

# Species traits, landscape quality and floral resource overlap with honeybees determine virus transmission in plant–pollinator networks

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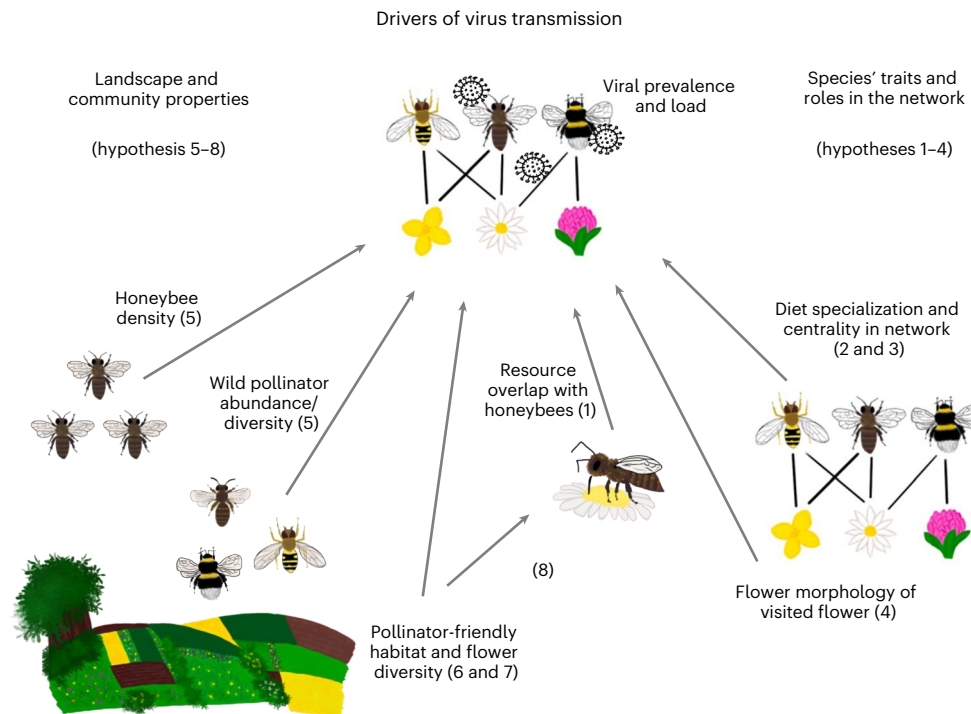
Emerging infectious diseases pose a threat to pollinators. Virus transmission among pollinators via flowers may be reinforced by anthropogenic land-use change and concomitant alteration of plant–pollinator interactions. Here, we examine how species' traits and roles in flower-visitation networks and landscape-scale factors drive key honeybee viruses—black queen cell virus (BQCV) and deformed wing virus—in 19 wild bee and hoverfly species, across 12 landscapes varying in pollinator-friendly (flower-rich) habitat. Viral loads were on average more than ten times higher in managed honeybees than in wild pollinators. Viral loads in wild pollinators were higher when floral resource use overlapped with honeybees, suggesting these as reservoir hosts, and increased with pollinator abundance and viral loads in honeybees. Viral prevalence decreased with the amount of pollinator-friendly habitat in a landscape, which was partly driven by reduced floral resource overlap with honeybees. Black queen cell virus loads decreased with a wild pollinator's centrality in the network and the proportion of visited dish-shaped flowers. Our findings highlight the complex interplay of resource overlap with honeybees, species traits and roles in flower-visitation networks and flower-rich pollinator habitat shaping virus transmission.

Transmission of newly emerging diseases can profoundly impact human and animal health<sup>1</sup>, as recently exemplified by the Covid-19 pandemic. Pathogen host shifts<sup>2</sup> leading to emerging diseases could potentially harm pollinator health and may contribute to pollinator declines<sup>3,4</sup>, jeopardizing the provision of vital pollination services<sup>5,6</sup>. RNA viruses such as the deformed wing virus complex (DWV-A and DWV-B) and black queen cell virus (BQCV) commonly detected in the western honeybee, *Apis mellifera*<sup>7</sup> show active replication in other bee species<sup>8,9</sup>. Indeed, shared viral strains between honeybees and wild pollinators, including non-bee taxa such as hoverflies<sup>2,10,11</sup>, suggest

ongoing transmission. This may impact the health of co-occurring pollinators<sup>12–14</sup> and affects the structure and functioning of pollinator assemblages<sup>15</sup>. Flowers shared by pollinators can be primary hubs of faecal–oral virus transmission<sup>16</sup>. Thus, anthropogenic land-use changes that alter the composition and interaction structure of plant–pollinator communities<sup>17,18</sup> may profoundly impact pathogen transmission among pollinators<sup>15</sup>.

The risk of exposure to pathogens of a potential pollinator host is probably mediated by the traits and roles of pollinator and plant species in an interaction network that, together with landscape effects,

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**Fig. 1 Hypothesized drivers of virus transmission via plant–pollinator interactions and landscape effects.** Virus transmission in plant–pollinator communities is hypothesized to be influenced by various mechanisms operating at the species, community and landscape levels. At the species and network level, we hypothesize that specific foraging traits such as (1) a high floral resource overlap of pollinators with other species, in particular honeybees (which are expected to act as a reservoir host<sup>9</sup>), (2) a high diet specialization and (3) a low centrality in the network<sup>19</sup>, as well as flower morphology of the visited plants such as (4) open

dish (dish-bowl-shaped) flowers<sup>22,24</sup> will lead to an increased viral prevalence and load in wild pollinators. At the landscape level, (5) a high abundance of honeybees and/or high viral loads or prevalence in honeybees and high abundance of wild pollinators or a low pollinator diversity as well as (6) a low amount of pollinator-friendly habitat and (7) flower diversity are predicted to increase viral prevalence and load in wild pollinators<sup>28,29</sup>, for example, (8) through increasing the floral resource overlap among pollinators, in particular between honeybees and wild pollinators<sup>30</sup>. Figure created using Procreate (<https://procreate.com/>).

have rarely been investigated within the same framework. For example, broader pollinator diets (that is, low floral specialization) and a well-connected network (and thus pollinator species with central roles) are predicted to dilute the risk of picking up a pathogen when the pollinator is visiting many different flowers<sup>19</sup>.

Flower morphology may also shape pathogen transmission risks. For instance, open dish flowers may increase the probability of insect defecation in the flower<sup>20,21</sup>, increase viral exposure to denaturing ultraviolet (UV) light and attract multiple pollinators (potential hosts) to easily accessible nectar rewards<sup>22–24</sup>. Flowers providing high amounts of nectar and pollen rewards (correlated to flower volume)<sup>25</sup> that are readily accessible are expected to be visited frequently by a broad range of pollinators. This will increase the probability of being visited by infected (or vectoring) hosts and the corresponding spread of pathogens to coforaging pollinators via faecal–oral virus transmission<sup>24</sup>. In contrast, easy accessibility of (open) flowers with short corollas could also lead to shorter flower handling times<sup>26</sup>, thus potentially reducing the temporal risk of depositing or picking up pathogens.

Community properties such as high flower and pollinator diversity may also reduce pathogen transmission through dilution processes<sup>27–29</sup>. Greater plant diversity might reduce overlap in floral resource use between (mostly) managed honeybees—predicted to act as a viral reservoir host<sup>9</sup>—and wild pollinators<sup>30</sup>, thereby potentially reducing pathogen transmission via shared flowers. In contrast, hotspots of attractive floral resources may concentrate foraging pollinators and the proportional abundance of competent hosts to increase transmission probabilities and pathogen prevalence in the community<sup>29,31</sup>. Consequently, landscapes poor in flower-rich pollinator habitat may lead to pollinators aggregating on the few available floral resource patches, thereby increasing the likelihood of pathogen transmission<sup>32</sup>.

Thus, an holistic understanding of the factors affecting interspecific transmission of pollinator pathogens at species, interaction network, community and landscape levels will help to design conservation strategies that mitigate pathogen transmission among pollinators.

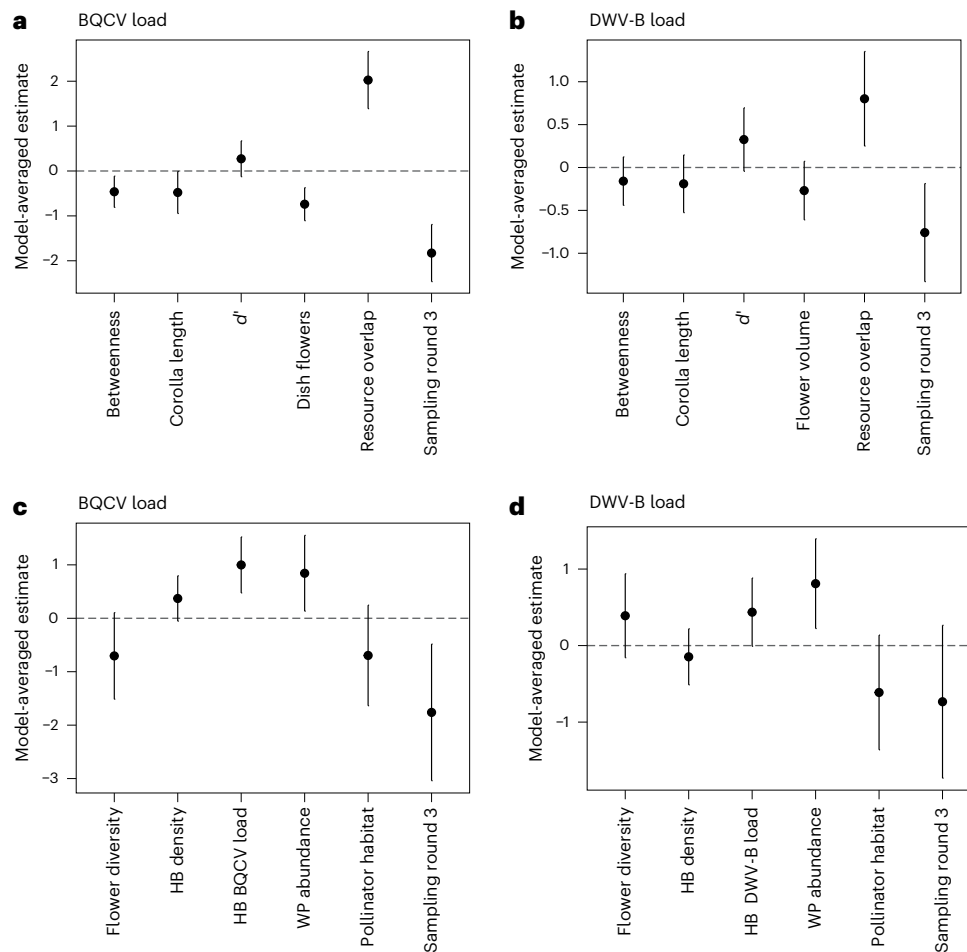
Here, we analyse plant–pollinator interaction networks, species traits and landscape composition to identify potential transmission pathways affecting prevalence and loads of RNA viruses (DWV-A, DWV-B and BQCV) in 19 wild bee (non-*A. mellifera*) and hoverfly pollinator species (hereafter wild pollinators for simplicity). We collected plant–pollinator interaction network data from 12 agricultural or more urbanized landscapes in northern Switzerland with varying amounts of pollinator-friendly habitat (flowering habitats playing important roles in sustaining pollinators, including urban green spaces) (Extended Data Fig. 1).

We hypothesized that viral prevalence and loads in wild pollinator species will increase with: (1) high floral resource overlap with managed honeybees (likely reservoir host); (2) high diet specialization; (3) low centrality in flower-visitation networks; (4) greater proportion of open (dish-bowl-shaped) flowers in the diet offering easy access to highly rewarding pollen/nectar; and (5) greater abundance of potential pollinator ‘hosts’ and high viral loads in honeybees in a landscape. We also hypothesized that viral prevalence and loads will decrease with (6) flowering plant diversity and (7) the amount of pollinator-friendly habitat in a landscape, (8) which together contribute to reduced honeybee–wild pollinator resource overlap (dilution of pathogen transmission) (Fig. 1).

## Results

### Viral prevalence and loads across pollinator communities

All three viruses were detected in honeybees (*A. mellifera*), with DWV-A being the least abundant virus (5.83% of individuals tested positive),



**Fig. 2 | Best ranked models predicting viral loads in wild pollinators.**

**a–d.** Averaged model estimates (modelled slopes of the relationships) and 95% confidence intervals of explanatory variables in best models (LMMs,  $\Delta\text{AICc} < 2$ ) explaining viral load of BQCV ( $n = 304$  virus-positive individuals) (**a,c**) and DWV-B ( $n = 288$  virus-positive individuals) (**b,d**) in wild pollinators (the response variable was log-transformed number of genome copies per microgram RNA of virus-positive individuals). **a,b.** display the results from modelling the effects of plant species traits and pollinator network roles (centrality measured as weighted

betweenness (Betweenness), corolla length, specialization  $d'$ , proportion of dish-bowl flowers among visited flowers (Dish flowers) and floral resource overlap with honeybees (Resource overlap)). **c,d.** display the results from modelling the effects of pollinator community properties (Shannon diversity of flowers (Flower diversity), honeybee density (HB density) and honeybee viral load (HB BQCV or DWV-B load), wild pollinator abundance (WP abundance) and percentage cover of pollinator habitat (Pollinator habitat)) in a landscape.

while more than ten times more individuals tested positive for DWV-B (64.17%) and BQCV (86.39%). Moreover, the maximum DWV-A viral load in honeybees (absolute number of genome copies per  $\mu\text{g}$  of RNA per individual sample) was lower by a factor of  $10^5$  and  $10^9$  than the maximum DWV-B and BQCV viral loads, respectively (Supplementary Table 1). This pattern was mirrored in the wild pollinator community, where 10 out of 19 (53%) screened species tested positive for DWV-A, whereas all 19 species (100%) tested positive for DWV-B and 18 out of 19 species (95%) tested positive for BQCV, although with loads and prevalence varying greatly among species (Extended Data Fig. 2 and Supplementary Table 1). For example, regarding numbers of copies per  $\mu\text{g}$  of RNA per individual: DWV-A ranged from  $7 \times 10^1$  (*Lasioglossum glabriusculum*) to  $9.7 \times 10^4$  (*Bombus terrestris*), DWV-B from  $4.3 \times 10^2$  (*Lasioglossum malachurum*) to  $9.0 \times 10^7$  in a single *Syrphus vitripennis* individual, while BQCV ranged from  $2.3 \times 10^2$  (*L. glabriusculum*) to  $3.5 \times 10^8$  (*B. humilis*). Low titres of DWV-A precluded statistical analysis of DWV-A (Methods). Thus, a total of 588 samples of 17 wild pollinator species and 240 samples of honeybees were used for statistical analyses. Median viral loads (log) of DWV-B and BQCV within a wild pollinator species (across landscapes) were positively correlated (Spearman's rank correlation  $\rho = 0.64$ ,  $P = 0.002$ ). Viral load (median (log)) and prevalence in the wild pollinator community in a landscape were also

strongly positively correlated (Spearman's rank correlations—BQCV for May/June  $\rho = 0.81$ ,  $P = 0.001$  and for July  $\rho = 0.81$ ,  $P = 0.002$ ; DWV-B for May/June  $\rho = 0.79$ ,  $P = 0.002$  and for July  $\rho = 0.88$ ,  $P = 0.0003$ ). Confidence intervals for apparent virus prevalence (BQCV and DWV-B) in each species can be found in Supplementary Table 3.

### Floral species' traits and pollinator network roles

In the best models ( $\Delta\text{AICc} < 2$ ) predicting BQCV load (Fig. 2a and Supplementary Table 4) and prevalence (Supplementary Table 5 and Extended Data Fig. 3a) in wild pollinators, floral resource overlap of a wild pollinator species with honeybees (community weighted mean (CWM) number of honeybee visits on flowers visited by a given wild pollinator species) had the strongest effect, positively affecting both BQCV prevalence (Supplementary Table 6) and load in wild pollinators (Table 1 and Fig. 3a; see Extended Data Fig. 4 for an example plant–pollinator network visualizing floral resource overlap). Weighted betweenness as a measure of a pollinator species' centrality within a network and the proportion of visited dish-bowl flowers were negatively related to its BQCV load (Table 1 and Fig. 3b,c) but only weakly to BQCV prevalence (Supplementary Table 6). Corolla length (CWM) of visited flowers was weakly negatively related to BQCV load (Table 1 and Fig. 3d), while specialization  $d'$  of pollinators or flower volume (CWM) of visited

**Table 1 | Model-averaged estimates (conditional average) of best models ( $\Delta AICc < 2$ ) investigating the effects of plant species traits and pollinator roles in the network**

Response		Estimate	s.e.	Adj. s.e.	z value	P value	FDR P value
<b>Species traits and roles models</b>							
BQCV load in wild pollinator	Intercept	12.05	0.58	0.58	20.65	<0.0001	
	<b>Betweenness</b>	<b>-0.46</b>	<b>0.18</b>	<b>0.18</b>	<b>2.60</b>	<b>0.009</b>	<b>0.027</b>
	Corolla length	-0.48	0.24	0.24	2.00	0.045	0.082
	$d'$	0.27	0.20	0.20	1.34	0.181	0.197
	<b>Dish flowers</b>	<b>-0.74</b>	<b>0.19</b>	<b>0.19</b>	<b>3.94</b>	<b>&lt;0.0001</b>	<b>0.001</b>
	<b>Resource overlap</b>	<b>2.03</b>	<b>0.32</b>	<b>0.32</b>	<b>6.24</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>
	<b>Sampling round 3</b>	<b>-1.83</b>	<b>0.32</b>	<b>0.32</b>	<b>5.63</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>
DWV-B load in wild pollinator	Intercept	8.47	0.50	0.50	16.96	<0.0001	
	Betweenness	-0.16	0.14	0.14	1.10	0.269	0.330
	Corolla length	-0.19	0.17	0.17	1.11	0.268	0.330
	$d'$	0.33	0.19	0.19	1.73	0.084	0.264
	Flower volume	-0.27	0.17	0.17	1.55	0.122	0.298
	<b>Resource overlap</b>	<b>0.80</b>	<b>0.28</b>	<b>0.28</b>	<b>2.85</b>	<b>0.004</b>	<b>0.050</b>
	Sampling round 3	-0.76	0.29	0.29	2.60	0.009	0.051
<b>Community and landscape models</b>							
BQCV load in wild pollinator	Intercept	11.45	0.83	0.83	13.73	<0.0001	
	H flowers	-0.70	0.41	0.41	1.70	0.088	0.135
	<b>HB load BQCV</b>	<b>1.00</b>	<b>0.27</b>	<b>0.27</b>	<b>3.74</b>	<b>0.0002</b>	<b>0.001</b>
	HB density	0.37	0.22	0.22	1.71	0.087	0.135
	Pollinator abundance	0.84	0.36	0.36	2.33	0.020	0.051
	Pollinator habitat	-0.70	0.48	0.48	1.45	0.147	0.189
	<b>Sampling round 3</b>	<b>-1.76</b>	<b>0.65</b>	<b>0.65</b>	<b>2.70</b>	<b>0.007</b>	<b>0.023</b>
DWV-B load in wild pollinator	Intercept	0.85	0.56	0.56	15.12	<0.0001	
	H flowers	0.39	0.28	0.28	1.39	0.164	0.306
	HB load DWV-B	0.44	0.23	0.23	1.92	0.055	0.202
	HB density	-0.15	0.19	0.19	0.79	0.432	0.475
	<b>Pollinator abundance</b>	<b>0.81</b>	<b>0.30</b>	<b>0.30</b>	<b>2.71</b>	<b>0.007</b>	<b>0.050</b>
	Pollinator habitat	-0.61	0.38	0.38	1.60	0.109	0.298
	Sampling round 3	-0.73	0.51	0.51	1.44	0.150	0.306

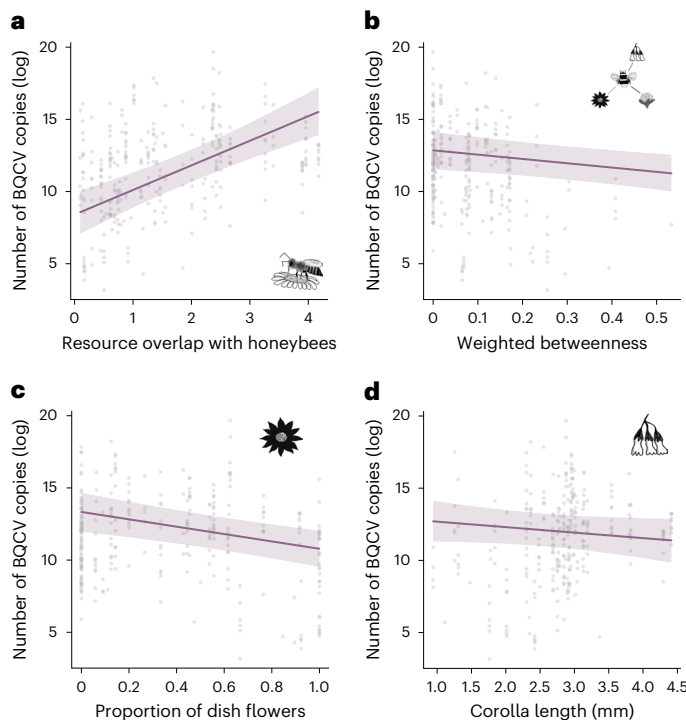
Plant species traits and pollinator roles in the network include: CWM flower volume, CWM corolla length of plants; specialization ( $d'$ ), resource overlap with honeybees (HB), proportion of dish flowers visited and weighted betweenness (Betweenness) of pollinators) or the effects of species community and landscape variables (percentage cover of pollinator habitat (%), flower Shannon diversity (H flowers), viral load in honeybees—BQCV or DWV-B—(HB load), honeybee density (HB density) and wild pollinator abundance) on viral loads of pollinator species (log-transformed, only virus-positive individuals). Sampling round was included in all models because of the data structure (two sampling rounds in each landscape). Z-tests were used to derive P values from averaged LMM. The table shows the estimates and (adjusted) standard errors (s.e., adj. s.e.), z and P values as well as P values corrected with the FDR correction. Significant results (FDR  $P < 0.05$ ) are shown in bold.

flowers did not affect BQCV prevalence (Supplementary Table 6) or load (Table 1).

In the best models ( $\Delta AICc < 2$ ) predicting DWV-B load (Fig. 2b and Supplementary Table 4) and prevalence (Supplementary Table 5 and Extended Data Fig. 3b) in wild pollinators, floral resource overlap with honeybees similarly had the strongest effect, positively affecting both DWV-B prevalence (Supplementary Table 6) and load (Table 1). Weighted betweenness, corolla length, specialization  $d'$  and flower volume did not affect DWV-B prevalence (Supplementary Table 6) or load (Table 1), respectively. Floral resource overlap between wild pollinators and honeybees decreased with increasing proportion of pollinator-friendly habitat in a landscape (linear model;  $R^2m = 0.021$ ,  $R^2c = 0.028$ , pollinator-friendly habitat (%)  $-F_{1,10} = 12.01$ ,  $P = 0.006$ ; sampling round  $-F_{1,228} = 0.13$ ,  $P = 0.717$ ).

Plants receiving the highest number of honeybee visits in May/June and July had open dish-bowl flowers (for example, *Centaurea jacea* and *Knautia arvensis*) as well as closed flag or gullet flowers

(for example, *Origanum vulgare* and *Trifolium repens*) (Fig. 4a,b). However, non-metric multidimensional scaling (NMDS) of pollinator species composition and flower traits of their visited flowers showed that wild pollinators visiting mainly dish-bowl flowers were those with generally lowest viral loads (permutation test: BQCV— $R^2 = 0.39$ ,  $P = 0.014$ ; DWV-B— $R^2 = 0.60$ ,  $P = 0.001$ ) (Fig. 4c,d), confirming the results reported above. A similarity of percentage analysis (SIMPER)<sup>33</sup> corroborated that flower volume, corolla length and dish-bowl shape were the traits of visited flowers most strongly associated with differences in viral loads among pollinators (Supplementary Table 7). To better understand the findings that dish-bowl flowers are highly visited by honeybees, while at the same time pollinators visiting a high proportion of dish-bowl-shaped flowers have lower viral loads, we separately tested the effect of resource overlap between honeybees and wild pollinators for dish-bowl and non-dish-bowl shaped flowers on viral loads. We found an interactive effect of resource overlap with flower shape on both BQCV and DWV-B loads: the positive relationship



**Fig. 3 | BQCV loads related to plant species traits and pollinator roles in the network.** **a–d**, Relationships of BQCV load of virus-positive wild pollinator individuals with floral resource overlap with honeybees (CWM number of honeybee visits on visited flowers) ( $P < 0.0001$ , corrected  $P < 0.0001$ ) (**a**), weighted betweenness as a measure of centrality in the network ( $P = 0.009$ , corrected  $P = 0.027$ ) (**b**), proportion of dish-bowl flowers among visited flowers ( $P < 0.0001$ , corrected  $P = 0.001$ ) (**c**) and corolla length (mm) of visited flowers (CWM) ( $P = 0.045$ , corrected  $P = 0.082$ ) (**d**). Z-tests were used to derive  $P$  values from averaged LMMs and  $P$  values were corrected with the FDR correction. Averaged model predictions of the best models ( $\Delta\text{AICc} < 2$ ) are plotted with 95% Bayesian credible intervals (shaded areas). All explanatory variables present in the best models ( $\Delta\text{AICc} < 2$ ) except the ones for which relationships with response variables are plotted were fixed at their mean values. Points show raw data. Figure created using Procreate (<https://procreate.com/>).

between viral load and resource overlap was steeper for resource overlap on non-dish-bowl flowers versus on dish-bowl flowers (Extended Data Fig. 5, LMMs; BQCV–interaction resource overlap  $\times$  flower shape  $F_{1,473} = 5.8$ ,  $P = 0.0167$  and sampling round  $F_{1,479} = 68.0$ ,  $P < 0.001$ ; DWV-B–interaction resource overlap  $\times$  flower shape  $F_{1,444} = 6.7$ ,  $P = 0.01$  and sampling round  $F_{1,460} = 10.5$ ,  $P = 0.001$ ).

### Influence of landscape and pollinator community properties

Testing for the influence of landscape and pollinator community properties at the landscape scale on BQCV loads (best models with  $\Delta\text{AICc} < 2$ ; Fig. 2c and Supplementary Table 8) and prevalence (Supplementary Table 9 and Extended Data Fig. 3c) in wild pollinators revealed that wild pollinator abundance was positively related to BQCV prevalence (Supplementary Table 6) and weakly to load (Table 1 and Fig. 5a). BQCV load in honeybees also explained a significant amount of variation of BQCV load in wild pollinators (Table 1 and Fig. 5b) but BQCV prevalence in honeybees did not explain prevalence in wild pollinators (Supplementary Table 6). The proportion of pollinator-friendly habitat was weakly negatively related to BQCV prevalence (Fig. 5c and Supplementary Table 6).

In the best models ( $\Delta\text{AICc} < 2$ ) predicting DWV-B load (Fig. 2d and Supplementary Table 8) and prevalence (Supplementary Table 9 and Extended Data Fig. 3d) in wild pollinators, wild pollinator abundance was positively related to DWV-B load but not to prevalence (Table 1 and

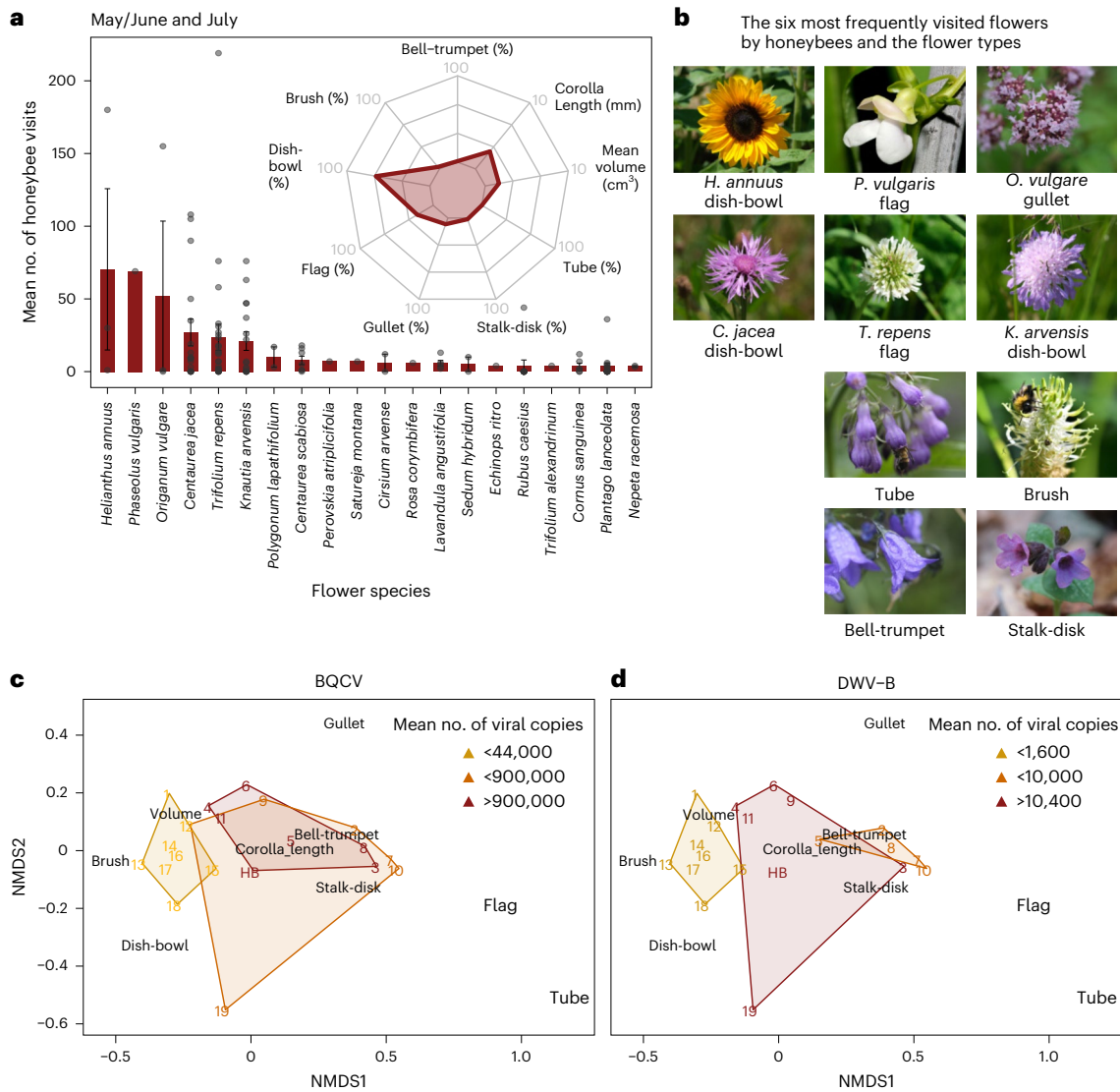
Supplementary Table 6). DWV-B load or prevalence in honeybees did not significantly affect DWV-B loads or prevalence in wild pollinators (Table 1 and Supplementary Table 6).

## Discussion

Our study demonstrates how pathogen transmission pathways among potential hosts are the product of complex, multiple interactions and processes operating across levels of ecological organization. The interplay of pollinator foraging roles within networks, preferences for particular plant traits, viral loads in coforaging honeybees and landscape composition together influenced viral prevalence and loads in wild pollinators. Both BQCV and DWV-B viruses were more prevalent with higher loads in wild pollinator species that had a high degree of floral resource overlap with honeybees and with a high wild pollinator abundance in the landscape. However, a more central position of a pollinator within a network, a high proportion of dish-bowl flowers in the diet and high amounts of pollinator-friendly habitat in the landscape reducing floral resource overlap, decreased the chance of pathogen transmission.

BQCV and DWV-B loads were markedly increased in many field-sampled bee and hoverfly species with high floral resource overlap with honeybees and with high viral loads in coforaging honeybees (for BQCV). Our results indicate that transmission of BQCV was more widespread, while transmission of DWV-B affected especially those wild pollinators with a particularly high floral resource overlap with honeybees. This is in line with our finding that BQCV was clearly more widespread in honeybees, wild bee and hoverfly pollinators screened in the study region than was DWV-B. Although we did not test for active replication of the virus in a pollinator (and thus infection), these findings, together with the generally substantially higher viral loads in honeybees compared to wild pollinators, provide strong evidence for virus spillover from honeybees to wild pollinators through foraging on shared floral resources. However, our data show also that a few wild bee species, especially bumblebee species such as *B. lapidarius* and *B. terrestris* which were frequently sampled in the plant–pollinator networks, had similarly high median loads or prevalence of BQCV and/or DWV-B, although clearly lower maximum viral loads, compared to honeybees. It is therefore conceivable that virus transmission could occur in both directions among honeybees and these wild bee species, potentially also including spillback<sup>21</sup> of viruses following spillover from honeybees (but see ref. 34 finding experimental evidence that the directionality of DWV transmission is predominantly from honeybees to bumblebees). We found some support for this hypothesis based on analyses showing that BQCV prevalence in *B. lapidarius* significantly predict BQCV prevalence in honeybees and similar positive associations between DWV-B prevalence in *B. terrestris* and honeybees as well as DWV-B loads in *B. lapidarius* and honeybees (Supplementary Table 10). It is important to note, however, that while these findings corroborate virus transmission among honeybees and these bumblebee species, we cannot unravel the directionality or determine the dominance of transmission in one or the other direction, which would require, for example, a controlled experimental approach<sup>34</sup>.

Transmission of viruses among pollinators via flowers can either occur through direct contact while foraging on the same flower<sup>34</sup> or more likely via visiting flowers contaminated through the transmission of contaminated pollen or oral secretions and faeces from infected pollinators<sup>16,35</sup>. In other pollinator–pathogen systems, trypanosomatid transmission can be strongly affected by flower morphology<sup>36</sup>. For example, increased defecation rates of bumblebees on large open flowers (dish-bowl flowers) may increase the spread of trypanosome pathogens<sup>21</sup>. In contrast to our hypothesis, our results indicate lower BQCV loads in pollinators visiting a high proportion of open dish-bowl flowers, suggesting that other factors associated with the dish shape of flowers played an important role in BQCV transmission<sup>24</sup>. For example, viruses in nectar and pollen of open dish-bowl flowers might degrade faster due to higher UV light exposure<sup>37,38</sup>, thereby potentially reducing



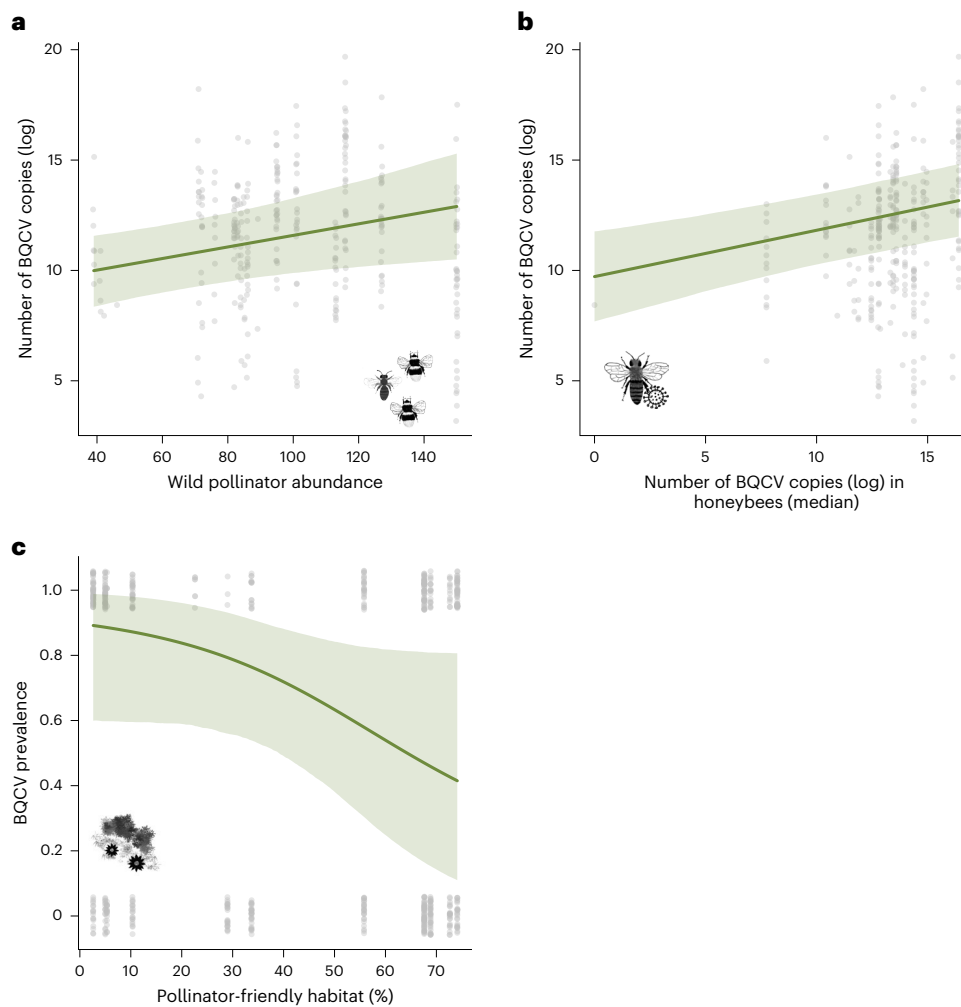
**Fig. 4 | Visited plants and their flower traits.** **a**, Plant species that received the most visits by honeybees in May/June and July (mean values  $\pm$  s.e.m.,  $n = 123$  observations from 12 landscapes). The insert is displaying the types of flowers most frequently visited by honeybees. **b**, The six species with the highest mean number of visits were *Helianthus annuus*, *Phaseolus vulgaris*, *Origanum vulgare*, *Centaurea jacea*, *Trifolium repens* and *Knautia arvensis* and their flower type is indicated. Additionally, examples for the flower types ‘tube’, ‘brush’, ‘bell-trumpet’ and ‘stalk-disk’ are given with images of *Symphytum officinale*, *Phyteuma spicatum*, *Campanula* spp. and *Pulmonaria* spp. as example taxa are shown. **c,d**, NMDS visualizing Bray–Curtis dissimilarity distances among the 20 pollinator species screened for viruses preferring plant species with different

flower traits. The pollinator species are grouped by load (mean number of genome copies per microgram RNA) of BQCV (**c**) and DWV-B (**d**). Numbers in **c** and **d** indicate specific pollinator species: HB, honeybees; 1, *Andrena humilis*; 2, *Bombus hortorum*; 3, *B. humilis*; 4, *B. hypnorum*; 5, *B. lapidarius*; 6, *B. lucorum*; 7, *B. pascuorum*; 8, *B. ruderatus*; 9, *B. subterraneus*; 10, *B. sylvorum*; 11, *B. terrestris*; 12, *Halictus scabiosae*; 13, *Lasioglossum glabriusculum*; 14, *L. malachurum*; 15, *L. morio*; 16, *L. pauxillum*; 17, *Melanostoma mellinum*; 18, *Sphaerophoria philanthus*; 19, *Syrphus vitripennis*. Credit: *Phaseolus vulgaris* photo © Thomas Bresson, <https://www.flickr.com/photos/computerhotline/>, under a Creative Commons licence CC BY 2.0.

transmission rates. Additionally, the open dish-bowl flowers and flowers with shorter corollas are generally easier to handle for many pollinators, leading to shorter flower handling times<sup>26</sup>, which may decrease the risk of picking up viruses. These potential mechanisms might explain the lower virus loads in species visiting proportionally more dish flowers and flowers with shorter corollas compared to species preferentially visiting flowers of other shapes, despite some pollinators having overlapping resources with honeybees. The pollinator species with lower virus loads most frequently visiting these dish flowers belonged to the families Halictidae, Andrenidae and Syrphidae, as revealed by the NMDS analysis. Thus, together with the potential mechanisms of increased UV light exposure and decreased handling time discussed above, it is conceivable that the observed usually high diversity of

pollinators visiting these readily accessible dish flowers included a particular high proportion of species with very low viral loads which may not act as viral reservoir hosts. This, along with a disproportionately high densities of dish flowers (as revealed by the flower abundance estimates for the sample plant–pollinator networks), could be associated with a reduced probability that individual flowers are actually shared among hosts, possibly further contributing to a reduced risk of virus transmission among pollinators through a dilution effect mediated by flower shape<sup>24</sup>.

Moreover, several of our other findings point to a dilution effect<sup>27</sup> at the pollinator species and the landscape level, although some of our findings also indicate processes that counter those of pathogen dilution. At the pollinator species level, our finding that pollinators with



**Fig. 5 | BQCV loads or prevalence related to drivers assessed at the landscape scale.** **a, b.** Relationships of either BQCV load of virus-positive wild pollinator individuals with wild pollinator abundance ( $P = 0.020$ , corrected  $P = 0.051$ ) (**a**) or BQCV load in honeybees (log) (median load of ten honeybees per landscape and sampling round) ( $P = 0.0002$ , corrected  $P = 0.001$ ) (**b**). **c.** The relationship between BQCV prevalence in wild pollinators and cover of pollinator-friendly habitat ( $P = 0.024$ , corrected  $P = 0.054$ ). *Z*-tests were used to derive *P* values

from averaged LMMs (viral load) or GLMMs (viral prevalence) and *P* values were corrected with the FDR correction. Averaged model predictions of the best models ( $\Delta\text{AICc} < 2$ ) with 95% Bayesian credible intervals (shaded areas) are plotted. All explanatory variables present in the best models ( $\Delta\text{AICc} < 2$ ) except the ones for which relationships with response variables are plotted were fixed at their mean values. Points show raw data. Figure created using Procreate (<https://procreate.com/>).

a central position in the networks (high weighted betweenness) are associated with lower viral loads points towards a dilution pathway: pollinators that visit a variety of different plant species also visited by other pollinators may experience a reduced risk of pathogen exposure compared to species focusing on few plant species<sup>19,29</sup>.

Finally, at the landscape level, our findings suggest that high amounts of pollinator-friendly habitat are related to reduced BQCV prevalence, both in bee and hoverfly pollinators. This was probably driven by the reduced floral resource overlap between honeybees and wild pollinators as a consequence of increased availability of different foraging habitat offering higher floral diversity levels<sup>39</sup>. High habitat amount and flower diversity generally reduce the probability of inter- and intra-species contact due to increasing complementarity in flowering plant species visitation<sup>30,40,41</sup>. At the same time, high amounts of suitable foraging habitat probably promote optimal nutritional conditions and thus general health of pollinators<sup>42</sup>. Therefore, our study of 17 wild bee and hoverfly species corroborates evidence for such a mitigation function of high-quality foraging habitats that have been found to reduce levels of viruses or microsporidia in four bee species in the United States<sup>39,43</sup> and to decrease virus prevalence in pollinators on farms participating in agri-environment schemes in

the United Kingdom<sup>29</sup>. Thus, pollinator-friendly habitat can reduce pathogen transmission and loads in wild pollinators via direct benefits through enhanced foraging, nesting and overwintering opportunities, and indirect benefits through reduced resource competition, in particular with honeybees<sup>30</sup>. However, such hotspots of high-quality foraging habitats attract at the same time a high abundance and diversity of pollinators. This can lead to increased pathogen transmission of density-dependent pathogens, such as BQCV and DWV-B (here) and for slow bee paralysis virus, microsporidia and acute bee paralysis virus<sup>29,31,44</sup>. This finding suggests that such high-quality foraging habitats may also trigger processes that counter those of a pathogen dilution effect, potentially confounding the beneficial effects of the latter on wild pollinator health. In fact, our findings imply that there is a potentially complex trade-off between the direct and indirect benefits of diverse floral resources enhancing pollinator nutrition and diluting pathogen transmission risks on the one hand and density-dependent elevation of pathogen transmission on the other hand.

In conclusion, by combining species traits, species interactions and landscape level factors, our study identifies several key drivers of viral prevalence and loads and potential transmission pathways of viral pathogens in pollinator communities. Our results highlight the

important role of floral resource overlap with honeybees, identified as a reservoir host<sup>9</sup>, as a primary driver of viral prevalence and loads in wild pollinators. Our findings also provide insights into how virus transmission and viral loads are mediated by foraging traits and roles of pollinator species in interaction networks, floral trait composition and the amount of pollinator-friendly habitat at the landscape scale. However, the direction of transmission and the extent to which detected viral loads affect health, fitness and population dynamics of wild pollinators in the field remains an important research gap<sup>14</sup> but see ref. 45; our results therefore serve to inform future hypothesis testing.

To follow the precautionary principle and reduce virus transmission among pollinators, our results highlight how conservation and restoration of flower-diverse pollinator-friendly habitat in a landscape may not only contribute to pollinator conservation through the provision of vital resources and a reduction in floral resource competition but also help to mitigate transmission of key viruses. Such habitats should be diverse in flowering plant species and not exclusively contain plant species that are highly visited by honeybees. Further, our study highlights the important role of high viral loads in managed honeybees as a driver of virus transmission to wild pollinators. It underpins the view that it is vital to increase efforts to implement best management practices to control *Varroa* mites in honeybee colonies as a key measure to reduce viral loads of honeybees, to minimize virus transmission to wild pollinators. In light of concerns about ongoing pollinator declines, our findings thus provide strong support for measures that promote pollinator-friendly habitats to maintain diverse and healthy pollinator communities and to secure the pollination functions and services they provide.

## Methods

### Study design

We selected 12 landscapes in the lowland of northern Switzerland ( $n = 12$ , 1 km radius, separated by  $>3$  km; Extended Data Fig. 1). This accounts for the typical foraging ranges of most of the studied pollinator groups being considerably less than 3 km (refs. 46,47), although honeybees can forage further if foraging resources dictate it but see refs. 46,48. The region is characterized by agricultural landscapes, seminatural habitats and settlements. The study landscapes thus varied from landscapes dominated by mixed production agriculture to landscapes dominated by settlements (many areas with one-family homes with gardens and other green space), with lower or higher amounts of seminatural habitat (forest, hedgerows and extensively managed grasslands). We classified each major land-use type as either a potential pollinator-friendly habitat or not based on previous studies in the study region that assessed the value of different land-use types to sustain bee and hoverfly pollinators<sup>49–54</sup>. Accordingly, grasslands (that is, extensively managed meadows and pastures; including traditional orchards and vineyards largely composed of extensively managed permanent grassland vegetation), sown flower strips, hedgerows and urban green spaces (urban area with  $>25\%$  green space, that is, houses with gardens, parks, green roadsides) were classified (ArcGIS Pro v.10.7, ESRI) as pollinator-friendly habitats. Arable crops, intensively managed grasslands, forests, urban space with  $<25\%$  green space area and water bodies were classified as not pollinator-friendly habitats. Although arable crops and forests can provide floral resources for pollinators, their overall importance for pollinators in the study region was found to be inferior in the studies cited above and their floral resource provision mainly concentrates on early in the season<sup>25</sup>, a period finally excluded from our analyses due to low numbers of species with minimum sample size for virus screening (see section on ‘Pollinator sample selection criteria and viral targets’). Consequently, we did not categorize them as pollinator-friendly in the present study. On the basis of raster maps (pixel size:  $2 \times 2$  m<sup>2</sup>), we calculated the percentage of pollinator-friendly habitat in a 500 m radius around the centre of each landscape using the R package *landscapemetrics*<sup>55</sup>.

The resulting gradient in pollinator-friendly habitat ranged from 2.6% to 74.1% (Supplementary Table 11).

### Sampling of plant–pollinator networks and flower surveys

Within each landscape, plant–pollinator visitation networks were sampled along different transect sections in habitats providing flowers at the time of the transect walks (for example, grasslands, forest edges, hedgerows, flowering crops, field edges and gardens) summing up to a total length of 1 km (2 m wide) per landscape in each sampling round (three rounds in total, April, May/June and July 2020). The transect section length per flowering habitat type was proportional to the cover of that specific flowering habitat type within the core sector (500 m radius) of a landscape<sup>52</sup>. Non-flowering habitats such as conifer plantations or cereal fields that were unlikely to contribute to flower–pollinator interactions in a landscape were not sampled. All flower-visiting bees (Hymenoptera: Anthophila), including the western honeybee, *A. mellifera* L. and hoverflies (Diptera: Syrphidae) were sampled as they are the most common pollinators in the study region<sup>4</sup>. The specimens were collected with a tube or a self-made ‘net’ consisting of a plastic bag fixed on a stick. After each catch, a fresh plastic bag was fixed on the stick to avoid contamination among specimens. Additionally, the species identity of all visited plants were recorded using the key ‘Flora Helvetica Exkursionsflora’<sup>56</sup> to allow construction of plant–pollinator interaction networks. Transect walks were standardized (3 min per 25 m, pausing the clock for catching and processing pollinator specimens) and conducted between 09:00 and 18:00 during dry and warm weather ( $>14$  °C). After each transect walk, we walked back the same transect at a steady pace to obtain an additional independent measure of honeybee densities by counting (without catching) each foraging or flying honeybee encountered within the transect. Immediately after sampling, all insects were placed on dry ice in the field and then at  $-80$  °C in the laboratory. All wild bee and hoverfly samples were assigned to species by barcoding the cytochrome oxidase subunit I gene region<sup>57</sup> by the company Microsynth Ecogenics GmbH. Barcoding is an objective and highly accurate method to identify species<sup>58</sup>. There are only a few cryptic species complexes that cannot be unequivocally identified using barcodes<sup>58,59</sup>, with only one present in our samples (*Halictus simplex* and *H. eurygnathus*). Abundance of wild pollinators was calculated as the number of flower-visiting wild pollinator individuals caught during the transect walks per landscape and sampling round, while wild pollinator richness was calculated as the number of different species caught per landscape and sampling round.

To obtain measures of flower abundance and flowering plant species richness independent of visitation (plant–pollinator network) data, flower abundance and richness were quantified in ten plots ( $2 \times 0.5$  m<sup>2</sup>) per 100 m along the transects (between one and three plots per 100 m for flowering crop monocultures) by a trained botanist, using the key ‘Flora Helvetica Exkursionsflora’<sup>56</sup>. The plots were either placed horizontally for herbaceous flowering vegetation or vertically along woody vegetation of hedgerows and forest edges. We estimated flower abundance as the number of single flowers (or inflorescences in the case of Asteraceae, *K. arvensis* and *Plantago* spp.) multiplied by their size (calculated as circle area as a proxy of floral resource availability, following ref. 25) for each flowering plant species. For flower/inflorescence size trait information see section on ‘Plant–pollinator network metrics and species traits’. The total number of flowering plant species per landscape and their flower abundance in each sampling round was used to calculate flower Shannon diversity.

### Virus quantification

**Pollinator sample selection criteria and viral targets.** Wild bee and hoverfly pollinator species were considered with  $n \geq 7$  samples (insect specimens per species) in a particular landscape and sampling round. A maximum of  $n = 10$  samples per wild pollinator species and ten individual honeybees (*A. mellifera*) were screened per landscape



and sampling round—a sample size used previously<sup>60</sup>. Further, this approach meant that we covered the most abundant species most likely to affect the plant–pollinator network structure in the respective landscapes. Samples ( $n = 986$ , 20 species (*A. mellifera*, 16 wild bee species and three hoverfly species); Supplementary Table 2) were screened for three viruses which are common in *A. mellifera*: DWV-A, DWV-B and BQCV<sup>7</sup>, all associated with the presence of and probably transmitted to *A. mellifera* by ectoparasitic mites *Varroa destructor*<sup>61</sup>. Owing to low numbers of species with minimum sample size for virus screening in the first sampling round (April) (Supplementary Table 2), data from this sampling round were not considered for statistical analyses. Further, due to very low titres of DWV-A, we refrained from data analyses of this virus (Supplementary Table 1 and Extended Data Fig. 2). Since the samples from April had to be dropped ( $n = 120$  honeybees,  $n = 38$  wild pollinator samples), this resulted in  $n = 588$  samples of 15 wild bee and two hoverfly species and 240 samples of honeybees which were used for statistical data analysis.

**RNA extraction and reverse transcription.** The pollinators were not surface sterilized before extraction because our main objective was to better understand possible virus transmission pathways rather than to detect and understand patterns of virus infections (we therefore did not test for replicating virus). This should be considered accordingly when interpreting results. Before RNA extraction, samples were randomized to avoid introducing any undesired bias (regarding species or collection site) during the sample preparation for viral quantification (RNA extraction, reverse transcription and PCR). Individual samples were crushed in PBS buffer (0.5 mg of tissue per  $\mu\text{l}$ ) with a 5 mm glass bead in 2 ml Eppendorf tubes using a Retsch MM 300 mixer mill for 1 min at the frequency  $25\text{ s}^{-1}$  (ref. 37). Then, RNA was extracted from 50  $\mu\text{l}$  (25 mg of tissue) of this homogenate using a NucleoSpin RNA II kit (Macherey-Nagel) following the manufacturer's recommendations. RNA was eluted in 60  $\mu\text{l}$  of elution buffer and stored at  $-80\text{ }^{\circ}\text{C}$  (ref. 37).

The RNA was reverse transcribed using a M-MLV RT Kit (Promega) following the manufacturer's recommendations. Briefly, 0.75  $\mu\text{l}$  of a random hexamer oligonucleotide (100  $\mu\text{M}$ ) and water were incubated for 5 min at  $70\text{ }^{\circ}\text{C}$  with 0.5  $\mu\text{g}$  of template RNA using a thermocycler (Biometra). Then, for a 25  $\mu\text{l}$  volume reaction, 5  $\mu\text{l}$  of  $5\times$  buffer, 1.125  $\mu\text{l}$  of dNTPs (10 mM) and 1  $\mu\text{l}$  of reverse transcriptase (M-MLV) were added and incubated at  $37\text{ }^{\circ}\text{C}$  for 60 min to synthesize complementary DNA.

**Quantitative PCR.** Absolute quantification of viral loads was performed by quantitative PCR (qPCR). Reactions were prepared with 6  $\mu\text{l}$  of  $2\times$  reaction buffer (SensiFAST SYBR No-ROX Kit, Meridian Bioscience), 0.24  $\mu\text{l}$  of forward and reverse primer (Supplementary Table 12), 2.52  $\mu\text{l}$  of water and 3  $\mu\text{l}$  of tenfold diluted cDNA. Then qPCR reactions were performed in a CFX96TM Real-Time PCR Detection Systems (Bio-Rad) with the following conditions: 3 min for  $95\text{ }^{\circ}\text{C}$ , 40 cycles of 3 s at  $95\text{ }^{\circ}\text{C}$  and 30 s at  $57\text{ }^{\circ}\text{C}$ . After amplification, we analysed the melting curve profile of all PCRs (strand dissociation) to verify product specificity (a single product with the correct dissociation temperature) by reading the fluorescence at  $0.5\text{ }^{\circ}\text{C}$  increments from 55 to  $95\text{ }^{\circ}\text{C}$ . Each sample was run in duplicate for each of the targeted viruses. A third technical run was included for samples that differed by more than one cycle. Amplification of the host insect's 28S ribosomal RNA gene using primer sequences conserved across suborder Apocrita<sup>62</sup>, which has been shown to perform well also for hoverflies<sup>63</sup>, was used as reference gene to assess the quality of the process (RNA extraction, cDNA synthesis and qPCR). Furthermore, each plate was run with seven tenfold serial dilutions ( $10^{-2}$  to  $10^{-8}$  ng) of synthetic strands (standard curve; Supplementary Table 13) which served as positive controls for the viral sequence target, plus two no-template negative controls<sup>64</sup>. For quantification, qPCR efficiencies ( $E$ ) were calculated on the basis of the slope of the standard curve, according to the following formula:  $E = 10(-1/\text{slope})$  (DWV-A- $E = 1.93$ , slope =  $-3.479$ , y intercept =  $38.907$ ,  $R^2 = 0.990$ ;

DWV-B- $E = 1.97$ , slope =  $-3.373$ , y intercept =  $39.187$ ,  $R^2 = 0.991$ ; BQCV- $E = 2.06$ , slope =  $-3.183$ , y intercept =  $38.195$ ,  $R^2 = 0.992$ ). Plates with no-template negative controls showing a signal matching the melting curve peak of the target viral gene were re-run. The quantification threshold (Cq) was set in the Bio-Rad CFX MAESTRO 1.0 software as auto calculated for all runs per target, assuring Cq was always set in the exponential phase of the amplification curve<sup>64</sup>. A qPCR quantification cycle (Cq) threshold of Cq < 35 was used to define a positive sample. This threshold is commonly accepted as it is interpreted that in general with an input of ten template copies in the reaction and a suitable PCR efficiency (between 1.8 and 2), a Cq value of  $\sim 35$  will be observed<sup>65</sup>. Moreover, melt curve analysis was also used to consider a sample positive or negative if their melting temperatures ( $T_m$ ) match or not those of their respective controls ( $81.5\text{--}82.5\text{ }^{\circ}\text{C}$   $T_m$  for DWV-A,  $79.0\text{--}80.0\text{ }^{\circ}\text{C}$   $T_m$  for DWV-B and  $82.5\text{--}83.0\text{ }^{\circ}\text{C}$   $T_m$  for BQCV). To calculate 95% confidence intervals (Clopper–Pearson interval) around the apparent virus prevalence in each species (per site and sampling round), we used the function propCI from the R package prevalence<sup>66</sup>. Although sequencing of viral variants from different species and sites would be necessary to provide unequivocal support for cross-species viral sharing (for example, ref. 67), the limited geographic scale of our sampling in northern Switzerland is unlikely to provide sufficient resolution to separate sharing of variants across species versus across sites.

### Plant–pollinator network metrics and flower species traits

We analysed flower–insect visitor networks for each landscape and sampling round with plant and pollinator species as nodes and interaction frequencies as links. The networks were constructed with the entire plant–pollinator community that was sampled during transect walks. We refer to plant–pollinator networks for simplicity, while acknowledging that not every flower visit necessarily results in a pollination event<sup>68</sup>. To test whether floral niche overlap with managed honeybees (hypothesis 1) influences virus prevalence and loads of wild pollinators, we calculated the CWM number of honeybee visits to flowering plant species visited by a given wild pollinator species. This metric of floral resource overlap correlated strongly positively with the potential for apparent competition (PAC) metric (Spearman's rank correlation  $\rho = 0.82$ ) often used to quantify resource overlap<sup>69</sup> but is simpler to interpret compared to PAC. To assess how pollinator species specialization determines viral loads (hypothesis 2), we calculated specialization  $d'$  based on observed floral resource use of a pollinator species in each network for those pollinator species that were screened for viruses. Specialization  $d'$  accounts for the presence and abundance of partner species available in an interaction network and denotes the degree of diet specialization of each species (0, no specialization; 1, perfect specialist)<sup>70</sup>. To assess how viral loads related to centrality of a pollinator species in a network (hypothesis 3), we calculated weighted betweenness of each screened pollinator species. It measures the proportion of shortest paths that pass through a focal species, indicating how central and closely connected a species is to other pollinators in the network. All network analyses were performed using R package bipartite<sup>71</sup>.

To assess the role of traits of flowering plants in the network hypothesized to affect pathogen transmission (flower morphology characterized through flower type and corolla length and flower volume as proxy for nectar rewards<sup>24</sup>), we linked information from the plant–pollinator networks with published information about traits of visited flowers. For hypothesis 4, we obtained data on flower (inflorescence) type from ref. 72 classified after ref. 73 as either dish-bowl type (for example, Asteraceae and Rosaceae), flag (for example, Fabaceae), gullet (for example, Lamiaceae), brush (for example, *Cirsium* and *Plantago*), bell-trumpet (for example, Campanulaceae), tube (for example, *Symphytum officinale*) or stalk-disk (for example, *Primula acaulis* and *Dianthus carthusianorum*), corolla length (mm) and average flower volume ( $\text{cm}^3$ , approximated as cylinder volume with height = corolla

length, radius =  $0.5 \times$  flower diameter)<sup>25</sup>. Flower diameter and corolla length were retrieved from a floral trait database including most plant species from the study region (D. Frey, L. Amman, M. A. & M. Moretti, manuscript in preparation) and from InfoFlora (<https://www.infoflora.ch/>), PlantNET (<https://plantnet.rbg.gov.au/>) and Naturegate (<https://luontoportti.com/>). Flower volume was calculated for individual flowers, except for Asteraceae, *K. arvensis* and *Plantago* spp., for which the volume of inflorescences (for example, entire flower heads) was calculated. We then calculated the CWM of each trait for all flowers visited by a pollinator species using R package FD<sup>74</sup>.

## Statistical analyses

**Floral species' traits and pollinator network roles.** To investigate how floral species' traits and pollinator roles in the plant–pollinator network drive viral prevalence and loads in wild pollinators (hypotheses 1–4), we used generalized linear mixed effects models (GLMMs, binomial error distribution) with viral prevalence (presence or absence of BQCV or DWV-B) in wild pollinators as response variable and linear mixed effects models (LMM, Gaussian error distribution) with viral load (log BQCV or log DWV-B) of each wild pollinator individual (considering only virus-positive individuals) as the response variable. Floral resource overlap of wild pollinators with honeybees, wild pollinator specialization  $d'$ , weighted betweenness of a wild pollinator, mean flower volume of visited flowers (CWM), mean corolla length of visited flowers (CWM) and the proportion of visited plant species with dish-bowl flowers were fitted as explanatory variables in the full models, with landscape ID and species ID as random factors. Exploratory analyses revealed no interaction between predictors and sampling round, which therefore was not included as a candidate interaction term in the full model. However, we accounted for the influence of sampling round by including it as a fixed factor in all models.

To visualize groups of pollinators visiting plants with similar floral traits, we used NMDS based on Bray–Curtis dissimilarity of the entire interaction matrix (pooled across landscapes and sampling rounds) using the R package *vegan*<sup>75</sup>. In this matrix, the rows represented the pollinator species, the columns represented the trait of the visited plants (flower volume, corolla length and inflorescence type) and the values were the CWMs of the respective trait. We then classified the pollinator species into three groups according to the lower, intermediate and upper third of the mean virus load (number of genome copies per  $\mu\text{g}$  RNA per individual sample) distribution (<33%, >33%, <66% and >66% quantiles; BQCV—<44,000; >44,000 < 900,000; >900,000 genome copies; DWV-B—<1,600; >1,600 < 10,000; >10,000 genome copies) and applied a permutation test to evaluate whether these groups of distinct levels of virus loads are associated with floral trait dependent visitation by pollinators. Since these virus-load groups significantly explained the differences in flower visitation, we performed a similarity percentage (SIMPER)<sup>33</sup> analysis in R package *vegan*<sup>73</sup> to evaluate which traits of visited flowers contributed most to these differences.

**Landscape and pollinator community properties.** To test how the explanatory variables landscape composition (proportion of pollinator-friendly habitat), flowering plant community composition (Shannon diversity of flowers at the landscape scale) and pollinator community composition (honeybee density and viral prevalence or loads in honeybees, species richness and abundance of wild pollinators at the landscape scale) affected the response variables viral prevalence or loads (log-transformed, virus-positive individuals only) of the wild pollinator community (hypotheses 5–8), we fitted GLMMs (binomial error distribution) and LMMs, respectively. We included sampling round as covariate and landscape ID and species ID as random factors. Viral loads in honeybees were calculated as the median number of viral copies (log-transformed) of the ten screened honeybees per landscape in a given sampling round, while viral prevalence in honeybees was the proportion of honeybees with viral load >0 per landscape in a given

sampling round. Because wild pollinator abundance and species richness were strongly positively correlated (Spearman's rank correlation  $\rho = 0.7$ ), we only used wild pollinator abundance in the full models due to its higher predictive power and goodness of model fit (lower AICc in univariate models).

Finally, we tested whether floral resource overlap between wild pollinators and honeybees (calculated as described above) was related to the proportion of pollinator-friendly habitat in a landscape (hypothesis 8). Owing to heteroscedasticity in the residuals of the model, we used an LMM with a 'power of the covariate' variance structure (varPower) to ensure correct estimation of regression parameters and standard errors<sup>76</sup>, with resource overlap as the response variable, proportion of pollinator-friendly habitat as the explanatory variable and landscape ID as a random factor using the R package *nlme*<sup>77</sup>.

Assessing correlation among explanatory variables in all full models using variance inflation factors (VIF)<sup>78</sup> in R package *performance*<sup>79</sup> showed low multicollinearity (VIF < 2.5). For all analyses, the set of best models was selected on the basis of the Akaike information criterion corrected for small sample size (AICc) using the R package *MuMIn*<sup>80</sup>. We considered all models with  $\Delta\text{AICc} < 2$  (that is, the difference of the AICc of the focal model to the best model < 2) and used model averaging (conditional average) to extract the final model coefficients<sup>81</sup>. To visualize the major effects (of the terms whose confidence intervals do not overlap with zero), we used a Bayesian framework to calculate averaged model predictions by drawing samples from the joint posterior distribution with the function *sim* of the R package *arm*<sup>82</sup>. Since we ran several models exploring species-specific as well as landscape and community level effects on viral load and prevalence, we did a false discovery rate (FDR) correction using the function *p.adjust* of R package *stats*<sup>83</sup>.

For all statistical analyses the software R v.4.2.1 (ref. 83) was used and models were fitted with the package *lme4* (ref. 84), except where stated differently. All continuous variables were scaled and centred to improve model convergence. Model assumptions were checked by inspection of residual plots using the R packages *DHARMa*<sup>85</sup> and *performance*<sup>79</sup>. The data used for all analyses of this study are openly available<sup>86</sup>.

## Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

## Data availability

The data is openly available via Figshare at <https://doi.org/10.6084/m9.figshare.25101977> (ref. 86).

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### Author contributions

A.J.V., O.S., H.S., R.J.P., P.N., A.G., O.Y. and M.A. conceived the study and developed the sampling and laboratory methodological protocols. C.M. collected the data. A.S., O.Y. and C.M. carried out the molecular analyses and performed the laboratory work. C.M., M.A. and L.P. conceived the data analyses. C.M. and M.A. analysed the data. C.M. led the writing of the manuscript. All authors contributed to the writing and gave final approval for publication.

### Competing interests

The authors declare no competing interests.

### Additional information

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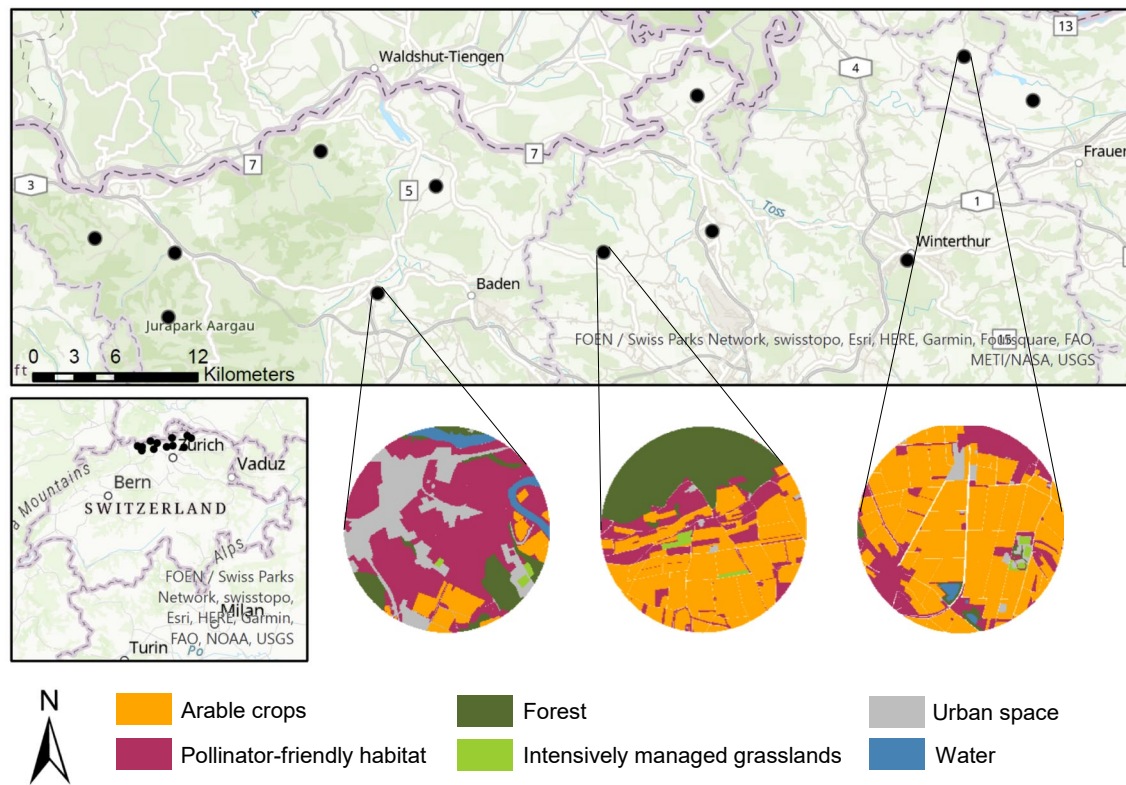
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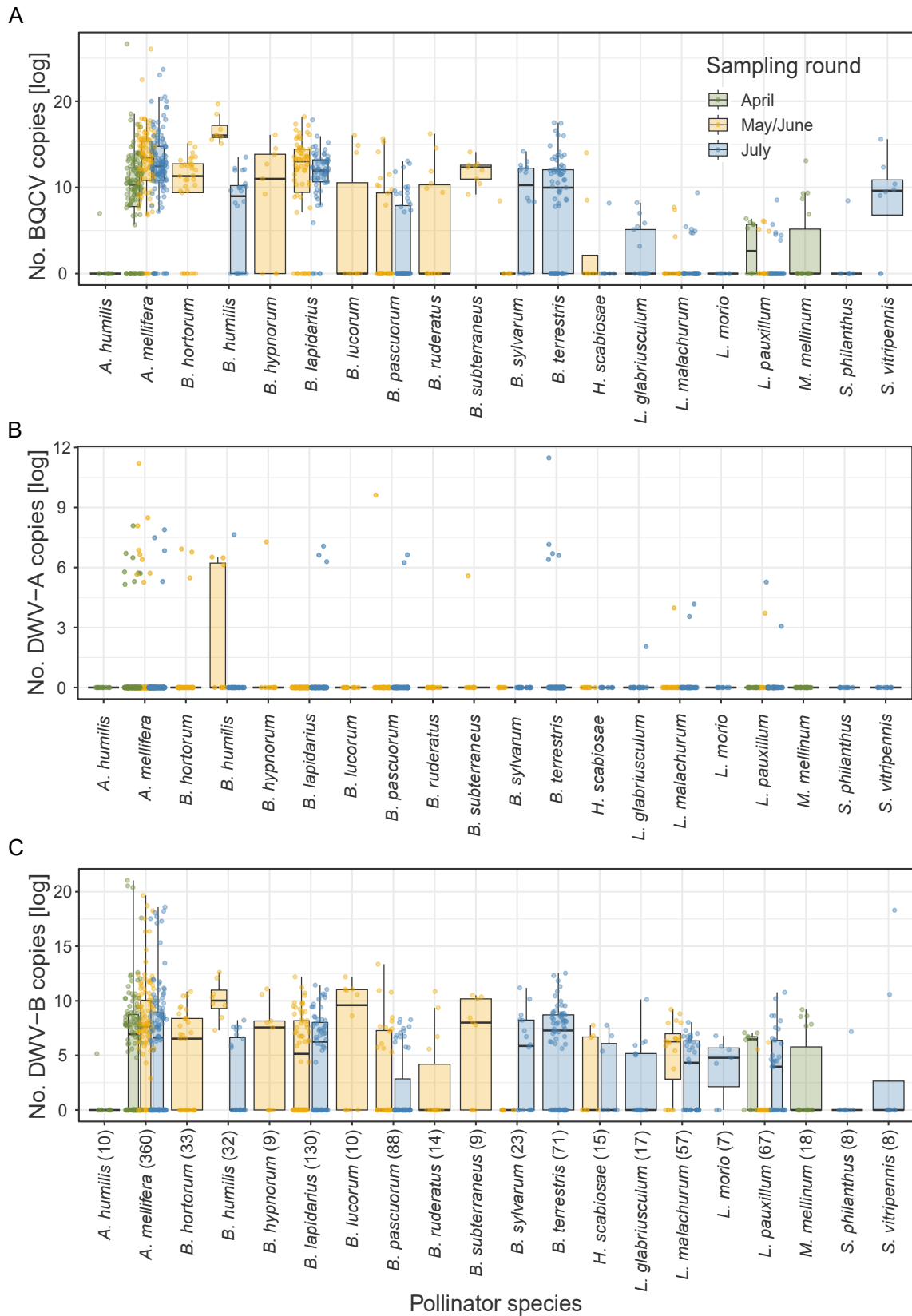
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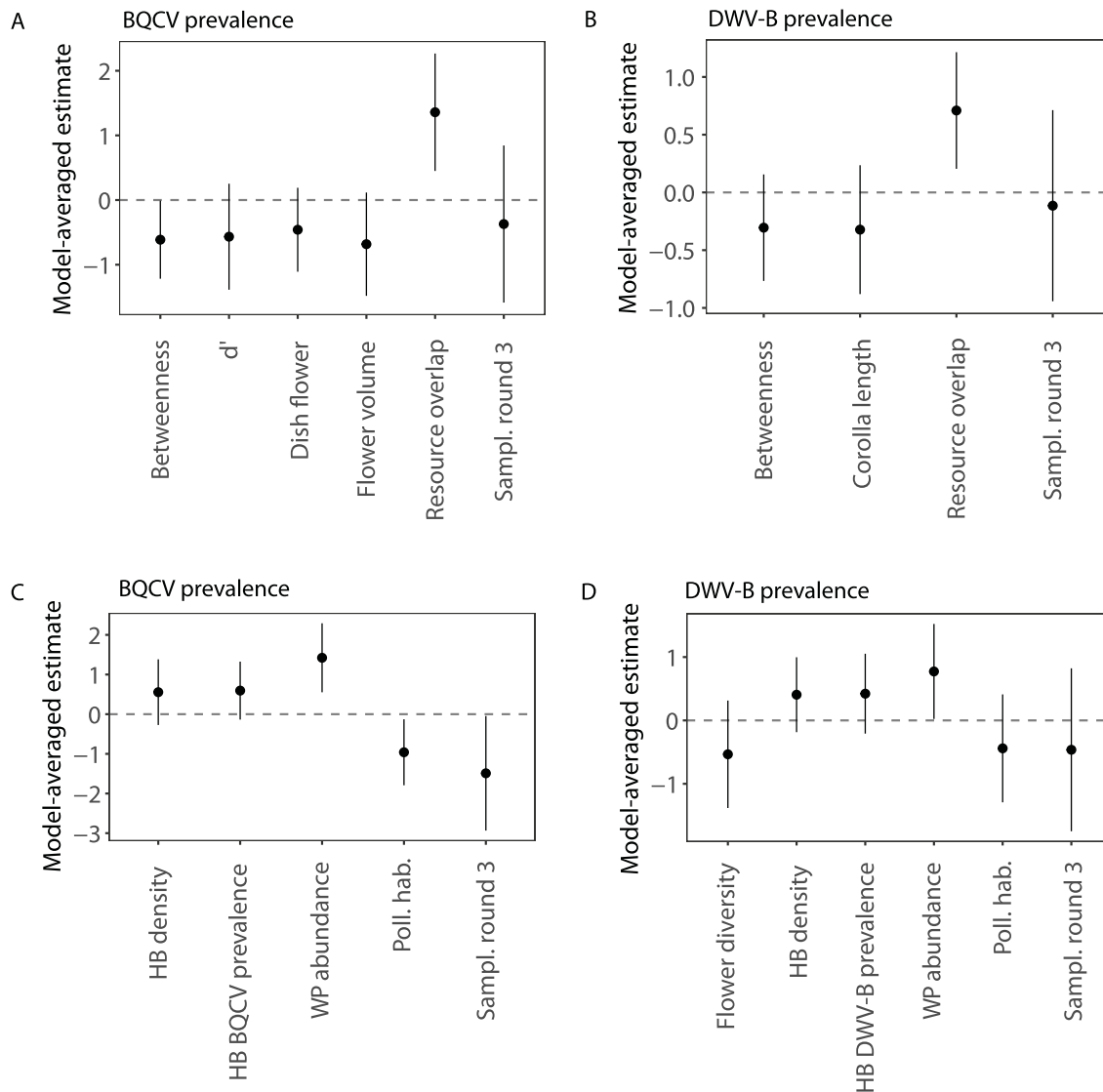
**Extended Data Fig. 1 | Map of the study landscapes.** The maps are showing the study landscapes located in the northern lowlands of Switzerland (orange = intensive agricultural landscape; green = rural habitat mosaic landscapes; grey = urban landscapes). Raster maps (1 km radius) show the land cover classes for three example landscapes (orange = arable crops; pink = pollinator-friendly

habitat; dark green = forest; light green = intensively managed grasslands; grey = urban space (< 25% green areas); blue = water bodies). Maps created using ArcGIS Pro software by Esri. ArcGIS Pro is the intellectual property of Esri and is used herein under licence. Copyright © Esri. All rights reserved. Additional credits for the map are listed in ref. 87.



**Extended Data Fig. 2 | Overview of virus loads in pollinators.** Displayed are boxplots of BQCV (A), DWV-A (B) and DWV-B (C) virus loads (log-transformed number of genome copies per individual) of all screened individuals per species in each landscape and sampling round. Wild bee and hoverfly species were screened when they were sampled with at least N = 7 individuals per landscape and sampling round (maximum N = 10 individuals per landscape and sampling

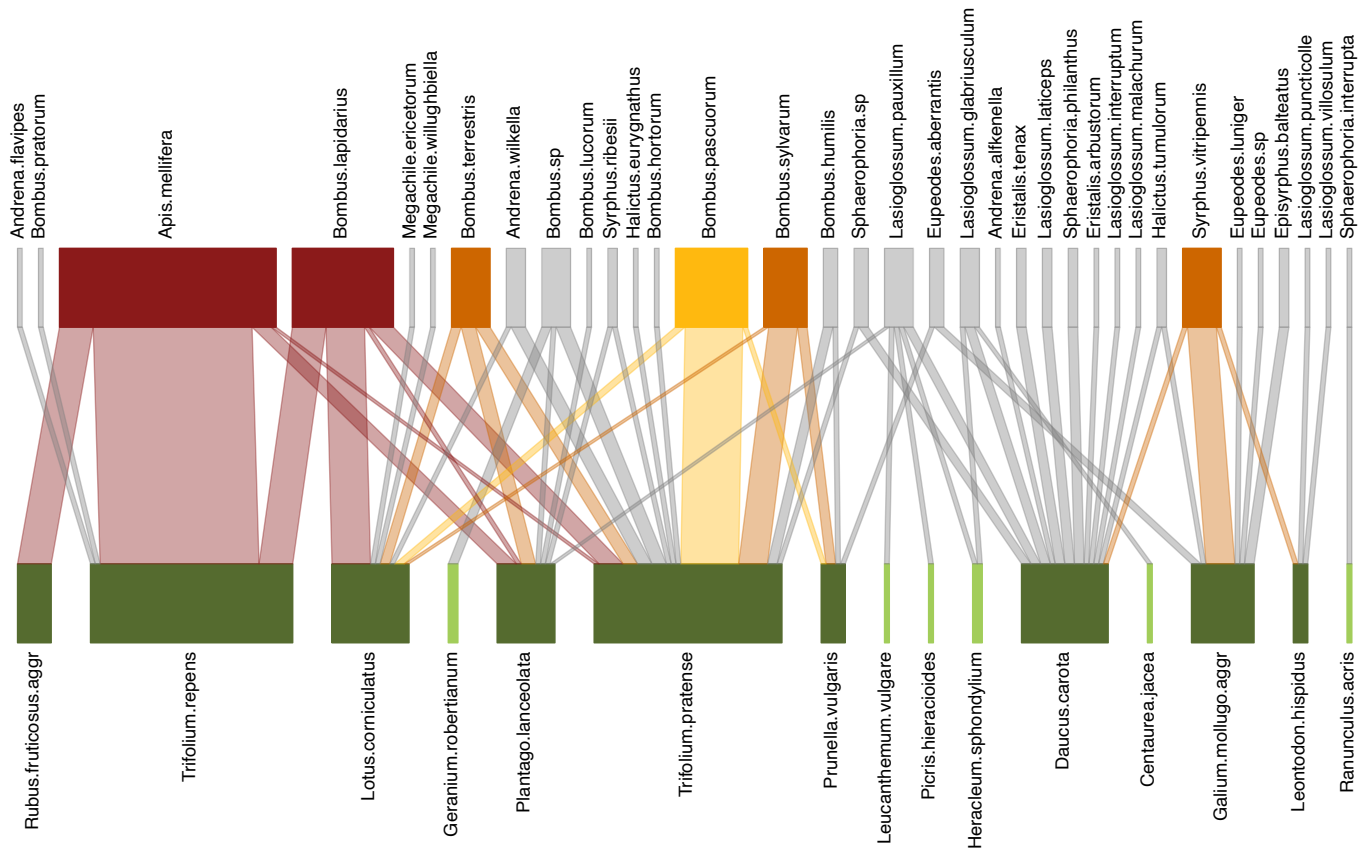
round). Boxplots show the median, the box representing the first and the third quartile, and the whiskers extend from the hinge to the largest and lowest values, respectively, no further than 1.5 times the interquartile range from the hinge. Points show raw log-transformed data. Colours represent the different sampling rounds. (Green = April, yellow = May/June, blue = July; BQCV = Black Queen Cell Virus; DWV = Deformed Wing Virus; see Table S1 for full species names).



**Extended Data Fig. 3 | Best ranking models predicting viral prevalence in wild pollinators.** Averaged model estimates (that is the modelled slopes of the relationships) and 95% confidence intervals of explanatory variables in best models ( $\Delta AIC_c < 2$ ) explaining viral prevalence of BQCV (**A, C**) and DWV-B (**B, D**) in wild pollinators ( $n = 588$  individuals). (**A, B**) display the results from modelling the effects of species traits and roles in the network (weighted betweenness

(Betweenness), corolla length, specialisation  $d'$ , proportion of dish-bowl flowers among visited flowers (Dish flowers) and floral resource overlap with honeybees (Resource overlap)). (**C, D**) display the results from modelling the effects of landscape and pollinator community properties (Shannon diversity of flowers (H flowers), honeybee density (HB density), wild pollinator abundance (Poll. abundance) and percentage cover of pollinator habitat (Poll. hab. %)).

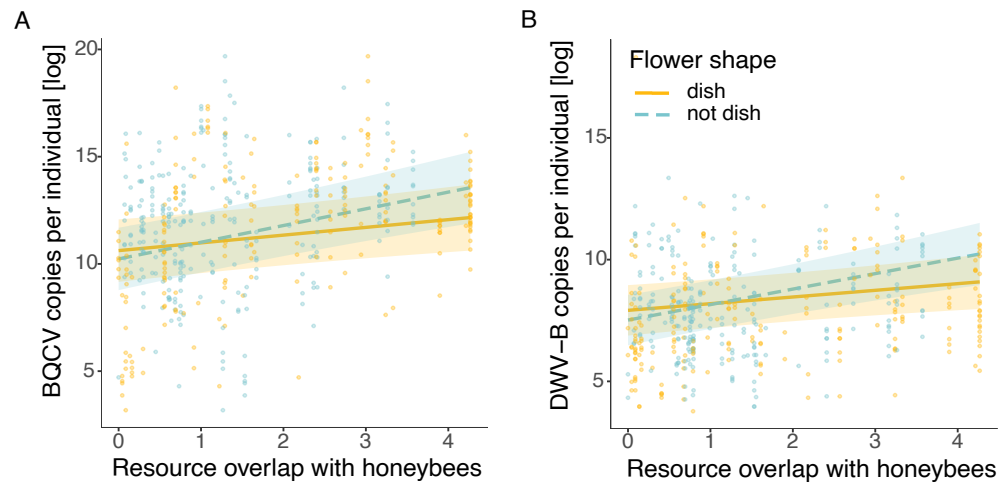




- 0–400 BQCV copies
- 400–10'000 BQCV copies
- >10'000 BQCV copies
- not screened pollinators
- plants visited by contaminated pollinators
- plants not visited by contaminated pollinators

**Extended Data Fig. 4 | Example plant-pollinator network** of a landscape with 56% cover of pollinator-friendly habitat in July. Nodes and links are weighted by the abundance of the species and number of observed interactions, respectively. The colours of the pollinator species and links indicate their mean viral load (log-transformed) of black queen cell virus

(BQCV copies; yellow = 0-400 BQCV copies; orange = 400-10000 BQCV copies; red = >10000 BQCV copies, grey = these species were not screened). Plant species coloured in dark green were visited by a pollinator carrying BQCV, while plant species coloured in light green were not visited by a pollinator carrying BQCV or a pollinator that was not screened for viruses.



**Extended Data Fig. 5 | Floral resource overlap on dish-bowl vs. non-dish-bowl flowers.** Model predictions and 95% confidence intervals of models (LMMs with landscape ID and species ID as random factors) testing the interactive effect of resource overlap between wild pollinators and honeybees on dish-bowl shaped

flowers vs. on non-dish-bowl shaped flowers on virus load (**A**: BQCV or **B**: DWV-B). Orange solid line = dish-bowl flowers; blue dashed line = non-dish flowers. BQCV = black queen cell virus; DWV = deformed wing virus. Points show raw data.

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The raw plant-pollinator interaction data, flowering plant survey and landscape data as used in the study as well as the raw virus (deformed wing virus A and B and black queen virus) load data are available on Figshare <https://doi.org/10.6084/m9.figshare.25101977>.

## Research involving human participants, their data, or biological material

Policy information about studies with [human participants or human data](#). See also policy information about [sex, gender \(identity/presentation\), and sexual orientation](#) and [race, ethnicity and racism](#).

### Reporting on sex and gender

Use the terms *sex* (biological attribute) and *gender* (shaped by social and cultural circumstances) carefully in order to avoid confusing both terms. Indicate if findings apply to only one sex or gender; describe whether sex and gender were considered in study design; whether sex and/or gender was determined based on self-reporting or assigned and methods used. Provide in the source data disaggregated sex and gender data, where this information has been collected, and if consent has been obtained for sharing of individual-level data; provide overall numbers in this Reporting Summary. Please state if this information has not been collected. Report sex- and gender-based analyses where performed, justify reasons for lack of sex- and gender-based analysis.

### Reporting on race, ethnicity, or other socially relevant groupings

Please specify the socially constructed or socially relevant categorization variable(s) used in your manuscript and explain why they were used. Please note that such variables should not be used as proxies for other socially constructed/relevant variables (for example, race or ethnicity should not be used as a proxy for socioeconomic status). Provide clear definitions of the relevant terms used, how they were provided (by the participants/respondents, the researchers, or third parties), and the method(s) used to classify people into the different categories (e.g. self-report, census or administrative data, social media data, etc.) Please provide details about how you controlled for confounding variables in your analyses.

### Population characteristics

Describe the covariate-relevant population characteristics of the human research participants (e.g. age, genotypic information, past and current diagnosis and treatment categories). If you filled out the behavioural & social sciences study design questions and have nothing to add here, write "See above."

### Recruitment

Describe how participants were recruited. Outline any potential self-selection bias or other biases that may be present and how these are likely to impact results.

### Ethics oversight

Identify the organization(s) that approved the study protocol.

Note that full information on the approval of the study protocol must also be provided in the manuscript.

## Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

Life sciences  Behavioural & social sciences  Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see [nature.com/documents/nr-reporting-summary-flat.pdf](https://www.nature.com/documents/nr-reporting-summary-flat.pdf)

## Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

### Study description

We selected 12 landscapes (1 km radius, separated by > 3 km) in the lowland of northern Switzerland. The study landscapes varied from landscapes dominated by mixed production agriculture to landscapes dominated by settlements, with lower or higher amounts of semi-natural habitat.

### Research sample

We sampled flower-visiting bees (Hymenoptera: Anthophila) and hoverflies (Diptera: Syrphidae), since these groups are the most common pollinators in the study region (IPBES 2016).

### Sampling strategy

Within each landscape, plant-pollinator interactions were sampled along different transect sections in habitats providing flowers at the time of the transect walks (e.g. grasslands, forest edges, hedgerows, flowering crops, field edges, gardens) summing up to a total length of 1 km (2 m wide) per landscape in each sampling round (3 sampling rounds in total). The transect section length per flowering habitat type was proportional to the cover of that specific flowering habitat type within the core sector (500 m radius) of the landscape. Transect walks were standardised (3 min per 25 m, pausing the clock for catching and processing pollinator specimens) and conducted between 9 am and 6 pm during dry and warm weather (>14°C). By choosing this high sampling effort (1 km transect length and 2 h sampling time per landscape), we assured to obtain a sufficient sample size.

### Data collection

The (flower-visiting) specimen were collected with a tube or a self-made "net" consisting of a plastic bag fixed on a stick. After each catch, a fresh plastic bag was fixed on the stick to avoid contamination among specimen. Immediately after sampling, all insects were placed on dry ice in the field and then at -80°C in the laboratory. Field data was collected by the first author. All wild bee and hoverfly samples were assigned to species by barcoding the cytochrome oxidase subunit I gene region (Hebert et al., 2003) by the company Microsynth Ecogenics GmbH (Balgach, Switzerland).

### Timing and spatial scale

Plant-pollinator interactions were sampled in a total of three sampling rounds (1st: 8.4.-8.5.2020; 2nd: 18.5.-13.6.2020; 3rd: 29.6.-22.7.2020). The specimen were collected along transects located within the inner 500 m radius of the study landscapes (see description above).

### Data exclusions

For the virus quantification, we considered wild bee and hoverfly species with  $n \geq 7$  samples in a particular landscape and sampling

Data exclusions	round and a maximum of $n = 10$ , as well as 10 individual honeybees ( <i>Apis mellifera</i> ) per landscape and sampling round. Samples ( $n = 986$ , 20 species ( <i>Apis mellifera</i> , 16 wild bee species and three hoverfly species) were screened for three viruses which are common on <i>A. mellifera</i> : Deformed wing virus A (DWV-A), Deformed wing virus B (DWV-B) and Black queen cell virus (BQCV). Due to low numbers of species with minimum sample size for virus screening in the first sampling round (April), data from this sampling round were not considered for statistical analyses. Further, due to very low titres of DWV-A, we refrained from data analyses of this virus (Table S1, Extended Data Fig. 1). This resulted in $n = 588$ samples of 15 wild bee and two hoverfly species and $n = 240$ samples of <i>A. mellifera</i> that were used for statistical data analysis.
Reproducibility	Since this is a field study, we did not repeat the experiment. However, we closely follow our pre-established protocols (field sampling and lab work) to ensure reproducibility.
Randomization	In each sampling round, we randomized the order by which we sampled the different landscapes. We also assured that we did not sample each time the same transect section in the morning or afternoon respectively. In the lab, we also randomized the samples so they were not ordered by landscape, sampling round or pollinator family/genus/species.
Blinding	Before starting with the lab work for virus quantification, we blinded the samples by assigning an "ID" (i.e. a number from 1 to 986) to each sample.
Did the study involve field work?	<input checked="" type="checkbox"/> Yes <input type="checkbox"/> No

## Field work, collection and transport

Field conditions	Pollinators were only sampled during dry and warm weather (temperatures above 14°C) and low wind.
Location	Landscapes were located in the lowlands of northern Switzerland (cantons Aargau, Zürich, Thurgau, approx. between 47°31'08.6"N 7°56'59.0"E and 47°35'47.8"N 8°51'13.9"E, approx. 350-550 m.a.s.l.)
Access & import/export	We ensured that we accessed/entered different habitats and arable fields (private land) with respect and carefully. (We obtained permits from local private land owners to access their land). We did not import or export any samples across country borders.
Disturbance	The disturbance to different habitats was held minimal, as we walked very slowly and carefully along our transects.

## Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

### Materials & experimental systems

n/a	Included in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> Antibodies
<input checked="" type="checkbox"/>	<input type="checkbox"/> Eukaryotic cell lines
<input checked="" type="checkbox"/>	<input type="checkbox"/> Palaeontology and archaeology
<input type="checkbox"/>	<input checked="" type="checkbox"/> Animals and other organisms
<input checked="" type="checkbox"/>	<input type="checkbox"/> Clinical data
<input checked="" type="checkbox"/>	<input type="checkbox"/> Dual use research of concern
<input checked="" type="checkbox"/>	<input type="checkbox"/> Plants

### Methods

n/a	Included in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> ChIP-seq
<input checked="" type="checkbox"/>	<input type="checkbox"/> Flow cytometry
<input checked="" type="checkbox"/>	<input type="checkbox"/> MRI-based neuroimaging

## Animals and other research organisms

Policy information about [studies involving animals](#); [ARRIVE guidelines](#) recommended for reporting animal research, and [Sex and Gender in Research](#)

Laboratory animals	The study did not involve laboratory animals.
Wild animals	We collected invertebrates (insects), flower-visiting bees (Hymenoptera: Anthophila) and hoverflies (Diptera: Syrphidae). Specimen were collected with a tube or a self-made "net" consisting of a plastic bag fixed on a stick. After each catch, a fresh plastic bag was fixed on the stick to avoid contamination among specimen. Immediately after sampling, all insects were placed on dry ice in the field and then at -80°C in the laboratory.
Reporting on sex	No information on sex of the bees and hoverflies was collected.
Field-collected samples	Field-collected samples were killed (as described above) and then analysed in the lab.

Ethics oversight

No ethical approval or guidance was required for collecting invertebrate species in our study area (i.e. no nature reserves).

Note that full information on the approval of the study protocol must also be provided in the manuscript.

## Plants

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Seed stocks

No plant specimen were collected from the field for this study.

Novel plant genotypes

n/a

Authentication

n/a