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BRIEF REPORT

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Genetic homogenisation of two major orchid viruses through global trade-based dispersal of their hosts

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Societal Impact Statement

Orchid viruses are capable of causing flower deformities and death, which can severely impact the horticultural industry and wild orchid conservation. Here we show how two of these quickly evolving viruses display few genetic differences since their first emergence, across countries and host plants. This is concerning as, despite biosecurity regulations to control the movement of orchids and their related pathogens, these patterns are suggestive of rapid and regular international movement of horticultural material. Poor biosecurity practices could threaten the orchid horticultural industry and result in the accidental translocation or reintroduction of infected plant material intended to recover wild populations.

KEYWORDS

Cymbidium mosaic virus, CymMV, horticulture, Odontoglossum ringspot virus, Orchidaceae, ORSV, phytosanitary, trade

1 | INTRODUCTION

With an estimated 28,484 species (WCSP, 2017), orchids are among the most speciose families of flowering plants (Joppa, Roberts, Myers, & Pimm, 2011). One of their most outstanding features is their diversity in floral form, resulting in a sizeable international horticultural industry where orchids consistently appear among the top horticultural commodities in terms of pot plants (Hinsley et al., 2017; Royal Flora Holland, 2015; United States Department of Agriculture, 2016), as well as comprise approximately 10% of the cut flower industry (De, Pathak, Rao, & Rajeevan, 2015; Hinsley et al., 2017). However, orchid viruses significantly affect flower quality and yield, and have the potential to cause substantial economic losses (Khentry, Paradornuwat, Tantiwiwat, Phansiri, & Thaveechai, 2006; Wong, Chng, Lee, Tan, & Zettler, 1994). Whilst more than 50 different viruses have been documented to infect orchids, Cymbidium mosaic virus (CymMV) and Odontoglossum ringspot virus (ORSV) are the most prevalent (Wong et al., 1994; Zettler, Ko, Wisler, Elliott, & Wong, 1990). Both viruses have a global distribution in cultivated orchids, though their presence in natural populations is currently unknown (Umikalsum, Bakar, Khairun, & Faridah, 2006; Zettler et al., 1990).

CymMV is a member of the potexvirus family with a single-stranded RNA (ssRNA) positive sense genome of approximately 6.3 kb (Wong et al., 1997). Signs of disease include flower necrosis, chlorotic or necrotic patches on the leaves, and growth retardation (Ajjikuttira et al., 2002; Pearson & Cole, 1991; Zettler et al., 1990), though asymptomatic hosts can occur (Ajjikuttira et al., 2002; Zettler et al., 1990). Although the virus appears not to have a natural vector for transmission (Namba & Ishii, 1971), it is stable and easily spread through contaminated horticultural tools, media, and pollen (Lawson & Brannigan, 1986; Moraes, Krause-Sakate, & Pavan, 2017). ORSV, a tobamovirus, also has a positive sense ssRNA genome of around 6.5 kb (Chng et al., 1996). ORSV infection can result in flower malformation and color breaking, and ringspots on the leaves. As with CymMV, the transmission of ORSV appears to be by means of mechanical inoculation (Cánovas, Ballari, & Nome, 2016; Hu et al., 1994; Zettler et al., 1990).

Whilst both of these viruses are currently only known from cultivated stock or domestic orchid collections, to date little emphasis has been placed on the dangers of viral spill-over into wild orchid populations through activities such as reintroduction and, consequently, what impacts this may have on biodiversity loss. We are aware of only a single study from Australia, in which several exotic viruses were described from wild *Diuris* orchid populations (Wylie, Li, Dixon, Richards, & Jones, 2013). The global spread of pathogens poses an increasing threat to biodiversity (Daszak, Cunningham, & Hyatt, 2000) and has been linked to the collapse of a number of wild populations and multiple species extinctions (Anderson et al., 2004). Most orchids are naturally rare and threatened with extinction through habitat loss and over-collection from the wild (Roberts & Dixon, 2008). For example, *Paphiopedilum vietnamense* was described new to science in 1999 only to be declared extinct in the wild five years later through over-collection for the horticultural trade (Averyanov, 2004). Due to the threat from trade, all orchids were placed on Appendix II, or higher, from the inception of the Convention on International Trade in Endangered Species (CITES) (Koopowitz, 2001; Roberts & Solow, 2008), and currently comprises over 70% of species listed on CITES (Hinsley et al., 2017). Within the orchid horticultural community there is a level of resentment toward CITES, as it is perceived to negatively impact on trade by restricting access and inhibiting the flow of plant material into the hobby (Hinsley et al., 2017; Koopowitz, 2001; Zelenko, 2005; Roberts pers. obs.). Along with national phytosanitary regulations, these regulations have the potential to limit the spread of orchid viruses across international borders by potentially reducing the movement of their hosts. However, phytosanitary certificates are not always required, as in the case of free movement of materials within economic unions such as the European Union (European Commission, 2000), and in some cases infected but asymptomatic plant material (Khentry et al., 2006) may be transported if prior screening is not carried out.

Here we investigate the molecular evolution of the two most prevalent orchid viruses, CymMV and ORSV, using datasets representing their global distribution in cultivated stock. We ask whether the considerable international trade of cultivated orchids has effectively "homogenised" the genetic diversity of the viruses or if their high mutation rate, as expected for RNA viruses (Duffy, Shackelton, & Holmes, 2008), and regulations on international movement has led to geographical and/or chronological differentiation.

2 | MATERIALS AND METHODS

2.1 | Sampling and data analyses

All available nucleotide sequence data for the capsid protein of CymMV and ORSV were obtained from the Genbank database (Accessed 8 January 2018), along with any associated data regarding host species from which they were isolated and sampling date where available (n = 211 for CymMV, Table S1, and n = 146 for ORSV, Table S2). Both viral isolate datasets were dominated by four host genera (62% for CymMV and 74% for ORSV), with *Cymbidium* being the most prevalent (28% and 30% respectively).

Geneious 8.1.7 (Kearse et al., 2012) DNA editing software was used to align and edit all DNA sequences. The programme jModelTest 2.1.7 (Posada, 2008) was used to infer the best fit nucleotide substitution model across each dataset. A TN93 transition model (Tamura & Nei, 1993) with gamma distributed rate variation was favoured for CymMV and an HKY85 transition and transversion model (Hasegawa, Kishino, & Yano, 1985) was favoured for ORSV. Evolutionary rates were determined using the programme Beast v1.8.2 (Drummond, Suchard, Xie, & Rambaut, 2012) using only those sequences available with a confirmed associated year of sampling (n = 116 for CymMV and n = 101 for ORSV). The Bayesian skyline coalescent demographic prior was used as it allows for temporal changes in population size (Drummond, Rambaut, Shapiro, & Pybus, 2005). Tracer v1.6 was used to ensure thorough model mixing and that a reasonable effective sample size (ESS > 200) had been reached for all parameters. Two runs, each consisting of ten independent Monte Carlo-Markov chains (MCMC) were implemented for 100 million generations each, with trees sampled every 10,000 generations. The evolutionary rate and time to most recent common ancestor (TMRCA) were estimated under an uncorrelated relaxed molecular clock (Drummond, Ho, Phillips, & Rambaut, 2006; Lemey, Suchard, & Rambaut, 2009). LogCombiner v1.8.2 was used to combine runs, TreeAnnotator v1.8.2 was used to obtain the tree with the highest clade credibility (Drummond et al., 2012) and FigTree v1.4.2 was then used to visualise and edit the consensus tree (Rambaut, 2009). Additionally, for greater analytical strength, maximum-likelihood (ML) phylogenies with 1,000 bootstrap replicates were generated for both genes to infer geographic relationships between all available sequences using PhyML 3.0 (Guindon et al., 2010). GENEIOUS v8.1.7 (Kearse et al., 2012) was used to generate the consensus tree prior to visualisation and editing in FigTree.

3 | RESULTS

Figure 1 shows the ML phylogeny of the CymMV capsid protein sequences depicting their biogeographic association. The tree comprises isolates from 29 host genera across 16 different countries or overseas territories, with numerous small clades displaying little apparent geographical or host genus pattern to their clustering. The Chinese and South Korean isolates, which are particularly well represented in this study, form several distinct groups indicating the presence of multiple viral genotypes within these regions. The rate of evolution calculated in the Bayesian analysis conducted over the dated subset of isolates (Figure S1) was determined to be 1.58×10^{-3} (95% HPD 7.32×10^{-4}–2.60×10^{-3}) substitutions per site (Table 1). The TMRCA was determined to be 43.24 (95% HPD 15.86–75.58) years before the most recent confirmed sampling event in 2015 (Table 1). Whilst, the clades in the Bayesian phylogeny appear to have slightly more structure with regards to their geographic origin

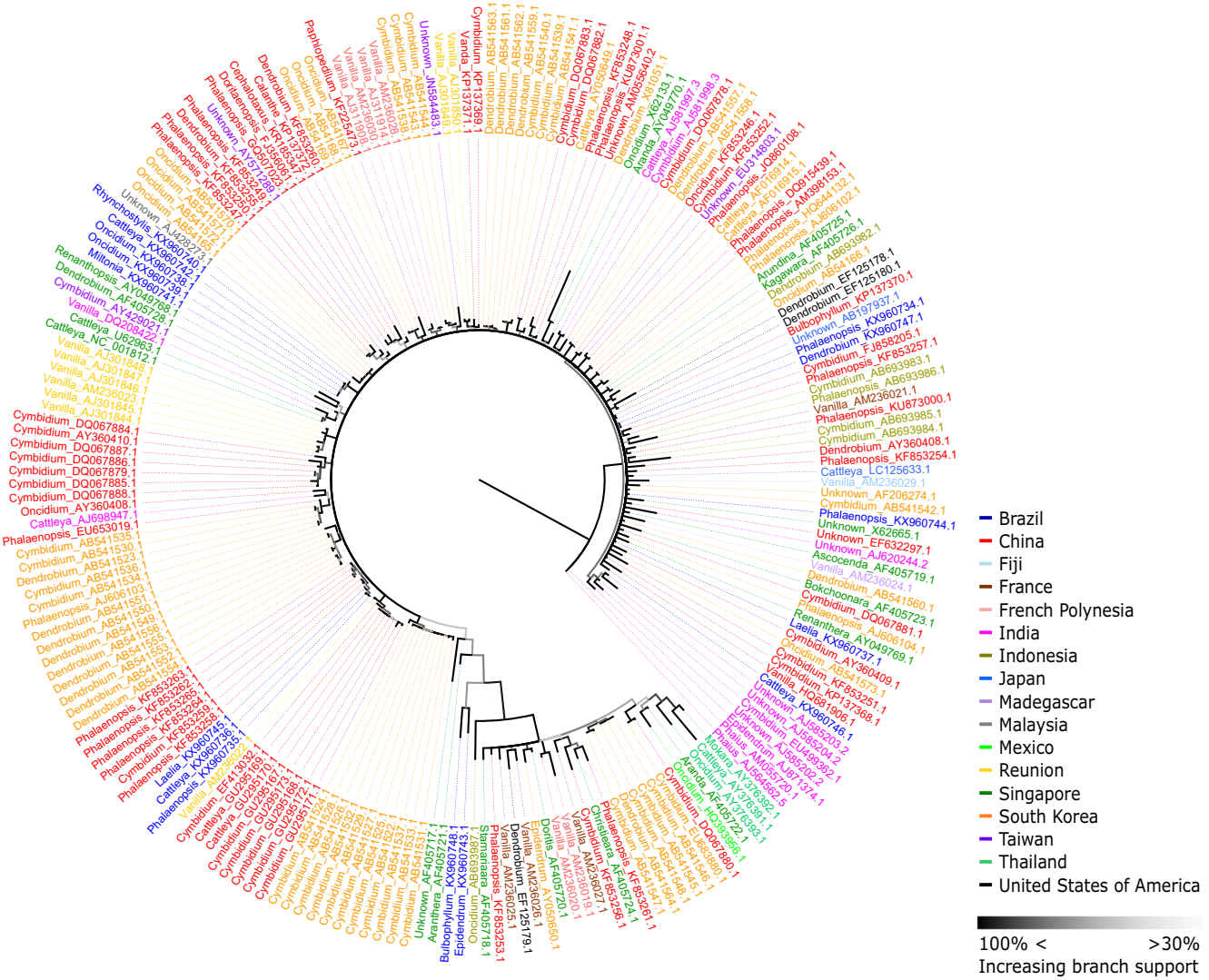

FIGURE 1 Maximum likelihood phylogenetic tree denoting relationships between Cymbidium mosaic virus (CymMV) capsid protein sequences obtained from cultivated orchid hosts. Branches are labeled according to host genus and colored according to bootstrap support. Labels are colored according to country of sampling, as denoted in the key

than with the ML tree, the analysis similarly suggests no host specificity (Figure S1).

Figure 2 shows the ML phylogeny of the ORSV capsid protein sequences comprising sequences isolated from 12 host genera across 14 countries. As with CymMV, both South Korean and Chinese isolates are highly represented in this dataset and little geographical, or host genus clustering is observed. The rate of evolution calculated in the Bayesian analysis conducted over the dated subset of isolates (Figure S2) was determined to be 1.93×10^{-3} (95% HPD 1.17×10^{-3}–2.72×10^{-3}) substitutions per site (Table 1). The ORSV TMRCA was determined to be 21.92 (95% HPD 21.01–23.41) years before the most recent confirmed sampling event in 2015 (Table 1). The Bayesian analysis has clustered the majority of South Korean isolates into four monophyletic clades but there was still no evidence of host specificity amongst sequences (Figure S2).

TABLE 1 Estimated substitution rate and TMRCA (along with their 95% HPD intervals) of the capsid protein of CymMV and ORSV inferred from an uncorrelated relaxed clock model

Virus	Marginal Likelihood	Mean substitution rate (site/ year)	95% lower HPD interval	95% upper HPD interval	TMRCA (years)	95% lower HPD interval (TMRCA)	95% upper HPD interval (TMRCA)
CymMV	−3,902.52	1.58×10^{-3}	7.32×10^{-4}	2.60×10^{-3}	43.24	15.86	75.58
ORSV	−1,261.73	1.93×10^{-3}	1.17×10^{-3}	2.72×10^{-3}	21.92	21.01	23.41

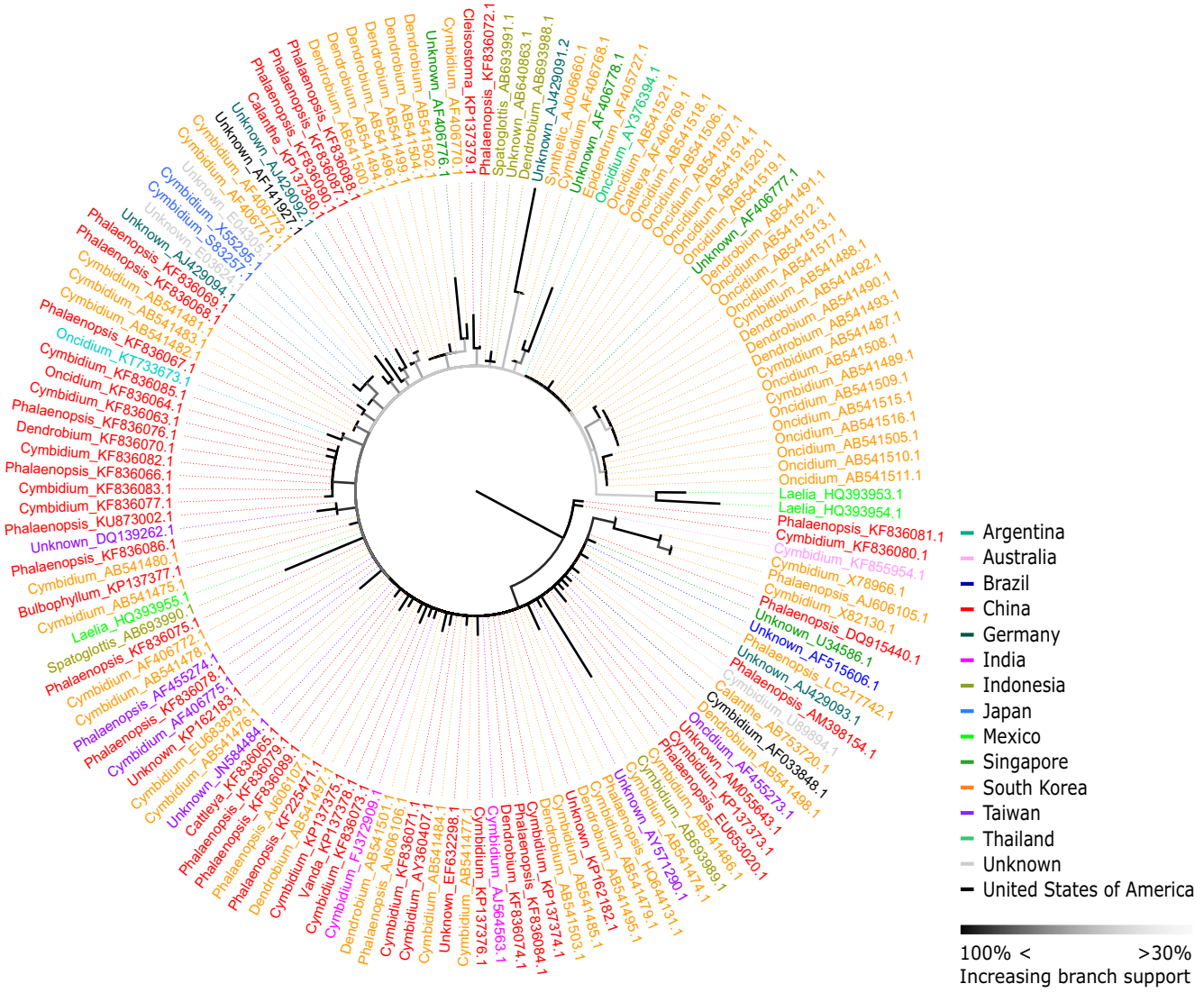

FIGURE 2 Maximum likelihood phylogenetic tree denoting relationships between Odontoglossum ringspot virus (ORSV) capsid protein sequences obtained from cultivated orchid hosts. Branches are labeled according to host genus and colored according to bootstrap support. Labels are colored according to country of sampling, as denoted in the key

4 | DISCUSSION

This study suggests that there is little geographical and temporal differentiation in global isolates of two of the most prevalent orchid viruses, CymMV and ORSV. There is also no indication that different genotypes of these viruses infect particular host species. This is in line with previous studies (Ajjikuttira et al., 2002; Moles, Delatte, Farreyrol, & Grisoni, 2007; Moraes et al., 2017) and suggests that there has been significant global transmission of these viruses. While acknowledging that only a partial fragment of the genome has been analyzed to determine the TMRCA, and that all but three of the sequences with confirmed sampling dates were obtained within a decade of the 2017 limit of this study (Table S1, S2), both viruses appear to have ancestral genotypes that originated within the last 50 years. This finding is in line with the period of mass expansion of trade in *ex situ* propagated orchids.

Our analyses date the CymMV common ancestor to around 1972 (95% HPD 1939–1999), while the date for ORSV is much younger at around 1993 (95% HPD 1992–1994). The broader confidence intervals surrounding the TMRCA for CymMV is likely due to a higher proportion of isolates from more diverse geographic regions, as opposed to the heavily biased ORSV dataset comprising predominantly Chinese and South Korean isolates used in the Bayesian analyses (Figures 1, 2 and S1, S2). While the early history of orchid cultivation up until the early 1900s is well-known (see Reinikka & Romero, 1995), little has been documented regarding the expansion of and changes within the industry over the last 50 years. As such, understanding the significance of the TMRCA for both viruses, as it relates to the orchid industry, is problematic. However, according to Motes (pers. commun.), the cloning of orchids, beginning in the 1950s, was a well-established technique by the 1970s. Many older plants were used in mass production through these micropropagation

techniques, some of which are likely to have carried viruses. During the 1970s, Singapore, Malaysia, Thailand, Hawaii, California, and the Netherlands were rapidly expanding their orchid sectors, particularly for the cut flower industry. As expected in a host-pathogen system, the frequency of contact to facilitate pathogen transmission and, therefore, the probability and persistence of infection increases when the host population reaches high densities (Lloyd-Smith et al., 2005).

The early 1990s, corresponding with the TMRCA of ORSV, saw the advent of mass production of *Phalaenopsis*, one of the most widespread orchid genera in the industry (Hinsley et al., 2017; Motes pers. commun.). After the controversy surrounding the use of the fungicide Benlate, that devastated the foliage growers in Florida and Hawaii (Geyelin, 2001; Motes pers. commun.), horticulturalists looked to new crops. This came at a time when the Taiwanese government were subsidising the growth in *Phalaenopsis* production and became the source of much of the stock for the United States and, potentially, growers in other regions such as Europe (Motes pers. commun.). This also saw the decline in then small growers, with the monopolisation of the industry by large horticultural corporations (Motes pers. commun.).

At approximately 10^{-3} substitutions per site per year we estimated very high evolutionary rates for both viruses, but well within that estimated for other RNA viruses of 10^{-5} and 10^{-2} substitutions per site per year (Duffy et al., 2008). Whilst we have only analyzed a portion of both genomes (~10%), studies of other positive sense ssRNA plant viruses also document evolutionary rates very similar to those we have estimated here for CymMV and ORSV (e.g. Fargette et al., 2006; Wu et al., 2011). This high evolutionary rate may be expected to result in divergence over time and geographic distribution, particularly in light of the restrictions on international trade imposed by national phytosanitary regulation and CITES. Even within the relatively short period estimated for the emergence of these viruses, we would have expected to see some evidence of geographically specific divergence within isolated populations. However, the phylogenetic patterns seen in Figures 1 and 2 suggests that the rate of dispersal of these viruses is high enough to result in any new variation being spread rapidly through the global distribution of cultivated orchids. Indeed, it is clear from our results that numerous introductions of both of these viruses have occurred globally. We frequently observe close phylogenetic relationships between isolates obtained from geographically distinct regions. For example, the well supported clade of CymMV isolates obtained from 12 different genera across eight countries (Figure 1). This rapid viral transmission is aided in part by their stability (Hu et al., 1994), ease of transmission through contaminated horticultural tools and media, and the presence of asymptomatic infections (Ajjikuttira et al., 2002). However, this is probably not enough to cause the global genetic homogenisation that we observe.

In a previous study of 85 viral isolates Moles et al. (2007) showed the presence of two sub-groups of CymMV. With the substantial increase in data (both in terms of the number of isolates and the geographical, temporal and host species coverage) our study has identified the presence of additional sub-groups (Figure 1), but with little differentiation based on geographic origin or host. The observed homogenisation is remarkable given the apparent lack of a known natural vector. Interestingly, this has occurred despite stricter international trade regulations for orchids under CITES, and phytosanitary regulations enforced by many countries (Khentry et al., 2006; Lawson & Brannigan, 1986). As CITES aims to ensure that the international trade in wild animals and plants does not threaten their survival, it does not act primarily as a means to enforce phytosanitary regulation and biosecurity. However, it does represent a significant constriction on the movement of plant material across international borders (Koopowitz, 2001; Roberts & Solow, 2008; Zelenko, 2005). Even so, the level of restriction on the movement of material caused by CITES does not appear to have resulted in any geographic separation of either virus. Homogenisation is only likely to increase further with the changes to CITES regulations which now allow the movement of large consignments of specific orchid hybrids from *Cymbidium*, *Dendrobium*, *Miltonia*, *Odontoglossum*, *Oncidium*, *Phalaenopsis* and *Vanda* without the need for CITES permits (see CITES, 2007).

Charles Darwin once speculated that "*… the great grandchildren of a single* [orchid] *plant would nearly … clothe with one uniform green carpet the entire surface of the land throughout the globe*", and noted "*minute seeds within their light coats are well fitted for wide dissemination…*" (Darwin, 1862). While the multi-billion-dollar international trade in orchids has certainly helped disperse orchids through the horticultural community, it has also dispersed their associated viruses, resulting in a homogenised, or rather "*uniform… carpet*" of CymMV and ORSV. While regulations are in place, such as plant health certification, that should, and others that could (i.e. CITES), potentially limit the dispersal of the virus, this clearly does not seem to be the case. It is also possible for virus-free plant material stocks for propagation and export to be readily generated with the application of heat and chemical treatments (Lim, Wong, & Goh, 1993; Wylie et al., 2013). The rapid global dispersal of viruses not only has the potential to impact this lucrative horticultural industry, it also threatens orchid species in the wild through poor biosecurity practices resulting in the reintroduction of infected stock or management of wild populations with infected horticultural tools.

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AUTHOR CONTRIBUTION

DR and SK conceived the study, DF and SK managed the genetic data and ran the analyses, DF created the figures and tables, DR compiled information relating to the orchid trade, all authors wrote and edited the manuscript.

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REFERENCES

Ajjikuttira, P. A., Lim-Ho, C. L., Woon, M. H., Ryu, K. H., Chang, C. A., Loh, C. S., & Wong, S. M. (2002). Genetic variability in the coat protein genes of two orchid viruses: Cymbidium mosaic virus and Odontoglossum ringspot virus. *Archives of Virology*, *147*, 1943–1954. https://doi.org/10.1007/s00705-002-0868-5

Anderson, P. K., Cunningham, A. A., Patel, N. G., Morales, F. J., Epstein, P. R., & Daszak, P. (2004). Emerging infectious diseases of plants: Pathogen pollution, climate change and agrotechnology drivers. *Trends in Ecology & Evolution*, *19*, 535–544. https://doi.org/10.1016/j.tree.2004.07.021

Averyanov, L. V. (2004). *Materials of Asia Pacific Orchid Conference 8* (p. 197). Tainan, Taiwan.

Cánovas, S. E., Ballari, M. C., & Nome, C. F. (2016). First report of Cymbidium mosaic virus and Odontoglossum ring spot virus in Argentina. *Australasian Plant Disease Notes*, *11*, 2. https://doi.org/10.1007/s13314-015-0189-7

Chng, C. G., Wong, S. M., Mahtani, P. H., Loh, C. S., Goh, C. J., Kao, M. C. C., … Watanabe, Y. (1996). The complete sequence of a Singapore isolate of odontoglossum ringspot virus and comparison with other tobamoviruses. *Gene*, *171*, 155–161. https://doi.org/10.1016/0378-1119(96)00046-7

CITES. (2007). CoP14 Prop. 34: Consideration of proposals for amendment of Appendices I and II. In Fourteenth meeting of the Conference of the Parties, 3–15 June 2007. The Hague (Netherlands).

Darwin, C. (1862). *On the various contrivances by which British and foreign orchids are fertilised by insects: And on the good effects of intercrossing*. London: J. Murray.

Daszak, P., Cunningham, A. A., & Hyatt, A. D. (2000). Emerging infectious diseases of wildlife - Threats to biodiversity and human health. *Science*, *287*, 443–449. https://doi.org/10.1126/science.287.5452.443

De, L. C., Pathak, P., Rao, A. N., & Rajeevan, P. K. (2015). *Commercial orchids*. In M. Golachowska (Ed.), Poland: DE GRUYTER OPEN.

Drummond, A. J., Ho, S. Y. W., Phillips, M. J., & Rambaut, A. (2006). Relaxed phylogenetics and dating with confidence. *PLoS Biology*, *4*, 699–710.

Drummond, A. J., Rambaut, A., Shapiro, B., & Pybus, O. G. (2005). Bayesian coalescent inference of past population dynamics from molecular sequences. *Molecular Biology and Evolution*, *22*, 1185–1192.

Drummond, A. J., Suchard, M. A., Xie, D., & Rambaut, A. (2012). Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*, *29*, 1969–1973. https://doi.org/10.1093/molbev/mss075

Duffy, S., Shackelton, L. A., & Holmes, E. C. (2008). Rates of evolutionary change in viruses: Patterns and determinants. *Nature Reviews. Genetics*, *9*, 267–276. https://doi.org/10.1038/nrg2323

European Commission. (2000). Part A, Annex V. In Council Directive 2000/29/EC. Bussels, Belgium.

Fargette, D., Konaté, G., Fauquet, C., Muller, E., Peterschmitt, M., & Thresh, J. M. (2006). Molecular ecology and emergence of tropical plant viruses. *Annual Review of Phytopathology*, *44*, 235–260. https://doi.org/10.1146/annurev.phyto.44.120705.104644

Geyelin, M. (2001). DuPont ordered to pay damages of $78.3 Million in benlate case. *The Wall Street Journal*.

Guindon, S., Dufayard, J.-F., Lefort, V., Anisimova, M., Hordijk, W., & Gascuel, O. (2010). New algorithms and methods to estimate maximum-likelihood phylogenies: Assessing the performance of PhyML 3.0. *Systematic Biology*, *59*, 307–321. https://doi.org/10.1093/sysbio/syq010

Hasegawa, M., Kishino, H., & Yano, T. (1985). Dating of the human-ape splitting by a molecular clock of mitochondrial DNA. *Journal of Molecular Evolution*, *22*, 160–174. https://doi.org/10.1007/bf02101694

Hinsley, A., de Boer, H. J., Fay, M. F., Gale, S. W., Gardiner, L. M., Gunasekara, R. S., …Phelps, J. (2017). A review of the trade in orchids and its implications for conservation. *Botanical Journal of the Linnean Society*, 1–21.

Hu, J. S., Ferreira, S., Xu, M. Q., Lu, M., Iha, M., Pflum, E., & Wang, M. (1994). Transmission, movement and inactivation of cymbidium mosaic and odontoglossum ringspot viruses. *Plant Disease*, *78*, 633–636. https://doi.org/10.1094/pd-78-0633

Joppa, L. N., Roberts, D. L., Myers, N., & Pimm, S. L. (2011). Biodiversity hotspots house most undiscovered plant species. *Proceedings of the National Academy of Sciences of the United States of America*, *108*, 13171–13176. https://doi.org/10.1073/pnas.1109389108

Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., … Drummond, A. (2012). Geneious basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics*, *28*, 1647–1649. https://doi.org/10.1093/bioinformatics/bts199

Khentry, Y., Paradornuwat, A., Tantiwiwat, S., Phansiri, S., & Thaveechai, N. (2006). Incidence of Cymbidium mosaic virus and Odontoglossum ringspot virus in Dendrobium spp. in Thailand. *Crop Protection*, *25*, 926–932. https://doi.org/10.1016/j.cropro.2005.12.002

Koopowitz, H. (2001). *Orchids and their conservation*. Portland, Oregon: Timber Press.

Lawson, R. H., & Brannigan, M. (1986). *Handbook on orchid pests and diseases*. West Palm Beach, Florida: American Orchid Society.

Lemey, P., Suchard, M., & Rambaut, A. (2009). Reconstructing the Initial Global Spread of a Human Influenza Pandemic: A Bayesian spatial-temporal Model for the Global Spread of H1N1pdm. *Plos Currents*, *1*, RRN1031. https://doi.org/10.1371/currents.rrn1031

Lim, S. T., Wong, S. M., & Goh, C. J. (1993). Elimination of cymbidium mosaic virus and odontoglossum ringspot virus from orchids by meristem culture and thin section culture with chemotherapy. *Annals of Applied Biology*, *122*, 289–297. https://doi.org/10.1111/j.1744-7348.1993.tb04034.x

Lloyd-Smith, J. O., Cross, P. C., Briggs, C. J., Daugherty, M., Getz, W. M., Latto, J., … Swei, A. (2005). Should we expect population thresholds for wildlife disease? *Trends in Ecology & Evolution*, *20*, 511–519. https://doi.org/10.1016/j.tree.2005.07.004

Moles, M., Delatte, H., Farreyrol, K., & Grisoni, M. (2007). Evidence that Cymbidium mosaic virus (CymMV) isolates divide into two subgroups based on nucleotide diversity of coat protein and replicase genes. *Archives of Virology*, *152*, 705–715. https://doi.org/10.1007/s00705-006-0897-6

Moraes, L. A., Krause-Sakate, R., & Pavan, M. A. (2017). Incidence and characterization of viruses infecting orchids in São Paulo state, Brazil. *Tropical Plant Pathology*, *42*, 126–131. https://doi.org/10.1007/s40858-016-0126-0

Namba, R., & Ishii, M. (1971). Failure of aphids to transmit the Odontoglossum ringspot and Cymbidium mosaic viruses to Orchid plantlets derived from meristem cultures. *Phytopathology*, *61*, 582–583. https://doi.org/10.1094/phyto-61-582

Pearson, M. N., & Cole, J. S. (1991). Further observations on the effects of cymbidium mosaic virus and odontoglossum ringspot virus on the growth of cymbidium orchids. *Journal of Phytopathology*, *131*, 193–198. https://doi.org/10.1111/J.1439-0434.1991.TB01187.x

Posada, D. (2008). jModelTest: Phylogenetic model averaging. *Molecular Biology and Evolution*, *25*, 1253–1256. https://doi.org/10.1093/molbev/msn083

Rambaut, A. (2009). FigTree v1.4.2.

Reinikka, M. A., & Romero, G. A. (1995). *A history of the orchid*. Portland, Oregon: Timber Press.

Roberts, D. L., & Dixon, K. W. (2008). Orchids. *Current Biology*, *18*, R325–R329. https://doi.org/10.1016/j.cub.2008.02.026

Roberts, D. L., & Solow, A. R. (2008). The effect of the Convention on International Trade in Endangered Species on scientific collections. *Proceedings of the Royal Society B: Biological Sciences*, *275*, 987–989. https://doi.org/10.1098/rspb.2007.1683

Royal Flora Holland. (2015). Flowering the world: Annual Report 2015.

Tamura, K., & Nei, M. (1993). Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. *Molecular Biology and Evolution*, *10*, 512–526.

Umikalsum, M. B., Bakar, U. K. A., Khairun, H. N., & Faridah, Q. Z. (2006). Cymbidium mosaic virus and odontoglossum ringspot tobamovirus genes cloned from infected Oncidium orchids. *Journal of Tropical Agriculture and Food Science*, *34*, 139–148.

United States Department of Agriculture. (2016). Floriculture Crops: 2015 Summary.

WCSP. (2017). *World checklist of selected plant families*. Kew: Facilitated by the Royal Botanic Gardens.

Wong, S. M., Chng, C. G., Lee, Y. H., Tan, K., & Zettler, F. W. (1994). Incidence of cymbidium mosaic and odontoglossum ringspot viruses and their significance in orchid cultivation in Singapore. *Crop Protection*, *13*, 235–239. https://doi.org/10.1016/0261-2194(94)90084-1

Wong, S. M., Mahtani, P. H., Lee, K. C., Yu, H. H., Tan, Y., Neo, K. K., … Chng, C. G. (1997). Cymbidium mosaic potexvirus RNA: Complete nucleotide sequence and phylogenetic analysis. *Archives of Virology*, *142*, 383–391. https://doi.org/10.1007/s007050050084

Wu, B., Blanchard-Letort, A., Liu, Y., Zhou, G., Wang, X., & Elena, S. F. (2011). Dynamics of molecular evolution and phylogeography of barley yellow dwarf virus-PAV. *PLoS ONE*, *6*, e16896. https://doi.org/10.1371/journal.pone.0016896

Wylie, S. J., Li, H., Dixon, K. W., Richards, H., & Jones, M. G. K. (2013). Exotic and indigenous viruses infect wild populations and captive collections of temperate terrestrial orchids (Diuris species) in Australia. *Virus Research*, *171*, 22–32. https://doi.org/10.1016/j.virusres.2012.10.003

Zelenko, H. (2005). *The Oncidium alliance with an emphasis on Caucaea*. In Proceedings of the 18th World Orchid Conference 11–20 March, 2005 (pp. 521–524). Dijon, France: Naturalia Publications.

Zettler, F. W., Ko, N. J., Wisler, G. C., Elliott, M. S., & Wong, S. M. (1990). Viruses of orchids and their control. *Plant Disease*, *74*, 621–626. https://doi.org/10.1094/pd-74-0621

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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