ORIGINAL RESEARCH ARTICLE

Bridging boundaries: Exploring vineyard, management and variety characteristics influencing long-term infection of grapevine pathogens

Ivett Kocsis[1], Marietta Petróczy[1] and Gábor Markó[1*]

[1] Hungarian University of Agriculture and Life Sciences, Institute of Plant Protection, Department of Plant Pathology, Ménesi út 44. Budapest, Hungary, H-1118

ABSTRACT

Globalisation, climatic changes, and increasing consumer demand have forced the intensification of agricultural production. Thus, vineyards have crossed the boundaries of the original production zones and extended towards suboptimal areas, increasing the potential risk of damaging disease outbreaks. Therefore, there is a rising need for a complex and empirical revision of the interfering effects between grape infection and other external, large-scale factors such as environmental conditions and management practices. Although external abiotic and biotic factors could determine the infection levels of grape disease in a complex way, existing studies focus on the short-term effects of only a single or very few potential factors. In this large-scale study, we aimed to reveal the long-term impact of specific factors regarding vineyard characteristics, applied crop management and grape variety features, which could determine the infection severity of primary grape diseases (grey mould, downy mildew and powdery mildew) using a citizen science approach in Hungary, a traditional wine- and grape-producing country. The present study has revealed that some vineyards (e.g., inclination, row orientation) and variety features (e.g., bunch structure) were considered crucial. At the same time, other factors were found to be less relevant in the present complex comparison, suggesting that the role of these factors might be overemphasised in the literature. In conclusion, the susceptibility or tolerance of grapevines to pathogens appears to be an integrated effect of several factors and cannot be assigned to a single characteristic. The global changes urge the revision of conventional agricultural traditions and deepen our knowledge about the infection process and pathogen-host-environment interactions.

KEYWORDS: *Botrytis cinerea*, citizen science, *Erysiphe necator*, fungi, grape cultivar, plant protection, *Plasmopara viticola*

INTRODUCTION

Agricultural systems and practices dynamically evolved throughout history in response to increasing demands for food production and environmental challenges. As a result, certain agricultural regions became more effective, producing top-quality crops in specific segments (e.g., Zabel *et al.*, 2019). The intensification of these crop-specific agricultural hotspots harnessed their excellent crop growth potential by the favourable climatic and edaphic conditions and improved the professional knowledge and technology as part of the cultural heritage. Moreover, production areas, reaching the highest quality product standards, could also benefit from the absence of pathogens or pests of the produced cultivars, which could be a significant source of crop loss in other areas. Therefore, these biotic, environmental and socio-economic factors interacted complexly, maintaining the privilege of a crop-production area (Savary *et al.*, 2012).

In the past decades, globalisation processes and global climatic changes have substantially modified conventional crop production practices, trends and developments in applied crop technology worldwide (Robinson, 2014). With the development of plant-growing technologies and the introduction of new crop species, the borders of previous growing areas have been significantly extended towards suboptimal areas for crop mass production, increasing the potential of the appearance of plant pathogens (Sirappa and Titahena, 2014) and abiotic stresses (Atkinson and Urwin, 2012). Moreover, global climatic changes have also had a significant impact on plant pathogens. Due to the environment-induced selection pressures, plant pathogenic agents gave an adaptive response compared to their previously described biology as part of the host-pathogen coevolution (Burdon and Thrall, 2009). Moreover, plants have a nutrient trade-off between their reproduction and chemical defence against their natural enemies. So, if a plant is constantly exposed to higher environmental or biotic stressors, the growth and reproduction outputs will be decreased, sharing the applied and limited nutrient sources (Herms and Mattson, 1992). Thus, suboptimal and non-traditional growing areas initiate higher biotic and abiotic stresses, leading to higher yield and quality losses due to plant protection problems. On the other hand, the specialisation of an agricultural sector in an area with optimal environmental conditions might be because the plant populations could acquire a better general physiological condition, causing higher crop yields and higher chemical defences against their pathogens, thus reducing the chance of the infection (Schoeneweiss, 1975).

Wine grape production is one of the most specialised and sophisticated production systems with an ancient history and traditions. However, it is beneficial to choose areas with optimal environmental factors for production; nowadays, vineyards have already crossed the boundaries of the original production zones and occur almost worldwide (Kok, 2014). Although the role of biological, environmental and cultivation factors in plant pathogen infestation has been extensively examined, existing studies focus on a few influential factors that need a more complex approach to the relationship between environmental and crop management issues, such as the incidence and severity of plant diseases. Revealing the complexity of the determinants of infection would be a huge step forward in developing pathogen-predicting models, and the accuracy and location specificity are crucial for more efficient pest control. Knowledge of the impact of planting features on diseases is essential in case of pathogens that are difficult to predict, such as the *Botrytis cinerea* Pers. (BC, hereafter), which causes an annual 2 billion USD economic loss in viticulture internationally (Elmer and Michailides, 2007), and also responsible for noble-rot, which is the basis of high-quality sweet wines such as '*Tokaji aszú*' (Fournier *et al.*, 2013). In addition, it is essential to know the impact of planting features on the most significant pathogens of viticulture, such as *Plasmopara viticola* (Berk and M.A. Curtis) Berl. and De Toni (PV, hereafter) and *Erysiphe necator* Schwein. (EN, hereafter), against which the vast majority of fungicide treatments are directed. Therefore, identifying the specific vineyard features can increase or decrease the long-term incidence of epidemic diseases, which could support the general pest management strategy.

There is a rising need for a complex and empirical revision of interaction effects on a broader spatial and temporal scale, including their practical applicability. Some features are determined for the whole duration of plant growth, while others can be changed flexibly. For instance, a farmer is powerless against unfavoured climatic conditions generally, which could influence the spreading of infection and planting conditions. However, locally, the development of growing areas can well serve the effectiveness of plant growth. The microclimate defining the disease outbreak can be effectively modified in the growing area by crop management (e.g., irrigation), even within a single vegetation.

The plantation circumstances and the agrotechnological procedures largely influenced the spread of grey mould, downy and powdery mildew diseases. Therefore, they are ideal models for studying the complex effects of plant-pathogen interactions, which could be indirectly shaped by the microclimatic environments within the vineyard. In the following, we briefly present the factors that can influence the success of grape production through the appearance of their most important pathogens.

A plantation's structure plays a crucial role in determining various plantation-specific features right from the beginning of production, which affects the long-term success of plant protection efforts. Plantation alignment establishes the quantity and duration of solar irradiation that affects the phenological sensitivity of the grape variety to grey mould (van Leeuwen *et al.*, 2018) through its ripening period (Deytieux-Belleau *et al.*, 2009). Similarly to BC, the UV-B radiation also harmed PV and EN by inhibiting the initial spore germination under daylight conditions (Rossi and Caffi, 2012; Willocquet *et al.*, 1998).

Proper crop management can alter environmental conditions in a narrow temporal frame, leading to disease. Different agrotechnical methods, such as using cover plants or mulch (Guerra and Steenwerth, 2012; Jacometti *et al*., 2007a) or leaf removal from the cluster zone (Evers *et al*., 2010; Romanazzi and Feliziani, 2014) can reduce the outbreak of BC. Leaf removal can be a practical agrotechnical element against PV (Ellis, 2008) and EN (Stapleton *et al*., 1995) pathogens by providing even assessment of pesticide coverage on leaves and clusters and a more favourable microclimate (i.e., better ventilation, reduced relative humidity). Although a moderate nitrogen application improves the resistance of plant tissues to the pathogen, further supplies significantly increase the canopy biomass, creating a more humid microclimate in the cluster zone, which promotes the development of BC and EN (Mundy and Beresford, 2007).

The role of environmental and plantation factors in influencing diseases can be traced back to complex effects. Still, previous research has only investigated factors considered the most biologically critical without any complex approach. However, studies with a univariate approach to aspects can often give an inaccurate picture of the importance of factors in the occurrence of diseases. With this in mind, our research aimed to identify specific relationships that could contribute to identifying vineyard properties as disease risks, such as the combined effects of climate, vineyard properties and crop management.

The resistance or susceptibility of different grapevine varieties to pathogens results from the systematic modification of some variety-specific morphological traits and the level of chemical defence systems. In terms of morphological characteristics, varieties with robust and thick leaves were more influential in inhibiting the penetration of EN and PV than varieties with soft and weak leaf tissues (Eftimová and Bacigálová, 2012), and berry skin thickness is also considered an important influencing factor in the BC infection process (Commenil *et al*., 1997). Fruit and berry characteristics could also play an essential role in the resistance against pathogens. For example, the number of natural pores on the berry surface and the quantity of sugar excreted onto the berry surface highly varied among the grape varieties, facilitating the pathogen invasion (Gabler *et al*., 2003). In addition to morphological factors, the chemical profile of the epidermis can also modulate mycelial penetration, even more, the production of chemical defence compounds may differ between species (Tříska *et al*., 2017).

In this large-scale study, we aimed to test the possible roles of the most relevant plantation and grape variety features, including the most relevant crop management characteristics on the long-term infection occurrence of primary grape pathogens such as BC, PV and EN, based on a citizen science approach. More specifically, we hypothesised that plantation characteristics and consistent crop management practices determine the general growing conditions and generate high spatial heterogeneity among vineyards in the occurrence of grape diseases. We predicted that average infection levels in the long term reflect the effectiveness of both in-season

and long-term crop management protocol, where regional and climatic effects determine these temporal effects (for the summary of the tested hypotheses, their assumptions and variables, see Table S1). The present study provides detailed information on the relationship between grape production and disease control, whose importance could be more relevant in production regions with suboptimal environmental conditions generated by the expansion of grape cultivation and global climate change.

MATERIALS AND METHODS

1. Data collection

To investigate the impact of plantation effects on disease prevalence and severity, a citizen science approach was used, following the methodology of previous studies (Beza *et al*., 2018). This widely used research approach has the advantage of allowing the collection of large amounts of data from both professional and non-professional volunteers and has been used successfully to explore general correlations in several topics (Silvertown, 2009). Furthermore, the method involved volunteers providing data on grapevine grey mould disease and the associated growing environment in different parts of the country, thus making it suitable for answering research questions at a large spatial scale (Gupta *et al*., 2022).

We collected geo-referenced data on the grey mould (*Botrytis cinerea*, BC), downy mildew (*Plasmopara viticola*, PV), and powdery mildew (*Erysiphe necator*, EN) diseases severity in a traditional wine- and grape-producing country, Hungary (area: 93,030 km^2, 9.7 million inhabitants). Citizen data were surveyed using an online, semi-quantitative questionnaire between July 2020 and March 2023. Around 5000 participants were recruited via e-mail, social media platforms and personally at professional events in Hungary interested in grape production (non-professional or professional). The questionnaire was completed by 181 volunteers, 112 of whom were qualified in plant protection (61.87 %) and gained independent observations (N = 239 vineyards) (Figure 1).

2. Questionnaire survey

Volunteers provided information on the variables of the cultivated area, the average cultivation and general average plant health conditions over the last five years. As a result, overall multi-year crop protection effects and trends could be quantified, and the long-term relationships between factors influencing pathogen infestation could be explored. The surveyed variables belonged to three main sections: infection evaluation, vineyard features, and crop management, as the surveyed variables are described briefly in the following.

2.1 Infection evaluation

To describe the long-term infection status, we surveyed two infection variables. The infection ratio (numeric-discrete) expressed the ratio of the infected vines within the focal vineyard by BC, PV and EN separately. The values based on the last five years by five infection ratio categories were used between the absent (or very low) to the high
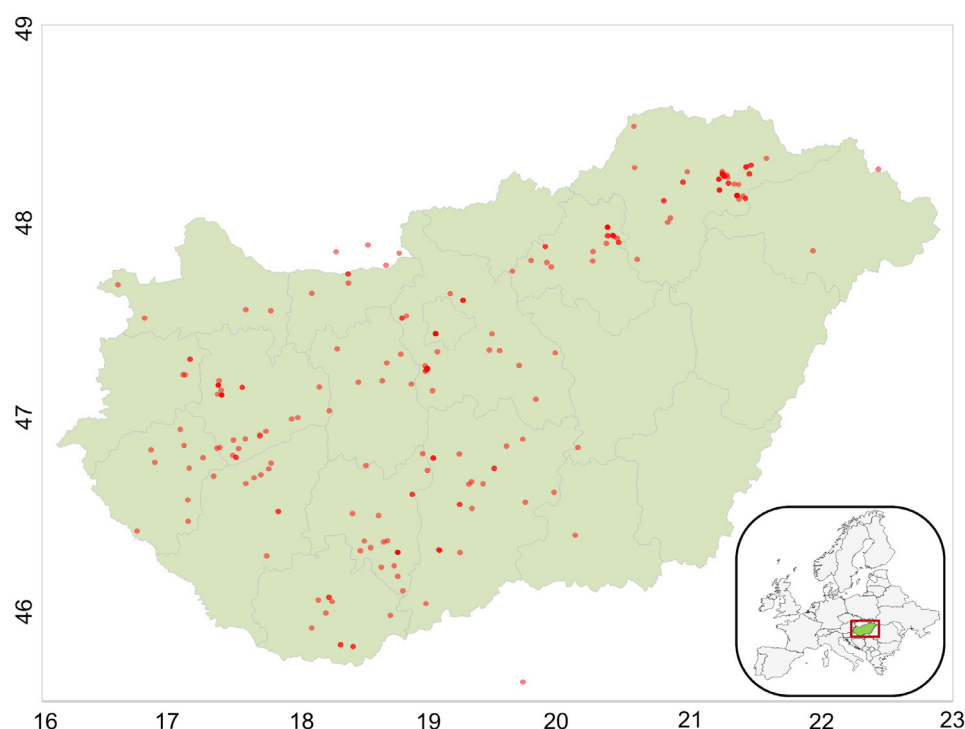
FIGURE 1. The map shows the geo-referenced vineyards from Hungary and nearby (red dot, N = 239 independent observations).

A point with a darker shade reflects more vineyards from the same or close locations. The x and y axes represent the longitude and latitude coordinate scales, respectively.

infection (0–5 %, 6–20 %, 21–50 %, 51–80 % and 81 % or higher). The infection severity (numeric-discrete) reflected the infection level of the cluster (in BC) or canopy (in PV and EN) of an average vine in each pathogen separately. Similarly, the values were based on the last five years using five infection severity categories between the absent (or very low) to the high infection (0–20 %, 21–40 %, 41–60 %, 61– 80 % and 81 % or higher).

2.2 Vineyard features

Volunteers were asked about their qualifications regarding plant protection ('*Qualification*', factor; yes and no) and labelled by a unique identification code for the anonymous identification of the volunteers ('*Farmer ID*', factor) to handle the statistical non-independent records of different vineyards (different location or variety) managing by the same person. The year of the survey ('*Survey year*', numeric-discrete) described the specific year when the focal data was recorded. Vineyards were geolocated using GPS coordinates or recording the closest Location and described the grape variety ('*Variety*', factor), the row orientation ('*Orientation*', factor; North–South, NorthEast–SouthWest, East–West and SouthEast–NorthWest, abbreviated as N–S, NE–SW, E–W and SE–NW, respectively, hereafter), and the slope of the plantation ('*Inclination*', numeric-discrete; 0, 1, 2, as plain: < 5 %, gently slope: 5–12 % and sloping: < 12 %, respectively). The ratio of the surrounding

vineyards ('*Surrounding vineyards*', numeric-discrete) around the focal vineyard within a 1 km radius was also classified into four numeric categories as 0, 1, 2 and 3, labelling none (0–5 %), scattered (6–50 %), many (51–80 %) and high (81 % or higher) classes, respectively. The height of the canopy wall described the vertical isolation distance between the ground surface and the canopy leaves at the lowest position, whose values were expressed in centimetres ('*Distance*', numeric-continuous). The plantation age ('*Age*', numeric-continuous) was calculated by the difference between the vineyard plantation and the survey year.

2.3 Crop management

In this study, we focused on three crop management practices. The inter-row management ('*Inter-row*'; factor) was classified into two categories, such as no (i.e., bare soil surface) and yes, if the inter-rows were covered by cover plants (e.g., mown grass) or organic materials (e.g., grass clippings, straw, mulches). The average number of crop protection treatments applied in a single growing season was defined by the number of pesticide applications ('*Treatments*', numeric-discrete) based on the last five years. Vineyards were characterised by one of the numeric categories, such as 1 (i.e., only dormant spraying without other chemical treatments or with non-chemical pesticides), 2 (range of spraying number: 1–5), 3 (range of spraying number: 6–10), and 4 (range of spraying number: 11 sprayings or more).

Removing the leaves from the cluster zone ('*Leaf removal*', factor) was surveyed, whether it is applied (yes) or not (no) during the fruit development period.

2.4 Grape variety features

Performing comparative analyses among grape varieties, we collected the most appropriate varieties' characteristics from the relevant and highly validated open-source international databases and manuals (Csepregi and Zilai, 1988; Maul *et al*., 2012; Maul and Töpfer, 2015; Tello and Ibáñez, 2018). In these sources, the information about pathogen susceptibility was quantified using the classification system applied in the Vitis International Variety Catalogue (VIVC) database (accessible via: https://www.vivc.de). Hereafter, the literature-based susceptibility values were defined according to the international database, while the observed susceptibility values were based on citizen science observations of the present study. We focused on the most relevant variety characteristics, which could determine or be linked to the level of pathogen infections, such as the pathogen susceptibility ('*Susceptibility*', numeric-discrete; a score between 1—resistant and 9—extremely susceptible, the ripening period ('*Ripening*', numeric-discrete; 0, 1, 2 as early, medium and late, respectively), and the primary postharvest usage of the grape production ('*Utilisation*', factor; classes: wine grape, table grape, both). Regarding the cluster and berry morphology, we tested the bunch compactness according to the berry density within a bunch ('*Bunch compactness*', numeric-discrete), scoring the varieties between 1 (very loose) and 9 (very dense), the thickness of the berry epidermis ('*Berry skin thickness*', numeric-discrete; scoring them as 0, 1 and 2 (thin, medium and thick, respectively) and the berry colour ('*Berry colour*', factor; blanc, rouge, noir) based on the colour classes at harvest.

3. Statistical analysis

Before running the statistical analyses, we applied a couple of transformations regarding the two infection variables (such as infection ratio and infection severity) in each pathogen separately. First, we calculated a single general infection occurrence index based on the average of the two infection variables. Second, we applied a min-max normalisation procedure on these pathogen-specific infection occurrence indexes in each year (when the given data were provided) separately. For this procedure, the used transformation formula was $x'=(x-xmin)/(xmax-xmin)$, where the x represented the general infection occurrence index, and the x_{min} and x_{max} were the yearly minimum and maximum infection values, respectively. As a result, all infection data were brought to a standard range between 0 and 1. Finally, due to the non-normal distribution of infection occurrences, these normalised infection variables were binarised based on the median of the corresponding year (0: below the median, 1: equal or higher median). These pathogen-specific, binarised infection occurrence (hereafter infection occurrence) variables were used in further statistical analyses.

In the present study, we tested the relationship between the infestation occurrence and the most relevant plantation characteristics by a Generalized Linear Mixed-Effect Model with binomial error structure (GLMER-b; using the 'lme4' package, Bates *et al*., 2015). Models were run separately for each grape disease, such as BC, PV and EN. In the models, the response variable was the infection occurrence, and the predictor variables were the following covariates: inclination, adjacent plantation, age, distance, treatments and the survey year. In addition, the orientation, the inter-row management, leaf removal and the region ID were represented as factors, while the grape sort and the farmer ID were entered as random factors. In each statistical model, we applied a combined statistical weight considering the inequality data points given by the responses of qualified or unqualified grape producers (qualification yes: 1, no: 0.5) or the newly established plantations (if age ≤ 4 years: age × 0.2; or 5 ≤: 1).

In separate statistical analyses, we revealed the possible role of the characteristics of grape varieties regarding the occurrence of infestation. First, we calculated the mean of the normalised infection occurrence by grape varieties in each tested pathogen. Then, we applied general linear models in which the variety-specific infection occurrence mean was entered as the dependent variable. At the same time, the pathogen sensitivity, ripening period, berry skin thickness and bunch compactness were entered as covariates, while berry colour and utilisation were factors. The observations were weighted by their relative sample size (also considering the qualification and plantation age) in the statistical models. Grape varieties with three or more observations were included in further analyses. Thus, the final models were based on 22 grape varieties.

BC infection followed by specific climatic conditions may cause 'noble-rot' as a part of some specific traditional wine production (dehydrated berries with increased sugar concentration) in some conventional grape varieties (i.e., *Furmint*, *Sárgamuskotály*, *Hárslevelű*) selected for this technology (Fournier *et al*., 2013). Therefore, we run the same model structure after excluding these varieties from the databases by eliminating the possible bias of these specific grape varieties in the relationship between BC infection and variety features.

In all statistical analyses, a likelihood ratio test (LRT) was applied to test the effects of each predictor in the extended models. In addition, the numeric predictors were centred and scaled before running the analyses, while the model diagnostics were always checked in the final statistical models. Finally, the derived variables were calculated, and all statistical analyses were run in the R environment (version: 4.1.0, R Development Core Team, 2019).

RESULTS

1. Roles of the plantation features and crop management

We found that the BC occurrence was significantly associated with the orientation (Figure 2A). Primarily, the NE–SW orientations increased the presence of the BC and the SE–NW row orientation less, while plantations

with the N–S and the E–W directions resulted in moderate infection occurrences. The ratio of adjacent plantations suggested an apparent increase in the presence of BC infections (Figure 2B). Similarly, the occurrence of BC infections increased with the number of chemical treatments (Table 1) and with the elevation of the canopy wall from the ground (Figure 3). We found significant spatial variation among the growing regions (Table 1, Table S2, Figure S1). A marginal association was revealed with the observation year. We failed to detect any effect regarding the other plantation and crop management features, such as plantation age, slopes, inter-row management and leaf removal (Table 1, Table S2).

We found that the infection of PV increased along with the magnitude of the inclination of the plantation (Table 1, Table S3). Similarly to the BC, different row orientations highly varied with the PV infection occurrence, such as an increased occurrence was revealed at the NE-SW and SE-NW row orientations and moderate ones at the N–S and the E–W directions (Figure 2C). In addition, the increased adjacent plantations around the focal plantations elevated the infection occurrence (Figure 2D). Furthermore, the observation year showed a significantly decreasing trend during the study. Similarly, growing regions reflected significant spatial variation in PV infection. Finally, a marginal association with the inter-row management was
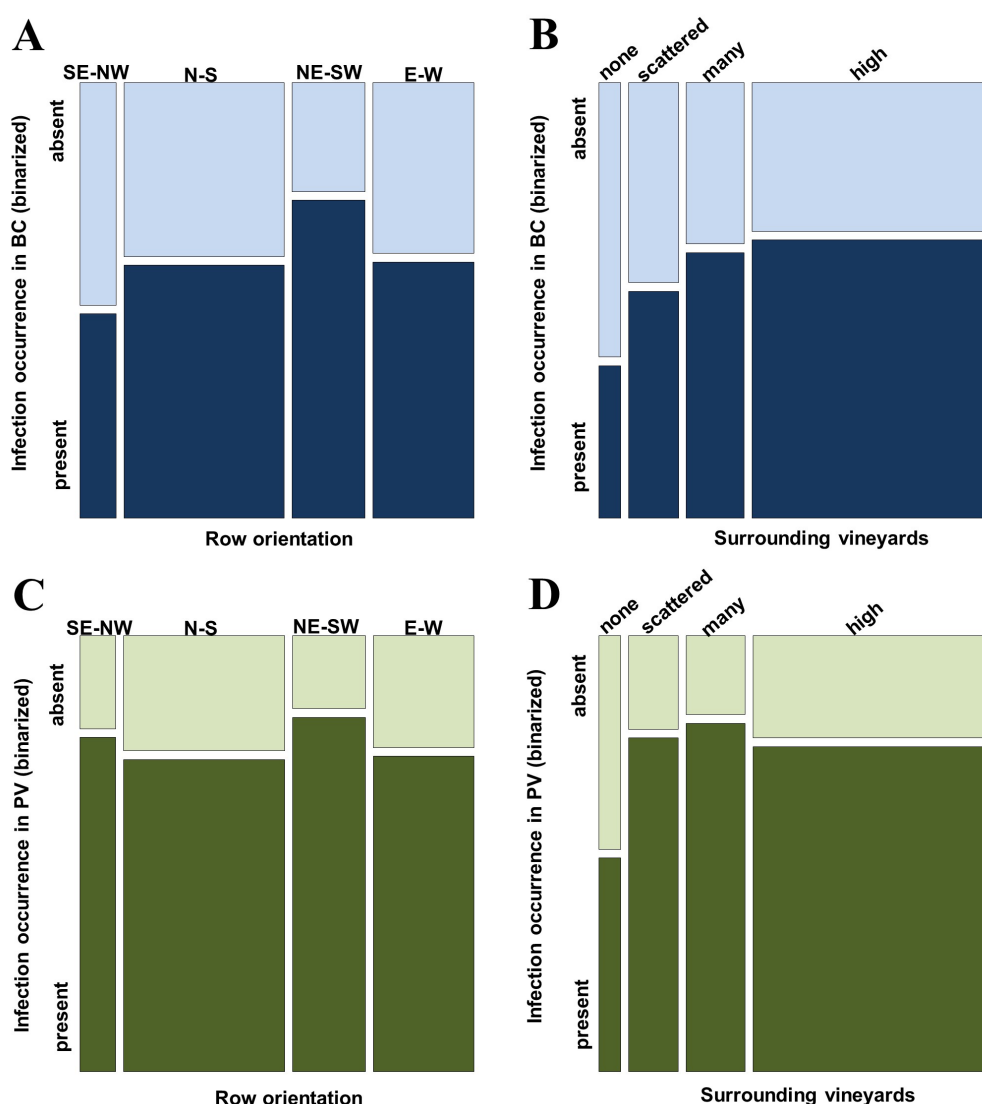
FIGURE 2. The figures show the relationships between the infection occurrence of grape pathogens, such as *Botrytis cinerea* (BC, blue) and *Plasmopara viticola* (PV, green), and two primary vineyard features, such as row orientation (A and C) and surrounding vineyards (B and D).

The tested row orientations, such as SouthEast–NorthWest, North–South, NorthEast–SouthWest and East-West, were abbreviated by SE–NW, N–S, NE–SW and E–W, respectively. The ratio of the surrounding vineyards around the focal vineyard within a 1 km radius was also classified into the categories such as none (0–5 %), scattered (6–50 %), many (51–80 %) and high (81 % or higher) classes, respectively. The light (absent) and dark (present) shades illustrate the occurrence of infection. The mosaic size represents the ratio of the observation numbers within each category (width) according to the infection occurrence (height).
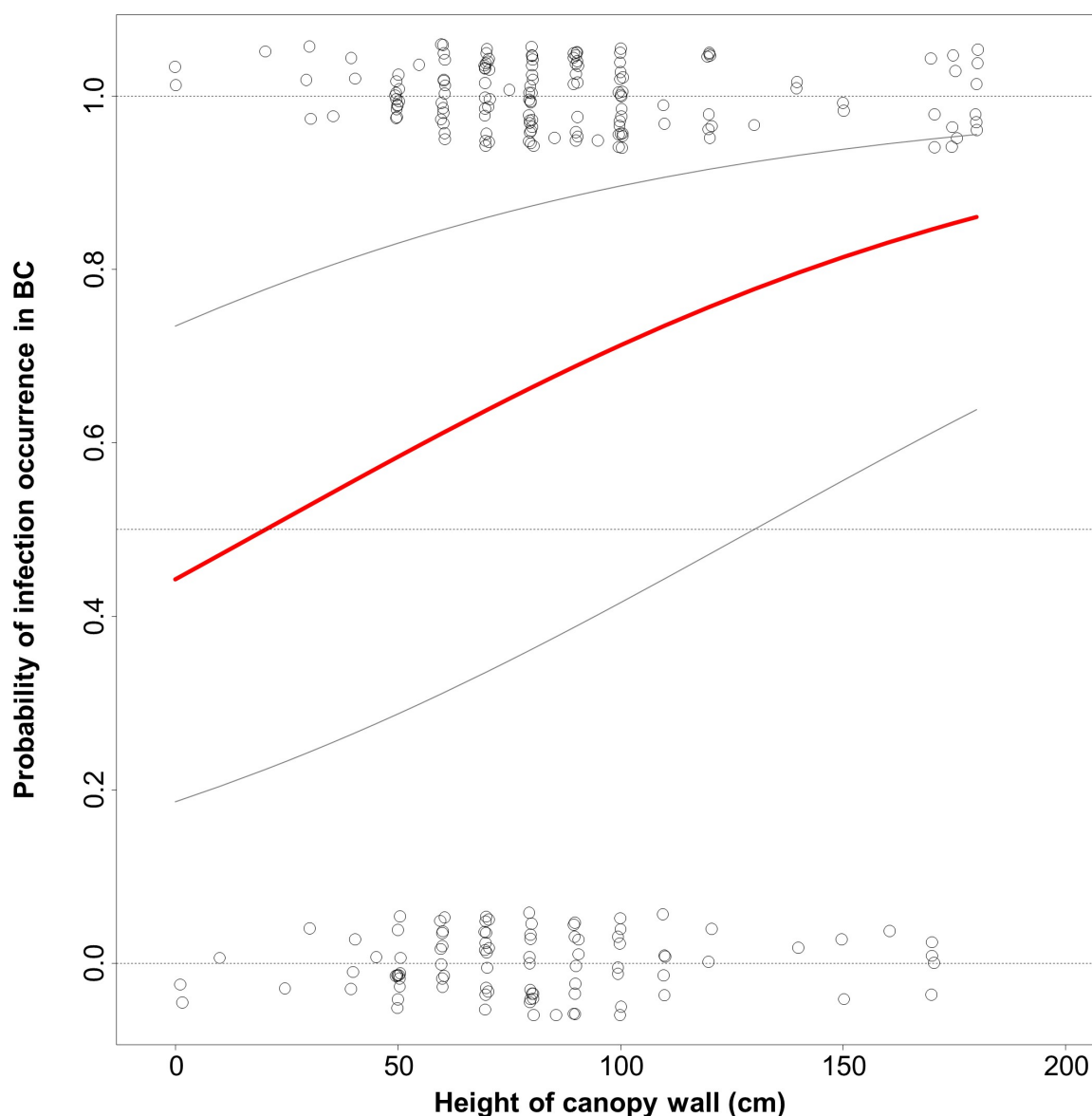
FIGURE 3. The figure shows the effects of the canopy wall height on infection occurrence in *Botrytis cinerea* (BC).

The regression line (red) represents the probability of BC infection occurrence for the cordon heights with the confidence intervals (grey). Points were slightly jittered vertically for better visualisation.

detected, suggesting that the covered inter-row caused more PV infection than the uncovered plantations. We could not detect any effect on plantation age, the elevation of the canopy wall, the number of chemical treatments, and leaf removal (Table 1, Table S3).

None of the tested variables affected the occurrence of EN. Besides these general results, some marginally insignificant effects were detected, suggesting patterns regarding row orientation, the height of cordon arms, leaf removal treatment and regional differences (Table 1, Table S4).

2. Roles of the grape variety

In BC, the observed infection occurrence means detectable increased with the level of literature-based susceptibility (Figure 4A). Infection increased with the delay of the ripening periods, so late-ripening varieties were more likely to be

infected than early- or middle-ripening varieties (Figure 4B). Infection means could also vary among the berry colours, as blanc varieties suffered more from BC infections, while noir varieties enjoyed a relatively higher defence. Interestingly, berry skin thickness and bunch compactness also positively increased the long-term chance of BC infection. Finally, we could not detect any effect of the utilisation (Table 2, Table S5).

After excluding grape varieties selected for BC noble rot in an independent statistical analysis, we revealed similar significant results for the ripening period, berry colour and skin thickness. However, the susceptibility became marginally insignificant, while the bunch compactness and utilisation showed no detectable effect on the BC infection means (Table 2, Table S5).

TABLE 1. The table summarises the statistical analyses of the fitted Generalized Linear Mixed-Effect Model with binomial error structure (GLMER-b) to test the association (highlighted in bold) of the pathogen occurrence and the vineyard and crop management characteristics (Predictor).

Pathogen model	Predictor	npar	AIC	LRT	p-value
	Full model		197.16		
	Inclination	1	196.62	1.464	0.226
	Orientation	**3**	**202.51**	**11.351**	**0.010 ***
	Surrounding vineyards	**1**	**199.01**	**3.853**	**0.050 ***
	Survey year	1	198.52	3.360	0.067
Botrytis cinerea	Age	1	195.88	0.718	0.397
	Distance	**1**	**202.06**	**6.898**	**0.009 ***
	Inter-row	1	195.70	0.545	0.460
	Treatments	**1**	**201.55**	**6.388**	**0.011 ***
	Leaf removal	1	196.27	1.108	0.293
	Region	**18**	**196.91**	**35.753**	**0.008***
	Full model		196.04		
	Inclination	**1**	**197.91**	**3.869**	**0.049***
	Orientation	**3**	**198.69**	**8.648**	**0.034***
	Surrounding vineyards	**1**	**198.64**	**4.600**	**0.032***
	Survey year	**1**	**200.66**	**6.623**	**0.010***
Plasmopara viticola	Age	1	194.12	0.076	0.782
	Distance	1	194.88	0.839	0.360
	Inter-row	1	197.60	3.557	0.059
	Treatments	1	195.35	1.315	0.251
	Leaf removal	1	194.42	0.377	0.539
	Region	**18**	**194.98**	**34.937**	**0.010***
	Full model		240.81		
	Inclination	1	239.85	1.039	0.308
	Orientation	3	242.27	7.459	0.059
	Surrounding vineyards	1	240.69	1.879	0.170
	Survey year	1	238.79	−0.015	1.000
Erysiphe necator	Age	1	238.84	0.029	0.866
	Distance	1	242.64	3.831	0.050
	Inter-row	1	239.49	0.681	0.409
	Treatments	1	239.93	1.124	0.289
	Leaf removal	1	241.36	2.553	0.110
	Region	18	229.78	24.972	0.126

The statistical tests were run separately in each pathogen (*Botrytis cinerea, Plasmopara viticola, Erysiphe necator*). The relevant statistical outputs (i.e., npar, AIC: Akaike Information Criterion, LRT and the p-value) were calculated from the corresponding likelihood ratio test (LRT) that tested the model fit of the full and the reduced model after excluding the given predictor. The asterisks indicated the level of significance of the given predictor (*p < 0.05, **p < 0.01, ***p < 0.001).
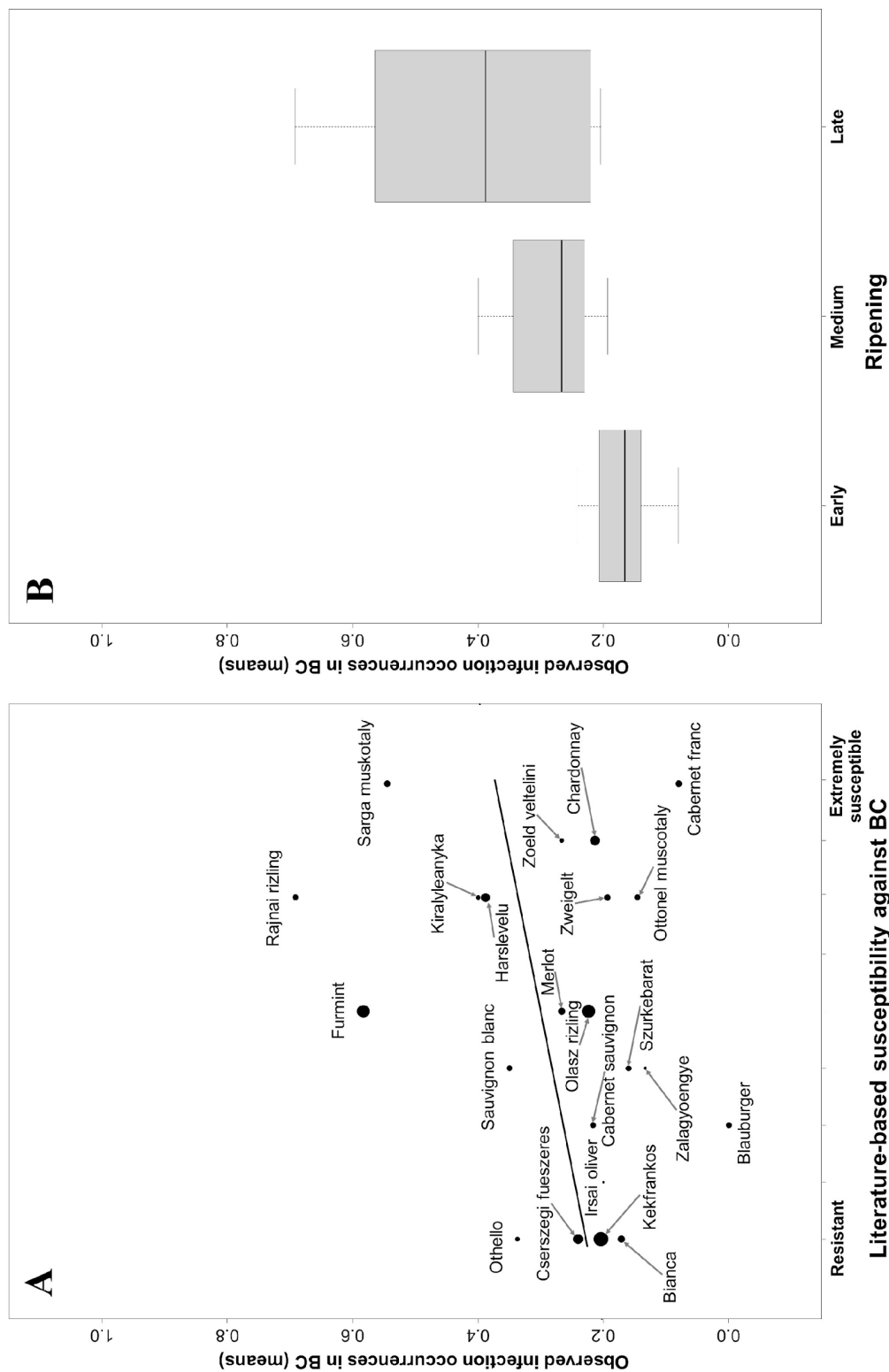
FIGURE 4. The figures show the relationship between the observed BC infection occurrence (variety means) and the literature-based susceptibility (A) and ripening (B).

Figure 4A: A black point represents a variety-specific literature-based susceptibility with the observed infection occurrences. The point size reflects the sample size of the given variety (a larger point represents more observations). The regression line (grey) shows the significant relationship between the tested variables. The labelling of the points was based on the varieties' names according to the VIVC database (see details, Table S6). Figure 4B: The box size corresponds to the interquartile, while the whisker shows the nonoutlier range. The bold horizontal line indicates the median of the corresponding ripening category.

TABLE 2. The table summarises the statistical analyses of the fitted General Linear Model to test the association (highlighted in bold) of the infection occurrence and the grape variety-specific characteristics (Predictor).

Pathogen model	Predictor	df	SS	RSS	AIC	p-value
Botrytis cinerea (Complete database)	Full model			0.684	−60.359	
	Susceptibility	**1**	**0.262**	**0.946**	**−55.230**	**0.007****
	Ripening	**1**	**1.156**	**1.840**	**−40.582**	**< 0.001*****
	Bunch compactness	**1**	**0.276**	**0.960**	**−54.891**	**0.006****
	Berry skin thickness	**1**	**0.767**	**1.451**	**−45.819**	**< 0.001*****
	Berry colour	**2**	**0.815**	**1.499**	**−47.098**	**< 0.001*****
	Utilisation	1	0.079	0.763	−59.956	0.121
Botrytis cinerea (Reduced database)	Full model			0.640	−48.435	
	Susceptibility	1	0.117	0.756	−47.247	0.074
	Ripening	**1**	**0.313**	**0.953**	**−42.865**	**0.006****
	Bunch compactness	1	0.067	0.706	−48.549	0.170
	Berry skin thickness	**1**	**0.470**	**1.110**	**−39.968**	**0.001****
	Berry colour	**2**	**0.558**	**1.198**	**−40.512**	**0.003****
	Utilisation	1	0.089	0.728	−47.970	0.116
Plasmopara viticola	Full model			1.018	−51.611	
	Susceptibility	1	0.038	1.056	−52.811	0.371
	Ripening	1	0.006	1.024	−53.478	0.716
	Bunch compactness	1	0.049	1.067	−52.579	0.310
	Berry skin thickness	1	0.121	1.139	−51.131	0.115
	Berry colour	2	0.037	1.055	−54.832	0.677
	Utilisation	1	0.004	1.022	−53.519	0.762
Erysiphe necator	Full model			0.795	−57.039	
	Susceptibility	1	0.001	0.796	−59.010	0.864
	Ripening	1	0.017	0.813	−58.563	0.490
	Bunch compactness	1	0.065	0.861	−57.303	0.188
	Berry skin thickness	1	0.040	0.835	−57.962	0.299
	Berry colour	2	0.033	0.828	−60.154	0.642
	Utilisation	1	0.001	0.797	−59.004	0.851

The statistical tests were run on each pathogen separately (*Botrytis cinerea, Plasmopara viticola, Erysiphe necator*). In *Botrytis cinerea*, two models were run based on the complete database (including all grape varieties) and the reduced database (excluding the noble-rot varieties). The relevant statistical outputs (i.e., df, SS: Sum of Squares, RSS: Residual Sum of Squares, AIC: Akaike Information Criterion and the p-value) were calculated from the corresponding likelihood ratio test (LRT) that tested the model fit of the full and the reduced model after excluding the given predictor. The asterisks indicated the level of significance of the given predictor (*p < 0.05, **p < 0.01, ***p < 0.001).

We could not detect any significant effects among the tested variables regarding the grape varieties in PV and EN (Table 2, Table S5).

DISCUSSION

In this large-scale study, we aimed to reveal the relative importance of the infection occurrence of plant pathogens and the most relevant vineyard characteristics and variety features in the most widely grown grapes. Previously, we hypothesised that the long-term infection occurrence of primary grape pathogens, such as BC, PV and EN, is determined by the general growing conditions and grape variety characteristics via the indirect negative impact of suboptimal conditions on plant health. Generally, the present long-term study successfully served some clear evidence to support the relevance of the primary hypothesis. In addition, we found some specific plantation and variety features that could influence the long-term occurrence of the tested grape pathogens; however, these factors shaped the

pathogen occurrence differently. In the following, the role of these factors will be discussed in detail, paying particular attention to the practical aspects of these possible impacts on viticulture.

1. Vineyard features

Before establishing a plantation, a farmer has to decide on several plantation characteristics that cannot be modified afterwards; however, these environmental and biological conditions could affect the production system and the cultivation practices in the long term. Therefore, these characteristics have a long-term impact on the growth conditions and the crop's success from crop management, including pest control. For example, appropriately selected planting structures could contribute to reducing infections by plant pathogens by ensuring the vines are in the proper condition and by inhibiting the spread of pathogen propagules (Ellis, 2008; Stapleton *et al.*, 1995).

Sloping and hilly areas are often preferred for vineyards due to favourable climatic conditions, such as higher solar radiation exposure and better air ventilation, especially in traditional grape-growing regions (van Leeuwen *et al.*, 2004). Previously, we expected that row orientation and slopeness generate a considerably high spatial variance in environmental conditions among vineyards, which could be associated with a higher variance in the occurrence of specific plant pathogens. Supporting this prediction (see Figure 2, Table 1, Table S2, Table S3), we found that specific row orientations increased the occurrence of BC (i.e., NE-SW) and PV (i.e., NE–SW, SE–NW) infections, while the higher slopes generated a similar increasing pattern in PV. The result regarding orientation could be linked to the prevailing wind direction (i.e., N and NW) in Hungary, which changes to NE during summer (Mezősi, 2017), thereby promoting the spatial dispersion of air-borne spores. Furthermore, previous studies showed that row orientation and slopeness could indirectly influence pathogen infections via the environmental conditions affecting plant health or growth (van Leeuwen *et al.*, 2018). The choice of row orientation also determines both the amount and the duration of irradiation reaching the vineyard, which also influences the ripening time of grape varieties through soil warming. Therefore, earlier ripening was expected in areas where the row orientations promote the rapid increase of the soil temperature better compared to those plantations with unfavoured row orientations (van Leeuwen *et al.*, 2018). Although the BC infection can develop at any phenological stage, berries are markedly more susceptible from the ripening stage onwards (Kretschmer *et al.*, 2007) since the susceptibility of berries to infection increases as the sugar content of the berries increases towards ripening (Deytieux-Belleau *et al.*, 2009). Contrary to the result of the present study, it was previously found that plain vineyards suffered a higher risk of infection with more severe symptoms than those with slight or steep downhills because the slopes receive higher solar radiation, favouring the growing and ripening conditions and causing healthier vines; however, the susceptible phenological stage was shifted earlier (Seguin, 1986; van Leeuwen *et al.*, 2018).

It may undoubtedly seem that increasing the distance between the lowest leaves and the ground makes work easier and isolates the foliage from the soil (Seguin, 1986). It also has plant protection benefits, as the distance of the lower leaves from the ground determines the chance of pathogens infecting the host plant from the ground, in case the pathogens overwinter on the soil surface or fallen plant residues, such as BC or PV. This is because leaves closer to the soil surface are more exposed to infection pressure from pathogens overwintering on fallen plant parts because the number and size of raindrops decrease as they move away from the soil surface (Rossi and Caffi, 2012). Nevertheless, our results indicate that canopy height increases BC infection incidence (Figure 3, Table S2). The potential role of the canopy height on pathogen infection has already been examined in grapes. For example, higher canopies result in larger shades for themselves, which affects the cluster environment and significantly affects the exposure of the fruit to solar radiation, leading to an increase in the incidence of BC (Smart *et al.*, 2017). Also, from the point of view of PV, a shaded canopy, where drying is more gradual, is favourable for the infection process. The survival of sporangia and the release and movement of zoospores are highly dependent on the relative humidity and the presence of water (Kast and Stark-Urnau, 1999). Thus, consistent with previous studies, our result suggests that canopy height could be a critical factor influencing plant health and the incidence of pathogens such as BC.

Cultivated crops of the same species grown over a large area favour large-scale multiplication of plant pathogens, as the pathogen will always find a suitable susceptible host plant in large populations (Wolfe, 2000). In addition, the presence of sufficient amounts of infective propagules in the plantation during the susceptible phenological phase of the host plant is a prerequisite for the pathogen's survival and infection (Coertze *et al.*, 2001). Supporting the expectations, our study revealed that a vineyard surrounded by a higher density of grape plantations suffered more from the infection of BC and PV but not EN (Figure 2, Table 1, Table S2, Table S3, Table S4). The combined results of several studies suggest that, although pathogen sporulation varies during vegetation (Mundy *et al.*, 2012), there are sufficient quantities of infective conidia available at the phenological stages of grapes susceptible to BC infection (Warren *et al.*, 1999).

Traditional grape and wine production is based on regional yield and quality specifications and standards, highlighting its characteristics as a brand mark of a specific terroir. Our large-scale study found similar regional variations in the prevalence of primary grape pathogens. The prevalence of BC and PV infections showed a high spatial heterogeneity, while the effect of EN infections remained hidden (Table 1, Table S2, Table S3, Table S4). Systematic spatial differences in grape infections may suggest a possible role of large-scale background mechanisms and their variations related to the macroclimatic, topographic and soil conditions. However, revealing these effects was out of the present study's focus; we noted that testing the relevance of grape production to

these effects could be a fruitful research objective in the future.

In many host-pathogen interactions, individuals' susceptibility may vary with time, as specific organs or whole plants may become more or less susceptible or have variable responses with age (Burdon *et al.*, 1989). Age-related susceptibility of a particular plant part is well-known in epidemic diseases; however, the link between infection susceptibility and the actual plant age was underrepresented in the literature. In the present study, we assumed that the infection rate would be higher and symptoms more severe in older plantations than in newly established ones. This is due to the reduced resistance of an older plant because the accumulation of endophytic parasites (i.e., viruses, trunk diseases) can be increased with years (Kovács *et al.*, 2017), generating higher biotic stress and resulting in susceptibility to epidemic diseases. Contrary to our expectations, the results showed that the plantation age did not affect the infection incidence in each tested pathogen (Table 1, Table S2, Table S3, Table S4). This can be explained by the fact that most of the plantations included in the study applied intensive crop production management. In a production environment, avoiding the physiological and condition deterioration of vines is one of the most crucial issues for keeping the quantity and quality standards of the cultivated crop. Therefore, most farmers carefully and regularly monitor physiological deterioration symptoms and continuously prevent or mitigate it with specific cultivation technology interventions. Thus, an older culture growing in an excellent cultivation environment could be more resistant to various plant pathogen infections, while these effects could be much more pronounced in the case of degraded growth environments. Moreover, the majority of the studied plantations were far below the age of senescence (75 % of the surveyed plantations were 30 years old or younger) based on the biological characteristics of the species, as a 40-year-old vine was considered to be old (Riffle *et al.*, 2022). Furthermore, according to grapevine production approaches, when the applied interventions were unsupported to prevent vineyard deterioration, farmers often completely eradicated the entire plantation. Thus, in cultivated grapes, the role of growing conditions on production is more substantial than age.

Grape studies draw special attention to the importance of the vintage effect (Khan *et al.*, 2020). However, our study approach was to explore long-term temporal patterns by asking volunteers for 5-year average infection rates. The yearly infection variance was smoothed out in the present study to long-term differences. It reflected a general average effect, which most describes the long-term cultivation success against pathogens. Since the collection of infection data also takes several years (3 consecutive years), the data for the 5-year average in the different years only partially overlapped in particular sampling areas. Due to the applied methodological sampling procedure, despite the prior annual correction of the infection data, we detected systemic changes in pathogen occurrences in PV (Table 1, Table S3), marginally insignificant in BC (Table 1,

Table S2). At the same time, this did not occur at all in the case of EN (Table 1, Table S4).

2. Crop management

Pest control treatments and other production management tools promote reducing the production risk in terms of crop quantity and quality, but the application frequency could be under consideration due to their long-term severe economic and agroecological consequences (Liere *et al.*, 2017). Therefore, we hypothesised that increased chemical crop protection could effectively reduce infection rates and symptoms. However, we also expected that applying more chemical treatments has no effect beyond a certain point, and therefore, some of the chemical treatments may be unnecessary. In the present study, we found a systematic change between the frequency of pesticide application and the infection occurrence only for BC, in which the BC infection increased with the level of chemical treatments (Table 1, Table S2).

The pathogen-specific association between pesticide applications and infection occurrence could be explained by two, not mutually exclusive, explanations. First, BC has the shortest incubation period of all the tested pathogens (Corio-Costet *et al.*, 2010; Gadoury *et al.*, 2012; Nair and Allen, 1993). Additionally, unexpected injuries caused by environmental (e.g., hail) or biotic (e.g., insects) factors can facilitate the rapid initiation of BC infection on berries, while PV and EN could infect intact berries. In case of these unwanted events, a farmer often prefers to insert an additional chemical treatment into the regular fungicide spray schedule to reduce the risk of BC infection (Romanazzi *et al.*, 2016). Due to the short incubation period of BC, these sprayings bore low efficiency or remained ineffective. In this way, the number of chemical treatments increased with the incidence of BC. Second, chemical fungicide resistance could determine the current infection rate (Hahn, 2014). The desired rotation of fungicides is challenging in the EU, as there are fewer and fewer authorised active substances available for plant protection in BC than in PV or EN, which is the main source of resistance. Although increasing the number of fungicide treatments may have the short-term effect of reducing pathogens, it may be counterproductive as this crop protection approach promotes the adaption of pathogens, leading to resistance and loss of fungicide efficacy in a long-term effect (Hahn, 2014).

In contrast with BC, we did not find detectable associations in PV and EN pathogens, suggesting that the frequency of the chemical treatments may represent a lower relevance compared to the quality (or effectiveness) of the applied pesticides and/or other external environmental factors on a long-term basis (Table 1, Table S3, Table S4). However, the applied active fungicide agents and their potential effectiveness (i.e., asked about an average of 5 years of application practice) would be an important influencing factor; we could not survey them in a separate question in the present questionnaire study (space limitations). Besides, it seems the fungicide spray schedules protect the

vines sufficiently against diseases caused by PV and EN. This information is rather lacking in the literature, which might be a relevant and focused topic of a systematic large-scale study in the future.

Our findings could not support the effect of inter-row management on the disease occurrence in BC, PV or EN (Table 1, Table S2, Table S3, Table S4). Therefore, our study suggests that inter-row effects have a minor impact on disease patterns in complex systems, compared to other factors, such as vineyard characteristics, crop production, and grape variety, when considering the long-term consequences. Contrarily, specific and short-term experimental studies demonstrated detectable direct or indirect effects of inter-row crops on disease prevalence and severity, which often interfered with other environmental impacts. Generally, inter-row crops could shift the microclimatic conditions and interfere with the soil properties (Guerra and Steenwerth, 2012). The inter-row management could enhance the biological activity of the soil by the application of cover crops and other organic mulch types, which could accelerate the decomposition rate of the infected plant debris (Jacometti *et al*., 2007a; Jacometti *et al*., 2007b). So, plant pathogens could be effectively inhibited indirectly via the beneficial shift of soil properties (e.g. increased nitrogen mineralisation rates, organic matter, microorganism populations) by appropriate inter-row management (Guerra and Steenwerth, 2012). For example, the decomposition of overwintering plant debris along with overwintering structures reduced the infestation rate of grapes due to the low survival rate of BC sclerotia as the organ of conidia production (Jacometti *et al*., 2007a). Comparing inter-row management types, plantations with inter-row coverage cut down the infection level of the flowers and clusters than vineyards without using that (Jacometti *et al*., 2007a).

Our study failed to detect the relationship between the leaf removal application and the long-term consequences of disease occurrence in BC, PV and EN (Table 1, Table S2, Table S3, Table S4). Thus, our results indicated that leaf removal might be less important than previously expected compared to a complex model. However, short-term studies revealed that the increased canopy mass was associated with a more humid microclimate in the cluster zone, which promoted the development of grape grey mould disease (Mundy and Beresford, 2007). So, removing the front leaves covering the clusters is a traditional and widely applied procedure to reduce the chance of BC infection by reducing the relative humidity (Romanazzi and Feliziani, 2014). In addition, the absence of foliage contributed significantly to the increased exposure of the berries to solar UV radiation, which resulted in increased berry resistance against the pathogen by a relatively thicker skin (Mundy *et al*., 2012). Furthermore, opening the foliage at the cluster zone facilitates faster wetness evaporation and ensures optimal pesticide coverage (Evers *et al*., 2010). The inconsistent results could be explained by the fact that the pathogen occurrence and climatic factors often show a high yearly fluctuation, so the effect of the leaf removal could enhance

the pathogen suppression only in specific years; however, the positive effects of this practice might be equalised on a longer temporal scale.

3. Grape variety features

Exhausted breeding efforts always attempt to improve production effectiveness, such as yield and quality, including tolerance and resistance against specific plant pathogens. Therefore, carefully selecting the most appropriate varieties is always crucial because the varietal-linked characteristics should fulfil the requirements regarding the production system, environmental regimes and consumer needs. This study found pathogen-specific infection associated with some variety-specific features only in BC but not in PV and EN, affecting the current infection rate (Figure 4, Table 2, Table S5). Thus, a promising variety can provide a complex and general response to the current production challenges. However, our results highlighted that relying exclusively on the beneficial features of a variety could not give an ultimate solution against all types of fungal attacks.

Grapevine varieties show high diversity in their phenotypic appearance due to their different genotypic backgrounds. Thus, the high variation of morphological traits and chemical properties (i.e. chemical defence) could be the primary source of the high heterogeneity in pathogen susceptibility. Supporting our expectations, the literature-based susceptibility to pathogen infections increased with BC's observed infection ratio but not PV or EN (Figure 4, Table 2, Table S5). These results suggested that BC infection could be primarily based on variety-specific features. In contrast, environmental and crop management factors could influence the infection in the other two tested pathogens. Moreover, some varieties were selected for botrytisation (i.e., facilitating noble-rot by the increased susceptibility to BC infection), which could bias the general pattern regarding BC infection. Thus, the susceptibility to a specific pathogen was linked strongly to the varieties as a complex representation of their properties as a whole package. Based on the reduced database, the additional analysis found that the susceptibility properties reduced the effect on the observed disease incidence (Table S5). Such a shift between the models supported the previous expectations that varieties represented a shared package regarding morphological and chemical features which could influence the pathogen attack. In the following, we provided a detailed description regarding the possible role of the specific features.

The general appearance of a cluster structure (i.e., compactness, berry number and size) is an inherited, variety-specific phenotypic feature determined by the genetic background; however, some environmental and production management factors could slightly shape it (Dai *et al*., 2011). Studies linked the bunch structure and the susceptibility to plant pathogens. Generally, a more dense cluster appearance explained the increased susceptibility to pathogens due to reduced isolation distance among berries (Gabler *et al*., 2003). Moreover, grape pests (e.g., vine moth larvae) could also contribute to the attack of the wound-induced pathogens

by their hidden feeding (Fermaud, 1998), against which the effectiveness of the pesticide treatments is limited for a more dense cluster. Our survey revealed that the likelihood of BC infection could not be varied among the tested varieties with different cluster structures (Table 2, Table S5). However, the noble-rot varieties played an important role in shaping this general pattern, making the relationship detectable after their inclusion into the analyses. These patterns suggested that the cluster compactness might not always confidently determine the BC attack on a long-term basis. Additionally, the specially selected noble-rot varieties showed a relatively higher infection ratio compared to varieties with similar characteristics; however, noble-rot varieties show a heterogeneous morphological profile (i.e., compactness) (Table S5).

The berry skin represents a primary host barrier, so its thickness could determine the level of the constitutive defence of a grape variety (Commenil *et al.*, 1997). Thus, varieties with thicker skins and more epidermis cell layers showed a greater defence capacity against pathogens (Gabler *et al.*, 2003). A similar pattern was found in the leaf penetration tested in different grape varieties by the infection of EN and PV (Eftimová and Bacigálová, 2012). Contrary to our expectation, varieties with thicker epidermis increased with a higher ratio of BC infection, even when varieties for botrytisation were excluded from the analysis (Table 2, Table S5). Similarly, previous results suggested that the relationship between the epidermis thickness and the degree of infection ratio could not always be trivial. A study (Kretschmer *et al.*, 2007) found that Riesling berries with thicker epidermis were more easily infected than the thin-skinned Pinot Noir ones, which pattern was explained by the fact that the Riesling had mechanically softer tissues and became more likely to rupture after infection than Pinot noir. Their further analysis revealed that the chemical defence could compensate for the greater vulnerability to physical injuries, reducing the negative consequences of the infection, which level of chemical defence shifted with ripening.

The chemical defence system is the second barrier against a berry infection manifested in the berry tissue (Gabler *et al.*, 2003). It is well known that the production of the plant secondary metabolisms involved in chemical defence strategies varies among varieties (Tříska *et al.*, 2017), and the more susceptible varieties tend to have lower concentrations of pathogen inhibitors (e.g., resveratrol) (Adrian *et al.*, 1997). In this study, we compared the infection ratios among grape varieties depending on the berry colour (used as an indicator), which reflect highly different chemical composition. We found that white or pale-coloured varieties suffered more from BC disease than those with higher pigment content (i.e., rouge, noir). However, BC infection may be desirable as noble-rot in some varieties (all blanc), but excluding these noble-rot varieties could not modify the revealed pattern (Table 2, Table S5). Therefore, the berry colour could be a suitable representation of the chemical defence determining the berry infection. Other studies highlighted that some specific secondary metabolisms shifted during the ripening,

which could define and represent an effective and inducible barrier against fungal attack (Kretschmer *et al.*, 2007). The effectiveness of the chemical defence could also vary among different tissues within a berry due to the pH variation (Manteau *et al.*, 2003).

Previous studies illustrated that the infection risk could change consistently with time, closely linked to fruit ripening. Due to morphological, structural and chemical properties changing over time, the ripening time is a variety-linked characteristic that could vary considerably from year to year according to the ongoing climatic conditions. Consequently, the known infection windows for grapevine pathogens also vary since the phenological development of plants (fruit ripening processes) is also linked to specific climatic conditions, and therefore, the risk of infection varies with time. Our results showed an apparent and detectable increase in BC infection rates with ripening time (Figure 4, Table 2, Table S5). The obtained pattern was consistent with the climatic requirements of BC (lower daily average temperature, more frequent precipitation) and the coincidence of the phenological stages of grape varieties suitable for infection (i.e., from pea-sized berries to harvest) (Ciliberti *et al.*, 2015). Moreover, the fungus can also cause latent infection in young berries, and the berries remain asymptomatic until ripening, then the fungus reactivates, causing severe symptoms (Keller *et al.*, 2003). Furthermore, the temporal variation in morphological and chemical processes previously described is well reflected in the differences in ripening processes observed between varieties. Since environmental, climatic and cultivation practices strongly influence these processes, deviations from optimal growing conditions can significantly increase the chances of BC infection.

CONCLUSION

The extensive growth of vineyards in suboptimal growing areas causes difficulties in plant protection, and exposure to fungal attacks is more likely. These results highlighted how different results could be obtained when the role of a variable was analysed in a complex system instead of testing them separately. Moreover, new or innovative grape varieties facilitate grape and wine production through their variety-specific feature profile based on the specific production system regarding environmental regimes, adverse biological conditions or consumer needs. Our study revealed that the importance of particular characteristics may be overemphasised in pathogen-host interactions and fungal susceptibility. Therefore, the susceptibility or tolerance of grapes to plant pathogens is the result of several combined factors and cannot be assigned to a single characteristic. This study revealed that long-term interferences could modify the infection of specific plant pathogens in a vineyard. Due to the complex interference, knowledge of the long-term relationship between plant infection and other important factors, such as soil properties and climatic conditions, is still limited. We believe that future studies could benefit more from Citizen science data collection, an increasingly popular method for gathering large-scale data. It offers an

excellent opportunity to complement monitoring efforts by involving farmers, experts and non-professionals. Volunteers can take ownership of scientific research and contribute to the knowledge transfer of a specific region, providing relevant and recent observations from different fields, such as sustainable crop production, plant protection and the occurrence of new pathogens.

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