with BYDV and CYDV (both 5%, Delmiglio et al. 2010). Festuca multinodis grows on rocks, cliffs and bluffs from coastal to alpine regions and has a high incidence of BYDV infection (30%, Davis and Guy 2001). CYDV infection was relatively rare in the native grasses but was more common in introduced grasses particularly in Dactylis glomerata (Davis and Guy 2001; Delmiglio et al. 2010). Both studies found there was generally a higher incidence of viruses in native species when infected introduced species were present at the same site.

The fungal endophytes (Epichloë spp), which have profound effects on growth and their host grasses’ responses to abiotic and biotic stress (Tanaka et al. 2012), are present in introduced Lolium spp and Festuca spp. However, the limited number of native pooid grasses studied to date, appear to be free of these associations (Davis and Guy 2001; Rolston et al. 2002; Leuchtmann et al. 2019). Two studies (Mahmood et al. 1993; Guy and Davis 2002) of tall fescue (Schedonorus phoenix syn. Festuca arundinacea) indicated that the tall fescue endophyte protected its host from BYDV infection indirectly by deterring feeding by its main aphid vector. The native grasses Dichelachne micrantha (Leuchtmann et al. 2019), Echinopogon ovatus (Miles et al. 1998) and Poa matthewsii (Stewart et al. 2004) have their own Epichloë endophytes but their interactions with insects and plant virus diseases have not been investigated.

Native species invaded by other viruses

CMV infects at least 93 species in NZ including 7 from the native flora (Veerakone et al. 2015). CMV infections of Sicyos and Solanum are discussed elsewhere. CMV infections of the native species Corynogapus laevigatus, Macropiper excelsum and Myosotidium hortensia and TuMV infection of Arthropodium cirratum and Pachycladon spp. have only been described from garden examples; there have been no field studies of these species (Ashby 1977; Thomson 1981; Fletcher et al. 2010; Blouin et al. 2016). Four percent of Clematis paniculata, a large woody vine which grows on lowland and
subalpine forest margins, were infected with CMV. These vines were declining and were showing leaf mottle symptoms (Guy 2011). The other viruses listed in Table 1: ageratum latent virus, tobacco ringspot virus, tomato mosaic virus and tomato spotted wilt virus have only been identified in specimens of native species in cultivation. Future work will determine if they are widespread and of concern in wild populations (Ward et al. 2009; Veerakone et al. 2010; Podolyan et al. 2020).

Knowledge gaps and potential threats

We have no information on virus invasions of five of the ten most specious families in NZ (Table 1).

As mentioned above, aphid transmitted viruses feature prominently as invasive species. Viruses present in exotic species (Veerakone et al. 2015) in these five families include lettuce mosaic virus and lettuce necrotic yellows virus (Asteraceae) a range of pome fruit and ornamental species viruses (Rosaceae), carrot motley dwarf virus complex and celery mosaic virus (Apiaceae). A range of viruses infect the Orchidaceae but there have been no investigations of the Cyperaceae.

The overseas origins and the timing of arrival of the viruses are unknown. The exception is TuMV where phylogenetic analysis of isolates from Australia and NZ, including the isolates from *Lepidium* spp, points to a European origin. Bayesian coalescent analyses showed that the virus probably migrated from Europe more than 80 years ago (Yasaka et al. 2015).

There are now more than 1992 plant viruses (EJ Lefkowitz personal communication: https://ictv.global/vmr/ extracted 27 July 2021) recognised by the International Committee for the Taxonomy of Viruses. With approximately 10 percent of the known viruses present in NZ there is clearly potential for future invasions. Many viruses excluded to date have host species present in NZ. The susceptibility of native species to the other viruses already present is unknown.

Current incursions are of concern too. Potato mop top virus was detected for the first time in 2018, and pepino mosaic virus in 2021, both have host ranges largely restricted to the Solanaceae (Harrison and Jones 1970; Jones et al. 1980) but their potential to infect poro poro is unknown. Wheat streak mosaic virus was accidentally imported in contaminated seed (Lebas et al. 2009) but so far has only been reported infecting wheat. This may be because its vector, an eriophyid mite has not been recorded in NZ. WSMV can also be transmitted by contact transmission. WSMV is of great concern because back in its original range in North America its mite vector feeds and the virus infects species from 22 genera of Danthonoid, Chloroid, Panicoid and Pooid grasses (French and Stenger 2002).

Worldwide, there are more than 2500 botanic gardens and arboreta (Barham 2016) curating collections of species from many parts of the world including NZ. Sentinel plants are plants found outside their native region that are, of a matter of course, exposed to the new regions’ native pests and diseases. Such plants can be monitored or casually observed to give advanced warning of potential future threats (Britton et al. 2010). They can be used to help focus and set research priorities, aid prevention and prioritise eradication measures. Sentinels can help increase information about the life histories and identify potential biocontrol agents for virus vectors.

Outbreaks of invasive pests and diseases in botanic gardens and arboreta have demonstrated the role that these plant collections can play in generating host relationship data for plant viruses and their vectors. For example, detailed information was compiled by Scott-Brown et al. (2018) on the host range of a molecularly characterized population of the thrips *Scirtothrips dorsalis* with access to over 3000 plant species in the Palm House at Kew Botanic Gardens. New hosts with commercial and traditional uses were identified as well as hosts that are endangered species.

Soil samples were taken from the root zones of New Zealand native plants growing at the Ventnor Botanic Gardens on the Isle of Wight (United Kingdom). Nematodes extracted from the soil revealed the presence of plant-parasitic lesion nematodes associated with *Olearia pachyphylla* (Asteraceae). As well as being pathogenic, these nematodes are also vectors of two groups of plant viruses (Walkey 1991). This revelation identifies potential threats to a very rare and critically endangered endemic shrub in New Zealand in a poorly investigated family (Asteraceae). The few remaining wild populations of *O. pachyphylla* in New Zealand may be at risk (Mansfield et al. 2019).
Conversely, information on virus invasions of the NZ flora will be useful to other regions. Many genera and some species also occur in other regions. Few genera are endemic (Allan 1961) with strong floristic links (Winkworth et al. 2002) to Southeast Asia, Papua New Guinea, Australia, Pacific Islands, Sub Antarctic Islands and South America. For example, some of our native solanums, cucurbits and cresses also occur in Australia but to our knowledge none have been tested for viruses outside NZ.

Control measures

Propagation of NZ native plants for conservation and restoration takes place in commercial nurseries, research institutes and universities located in urban or rural environments. The importance of virus spread from weeds in agricultural systems is well known (Walkey 1991; Wilson 2014) and there is emerging evidence that they are important reservoirs in natural systems (Davis and Guy 2001; Delmiglio et al. 2010). Herbaceous reservoirs of infection can be eliminated by cultivation or the application of herbicide. Virus spread from perennial ornamentals and amenity plantings may be more difficult as their destruction is undesirable (Cooper 1993). ‘Roguing’ or removal of diseased individuals is an important technique in the control of virus spread through establishing seedlings and avoiding their deployment to the field. Seed transmission of some viruses is a risk (e.g. CMV, WSMV, ZYMV) and is another source of seedling infection that needs to be controlled (Constable et al. 2021).

The majority of viruses discussed in this review are spread by contact transmission. Contamination of protective clothing, hands and tools can be avoided, in plant propagation facilities, by the use of heat and cleaning products. Most of the viruses are also spread by invertebrate vectors; mainly by aphids. Insecticides are more likely to be effective in protecting against persistent viruses (BYDV, CaMV, CMV, CYDV, TuYV) than non-persistent viruses (TuMV, WMV, ZYMV) where the insecticide is likely to agitate the aphid and increase short-probing activity which favours the spread of non-persistent viruses (Walkey 1991). In contrast, the application of mineral oils is more effective in controlling non-persistent viruses by disrupting probing and feeding behaviour (Wilson 2014) particularly on slower growing species. Again the use of these chemicals is only practicable in propagation facilities.

Concluding remarks

The control measures outlined above were devised for the protection of economically important agricultural and horticultural species however they can be used to help mitigate the spread and effects of viruses in native floras. Similarly, border security and surveillance measures with legislative controls to control the movement of plants and with requirements for inspecting and testing materials protect agriculture and the native flora against the introduction of new pests and diseases. Weed control is mandated and practised in conservation areas and as well as restricting the spread of these unwanted species, is also restricting the spread of virus reservoirs and virus vectors. For example, controlling the invasive weed Japanese honeysuckle (Lonicera japonica) also controls the reservoir of honeysuckle yellow vein virus and its whitefly vector (Bemisia tabaci) which is capable of transmitting a number of viruses (Lyttle and Guy 2004).

All in all, the protection of native floras from virus invasion is another justification for the control measures and legislative procedures already in place to protect agriculture. We should also look further afield to genetics to help protect the flora as suggested by van Vianen et al. (2015) for the endangered cresses. They generated good sources of virus resistance by crossing individuals from different populations. RNA interference (Tenllado et al. 2004) and genetic engineering (Nejidat et al. 1990) are also potential tools to mitigate virus invasions. High throughput sequencing (HTS) shows great potential for assessing the phytosanitary status of plants before they enter the country. Theoretically, HTS can detect all viruses in a single assay. The technology still needs to show that detection across a range of host and virus species is robust. The databases used to interrogate the HTS generated sequences are improving as the number of viruses being characterised and sequenced increases (Maree et al. 2018).

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**Declarations**

**Conflict of Interest** The authors declare they have no conflict of interest.

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