Doctoral (PhD) Dissertation

Ivett Kocsis

Budapest

2025

HUNGARIAN UNIVERSITY OF AGRICULTURE AND LIFE SCIENCES

Multivariate analysis of factors influencing the development of plant pathogen infections

Doctoral (PhD) Dissertation

Ivett Kocsis

Budapest

2025

Ph.D. School

Name: Doctoral School of Horticultural Sciences

Discipline: Crop Sciences and Horticulture

Head of Ph.D. School: **Prof. Dr. Éva Németh Zámboriné**
Doctor of the Hungarian Academy of Sciences
Head of Department of
Medicinal and Aromatic Plants
HUNGARIAN UNIVERSITY OF
AGRICULTURE AND LIFE SCIENCES,
Institute of Horticultural Science

Supervisor: **Dr. Gábor Markó**
Associate professor, Ph.D.
Department of Plant Pathology
HUNGARIAN UNIVERSITY OF
AGRICULTURE AND LIFE SCIENCES,
Institute of Plant Protection

The candidate has fulfilled all the conditions prescribed by the doctoral school of the Hungarian University of Agriculture and Life Sciences, and the thesis is accepted for the defence process.

…… ……

Head of Ph.D. School Supervisor

TABLE OF CONTENTS

1. GENERAL INTRODUCTION 10

2. POLLEN-SPORE INTERACTION 12

2.1 Literature overview 12

2.2 Aims and objectives 14

2.3 Material and methods 15

2.4 Results 19

2.5 Discussion 24

3. VINEYARD, MANAGEMENT AND VARIETY CHARACTERISTICS INFLUENCE ON DISEASE PREVALENCE 28

3.1 Literature overview 28

3.1 Aims and objectives 31

3.3. Material and methods 31

3.4 Results 40

3.5 Discussion 48

4. IMPACT OF VINEYARD PROPERTIES ON SHIFTING GRAPE PHENOLOGY AND ITS IMPLICATIONS FOR PLANT DISEASES 58

4.1 Introduction 58

4.2 Aims and objectives 59

4.3 Material and methods 60

4.4 Results 66

4.5 Discussion 71

5. LONG-TERM INFLUENCES ON DISEASE OCCURRENCE: A META-ANALYTIC COMPARISON OF VINEYARD, TECHNOLOGY AND SOIL FEATURES 75

5.1 Introduction 75

5.2 Aims and objectives 78

5.3 Material and methods 80

5.4 Results 89

5.4 Discussion 101

8. NEW SCIENTIFIC RESULTS 109

8.1 Pollen-spore interaction 109

8.2 Vineyard, management and variety characteristics influence disease prevalence 109

8.3 Impact of vineyard properties on shifting grape phenology and its implications for plant diseases 109

8.4 Long-term influences on disease occurrence: a meta-analytic comparison of vineyard, technology and soil features. 109

9. SUMMARY 110

10.CONTRIBUTION 114

ACKNOWLEDGMENT 115

SUPPLEMENTARY 116

REFERENCES 166

LIST OF ABBREVIATIONS

AIC: Akaike Information Criterion

BBCH: a standardized scale for coding system describing the phenological development stages of plants (acronym for Biologische Bundesanstalt, Bundessortenamt and CHemical industry)

BC: *Botrytis cinerea*

CI: Confidence Interval

EN: *Erysiphe necator*

ES: Effect Size

E–W: East–West

GDD ST8: GDD model with a baseline temperature (Tbase) of 8°C

GDD: Growing Degree Days

GDDa: GDD Single threshold model

GDDb: GDD Lower and upper threshold model

GDDc: GDD Heat threshold model

GLM: Generalized Linear Model

GLMM-nb: Generalized Mixed Effect Model with a negative binomial error structure

GLM-qb: Generalized Linear Models with quasibinomial error structure

GPS: Global Positioning System coordinates

LRT: Likelihood Ratio Test

MCMC: Markov Chain Monte Carlo sampler

MISH: Meteorological Interpolation based on Surface Homogenized Data Basis

NE–SW: Northeast–Southwest

N–S: North–South

OR: Odds Ratio

PDA: Potato Dextrose Agar

PP: Precipitation

PV: *Plasmopara viticola*

REML: Restricted Maximum-likelihood Estimator Methods

RMSE: Root-Mean-Squared-Error

SE–NW: Southeast–Northwest

TMB: Template Model Builder

UV-B: Ultraviolet B radiation

VIVC: Vitis International Variety Catalogue

LIST OF TABLES

Table 1 *Botrytis cinerea* conidia germination association with specific predictors and their interactions 20
Table 2 Summary of surveyed variables on infection status of vineyard 33
Table 3 Summary of surveyed variables on vineyard features 34
Table 4 Summary of surveyed variables on crop management 35
Table 5 Summary of surveyed variables on grape variety features 36
Table 6 Summary of model used for assessment the relationship between vineyard features, crop management and variety characteristics 39
Table 7 The association between pathogen occurrence and the vineyard and crop management characteristics 43
Table 8 The association between pathogen occurrence and the grape variety-specific characteristics 47
Table 9 The association of the grape development and the most relevant vineyard features and crop management characteristics 66
Table 10 The relationships between the long-term disease occurrence and corrected grapevine phenological shift, plantation and crop management features 69
Table 11 General descriptive table of the glmmTMB model structures for the Vineyard, Technology, and Soil domain variables to analyse the relationships between the infection and specific domain variables. 84
Table 12 Comprehensive table of the environmental factors for each moderator variable. 87
Table 13 The overall and pathogen-specific effects on the relationship between long-term disease occurrence and production-related environmental factors in vineyards 91
Table 14 Heterogeneity estimates for meta-analytic models: overall and pathogen models 92
Table 15 The effect of moderator variables on the relationship between long-term disease occurrence and production-related environmental factors in vineyards 93
Table 16 Summary of heterogeneity estimates for all meta-analytic models with moderators ... 96
Table 17 Estimates of the subgroup heterogeneity within Domain moderator for each pathogen 100

LIST OF FIGURES

Figure 1 Leaf as natural pollen trap (Kocsis 2020) 13
Figure 2 *Botrytis cinerea* conidia germination under a light microscope..... 17
Figure 3 The species-specific stimulation effect of pollen on *Botrytis cinerea* conidia germination rate over time and concentration 19
Figure 4 The species-specific stimulation effects of pollen on *Botrytis cinerea* conidia germination within species-specific attributes 21
Figure 5 The temporal- and concentration-dependent pattern of *Botrytis cinerea* conidia germination rate..... 22
Figure 6 The relationship between the volume-corrected concentration and *Botrytis cinerea* conidia germination rate 23
Figure 7 The geo-referenced vineyards from Hungary and nearby 32
Figure 8 The relationship between the infection occurrence and vineyard features 41
Figure 9 Effect of the canopy wall height on infection occurrence of *Botrytis cinerea*..... 42
Figure 10 The relationship between the observed *Botrytis cinerea* infection occurrence (variety means) and the literature-based susceptibility (A) and ripening (B)..... 46
Figure 11 Locations of phenological observation across Hungary 61
Figure 12 Graphical summary of the material and methods regarding climate, variety and vineyard features influence on disease prevalence 64
Figure 13 Effect of tested predictors on long-term disease occurrence..... 68
Figure 14 A visual representation of our predictions regarding various effect sizes and their heterogeneity is illustrated by mini-forest plots..... 79
Figure 15 The overall effects of tested domains in *Botrytis cinerea*..... 97
Figure 16 The overall effects of tested domains in *Plasmopara viticola* 98
Figure 17 The overall effects of tested domains in *Erysiphe necator* 99

LIST OF SUPPLEMENTARY

Supplementary 1 Summary of the taxonomic and biological differences of the tested plant species, including the sampling events 116
Supplementary 2 The associations between conidia germination of *Botrytis cinerea* and a set of predictors: temporal, concentration, species and their interactions..... 119
Supplementary 3 The associations between conidia germination of *Botrytis cinerea* and a set of predictors: temporal, concentration, host compatibility (host, non-host) and their interactions 122
Supplementary 4 The associations between conidia germination of *Botrytis cinerea* and a set of predictors: temporal, pollen concentration, cultivation (crop, non-crop) and their interactions 123
Supplementary 5 The associations between conidia germination of *Botrytis cinerea* and a set of predictors: temporal, concentration, pollen volume and their interactions 124
Supplementary 6 The association between grape disease occurrence and vineyard features, crop management, and grape variety features 125
Supplementary 7 The association between *Botrytis cinerea* infection occurrence and plantation and crop management characteristics 127
Supplementary 8 The spatial variations of grape disease occurrence among regions 129
Supplementary 9 The association between *Plasmopara viticola* infection occurrence and plantation and crop management characteristics..... 130
Supplementary 10 The association between *Erysiphe necator* infection occurrence and plantation and crop management characteristics 132
Supplementary 11 The association between the infection occurrence and the grape variety-specific characteristics 134
Supplementary 12 Summary of the formal grape variety name based on the VIVC database, the reference variety number and the common name used in Hungarian. 136
Supplementary 13 Summary of grape varieties based on VIVC database 137
Supplementary 14 The plot shows combined indicator values for dAIC and RMSE at different base temperatures using the GDDa approach 143
Supplementary 15 Growing Degree Days: Scientific Relevance, Explanations and Methodical Implications..... 143
Supplementary 16 The heat map plot provides a graphical representation of the combined indicator values for dAIC and RMSE at various lower and upper temperature ranges, using the GDDb approach..... 149

Supplementary 17 The heat map plot provides a graphical representation of the combined indicator values for dAIC and RMSE at various lower and upper temperature ranges at different heat threshold levels, using the GDDc approach 150
Supplementary 18 The plot shows the association between the standard deviation and the threshold differences (i.e., T_{upper} - T_{lower}) in the GDDb predictors..... 151
Supplementary 19 The multiple plots compare the density distribution of the model fits regarding the GDD predictors and their relative positions..... 152
Supplementary 20 The relationship between the grape development and growing degree days (GDDa, Tbase=8°C, 'GDD ST8')..... 153
Supplementary 21 The relationship between grape development and cumulative precipitation 154
Supplementary 22 The relationship between grape phenological shift and other plantation-related factors, such as vineyard and crop management features..... 155
Supplementary 23 The relative importance of climate-corrected grape phenological shift, plantation features, and crop management characteristics in the long-term occurrence of diseases 156
Supplementary 24 The roles of variety, ripening classes and local climate 158
Supplementary 25 The association between grape development (i.e., BBCH) and the climatic characteristics, testing the effects of Ripening and Variety..... 159
Supplementary 26 Effects of climatic characteristics and variety on grape phenological shift 159
Supplementary 27 Effects of the climatic characteristics and variety-specific ripening categories on grape phenological shift..... 165

1. GENERAL INTRODUCTION

Living organisms are not the simple receivers of environmental impacts, but they attempt to response adaptively to the current environmental factors of their habitat (CORRIS 2020). Global climatic changes are one of the main drivers of the phenotypic shift of plants. The climate change is accelerated directly or indirectly by anthropogenic activities such as the intensification of agricultural production (AZHAR KHAN et al. 2014; PRAKASH and VERMA 2022). As a consequence of changes in climatic conditions, the distributions of many species have shifted to previously unfavourable considered regions, resulted modification not only in the spatial but the temporal distribution too, such as accelerated phenological development due to modified climatic conditions (ANDERSON and SONG 2020; FRAGA et al. 2017).

Vineyards are one of the most significant examples of these outbreaking crops, since most of the original wine-producing regions are located in the temperate climatic belt (ILAND et al. 2009). In the last decades, vines conquered new growing areas and have become nearly the largest volume produced crop in the tropics and subtropics area (POSSINGHAM 2004). The conquest of new areas with favourable conditions is the strategy of plant pathogens too, as they are forced to follow the migrating hosts (CHAKRABORTY 2013). Thus, requirement of dynamic evolution is more pronounced in grape pathogen fungi, where pathogens are shaped by the environmental changes and grapevine at the same time. The adaptation to the growing environment is essential for survival since the complex growing environment affects highly the lifecycle of grape pathogens (e.g.: required temperature for spore germination etc.).

Frequency and severity of grape diseases could vary within and among years and the occurrence and severity show a diverse spatial pattern. The most common grape diseases as grey mould (*Botrytis cinerea* Pers.), downy mildew (*Plasmopara viticola* (Berk. & M.A. Curtis) Berl. & De Toni.) and powdery mildew (*Erysiphe necator* Schwein.) are regularly present in vineyards with various magnitude and are highly exposed to a wide range of environmental factors. *Botrytis cinerea* is a necrotrophic fungus, which causes an annual 2 billion USD economic loss in viticulture internationally and its conidia production depends highly on temperature and humidity (20–25 °C and 92–96% relative humidity) (CILIBERTI et al. 2016; ELMER and MICHAILIDES 2007; THOMAS et al. 1987). *Plasmopara viticola* is a biotrophic pathogen causing serious losses under warm and wet conditions, thus pathogen sporulation depends mostly on temperature and relative humidity (18-22 °C and 95-100% relative humidity) (KASSEMEYER and BERKELMANN-LÖHNERTZ 2009). *Erysiphe necator* is a biotrophic pathogen which conidia formation is determined by temperature and humidity (25 °C and 85% relative humidity)

(GADOURY et al. 2012). Therefore, the growing environment is the most important influencing factor for pathogen survival.

At the micro spatial scale, plant pathogens are exposed to a wide variety of organic materials, including airborne pollen grains and fungal spores, which microbiome can interact on the surface of grapes (HENNEBERT 1973; KOCSIS et al. 2022; SCHERMAN et al. 2025). At the large spatial scale, various environment-induced selection pressures could modify the occurrence of grape pathogen agents. Due to the increased anthropogenic activity and the intensification of agricultural production the traditional production practices have changed. There is strong evidence that vineyard features (e.g. row orientation), crop management (e.g. number of chemical treatments) and grape variety features (e.g. ripening) influence the long-term disease prevalence (KOCSIS et al. 2024). The local climatic conditions act as a selection pressure on the level of a large spatial scale, the climate could generate shifts in grape phenology patterns (MOSEDALE et al. 2016). The shifted phenological development could set back the plant protection through less accurate forecast and prolonged exposure to infection, while agrotechnical activities and chemical treatments are timed to the optimum development stage of grapes (SCHULTZ et al. 1987). The soil parameters may have an additional impact on the long-term occurrence of grape diseases as a component of the macro-environment as vines are exposed to the effect of soil quality and composition due to being located on the same soil over a long period and anthropogenic activity could accelerates the changes of soil via preferred cropping practices and intensive land-use (LAL 2012; TSIAFOULI et al. 2015; YANG et al. 2020). Consequently, the susceptibility to plant pathogens is the result of a complex growing environment and cannot be assigned to a single characteristic. Thus, the interpretation of combined effect of the complex growing context together is essential to detect the mechanism of pathogen infection.

Therefore, to investigate the influencing factors of grape disease, it is necessary to amalgamate to synthesize and integrate knowledge among disciplines plant production, biology of plant pathology and environmental sciences. In this cross-disciplinary research series, we aimed to identify the most meaningful factors of a complex growing environment which define the long-term disease risk.

2. POLLEN-SPORE INTERACTION

2.1 Literature overview

The airborne components fundamentally determine a wide range of biological processes (e.g. pollination) and often can be the source of several adverse environmental, agricultural and human impacts (RANDALL 1990). The vast majority of the airborne organic mass is plant pollen grains and fungal spores, which are often transported together (MAGYAR 2008). However, a considerable amount of evidence has been collected regarding the pollen and spore airborne transportation and related issues; there is still a lack of information about the biological processes after the accumulation of the pollen and spore grains, especially their interspecific interactions.

The natural pollen trap is a specific surface of an inanimate object or a living organism where the accumulation of atmospheric plant pollens takes place Figure 1 (ZHANG et al. 2019). However, the term of pollen trap is mainly referred to the deposit place of plant pollens, other airborne particles with similar sizes could also be deposited massively, such as fungal spores (MAGYAR 2008). So, we used this term as an accumulation place for both pollen and spore hereafter. The plant surface can be a very effective pollen trap if the particular organ has a relatively large surface with depressions and complex structures, such as leaf stalks, flowers, fruits or bark (FÆGRI et al. 1989; GROENMAN-VAN WAATERINGE 1998; SONG et al. 2014), and can also preserve surface moisture and wetness (SOSA-ALVAREZ et al. 1995). A pollen trap containing a considerable amount of pollen and other organic materials with moisture could provide an ideal microenvironment, nutrient source and chemical trigger molecules for spore germination and the initial fungal growth (HENNEBERT 1973). A crop plant is often exposed to a massively produced pollen by the cultivated or other plants and spore grains due to the sporulation of the crop-specific plant pathogens. Furthermore, the pollen trap effect may be even more pronounced in a crop plant growing in large-scale agricultural areas than in a plant living in a natural habitat. Therefore, if a pollen trap accumulates pathogenic fungus spores and creates ideal environmental conditions to support the initial development of specific pathogens, a pollen trap could be a potential infection risk zone for the plant pathogen infection depending on the host-pathogen compatibility.

Figure 1 *Leaf as natural pollen trap (Kocsis 2020)*

The stimulatory effect of pollen grains on conidia germination and initial colonisation was barely documented previously, focusing on a few plant-pathogen pairwise comparisons. However, these early studies only revealed the presence or absence of the stimulation response in the particular pollen-spore interaction (BACHELDER and ORTON 1962; CHOU and PREECE 1968). These early studies showed clear evidence for the spore stimulation by exposure of the pollen's aqueous extracts, which were exposed to different concentration levels, but the comparison of these results was challenging due to the heterogeneity of the applied methods among studies. The high variation of the described concentration thresholds suggested a powerful species-specific stimulation effect in the plant-pathogen interactions. Similarly, other studies also reported high variance in the pollen chemical composition within and between species or pollination types (KOSTIĆ et al. 2017; NICOLSON et al. 2018; NICOLSON and HUMAN 2013). Thus, the chemical composition could be a potential source of the high heterogeneity of the pollen-spore interactions. At the same time, these patterns could also be driven by the consequences of the specific host-pathogen coevolution and breeding processes, which could be the primary selection forces shaping the pollen variation in crop plants' morphology and physiology (LYU et al. 2021; OCCHIPINTI 2013; PISKORSKI et al. 2011). Thus, these factors may also play an important role in the pollen stimulatory effect, generating differences between host and non-host or crop and non-crop plants. These species-specific and functional attributes may explain the heterogeneous pollen-spore interactions, which urges the need to reveal these unknown mechanisms using a multispecies study approach.

Regarding the potential role of the pollen-spore interaction in the initial development of specific pathogens, studying the pathological risk of plant pollen exposure would not be essential only for a theoretical purpose, but it could be helpful for practitioners in crop production. These effects could be more emphasized in those plant pathogens of which spores transferred and accumulated together with pollens, and so the airborne pollens could constantly stimulate the conidia germination in cultivation, such as in *Botrytis cinerea* (CHOU and PREECE 1968; OGAWA and ENGLISH 1960). The causal agent of grey mould is *Botrytis cinerea*, a facultative parasite fungus, being a significant pathogen with a wide range of host plants, causing critical yield losses worldwide year by year in several cultivations such as strawberry (*Fragaria* x *ananassa*), raspberry (*Rubus idaeus*) and grape (*Vitis vinifera*). Airborne conidia of *Botrytis cinerea* are produced intensively and, as a primary source of inoculum, can infect plant organs, such as flowers and fruits (ROMANAZZI and FELIZIANI 2014). Moreover, these conidia are transported through advection and can be easily trapped in natural pollen traps on the surface of crop plants. These species-specific features and the positive conidia germination response to the pollen extract make *Botrytis cinerea* an ideal model organism to test the general patterns of pollen-spore interaction.

2.2 Aims and objectives

The pollen grains have a species- or function-specific chemical composition profile (HESSE 1981; NICOLSON and HUMAN 2013), so their aqueous extracts could generate a high variance among plant taxa along with the pollen concentration and the temporal gradients in the conidia germination (CHOU and PREECE 1968). Therefore, in this multispecies comparison, we paid particular attention to the species and function-specific pollen attributes which could interfere with the pollen-spore interactions, generating differences in the concentration- and time-dependent stimulatory effect on conidial germination in *Botrytis cinerea*. Specifically, we tested the possible role of the species-specific functional characteristics such as host-pathogen compatibility (non-host or host), cultivation (non-crop or crop), pollination type (anemophilous or entomophilous) and pollen size. Regarding the tested factors, we formulated to following predictions.

First, due to the long-term coevolutionary background between the host plants and their pathogens by chemical composition-based cue recognition mechanisms (e.g., REZZONICO et al. 2017), we hypothesized that pollen from the host plant of *Botrytis cinerea* has a more substantial effect on conidia germination than an incompatible plant.

Second, we predicted that a crop plant has a more significant stimulating effect on *Botrytis cinerea* conidia than a non-crop, a weed or free-living species because the selective breeding processes could affect the pollen morphological attributes and chemical compositions.

Third, we hypothesized functional and chemical differences between anemophilous and entomophilous plants, which may explain the variance in stimulatory effect.

Fourth, if the pollen variances in chemical composition determine the temporal dynamics of conidia germination, we assumed that pollen with greater biomass contains more stimulants and/or represents a higher nutrient value for the initial conidia development, which may influence conidial germination more effectively. Therefore, in the present study, we provided a detailed overview of the pollen-spore interaction to deepen our understanding of the pollen stimulatory effect on *Botrytis cinerea*.

2.3 Material and methods

Pollen collection, isolation, identification and maintenance of the pathogen

Testing biologically relevant pollen-spore interactions, we targeted to test specific pollinating plants potentially living in agricultural or rural habitats and overlapping their flowering period with the susceptible phases of the potential host infection by *Botrytis cinerea*. The susceptible phenological stage to *Botrytis cinerea* infection was defined based on the vegetation of strawberry, raspberry and grape hosts. At the same time, the overlapping flowering periods were explicitly selected based on a long-term descriptive national survey (UDVARDY et al. 2019). Additionally, we selected plants with high pollen production categorizing them into different functional groups. Specifically, the tested species included host plants of the pathogen and non-host plants, anemophilous and entomophilous plants, and non-crop and crop species (e.g. cover plants, weeds).

To extract fresh pollen for laboratory analyses, we collected flowering plant parts in full blooming from the focal species based on the species-specific blooming periods (between May and September) in two consecutive years (2018, 2019) in agricultural habitats (for sampling details, see Supplementary 1). The plant samples were labelled individually and transported into the laboratory for further preparation. Only the freshly opened flowers were selected to extract the pollen grains manually in the laboratory, attempting to collect 1-1.5 cm^3 pollen grains in each species. Then, the pollen grains were stored in a paper envelope (7 °C) for further use. To approximate the pollen size, we estimated the pollen grain volume by measuring the polar and equatorial diameters of pollen grains (N=10 in each species with the accuracy of 0.1 µm) and calculated the spherical volume according to (DIMOU et al. 2020). The measurement was carried out under a light microscope (Nikon Eclipse 50i) at 400× magnification using QCapture Software (version 6.0). Next, we created a derived variable called ‘volume corrected concentration’ after multiplying the values regarding species-specific pollen size, approximate pollen volumes (approximated by the volume of a sphere: r3×PI, in which *r* is the species-specific radius of pollen)

and the pollen concentration (zero, medium and high, see later). This variable can express the pollen exposure in the aqueous extracts more accurately than the concentration alone.

In the laboratory, we established a *Botrytis cinerea sensu lato* strain isolated originally from an infected bunch of grapes (cv. Furmint) collected near Szekszárd (Hungary). The applied *Botrytis cinerea* strain (BC2108; Institute Type Collection, Hungarian University of Agriculture and Life Sciences, Institute of Plant Protection, Budapest, Hungary) was previously analysed, including morphological features, cultural characteristics, pathogenicity tests, and molecular tools also confirmed the identification. Conidia were cultured on PDA plates (Biolab Inc., Budapest, Hungary) with five replications at 24 °C in the dark. On the 14th day of the incubation period, colony and conidial morphology were visually observed and checked. Morphological identification was performed according to (COLEY- SMITH 1980). The *Botrytis cinerea* cultures were maintained on malt extract agar (GREEN et al. 2006). Before each pollen-spore test, the conidia were harvested manually from the sporulating part of the colony in a sterile environment.

The pathogenicity test was conducted on mature grape berries (cv. Furmint) with conidia in three parallel replications. First, the surface-sterilized berries with pedicels were placed in sterilized glass containers on moist filter paper. After that, the conidial suspension (4×10^4 conidia/mL) was added dropwise to the surface of the fruits. The inoculated berries were incubated with 95-100% relative humidity at room temperature (21±2 °C). Finally, *Botrytis cinerea* was re-isolated from the necrotic tissues to confirm Koch's postulates (data not shown).

Measuring pollen stimulating effect

Firstly, three different pollen suspensions were prepared with different concentrations, including zero, medium and high (0, 5×10^4 and 1×10^5 pollen grains per ml, respectively). The proper concentration was validated by using the Bürker chamber. After the validation process, the suspension was allowed to stand for 18 hours for the dissolution of the pollen constituents at room temperature (21±2 °C) (BÉKÉSI 1977). Only the supernatant fraction (aqueous pollen extracts without pollen grains) was added for stimulation. Secondly, the sporulating *Botrytis* culture was washed with sterile water to harvest the produced conidia. After validation, we applied a standard concentration of conidia suspension in all tests (5×10^5 conidia grains per ml).

The pollen-spore interaction test started when the aqueous pollen extract was added and gently mixed with the conidia suspension in a ratio of 1:5 (0.08 mL and 0.4 mL, respectively) onto the microscopic slides with reaction wells (Omano, diameter depression 15 mm). The microscopic slides were then placed into sealed sterile Petri dishes for incubation to maintain the humid and sterile environment. Three microscopic slides were prepared as repetitions in each pollen

concentration, and we examined them separately in each plant species. Conidia germination was measured at four, six and eight hours after the beginning of the treatment by visual observation using a light microscope (Nikon Eclipse 50i) at 400× magnification. We examined five microscopic views in each sampling event, counting ten random conidia. A conidium was considered to be germinated if the germ tube length reached or exceeded the largest diameter of the conidia (Figure 2). Finally, we expressed our observations as a percentage of the germinated conidia in each sampling unit and used them as a response variable in the statistical analyses.

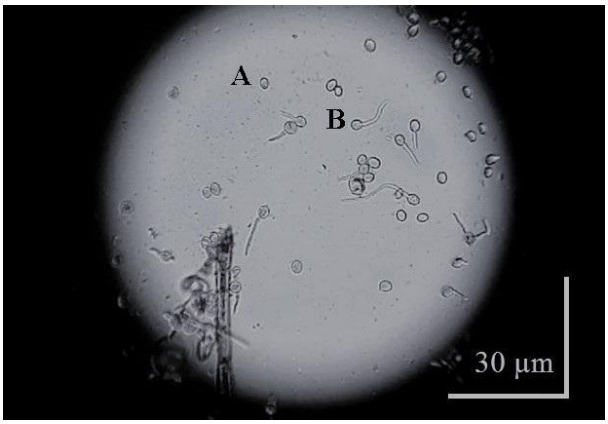


Figure 2 Botrytis cinerea *conidia germination under a light microscope*

Non-germinating (A) and germinating (B) conidia of Botrytis cinerea *under light microscope at 400× magnification (Kocsis, 2020).*

Statistical analysis

Merely for validation of the applied measuring procedure, we quantified the repeatability as the ratio of the within-group and the total residual variances calculated by Markov Chain Monte Carlo sampler for multivariate Generalized Linear Mixed Models based on repeated measurements of the identical sample units (R package: 'MCMCglmm', HADFIELD 2010). The mean and the quantiles (2.5% and 97.5%) of the MCMC outputs represented the repeatability index and the confidence intervals (CI_{95}), respectively, based on 1000 permutations. As a result, we derived a high repeatability index (0.701; CI_{95}: 0.681/0.721), which means that data of independent measurements carried out under the same conditions were in close agreement. This result indicated that our test series followed a valid methodology.

Models

First, we tested the basic concentration- and temporal-dependent patterns on the germination ratio by a Generalized Mixed Effect Model with a negative binomial error structure (GLMM-nb), approaching a better distribution of the response variable. In this 'basic' model (model formula: Germination ratio ~ Concentration+ Time+ Concentration:Time+ (1|Slide_ID)), we entered the percentage of the germinated conidia as the response variable, and the predictor variables were the concentration of the pollen extract ('concentration'), the measuring time ('time') presented as covariates, and their interaction (concentration × time). At the same time, the random factors represented the slide identification number due to the repeated measuring of the identical slides, and a hierarchical nested random structure (family nested in the order) provided a statistical control to the botanical origin.

Second, we tested the species- and functional-specific related predictors such as 'Species', 'Host compatibility', 'Cultivation' and 'Pollination' (as factors). The basic GLMM-nb model structure was supplemented with a single predictor one by one in each model and running them separately. Integrating all the tested variables into a single model could not be performed because each predictor carried a species-dependent attribute generating zero variances. We applied a likelihood ratio test (LRT) to test each predictor's effect in these extended models. After that, models with significant predictors were further analysed by testing the specific interactions, such as concentration × predictor and time × predictor.

Final, we tested the effect of pollen volume on the pollen-spore interactions. As a first step, we tested the presence of an a priori systematic variance of the pollen volume between the functional groups by Welch's t-test. If the functional groups were the same, we could consider the pollen volume as a separate, species-specific attribute.

Next, we tested the effect of the pollen volume corrected concentration ('Concentration-volcorr') using a separate GLMM-nb model. In this model, we entered the germinated conidia ratio (percent) as the response variable, and the 'Time' and the 'Concentration-volcorr' represented the covariates, and their interactions, while the random factors were the same as in the basic model.

The numeric predictors were centred and scaled in all statistical models before running the analyses. The model diagnostics were always checked in all final models. The post-hoc tests were calculated by pairwise Student's t-test comparisons between group levels with 'Holm' adjustments of the P-values due to the planned multiple testing. The statistical analyses were carried out in the R statistical environment (R Development Core Team 2019) using the 'lme4' package (BATES et al. 2014a).

2.4 Results

To explain the variation of the pollen aqueous extracts' stimulation effect on the spore germination in *B. cinerea*, we tested the species- and several function-specific attributes such as host compatibility, cultivation, pollination type, and pollen volume.

Overall impact

First, we found robust and general concentration and temporal-dependent patterns in the germination ratio (Figure 3). The spore germination increased with the measuring time along with the concentration gradient of the aqueous pollen extract. The significant interaction between time and concentration suggested non-zero temporal dynamics in the germination ratio among the concentration treatments.

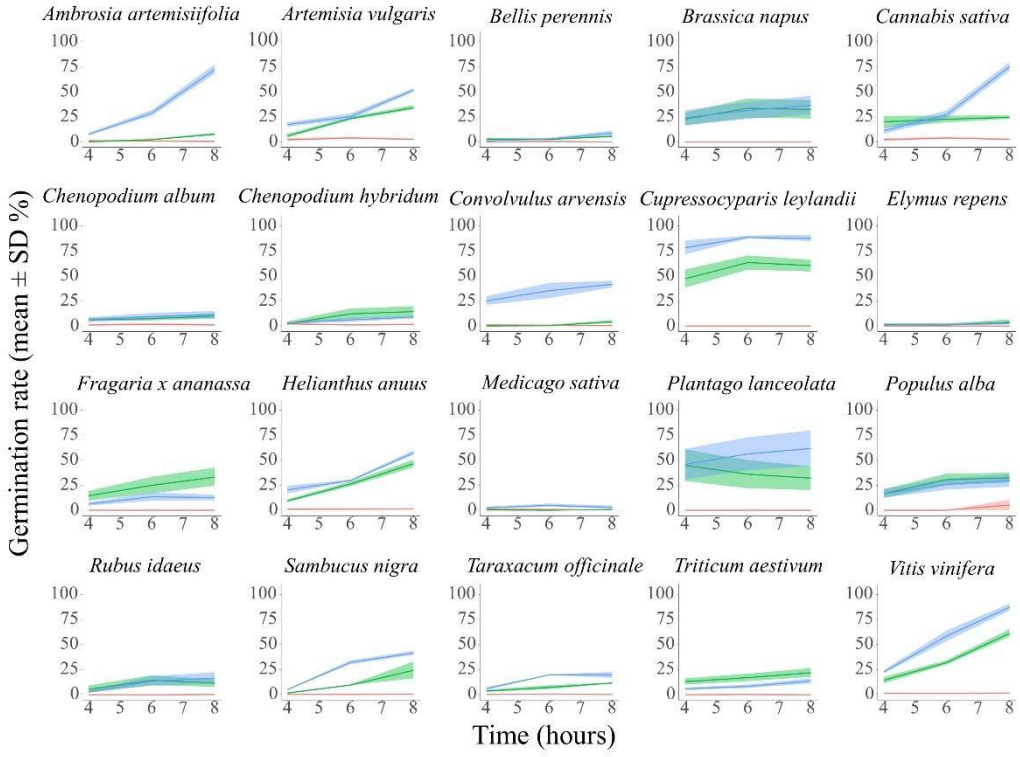


Figure 3 *The species-specific stimulation effect of pollen on* Botrytis cinerea *conidia germination rate over time and concentration*

Plot summarizes the species-specific stimulation effect of the pollen aqueous extracts on the conidia germination rate within the measuring period along with three different concentration levels. The lines with different colours represent the different concentration treatments of the aqueous pollen extracts (red: zero, green: medium, blue: high concentration). The shaded zones around a line indicated the standard deviation of the corresponding mean value.

Functional attributes

Second, we tested the specific functional attributes by expanding the basic model using a focal predictor. We found that the species, host compatibility and cultivation highly affected the germination ratio, while the pollination type did not affect germination ratio significantly. In all expanded models, the basic relationships regarding concentration and temporal patterns were consistently the same as we revealed previously in the basic model (Table 1).

Table 1 Botrytis cinerea *conidia germination association with specific predictors and their interactions*

Results from generalized mixed effect model with a negative binomial error structure (GLMM-nb), in which the conidia germination was the response variable, testing the association with specific predictors and their interactions.

Model name	Predictor variable	χ^2	df	p-value
Basic	Time	135.677	1	<0.001***
	Concentration	296.148	1	<0.001***
	Time × concentration	9.128	1	0.002**
Species (20 factors)	Time	147.287	1	<0.001***
	Concentration	332.129	1	<0.001***
	Species	148.045	19	<0.001***
	Time × concentration	11.248	1	<0.001***
	Concentration × species	48.760	19	<0.001***
	Time × species	47.529	19	<0.001***
Compatibility (2 factors)	Time	137.098	1	<.001***
	Concentration	297.792	1	<0.001***
	Host compatibility type	4.413	1	0.036*
	Time × concentration	9.968	1	0.002**
	Concentration × host compatibility type	2.249	1	0.133
	Time × host compatibility type	4.694	1	0.03*
Pollination (2 factors)	Time	135.557	1	<0.001***
	Concentration	297.209	1	<0.001***
	Pollination type	1.413	1	0.234
	Time × concentration	9.088	1	0.003**
Cultivation (2 factors)	Time	136.064	1	<0.001***
	Concentration	306.461	1	<0.001***
	Cultivation type	8.699	1	0.003**
	Time × concentration	9.505	1	0.002**
	Concentration × cultivation type	5.347	1	0.021*
	Time × cultivation type	0.601	1	0.438
Pollen volume	Time	140.879	1	<0.001***
	Volume-corrected concentration	69.120	1	<0.001***
	Time × volume-corrected concentration	0.006	1	0.941

*Note: The Chi-square values, the degree of freedom (df) and the significance levels (p-value) were calculated from the corresponding likelihood ratio test that compared the model fit of the full model and the reduced model after excluding the given predictor. The stars indicated the level of significance of the given predictor (*p < 0.05, **p < 0.01, ***p < 0.001).*

Focusing on the botanical differences (Figure 4 and 5), we detected high species-specific variations, including weak (e.g., *Medicago sativa*, *Elymus repens*), medium (e.g., *Fragaria* × *ananassa*, *Sambucus nigra*) and strong (e.g., *Vitis vinifera*, *Cupressocyparis leylandii*) stimulation effects. Furthermore, this general level of the spore germination showed considerably different temporal dynamics in germination along the concentration gradients (for more details, see Supplementary 2).

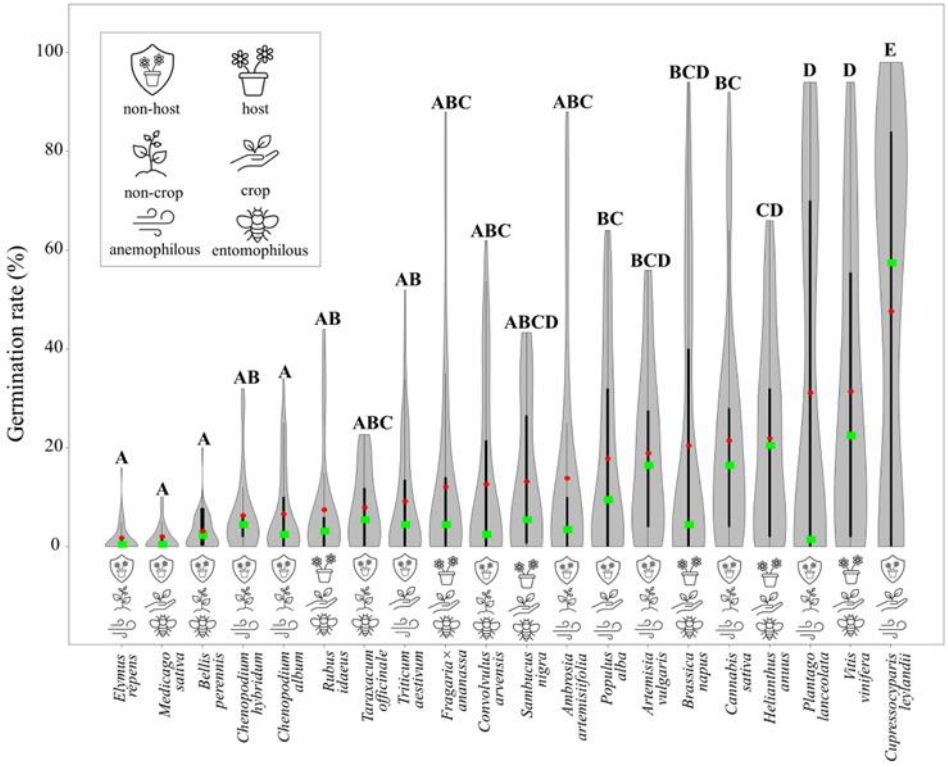


Figure 4 *The species-specific stimulation effects of pollen on* Botrytis cinerea *conidia germination within species-specific attributes*

Violin plot illustrates the general species-specific stimulation effects of the pollen aqueous extracts on the spore germination rate of Botrytis cinerea. *In each species, the vertical black line represents the interquartile data range, while the points indicate the mean and median germination ratio by a red circle and a green square, respectively. The different letters show significant differences at* $p < .05$ *level according to the post hoc tests. The icons represented the species-specific attributes (host compatibility: host, non-host; cultivation: crop, non-crop; pollination type: anemophilous, entomophilous).*

Interestingly, we could detect spore stimulation effects in most non-host and non-crop species, and only a few pollen extracts (with non-zero concentrations) caused undetectable responses. Specifically, in the host species, the medium and high pollen concentration extracts stimulated a similarly high and consistent temporal increase in the germination ratio (Figure 5, Table 1, Supplementary 3 and 4). In contrast, the non-host pollen extracts showed a concentration-dependent response at the medium and high concentration treatments 8 hours after the tests started. Similarly, a stimulation difference emerged in the crop and non-crop comparisons, with a difference appearing after 6 hours between the medium and high treatments in the crop plants, while in the non-crop species, this effect was consistently the same in the non-zero concentration groups throughout the study.

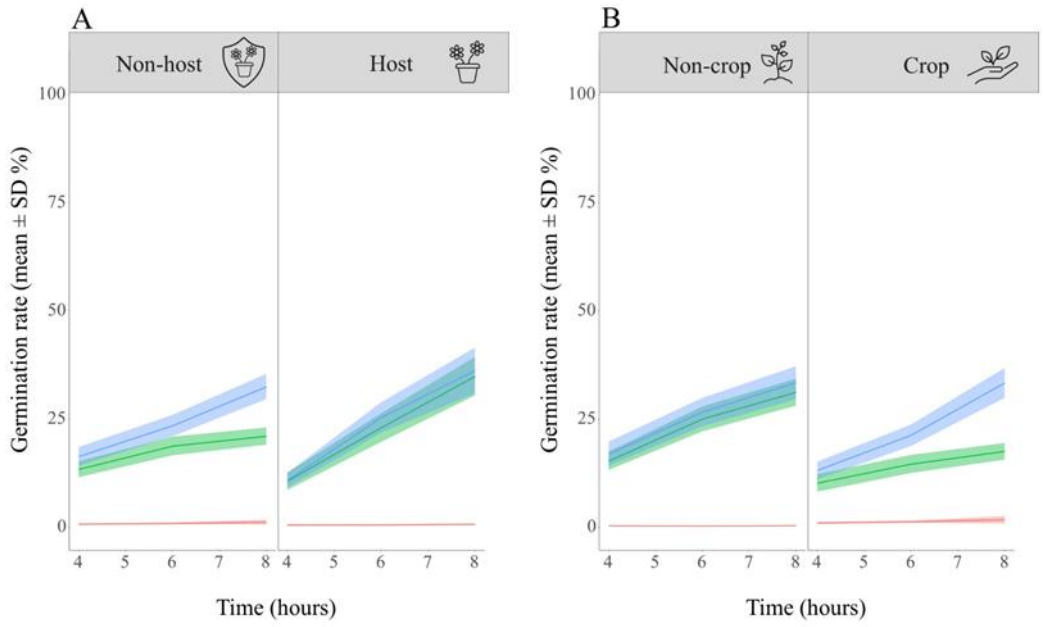


Figure 5 *The temporal- and concentration-dependent pattern of* Botrytis cinerea *conidia germination rate*

Plot shows the conidia germination rate's temporal- and concentration-dependent patterns regarding the host compatibility (A) and cultivation types (B). The lines with different colours represent the different concentration treatments of the aqueous pollen extracts (red: zero, green: medium, blue: high concentration). The shaded zones around a line indicate the standard deviation of the corresponding mean value.

Pollen volume

Third, we tested the effect of pollen volume on the pollen-spore interactions. Nevertheless, before testing a quantity feature, we tested whether there was a priori systematic variance in the pollen volume between the functional groups, which could result from differential selection environments. Then, we confirmed that all functional groups were homogenous in pollen volume (Host-compatibility: t = -1.217, df = 16.14, p-value = 0.24; Cultivation: t = 0.399, df = 15.06, p-value = 0.69; Pollination: t = 0.264, df = 17.51, p-value = 0.79). So, we could test this species-specific feature as a separate attribute. Similarly to previous models, we found a temporally consistent stimulation effect and detected a robust increase with the exposition of the volume corrected concentrations (Figure 6, Supplementary 1 and 2).

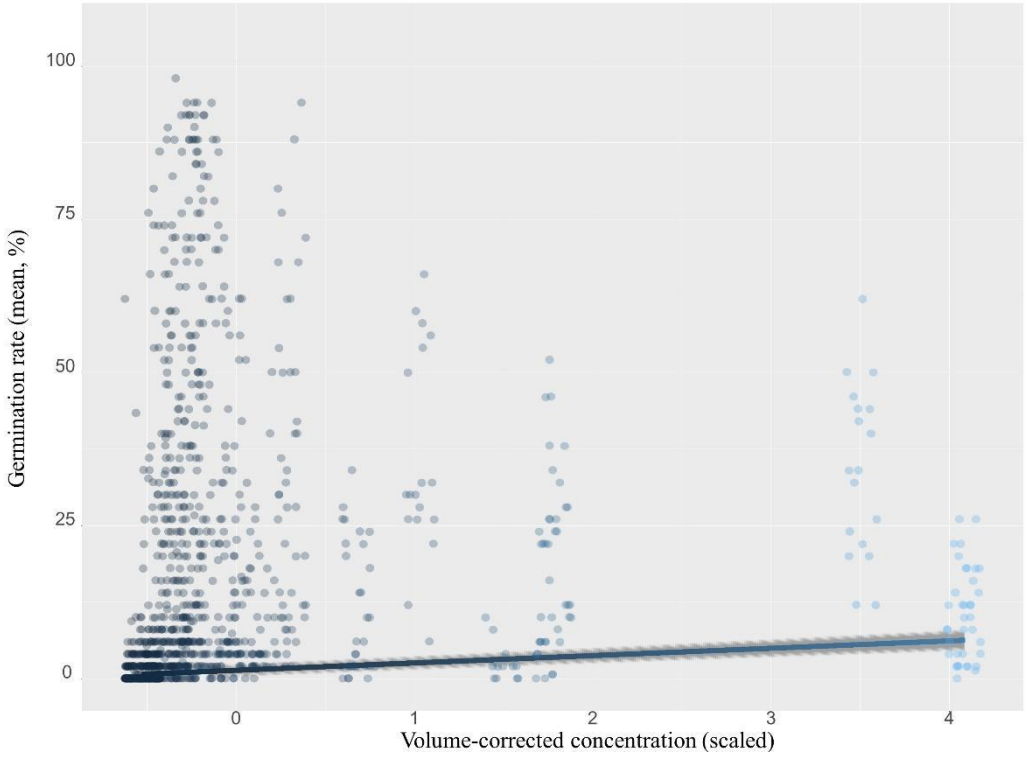


Figure 6 *The relationship between the volume-corrected concentration and* Botrytis cinerea *conidia germination rate*

Plot shows the relationship between the volume-corrected concentration (scaled data shown) on the conidia germination rate (mean, %). The line represents the regression slope with the confidence intervals (shaded zone). The data (horizontal, x axis) were slightly jittered both directions equally to improve the visualization.

2.5 Discussion

This study investigated the pollen's possible role, which could effectively interfere with the pollen-spore interactions. We compared 20 plant species with functionally diverse attributes and estimated the stimulatory effect of their aqueous pollen extracts on spore germination in *Botrytis cinerea* as a polyphagous and widely distributed fungus. In general, we found robust concentration- and temporal-dependent stimulatory effects, which highly varied among species. Furthermore, the dose-response patterns reflected a considerably high species-specific pollen difference in the response's magnitude and speed (Figures 3 and 4, Supplementary 1). These results supported the previous assumptions that pollens might bear a unique chemical composition which could generate species-specific differences as germination stimulants of fungal spores.

Regarding small water-soluble molecules, the results provided indirect evidence for the validity of the basic assumptions that the pollen grains' chemical profile and their taxonomic variance in quality and quantity could play an essential role in interspecific interactions. Generally, pollen and other pollen-based food products were often considered high in nutrient and vitamin values due to the specific carbohydrates and protein compositions (NICOLSON and HUMAN 2013). In close agreement with our results, similar species-specific chemical composition patterns (e.g. carbohydrates, proteins, lipids, trace elements) were revealed in different plant pollens and pollen-kitts (DOBSON 1988; PISKORSKI et al. 2011; STANLEY and LINSKENS 1974). Recently, only a handful of studies attempted to describe a detailed chemical composition of the hand-collected pollens, mainly for the descriptive purpose of their nutrient values (KOSTIĆ et al. 2017; NICOLSON et al. 2018; NICOLSON and HUMAN 2013).

The natural selection and crop breeding processes can generate a driving force for the fitness-related traits shaping systematic functional differences among plants, such as fertilisation and the pathogen infection (OCCHIPINTI 2013). So, these selection forces could also affect the pollen's chemical and morphological attributes. Therefore, we predicted that if the pollen morphological structure and chemical composition were shaped by the same long-term selection process, such as host-pathogen coevolution, plant breeding or pollination, we could detect similar systematic variation in the dose-response spore stimulation among taxa within the same functional group. Supporting the previous expectations, we detected systematic differences in the functional attributes, such as host-pathogen compatibility and the type of cultivation (Figure 5, Table 1, Supplementary 3 and 4), but no differences between the pollination types. Thus, the non-random spore responses indirectly reflected the species- and function-specific differences via the pollen extracts' chemical composition profile. If so, the chemical profile within the same functional group

would be more similar expectedly than between groups which prediction would be worth studying in the future.

Focusing on the relevance of the host-pathogen compatibility, the spore responses reflected taxonomic differences, which might be associated with the host-pathogen coevolution due to the differential qualitative and quantitative pollen properties. However, both compatibility groups elicited stimulation effects in all non-zero concentrations, and the efficiency of the non-host pollen extracts was reduced than the extracts of the host's pollens (Figure 5, Table 1, Supplementary 5). An essential selection factor in a host-pathogen interaction is the host's chemical recognition of a pathogen and how effective and sensitive this system is, in which a plant pathogen could exert considerably high selection pressure on its host plants (OCCHIPINTI 2013). If such a process is under selection, we expected that a pathogen fungus could gain adaptive benefits by increasing the efficiency of the host recognition, generating a similar response at a reduced concentration of the chemical stimulants, as illustrated in the results of this study similarly. On the other hand, plants also developed strategies to cope with their pathogens, such as evolving new chemical compounds (e.g. organic acids) for masking host recognition of the pathogens (LYU et al. 2021).

Crop breeding could also trigger directional phenotypic changes, evolving beneficial changes for plant management, while less direct selection forces shape the non-crop plants occurring in natural or semi-natural environments (WINK 1988). Despite the expected chemical diversity in pollens, this study revealed systematic variations in the stimulation effect between crop and non-crop groups. Like the effects of host-pathogen compatibility, crop and non-crop groups triggered the spore stimulation at medium and high concentrations (Figure 5, Table 1, Supplementary 3). However, the effect of non-crop plants generates a more intense response at medium concentration than the effects of the crop plants at a similar treatment. These relationships supported accepting the predictions that breeding processes could also generate differential phenotypic variations providing positive benefits for the crop plants and reducing the harmful interference of the host-pathogen interactions.

The pollination type can fundamentally determine the pollen's morphological structure and chemical composition. For example, anemophilous plants always produce powdery pollen, while the pollen grains produced by entomophilous plants are mostly sticky, facilitating attachment to the pollinator (HESSE 1981). Therefore, the effect of the pollination type was a biologically relevant functional attribute worth testing. However, besides the expectedly high variations between pollination types, the result showed that the pollination could not affect the conidia germination. This pattern can be interpreted by the partially overlapped selection forces shaping the host-pathogen interactions rather than the processes regarding pollination differently.

Therefore, this result suggested that the morphological adaptations to a specific pollination form were not enough to increase the spore stimulation effects. So, the potential role in spore stimulation could be less relevant.

Finally, we tested the hypothesis that the stimulation of the conidia germination increases with the pollen size, assuming that a larger pollen grain contains more nutrients and other stimulants than a smaller one (STANLEY and LINSKENS 1974). According to the expectations, the results showed that the effects were more pronounced in taxa producing larger pollen grains than plants with smaller ones (Figure 6, Table 1, Supplementary 5). Therefore, the pollen volume could be considered as a relevant species-specific attribute that varied independently on the variations related to host-pathogen compatibility, the cultivation, or the pollination types. Moreover, similar to previous results (STANLEY and LINSKENS 1974), this relationship also suggested that the spore stimulation effect of pollen could be based on qualitative and quantitative indicators due to the consistent and robust dose-dependent relationship and the high species-specific variances, respectively.

This study provided highly varied pollen-spore interactions between certain relevant plant species and a fungus, *Botrytis cinerea*. The results agreed with previous studies, which only demonstrated the presence or absence of the pollen-spore interactions between certain fungi and plant species (CHOU and PREECE 1968; FOKKEMA 1971; OGAWA and ENGLISH 1960), but our detailed multispecies study showed that the spore stimulation by plant pollens could be regulated by a more complex mechanism than previously expected. Therefore, further studies should pay particular attention to these small, water-soluble precursor molecules that could be responsible for regulating specific biochemical mechanisms. In addition, these pollen components might be structurally and functionally analogous to specific precursors in the spore, which could cause interference in similar processes during plant fertilization and spore germination.

In a comprehensive ecological approach, the plant organs (i.e. leaves pollen grains) could provide unique habitats (i.e. not only as chemical environments or nutrient sources) for specific microbiome assemblages composed of members from the fungal and bacterial kingdoms (FOKKEMA 1971; JUNKER and KELLER 2015; MANIRAJAN et al. 2018). Thus, the species-specific host-pathogen compatibility could also be driven by the diversity of the epiphytic and endophytic microorganism assemblages, which could shape the effectiveness of the natural plant-defence systems against pathogens via their intra- and interspecific competitions (MANIRAJAN et al. 2018; VANDENKOORNHUYSE et al. 2015). However, so far, the role of the microbiome structures and associations is still less known in the specific host-pathogen interactions, which knowledge would be beneficial in agricultural practice.

In summary, the results of the present study suggested a non-random taxonomic variation as a consequence of the differential selection forces, which might be manifested via the quality and quantity of the pollen chemical profile, and these effects might be the fundamental source of the heterogeneity in the spore-pollen interactions. Thus, a pollen trap could be an ideal environment for interspecific interactions via pollen and spore. However, the role of these specific molecules and other influential factors are still unknown, which could be essential in these biological mechanisms. Furthermore, the revealed mechanism in the plant-pathogen interactions may have many practical implications for crop production and protection management. For example, the pollen-spore interactions could generate additional infection risks in crop plants as natural pollen traps by the pollen-sourced stimulating factors. Therefore, future studies should pay more attention to revealing the functional comparisons regarding the form of cultivation, host-pathogen compatibility, or pollen size, especially in the initial development of plant pathogenic fungi.

3. VINEYARD, MANAGEMENT AND VARIETY CHARACTERISTICS INFLUENCE ON DISEASE PREVALENCE

3.1 Literature overview

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 et al. 1989). 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 required 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* (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* (PV, hereafter) and *Erysiphe necator* (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 unfavourable 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).

3.1 Aims and objectives

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 hypothesized 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 Supplementary 6. 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.

3.3. Material and methods

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. 2021). We collected geo-referenced data on the grey mould (*Botrytis cinerea*, BC), downy mildew (*Plasmopara viticola*, PV), and powdery mildew (*Erysiphe necator*, EN) disease severity in a traditional wine- and grape-producing country, Hungary (area: 93,030 km2, 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 7).

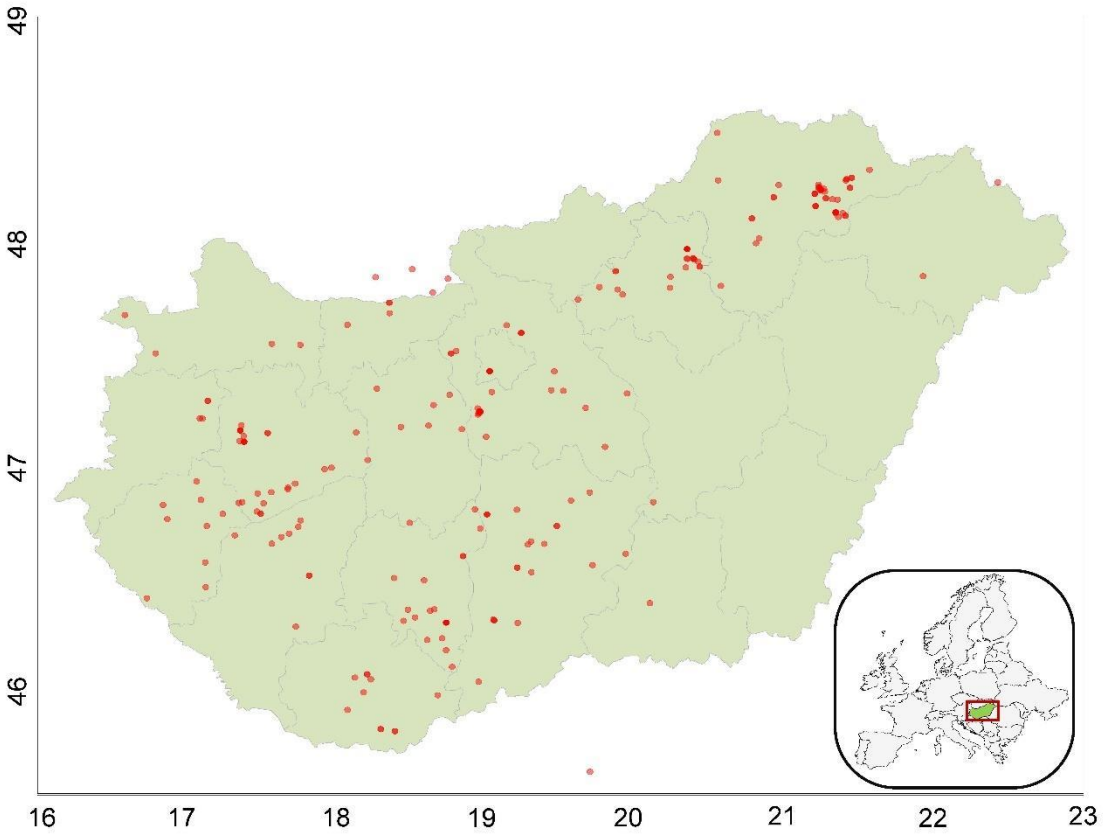


Figure 7 *The geo-referenced vineyards from Hungary and nearby*

Red dot, N = 239 independent observations

Questionnaire survey

Infection evaluation

To describe the long-term infection status, we surveyed two infection variables (Table 2). The infection ratio (numeric-discretee) 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 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) and the high infection (0–20 %, 21–40 %, 41–60 %, 61– 80 % and 81 % or higher).

Table 2 *Summary of surveyed variables on infection status of vineyard*

Variable	**Categories**				
Infection ratio	0–5%	6–20%	21–50%	51–80%	81%<
Infection severity	0–20%	21–40%	41–60%	61–80%	81%<

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 (Table 3).

Table 3 *Summary of surveyed variables on vineyard features*

Variable	**Categories**			
Qualification	Yes		No	
Survey year	Open question			
Variety	Open question			
Orientation	N-S (North–South)	NE-SW (NorthEast–SouthWest)	E-W (East–West)	SE-NW (SouthEast–NorthWest)
Inclination	0 (plain: < 5 %)	1 (gently slope: 5–12 %)		2 (sloping: < 12 %)
Surrounding vineyards	none (0–5%)	scattered (6–50%)	many (51–80%)	high (81% or higher)
Distance	Open question (cm)			
Age	Calculated by the difference between the vineyard plantation and the survey year			

Crop management

In this study, we focused on three crop management practices (Table 4). 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 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.

Table 4 *Summary of surveyed variables on crop management*

Variable	**Categories**			
Inter-row	Yes		No	
Treatments	1 Only dormant spraying/non-chemical pesticides	2 1-5 chemical spraying	3 6-10 chemical spraying	4 11 spraying or more
Leaf removal	Yes		No	

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. 2015; 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 (Table 5), 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.

Table 5 *Summary of surveyed variables on grape variety features*

Variable	Categories		
Susceptibility	Score between 1 (resistant) — 9 (extremely susceptible)		
Ripening	0 (early)	1 (medium)	2 (late)
Utilisation	Wine grape	Table grape	Both
Bunch compactness	Score between 1 (very loose) — 9 (very dense)		
Berry skin thickness	0 (thin)	1 (medium)	2 (thick)
Berry colour	Blanc	Rouge	Noir

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 $x'=(x-x_{min})/(x_{max}-x_{min})$, 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 based on the median of the corresponding year (0: below the median, 1: equal or higher median). These pathogen-specific, binarized 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. 2014a) (Table 6). 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 since the identification of pathogens in the initial stage is difficult (qualification yes: 1, no: 0.5). Furthermore, we used weight at the newly established plantations, since we examined the average infection of the last 5 years (if age $\leq$ 4 years: age $\times$ 0.2; or 5 $\leq$: 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).

Table 6 *Summary of model used for assessing the relationship between vineyard features, crop management and variety characteristics*

Assessment	Model
Effect of **Vineyard features** and **Crop management** practices on BC/PV/EN infection occurrence	BC/PV/EN~ Inclination+ Adjacent plantation+ Age+ Distance+ Treatments+ Survey year+ Orientation + Inter row management+ Leaf removal+ Region_ID + (1|Grape sort) + (1|Farmer ID), data=data2[data2$plant_age>4,], weight = qualif_vineyard_age In each statistical model, we applied a combined statistical weight considering the inequality data points given by the responses of qualified or unqualified grape producers (qualification yes: 1, no: 0.5) or the newly established plantations (if age ≤ 4 years: age × 0.2; or 5 ≤: 1).
Effect of **Grape characteristics** on BC occurrence: with noble rot varieties	BC~ Susceptibility+ Ripening+ Berry skin thickness+ Bunch compactness+ Berry colour + Utilisation, data = inf_varie_data, weights = bc_infbin_agequal_wght)
Effect of **Grape characteristics** on BC occurrence: varieties without noble rot varieties	BC~ Susceptibility+ Ripening+ Berry skin thickness+ Bunch compactness+ Berry colour + Utilisation, data = inf_varie_data[inf_varie_data$leading_sort != "furmint" & inf_varie_data$leading_sort != "sargamuskotaly"& inf_varie_data$leading_sort != "harslevelu",weights= bc_infbin_agequal_wght)

3.4 Results

Roles of the plantation features and crop management

We found that the BC occurrence was significantly associated with the orientation (Figure 8). Primarily, the NE–SW orientations increased the presence of the BC and the SE–NW row orientation less increased, 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 8). Similarly, the occurrence of BC infections increased with the number of chemical treatments (Table 7) and with the elevation of the canopy wall from the ground (Figure 9). We found significant spatial variation among the growing regions (Table 7, Supplementary 7, Supplementary 8). 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 7, Supplementary 7). We found that the infection of PV increased along with the magnitude of the inclination of the plantation (Table 7, Supplementary 9).

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 8). In addition, the increased adjacent plantations around the focal plantations elevated the infection occurrence (Figure 8). 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 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 7, Supplementary 9).

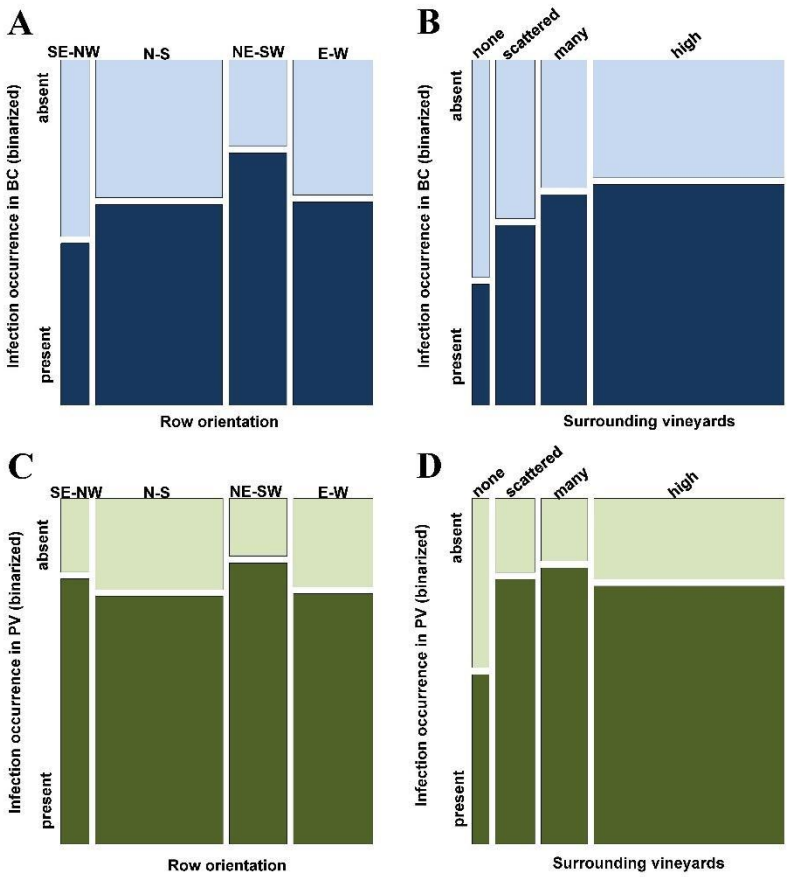


Figure 8 *The relationship between the infection occurrence and vineyard features*

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).*

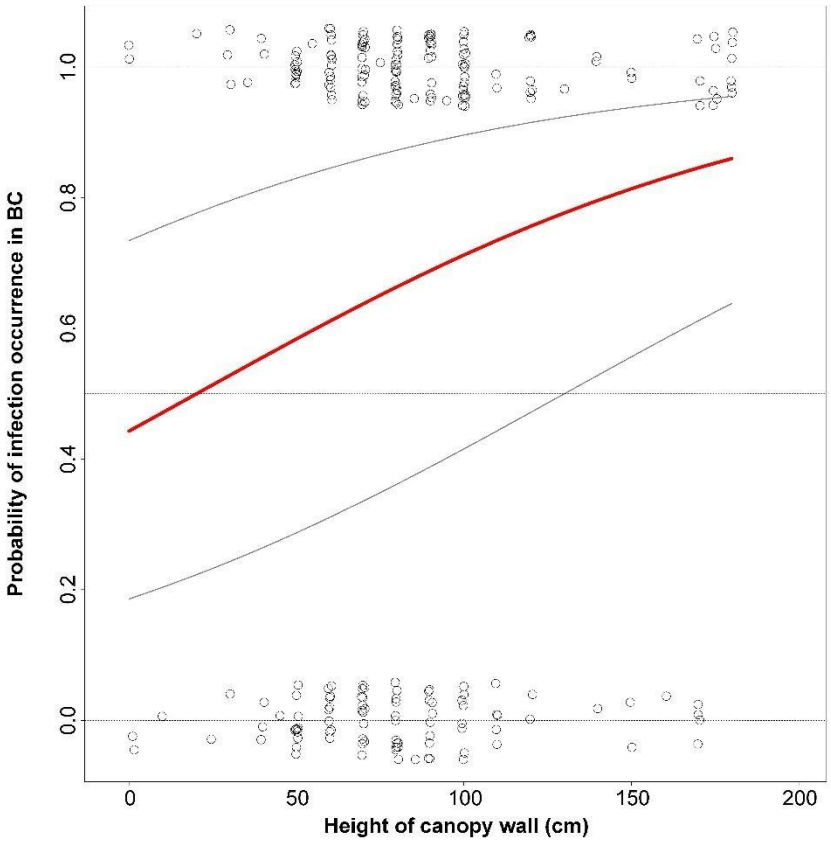


Figure 9 *Effect of the canopy wall height on infection occurrence of* Botrytis cinerea

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.

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 7, Supplementary 10).

Table 7 *The association between pathogen occurrence and the vineyard and crop management characteristics*

The table summarises the statistical analyses of the fitted Generalized Linear Mixed-Effect Model with binomial error structure (GLMM-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
Botrytis cinerea	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
	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****

Plasmopara viticola	Full model		196.04		
	Inclination	**1**	**197.91**	**3.869**	**0.049***
	Orientation	**3**	**198.69**	**8.648**	**0.034***
	Surrounding	**1**	**198.64**	**4.600**	**0.032***
	Survey year	**1**	**200.66**	**6.623**	**0.010***
	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****
Erysiphe necator	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
	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

*Note: The statistical tests were run in each pathogen (*Botrytis cinerea, Plasmopara viticola, Erysiphe necator*), separately. 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).*

Roles of the grape variety

In BC, the observed infection occurrence means detectable increased with the level of literature-based susceptibility (Figure 10A). 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 10B). 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 8, Supplementary 11). 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 8, Supplementary 11). We could not detect any significant effects among the tested variables regarding the grape varieties in PV and EN (Table 8, Supplementary 11).

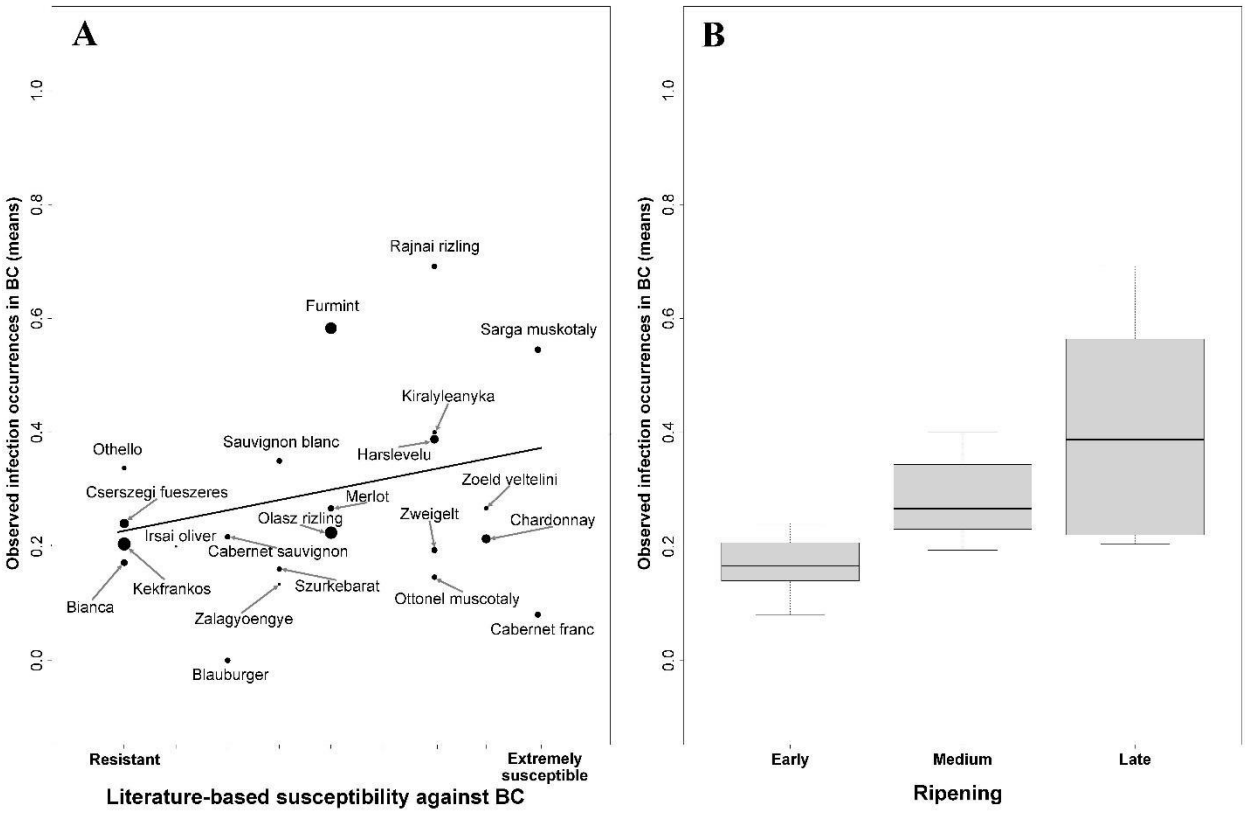


Figure 10 *The relationship between the observed* Botrytis cinerea *infection occurrence (variety means) and the literature-based susceptibility (A) and ripening (B)*

Figure 10A*: 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, Supplementary 12).* ***Figure 10B:*** *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 8 *The association between pathogen occurrence and the grape variety-specific characteristics*

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	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	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

*Note: 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).*

3.5 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. 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.

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 slope 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 Supplementary 6) 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 (Figure 8, Table 7, Supplementary 7 and 8). 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 2017a), thereby promoting the spatial dispersion of airborne spores. Furthermore, previous studies showed that row orientation and slope 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 9, Supplementary 7). 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 8, Table 7, Supplementary 7 and 9-10). 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 7, Supplementary 7-10). 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 7, Supplementary 7 and 9-10). 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 them 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 in the prevention 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 7, Supplementary 9), marginally insignificant in BC (Table 7, Supplementary 7). At the same time, this did not occur at all in the case of EN (Table 7, Supplementary 10).

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 hypothesized 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 7, Supplementary 7).

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 the long-term (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 7, Supplementary 9 and 10). 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 for a systematic large-scale study in the future.

Our findings could not support the effect of inter-row management on disease occurrence in BC, PV or EN (Table 7, Supplementary 7 and 9-10). 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, 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 7, Supplementary 7 and 9-10). 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.

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 10, Table 8, Supplementary 11). 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 10, Table 8, Supplementary 11). 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 (Supplementary 11). 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 of 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 8, Supplementary 11). However, the varieties susceptible to noble rot 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) (Supplementary 11).

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 8, Supplementary 11). 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 metabolites 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 reflects 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 8, Supplementary 11). 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 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 10B, Table 8, Supplementary 11). 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.

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 overemphasized 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.

4. IMPACT OF VINEYARD PROPERTIES ON SHIFTING GRAPE PHENOLOGY AND ITS IMPLICATIONS FOR PLANT DISEASES

4.1 Introduction

Grape growers are facing increasing challenges posed by global climate change, which has significantly altered agricultural production over the past decades (ARORA 2019; PAREEK 2017). Specifically, general climatic conditions have become more unpredictable, and the erratic weather events (e.g., heat waves, frosts, droughts) have become more frequent and extreme (JORGENSON et al. 2019; KRON et al. 2019; MAHATO 2014). Due to accelerated climate change, plants are forced to adapt to changing conditions in their physiology, morphology, and developmental processes. Adaptation related to development is reflected in changes to initial growth patterns and alterations in the timing of phenology (GRAY and BRADY 2016). This variability in phenological development, known as phenological shift, occurs as a result of the growth environment and can lead to changes in the climate-dependent phenology of grapevines.

Vine phenology is a temperature-dependent process which demonstrates the impact of global warming. The length of the ripening period was extended in several wine-growing regions over the last 50 years, along with global warming, which originated in the earlier start of initial development (FRAGA et al. 2017; VAN LEEUWEN, CORNELIS and DARRIET 2016). Faster initial development indicates earlier budbreak, flowering, veraison and biological ripeness of clusters, which define the plant protection strategy of the vineyard, since agrotechnical activities and chemical treatments are timed to the optimum development stage of grapes (SCHULTZ et al. 1987). Harmful organisms of vines, such as fungal pathogens (e.g., *Botrytis cinerea*, *Plasmopara viticola*, *Erysiphe necator*; hereafter BC, PV, and EN, respectively; see ELMER REGLINSKI (2006); FERNÁNDEZ-GONZÁLEZ et al. (2013); KENNELLY et al. (2005) or pests (e.g., *Drosophila suzukii*, *Eupoecilia ambiguella*; see RICCIARDI et al. (2024); WALSH et al. (2011) attack their hosts at defined growth stages, therefore identifying the susceptible phenological stages is essential for effectively timing plant protection treatments (DESPREZ-LOUSTAU et al. 2010; LAWRENCE et al. 1997; MOLITOR and BERKELMANN-LOEHNERTZ 2011). The onset and duration of these susceptible phenological stages are a variety-specific trait, showing a high temporal and spatial variation among grape-growing regions (JONES 2018). Extended periods of susceptibility can lead to increased inoculum production, raising the risk of long-term infection following overwintering (KÖNIG et al. 2017; REDL et al. 2021). Recognizing phenological growth stages allow for more accurate estimation of the grapevine stage at which susceptibility to infection begins. Thus, examining grape phenology has a key role in predicting

grape disease in the long term. Since vine phenological development is primarily driven by temperature, the Growing Degree Days (GDD) approach is an appropriate method to describe the relationship between temperature and the phenological development of the grapevine (HALL and BLACKMAN 2019; MOLITOR et al. 2014). This method relies on the concept that plants require a certain amount of heat units for their metabolic processes to reach a certain developmental stage, regardless of how long it takes to accumulate the necessary heat units for the next phenological stage, thus making this method suitable for monitoring plant development across various locations (FRAISSE et al. 2018). Furthermore, the role of the complex growing environment (e.g., grape variety, vineyard features, crop management) in grape phenological shift has not been clarified in comprehensive research, although the relative importance of biological and environmental factors on phenological responses to climate requires further investigation (PIAO et al. 2019).

Strong evidence suggests that vineyard features, combined with crop management practices, can cause shifts in the climate-dependent phenology of grapevines. For example, row orientation, inter-row management, and inclination affect soil warming through solar radiation, influencing grape phenology (VAN LEEUWEN et al. 2018). Crop management techniques (e.g., chemical treatments) can reduce plant growth due to a negative impact on photosynthesis (PETIT et al. 2012). Furthermore, different grape varieties require different heat units to ripen, resulting in differential development rates among the varieties (GRIS et al. 2010; KÖSE 2014). Therefore, site-specific adaptation of climatic models to the local environment is essential, as vineyard features, crop management practices, and variety-specific traits could simultaneously generate shifts in climate-driven phenological development. Moreover, the phenological shift driven by the production environment in grapevine could also define the prevalence of pathogens and the long-term disease severity of vineyards via influencing the initiation and duration of phenological phases, as extended susceptible periods increase the risk of inoculum and overwintering formula production (KÖNIG et al. 2017; REDL et al. 2021). However, the triple interactions among the production environment, the environment-modulated phenological shift, and long-term disease prevalence of vineyards are still unknown.

4.2 Aims and objectives

Based on these research gaps, the current study aimed to identify the influence of climate, environment, and crop management on the grape phenological shift and explore the potential outcomes on the long-term severity of grape primary diseases. Therefore, we conducted comprehensive research using a citizen science approach on a massive, variety-specific phenological dataset linked to geo-referenced data regarding local climatic conditions, complemented by vineyard features.

First, we aimed to test whether vineyard features, including the most relevant crop management practices and the effect of grape varieties, could influence grape phenology. More specifically, we hypothesized that vineyard characteristics (e.g., inclination, row orientation), consistent crop management practices (e.g., intensity of plant protection), and grape variety (e.g., ripening profile) could generate phenological shifts due to their impact on the growing environment (PARKER et al. 2011; PETIT et al. 2012; VAN LEEUWEN et al. 2018).

Our second goal was to reveal the relative importance of phenological shifts (i.e., earlier or delayed development due to the modifying effect of the growing environment) compared to other environmental factors, crop management strategies, and the ripening categories of grape varieties on the long-term disease severity of primary pathogens in grapes, such as BC, PV, and EN. We expected that phenological shifts (led by plantation features) could determine long-term disease occurrences by affecting the timing and duration of the susceptible phenological period for infection, and also by the amount of inoculum source (KÖNIG et al. 2017; REDL et al. 2021). This is particularly relevant in production regions where grapevines are exposed to numerous plant pathogens, depending on the stage of grape phenological development.

4.3 Material and methods

Data collection

To estimate the regional development of different grape varieties, we used a citizen science approach, following the methodology of previous studies (BEZA et al. 2018; KOCSIS et al. 2024). This widely applied research methodology facilitates the collection of a considerable amount of data involving professional and non-professional volunteers (SILVERTOWN 2009). This methodology is especially useful for studies testing patterns along large spatiotemporal scales (GUPTA et al. 2022).

Geolocated data were collected between July 1, 2020, and March 31, 2023, in Hungary. A standard online questionnaire was created based on KOCSIS et al. (2024) and distributed to nearly 5,000 vine growers via email, different social media platforms and personal contact at professional events. The questionnaire survey gathered systematic information on grape variety, phenological status across seasons (including repeated observations), date of observation, growing location (i.e., GPS coordinates, nearest location), and the most relevant growing environment properties (see later). During data collection, we made exhaustive efforts to collect repeated observations from the same vineyard. The variety-specific ripening classes (‘Ripening’, factor; Early: from early June to mid-July, Medium: from mid-July to the end of August, Late: early September to the end of October) were gathered from validated open-source international databases and breeders’ manuals

(Supplementary 13) (CSEPREGI and ZILAI 1988; MAUL et al. 2015). Additionally, georeferenced phenological observations were collected through data scraping methods on popular social media platforms. After data curation, only those observations that contained the most relevant information, such as the name of the variety, date of observation and location, were included in the statistical analyses. A total of 1,196 phenological observations were collected across Hungary during the survey period (Figure 11). Hungary is a country that produces wine and grapes with unique traditions. The vine-growing regions are diverse in terms of geography and climate, and grape production is carried out in arid plains and humid hilly areas (HAJDU 2018; MEZŐSI 2017a, 2017b). This diverse environment of the focal country serves as an ideal model location to examine phenological development and shift.

For the analyses regarding long-term disease occurrence, this database incorporated different vineyards (N=100), in which most of the volunteers (75%) were qualified in plant protection.

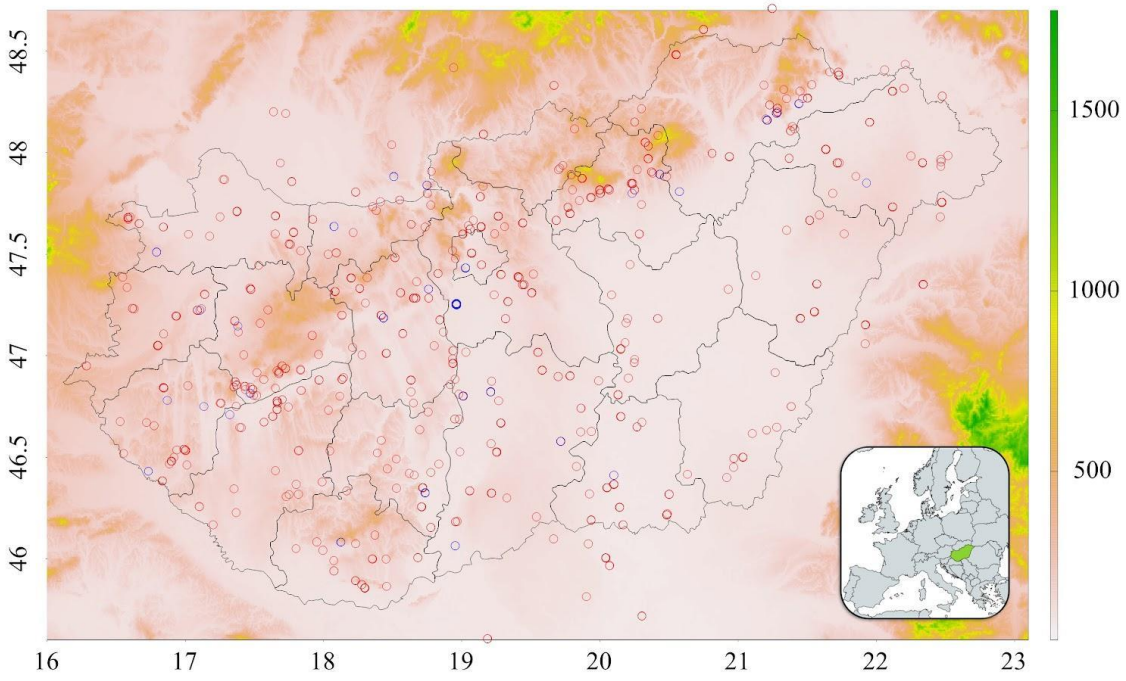


Figure 11 *Locations of phenological observation across Hungary*

The map displays geo-referenced phenological data from Hungary and its surrounding areas. Red circles (N = 1,211) represent phenological data only, while blue circles (N = 100) indicate phenological data combined with vineyard property data. A circle with a darker shade reflects more vineyards in the same or neighbouring locations. The colour of the map indicates altitude above sea level; the darker shades represent higher altitudes. The x and y axes represent longitude and latitude coordinate scales, respectively; the scale on the right shows the altitude above sea level.

Surveyed variables

The BBCH scale is widely adopted worldwide as a standard for describing crop growth stages(LORENZ et al. 1995). According to the BBCH scale, volunteers provided information on the current phenological stage of their grapevines, ranging from 50 to 99 (LORENZ et al. 1995). To enhance the accuracy and validity of the collected data regarding the BBCH stages, standard visual illustrations were provided to the survey to support the participating volunteers. The photos scraped from social media were assessed for BBCH values in the same way as described previously by a grape expert (Ivett Kocsis).

Furthermore, the farmers provided information on the most important vineyard features and crop management practices as row orientation, slope of the vineyard, number of pesticide applications, vertical isolation distance between the ground surface and the lowest canopy leaves, age of vineyard, inter-row management, ratio of surrounding vineyards, following the guidelines established in our previous citizen science study (KOCSIS et al. 2024). For more details see Chapter 3.3 Material and methods, Vineyard features and Crop management section (Table 3-4).

Plant health conditions

Finally, volunteers provided data on the overall plant health conditions. We surveyed two infection variables to describe the long-term infection status over the last five years (KOCSIS et al. 2024), following the guidelines established in our previous citizen science study (KOCSIS et al. 2024). For more details see Chapter 3.3 Material and methods, Infection evaluation section (Table 2).

Climatic variables

Meteorological data were collected for each georeferenced observation site using the Hungarian Meteorological Service (HungaroMet) open-sourced Meteorological Database (odp.met.hu). The meteorological data were generated by MISH interpolation methods (grid resolution: 10×10 km) from the measured, quality-controlled, homogenised, and completed data (IZSÁK 2023; SZENTIMREY et al. 2005). We gathered site-specific precipitation (daily sum, in mm, resolution: 0.01) and temperature (daily average, in °C, resolution: 0.01) values from January 1 to the observation date of the corresponding year.

Climatic predictors

Cumulative precipitation is the total amount of rain (or other forms of precipitation) that has fallen during the period from January 1 to the observation day in the corresponding year (expressed in mm, resolution: 0.01, ‘Precipitation’ hereafter).

For the statistical analyses, we selected the GDD predictor, which is calculated using the single threshold GDD model with a baseline temperature (Tbase) of 8°C ('GDD ST8', hereafter). This selection is based on the previously analysed GDD predictor (for more details, see Supplementary 14-19).

Statistical analysis

All statistical analyses were run in the R environment (version: 4.3.1, R Development Core TEAM 2019). In all models, all numeric variables were centred and normalised by the '*scale*' function before running the statistical analyses. The significant effects of the model predictors were tested by Likelihood Ratio Tests (LRT) using '*drop1*()' functions and combining ANOVA (Type II) and Wald Chi2 tests. Figure 12 provides a graphical illustration of the entire flow of the statistical analyses in the study, including the main steps, the calculation of each variable, and the statistical models applied. For a detailed explanation of the calculation methods (i.e., calculation and selection procedure of GDD predictors), see Supplementary 15.

Calculation of phenological shift

The grape phenological shift is described by the residuals derived from a statistical model that fits a regression between grape development and climatic factors, due to the strong dependence of grape development on climate, which can vary highly across varieties (Supplementary 20-21). The size and sign of the residual value denote the extent and direction (i.e., negative: delayed, positive: earlier development than predicted) of the phenological change. Furthermore, the use of a complex multivariate statistical approach was necessary to account for other confounding factors. Thus, this statistical correction procedure was crucial; otherwise, this variable would also be loaded by the unwanted noise of local-specific variances in grape development sourced from the different climatic and variety-specific features. Since the estimate is based on a considerably large sample size, the specific BBCH (i.e., original values) was less crucial, but rather its deviation, reflecting the phenological shift.

Therefore, we used a Generalised Linear Mixed Model using Template Model Builder ['glmmTMB', using the 'glmmTMB' package (BATES et al. 2014b), with t-family distribution ('t_family', Student-t provides flexible adjustment for scale and location parameters). In this model, the BBCH value was the response variable, while the predictor variables were the following covariates: GDD ST8, the precipitation, as continuous numeric variables, and the ripening class ('Ripening') as a factor. The random factors were entered as the observation year (numeric, discrete) and the observation identifier ('Observation ID', factor), which can identify the data points originating from the same location, grape variety, and farmer (or observer). This

identification method allowed us to account for repeated observations from the same vineyard in the statistical analyses, addressing issues of statistical non-independence. The derived model residuals represented the phenological shifts and were used in further statistical analyses.

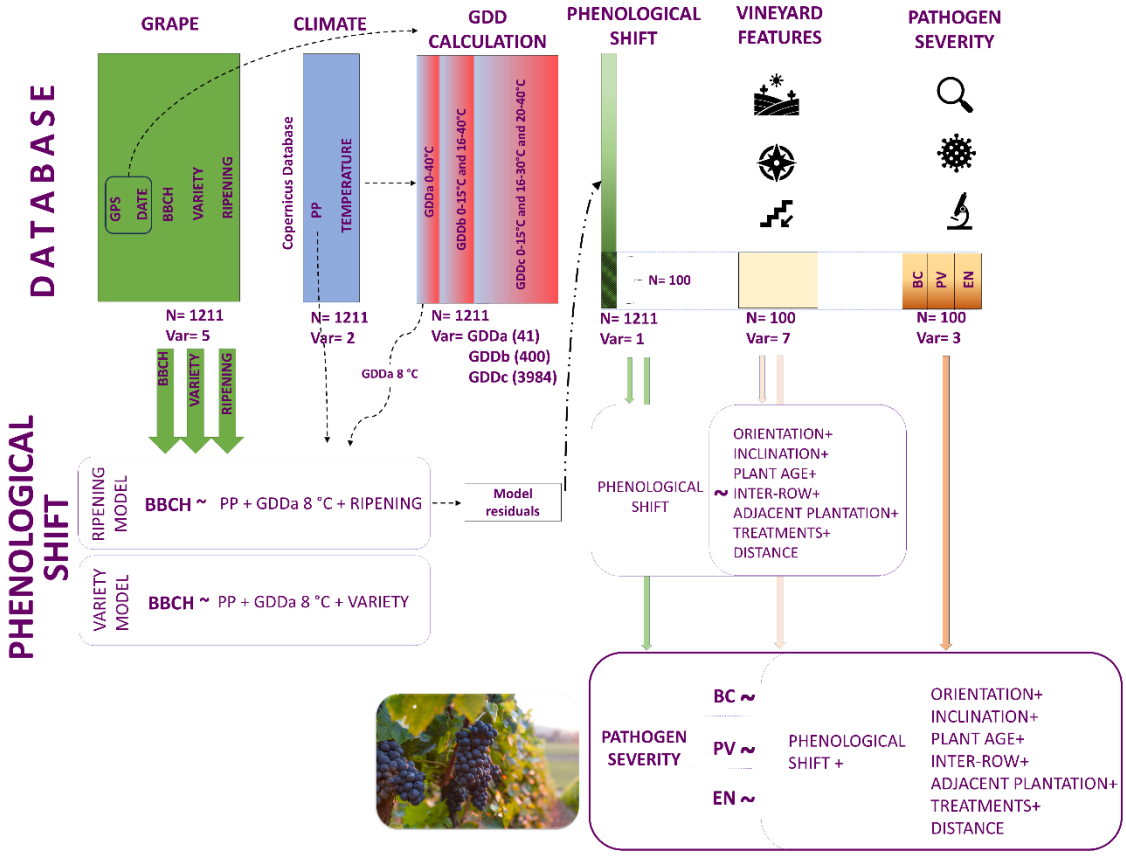


Figure 12 *Graphical summary of the material and methods regarding climate, variety and vineyard features influence on disease prevalence*

Abbreviations: Precipitation (PP), Growing Degree Days (GDD), GDD Single threshold model (GDDa), GDD Lower and upper threshold model (GDDb), GDD Heat threshold model (GDDc), Botrytis cinerea *(BC),* Plasmopara viticola *(PV) and* Erysiphe necator *(EN). For a more detailed explanation about the calculation methods of the selected variables and model structures, see Supplementary15-27.*

Effects of the vineyard features

We tested the modifying effect of vineyard features on the variety- and climate-corrected phenological growth using linear regression. In the model, the response variable was the Phenological shift (i.e., model residuals of the Ripening model), and the predictor variables were the Orientation, the Inclination, the Treatments, the Distance, the Age, and Adjacent plantations as covariates, and the Inter-row as a factor (Figure 12).

Long-term occurrence of grape pathogens

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, following the methods outlined by KOCSIS et al. (2024). These pathogen-specific, normalised infection occurrence (hereafter infection occurrence) variables were used in further statistical analyses; for more details, see Chapter 3.3 Material and methods, Statistical analysis section.

We applied a Generalized Linear Model (GLM) with a quasibinomial error structure to investigate the relationship between the infection occurrence as a response variable and several covariate predictors, such as Phenological shift, and vineyard features (i.e., Orientation, Inclination, Treatment, Distance, Plant age, and Adjacent plantations), and Inter-row and Ripening as factors. The same model structure was run separately for each plant pathogen. Finally, to enhance clarity, we provided the Odds Ratio (OR) for the model variables associated with each pathogen, separately. The OR represents the ratio of odds of the outcome (e.g., the BC infection) occurring in the exposed group compared to the unexposed group. The calculation based on the following formula OR = (a/b) / (c/d) = a×d/b×c, where, ‘a’ means the number of exposed with event (e.g., early ripening with BC infection); ‘b’ means the number of exposed without event (e.g., early ripening without BC infection); ‘c’ means the number of not exposed with event (e.g., not early ripening with BC infection), and ‘d’ means the number of not exposed without event (e.g., not early ripening without BC infection).

4.4 Results

The effect of vineyard features

We comprehensively examined how vineyard features, and crop management practices influence the phenological shifts of grapes, after statistically accounting for climate and variety differences. The grapevine phenological shift was significantly associated only with the row orientation (Table 9, Supplementary 22), increasing with the systematic deviation from the northern direction. However, we failed to detect any effects for other vineyard or crop management features, such as inclination, pesticide treatments, distance, plant age, inter-row management, and adjacent plantations (Table 9, Supplementary 22).

Table 9 *The association of the grape development and the most relevant vineyard features and crop management characteristics*

*The table summarises the statistical analyses of the fitted General Linear Model to test the association of the grape development and the most relevant vineyard features and crop management characteristics (Predictor). The statistical outputs were calculated from the corresponding likelihood ratio test (LRT). Significant results are highlighted in bold. The asterisks indicate the level of significance of the given predictor (*p<0.05, **p<0.01, ***p<0.001).*

Predictors	**Df**	**Sum of Squares**	**RSS**	**AIC**	**p-values**
Full model			12.420	-192.59	
Orientation	**1**	**1.49**	**13.91**	**-183.24**	**<0.001*** **
Inclination	1	0.22	12.64	-192.81	0.183
Treatments	1	0.26	12.68	-192.50	0.148
Distance	1	0.01	12.43	-194.52	0.796
Plant age	1	0.003	12.42	-194.56	0.868
Inter-row	1	0.10	12.52	-193.76	0.363
Adjacent plantation	1	0.35	12.76	-191.84	0.097

*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).*

Long-term occurrence of grape pathogens

This complex model provided insights into the relative importance of the most relevant production-related factors (e.g., vineyard features, crop management practices) and the phenological shift on the long-term occurrence of major grape pathogens. The results reflected that the tested variables showed a considerably high heterogeneity among grape diseases (Figure 13). Interestingly, we detected a significant impact of phenological shift only on the occurrence of EN disease. Ripening significantly reduced the BC disease occurrence, specifically, based on the ORs, the BC occurrence was more likely in the medium and late ripening classes than in the early ripening classes (Supplementary 23). In EN, the early and medium ripening classes were associated with low disease occurrence, while ripening had no effect on PV occurrence (Supplementary 23). Most of the tested vineyard features, such as orientation, inclination, distance, plant age, and inter-row management, had a great impact on BC, increasing the long-term infection occurrence, while the other variables were considered insignificant (Table 10). In PV, only the adjacent plantations increased the infection occurrences. Regarding EN, we failed to detect any significant effects related to the vineyard features and crop management practices (see more details, Table 10, Supplementary 23).

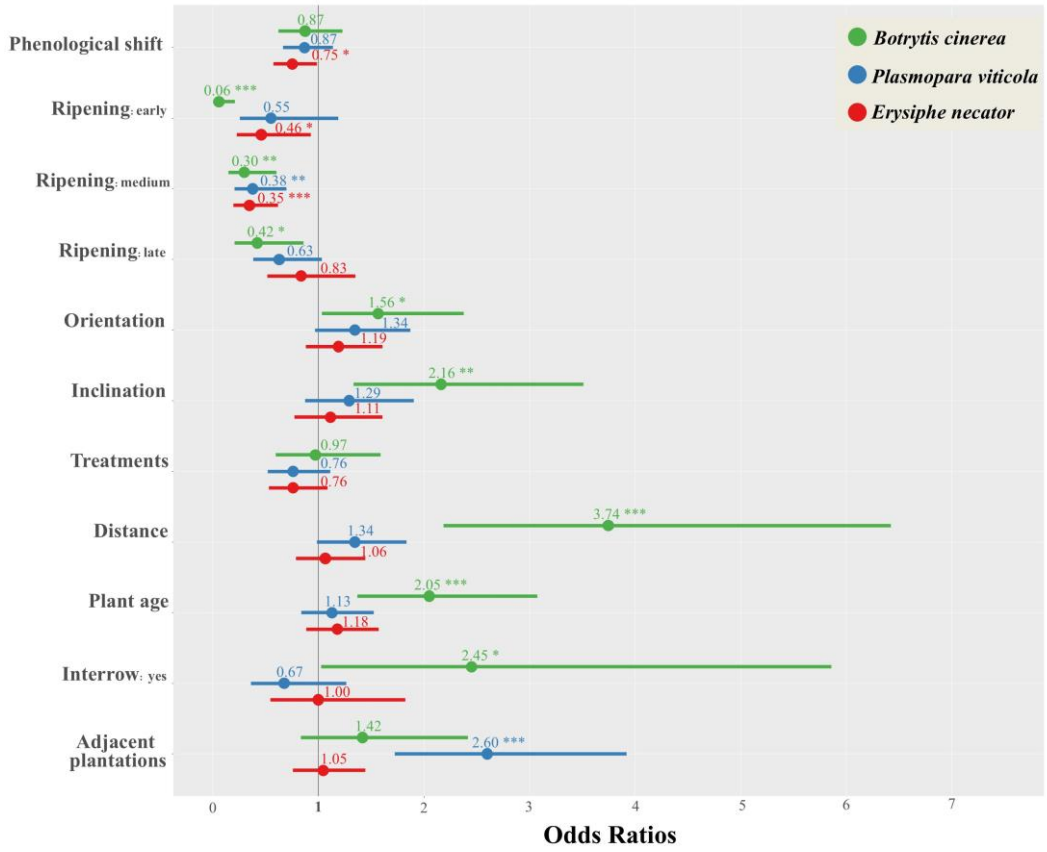


Figure 13 *Effect of tested predictors on long-term disease occurrence*

The plot shows the effects of the tested predictors on long-term disease occurrence of grapevine main diseases, such as Botrytis cinerea *(green),* Plasmopara viticola *(blue),* Erysiphe necator *(red). The dots represent the species-specific model estimates (Odds ratio, OR) with their confidence intervals (CI_{95} horizontal lines). The asterisks indicate the level of significance (*p<0.05, **p<0.01, ***p<0.001). The vertical black line represents the value of 1. If a model estimate is around 1 (i.e., the range of CI_{95} includes the value 1), it represents that there are no detectable effects or differences between groups. When an OR is greater than 1, it indicates a positive association, suggesting that the likelihood of disease occurrence is higher with that specific predictor. Conversely, an OR less than 1 indicates a negative association, showing that the likelihood of disease occurrence is lower with that specific predictor.*

Table 10 *The relationships between the long-term disease occurrence and corrected grapevine phenological shift, plantation and crop management features*

The table summarizes the relationships between the long-term disease occurrence of grapevine main diseases and phenological shift (variety and climate corrected, phenological shift), plantation and crop management features (Predictors) fitted by the Generalized Linear Models with quasibinomial error structure (GLM-qb). The statistical tests were run separately on each pathogen. The statistical outputs were calculated from the corresponding likelihood ratio test (LRT) that was tested by single-term deletions. Significant results are highlighted in bold, while the marginally significant effects (0.05 < p ≤ 0.1) are in italics. The asterisks indicate the level of significance of the given predictor (p < 0.05, ** p < 0.01, *** p < 0.001).*

Predictors	**Df**	**Deviance**	**Scaled dev.**	**p-value**
		Botrytis cinerea		
Full model		34.81		
Phenological shift	1	35.08	0.642	0.423
Ripening	**2**	**40.36**	**13.30**	**0.001****
Orientation	**1**	**36.77**	**4.70**	**0.030***
Inclination	**1**	**39.29**	**10.73**	**0.001****
Treatments	1	34.82	0.01	0.906
Distance	**1**	**49.59**	**35.39**	**<0.001*****
Plant age	**1**	**40.81**	**14.35**	**<0.001*****
Inter-row	**1**	**36.63**	**4.34**	**0.037***
Adjacent plantation	1	35.54	1.75	0.186

Plasmopara viticola				
Full model		31.09		
Phenological shift	1	31.45	1.13	0.289
Ripening	2	31.75	2.09	0.351
Orientation	*1*	*32.10*	*3.19*	*0.074*
Inclination	1	31.64	1.73	0.189
Treatments	1	31.76	2.11	0.146
Distance	*1*	*32.28*	*3.66*	*0.056*
Plant age	1	31.29	0.64	0.423
Inter-row	1	31.59	1.58	0.209
Adjacent plantation	**1**	**39.27**	**25.90**	**<0.001*** **
Erysiphe necator				
Full model		34.94		
Phenological shift	**1**	**36.48**	**4.62**	**0.032***
Ripening	**2**	**37.42**	**7.45**	**0.024***
Orientation	1	35.38	1.32	0.250
Inclination	1	35.05	0.34	0.558
Treatments	1	35.74	2.41	0.120
Distance	1	34.99	0.17	0.682
Plant age	1	35.37	1.31	0.252
Inter-row	1	34.94	0.001	0.992
Adjacent plantation	1	35.96	0.01	0.785

4.5 Discussion

In this study, we aimed to explore the leading drivers and the impact of the local phenological shift in grapevines using a large-scale spatiotemporal data collection approach involving citizen science toolkits, which allowed us to effectively obtain a massive dataset. First, we investigated the phenological shift as a function of vineyard properties. The results indicated that these variables play a smaller role in modifying the grape phenological shift than our hypothesis suggested. Then, we assessed the long-term occurrence of globally significant grape diseases, such as grey mould, downy mildew, and powdery mildew, along with the variation in phenological shifts, vineyard features, and crop management practices. This study provides valuable insights into the specific grape-pathogen interactions during seasonal phenological development, which is essential for establishing new vineyards and making informed decisions. After this general overview of our findings, we provide detailed explanations and relevance regarding the grape phenological shifts.

Vineyards are climate-sensitive agricultural systems where temperature has the most significant impact on development compared to other climatic factors. This environmental factor is often the main driver of growth-related primary metabolic processes, such as shoot elongation and root growth (BAHUGUNA and JAGADISH 2014; JONES et al. 2005; OKE et al. 2017). The GDD approach is based on the concept that a certain amount of daily heat units is required to facilitate the biochemical processes necessary for growth and tissue development (MILLER et al. 2001). Therefore, applying GDD models has become a popular and suitable method for predicting the phenological development of plants, including grapevines (MOLITOR et al. 2014). Estimation accuracy is extremely important because it helps identify the onset of the susceptible phenological phase when fungal pathogens, such as BC, PV, and EN, could start to infect (CAFFARRA et al. 2012; KENNELLY et al. 2005; ZAPATA et al. 2015). Rather than investigating the well-documented relationship between growing degree days (GDD) and other climatological parameters affecting phenological development in grapevines, we shifted our focus to environmental factors in plantations that can influence the timing of phenological events. While examining grape development is important, we address these methodological details in the supplementary material (Supplementary 15-27).

Grape vines follow variety-specific patterns of phenological development over seasonal change. Originally, these grape varieties were classified into ripening groups based on their average harvesting dates in Hungary (CSEPREGI and ZILAI 1988), which closely reflects seasonal phenological development and maturity. Similarly, our results showed that variety-specific features can determine the ripening and shape of climate-modulated phenological growth in grapevines (Supplementary 25-26). However, the differences among ripening groups were less

pronounced in the present study. Specifically, the early and mid-ripening varieties reached similar stages of ripeness without clear differences, while the late-ripening varieties showed delayed ripening (Supplementary 25, 27). This pattern aligns with previous results, which showed that different grape varieties require variety-specific heat units to achieve a comparable ripening stage (GRIS et al. 2010; KÖSE 2014). The developmental similarity between early and medium-ripening varieties suggests that changes in climatic influences, such as warmer periods at the beginning of the growing season, could eliminate the variety-specific physiological differences and reduce variability in growing patterns during the intensive growing period among varieties. Furthermore, from a macroclimatic perspective, weather patterns have historically shown a relatively consistent pattern during the critical grapevine growing season in Hungary (MEZŐSI 2017a). This climatic consistency, combined with the country's small geographical size, has led to similar heat accumulation across locations, thereby reducing regional differences in grapevine development. Consequently, variety-specific ripening details appeared less relevant over the decades, but recent shifts in climate could disrupt these long-standing patterns. Accordingly, it is essential to re-evaluate the grape varieties, considering the climate-specific conditions and other environmental factors of each production area.

A vineyard with consistent crop management practices could represent a stable environment, which could indirectly affect the development rate via its favourable climatic and biological impacts on the growing environment. However, these factors could modify the long-term macroclimatic regimes by altering the growing environment, influencing the grape phenological shift. We carefully tested various vineyard features to assess their potential impact on plant growth and development. These factors could permanently determine and affect the production's success in each growing period, starting from the vineyard establishment. Surprisingly, our findings revealed that these factors have a less significant impact on grape phenological shifts than earlier studies have previously demonstrated (GRIESSER et al. 2022; PETIT et al. 2012; VAN LEEUWEN et al. 2018). In line with our expectations, our study revealed that only the row orientation had an impact on grape phenological shift. We observed that the level of development increased with the deviation from the northern direction, while the effects of all other vineyard features remained undetectably hidden (Table 9, Supplementary 22). Our results indicated that the SE-NW row orientation maximised light interception and, therefore, the rate of phenological advancement. Generally, the row orientation modulates the intensity of solar exposure and the heat environment by warming the canopy wall and the soil. Thus, this influences the quantity and duration of solar radiation, which affects grapevine phenological shifts via soil warming, leading to an enhanced phenological development rate in warmer soils (VAN LEEUWEN et al. 2018).

Previous studies demonstrated that various commonly applied crop management techniques could also modify grapevine development. For example, some pesticide treatments could create a non-transparent layer, which could negatively affect photosynthesis due to reduced light penetration (PETIT et al. 2012). Conversely, our extensive study found that the factors linked to the production environment may not be relevant, as climatic and variety-specific features appear to play a more crucial role in vine development. Moreover, our study demonstrated these general patterns on a large scale, which implies that they might be robust and less sensitive to detecting interferences among environmental factors at local-specific scales.

Finally, we examined how long-term infections and climate-adjusted phenological shifts, along with other production-related cues, could potentially interfere with each other. Previous studies effectively illustrated the key role of the timing of phenological development in infection occurrences in vineyards, accomplished by shaping the onset and duration of the susceptible phenological stages for the main plant pathogens (CAFFARRA et al. 2012; KENNELLY et al. 2005). Moreover, previous results shed light on how environmental factors influence disease occurrence in vineyard production (KOCSIS et al. 2024). Among the pathogens, BC infection occurrence was mainly exposed to the effect of vineyard features such as orientation, inclination, distance, plant age, and inter-row management. In contrast, infection occurrences related to PV and EN showed less variation in relation to these environmental factors (Figure 13, Table 10, Supplementary 23). After the statistical adjustment of climatic and variety-specific differences, only the occurrence of EN infection was influenced by the long-term phenological shift, confirming the significant impact of an extended susceptible phenological phase on the disease prevalence of powdery mildew. In contrast, it appeared that the grapevine phenological shift had a minor impact on the emergence of BC and PV pathogens, compared to environmental and vineyard effects. These patterns were unexpectedly observed; the phenology-modulated infection occurrence appeared to play a significantly less crucial role on a larger scale.

The accelerated process of global climate change creates unprecedented challenges for farmers, as the weather patterns become increasingly unpredictable and erratic conditions become more frequent. Grapevines have to adapt to these changes, which could lead to shifts in previously known grape phenology patterns. However, the reliable determination of the grapevine's growing cycle is a major issue, since agrotechnical activities and chemical treatments are timed to the optimal development stage of the grape. Previous research has focused on the GDD method without a complex approach; nevertheless, the local climate and vineyard features co-induce the phenological growth of the grapevine, thereby determining the length of a susceptible phenological

phase for the main grape pathogens. Our study highlighted how different results could be obtained when a relationship is analysed with a complex approach instead of testing each factor separately.

In our Citizen Science study, we used a multivariate approach to understand grape development in viticulture. Our results showed that the best method for calculating GDD is the simple threshold approach, having direct implications for vineyard management. We constructed a model that explains the phenological shift, taking into account grape variety and climatic factors. Our findings highlighted the importance of considering some environmental factors in grape development, emphasising the need to look beyond just climatic data. Additionally, we compared the impacts of grape phenological shift, vineyard features, and management practices on disease occurrence. We found that the length of the susceptible phenological period is largely determined by the local climate, while the long-term occurrence of plant diseases is more influenced by vineyard features than by the phenological shift. Although climatic factors are the primary drivers of grape phenological growth, our study revealed that other environmental and biotic cues also play a significant role. Therefore, we emphasise the urgent need for future studies to adopt a comprehensive statistical approach to test the interfering effects simultaneously. This approach will help us prioritise the environmental and cultivation impacts of climate, variety use, and vineyards, providing a deeper understanding of the complex growing environment.

5. LONG-TERM INFLUENCES ON DISEASE OCCURRENCE: A META-ANALYTIC COMPARISON OF VINEYARD, TECHNOLOGY AND SOIL FEATURES

5.1 Introduction

Agricultural systems are complex environments shaped by various factors that directly influence plant conditions, crop yield, and quality (BENJAMIN et al. 2003; REDDY et al. 2003). These systems can be objectively characterised by describing them according to the most important factors influencing production, thus enabling these complex areas to be compared based on these environmental variables. Furthermore, these variables, rather than acting independently, operate simultaneously to produce a combined effect on crop production (e.g., BOYER 1982; CABAS et al. 2010; CLEMENTS 1964; LILIANE and CHARLES 2020; TENG et al. 2024). The purpose of production determines the environmental complexity, along with the crop type, the associated plant management and technology used (CAMERON et al. 2024; ROUPHAEL et al. 2012; VOSS et al. 1970). These effects are more pronounced and consistent in perennial plantations than in annual crops, because the same plants remain in the same growing conditions over a long period, and there are few opportunities to modify the overall growing environment (JUNGERS et al. 2023; PLOETZ 2007). Moreover, certain plantation characteristics are more closely related, sharing similarities, than others based on their agrotechnical purposes, biological functions, and the level of flexibility in the management control.

Viticulture has expanded production worldwide, representing a complex production environment with diverse technologies applied (JONES 2015). Moreover, in viticulture, environmental and production-related factors have long-term and cumulative effects on plant performance spanning decades (CAMERON et al. 2024; JOGAIAH 2023; RIPOCHE et al. 2011). Therefore, understanding and categorising the production-related and environmental factors is essential for optimising grape production and management practices. Considering these aspects, these environmental factors in viticulture can be classified into three main ‘domains’. The ‘vineyard domain’ includes variables related to vineyard characteristics, which are mostly determined when the vineyard is established (i.e., low modification level) (LANYON et al. 2004). The ‘technology domain’ refers to the specific agricultural technologies applied and production management strategies (i.e., high modification level) (SURAMWAD and KOLGANE 2017). The ‘soil domain’ encompasses variables related to soil properties, where some properties are determined and fixed due to region-specific conditions, while others can be gradually improved through management (i.e., moderate modification level) (LI, Q. et al. 2024). Together, these domains cover the primary sets of factors that shape and determine the production outcomes in grape production.

Healthy plants can yield the highest agricultural output; thus, producers endeavour to create ideal growing conditions (FAGERIA et al. 2008; GAUNT 1995). There is strong evidence that certain vineyard properties can influence the health conditions of grapes. For example, inclination influences solar radiation in vineyards, receiving higher solar radiation in sloping areas, which favours the growing and ripening conditions, thus indicating a lower occurrence of *Plasmopara viticola* (Berk. and M.A. Curtis) Berl. and De Toni, PV (hereafter), on a long-term basis (VAN LEEUWEN et al. 2018). The row orientation aligned with the prevailing wind direction could promote the dispersion of airborne spores of *Botrytis cinerea* Pers. (BC hereafter). Additionally, a vineyard surrounded by denser grape plantations increases the infection rates of BC and PV due to enhanced inoculum production from neighbouring plantations (KOCSIS et al. 2024; MEZŐSI 2017a).

Similarly, the cultivation technology applied aims to prevent or reduce the risk of the main grape pathogens. Grape growers make exhaustive efforts to reduce the risk of infection via chemical treatments. Besides chemical solutions, agrotechnical practices indirectly support growers in reducing the pressure of pathogens. For instance, a higher canopy wall increases the incidence of BC, as the self-shading effect shifts the microclimate (KOCSIS et al. 2024; SMART et al. 2017). Similarly, appropriate inter-row management in vineyards can have a beneficial indirect effect on plant pathogens, thereby suppressing the risk of pathogen infection (GUERRA and STEENWERTH 2012). This is due to the application of cover crops and other organic mulch types, which can enhance the biological activity of the soil, accelerating the decomposition rate of the infected plant debris, the primary source of fungal inoculum (JACOMETTI et al. 2007a, 2007b). Furthermore, defoliation is a widely used technique in viticulture to open the foliage at the cluster zone by removing the front leaves, which facilitates the faster evaporation of moisture from clusters and ensures optimal pesticide coverage. Thus, this leaf removal in practice reduces the infection risk of *Erysiphe necator* Schwein. (EN hereafter) leading grape pathogens (EVERS et al. 2010; ROMANAZZI and FELIZIANI 2014).

The unique soil properties are crucial in shaping the region-specific characteristics and distinctive quality of a grape product, which is often known as one of the key elements of the ‘terroir-concept’ (VAN LEEUWEN et al. 2018). However, soil properties have also direct effects on the general health conditions of vineyards within the same growing region or climatic conditions (DARRIAUT et al. 2022; GHORBANI et al. 2008; REISENZEIN et al. 2007). Additionally, plantations are often located in the same place for an extended period, thereby their soil characteristics can directly affect the overall health of vineyards on a long-term basis, even within the same growing region or under similar climatic conditions (DARRIAUT et al. 2022;

GHORBANI et al. 2008; REISENZEIN et al. 2007). For example, soil organic matter and nitrogen sources primarily supply nutrients for grape development, particularly shoot and leaf biomass, whose qualities of these tissues have an impact on the success of infections and the subsequent development of plant pathogens (DE NEVE 2017; NEWMAN 1985). Furthermore, the soil pH is one of the key factors which modify the nutrient availability and uptake efficiency. In grapes, the optimal soil pH falls into the range from slightly acidic to neutral soil (pH 6.0–7.0) (CHEN et al. 2024), similar to that of most agricultural crops (pH 5.5–7.5) (OSHUNSANYA 2019), in which range the essential nutrients are most available (MSIMBIRA and SMITH 2020). Thus, any deviations from this optimal range can lead to nutrient deficiencies, which in turn reduce plant growth and general deterioration in plant health (BAVARESCO et al. 2010). To prevent overall decline, grape growers commonly use soil liming to adjust soil pH, which indirectly reduces the risk of pathogen infection (HARTEMINK and BARROW 2023; NDUWUMUREMYI 2013). For suitable nutrient uptake, the water-holding capacity of soil is also crucial, which is determined by the size of the mineral particle. Soil with small mineral particles has a greater water-holding capacity than soil with larger particles, which is important in areas where abiotic stress is higher due to lower capacity for waterlogging, resulting in more frequent plant diseases (FINCH et al. 2014; GHORBANI et al. 2008; VANDECASTEELE et al. 2018).

The interactions and contributions of Vineyard, Technology, and Soil domains to long-term disease occurrence have rarely been comprehensively compared. However, the individual interpretation of particular variables within or between domains in long-term disease occurrence may lead to incorrect conclusions, as these factors form a complex, growing environment that simultaneously influences disease occurrence. An illustrative example of this synergistic effect is that warming of soil due to solar irradiation depends on both the intensity of solar radiation and the type of soil. This relationship is influenced by factors such as row orientation, vineyard inclination, and inter-row management, and also contribute to earlier ripening even for late varieties, when grape berries become more exposed to BC infection due to increased sugar content during ripening (DEYTIEUX-BELLEAU et al. 2009; KOCSIS et al. 2024; KRETSCHMER et al. 2007; VAN LEEUWEN et al. 2018). Consequently, susceptibility to plant pathogens results in a complex production context that cannot be attributed to a single factor; thus, interpreting environmental factors requires a comprehensive, transdisciplinary study approach.

In grape production, there is an urgent need to understand the role of complex production contexts in the long-term occurrence of grape pathogens, alongside global technological and climatic challenges. Therefore, in this large-scale study, we examined the key factors influencing grape production, classified into three leading environmental domain groups: Vineyard, Technology, and

Soil. Our focus was on understanding how these factors affect the long-term occurrence of main grape pathogens, such as *Botrytis cinerea*, *Plasmopara viticola* and *Erysiphe necator*. Due to the complex and combined nature of the environmental variables throughout the vineyard, technology, soil, and their simultaneous presence, these factors can reinforce and weaken each other simultaneously. So, testing these interactive effects is particularly challenging because it is difficult to separate the effects of each factor on the other. Moreover, the domain concept categorises environmental factors into distinct categories, along with the scientific disciplines and practical approaches in viticulture. This discipline-specific classification approach facilitates a more interpretable transition from human-induced factors to natural conditions. However, the domain-specific grouping can be too robust and overlooks other relevant aspects for the production management of grapes. Therefore, additional grouping factors (i.e., moderator variables) are necessary to address the overall complexity by considering plant health aspects, management perspectives, and spatiotemporal scales in the relationships between disease occurrence and environmental factors.

5.2 Aims and objectives

Therefore, we aimed to address three main objectives: 1) What is the overall effect on the relationships between long-term disease occurrence and relevant environmental variables? 2) Are there any pathogen-specific roles in the overall effect and their heterogeneity? 3) What type of environmental factors can affect disease occurrence in response to environmental factors in each grape pathogen? To analyse such complex effects and global patterns, we used a meta-analytical approach, which is the most appropriate statistical method, allowing us to create a common platform for performing a valid and objective comparison of various statistical outputs (BORENSTEIN et al. 2009). Alternatively, this approach can also be utilised in specific research studies designed to test various correlational structures. This statistical procedure provides an overall effect size (ES) that describes the combined effect of the different studies, along with weighted effect size values based on their sample sizes. Moreover, the procedure can also quantify the degree of heterogeneity, which is the variance of the particular effect size values (HARDY and THOMPSON 1998). Significant heterogeneity could suggest a biological mechanism modulating the patterns of the particular effect sizes (i.e., factors within domains), which could be tested with moderator variables using meta-regression. Heterogeneity and ES size are related; the ES shows the magnitude of the effect, and the heterogeneity indicates the variance of within-domain features. If the effects of within-domain features are varied within a domain, opposing effects could counterbalance each other, resulting in a low ES. The predictions of the present study, based on the relationship between overall ES and their heterogeneities, are illustrated in Figure 14.

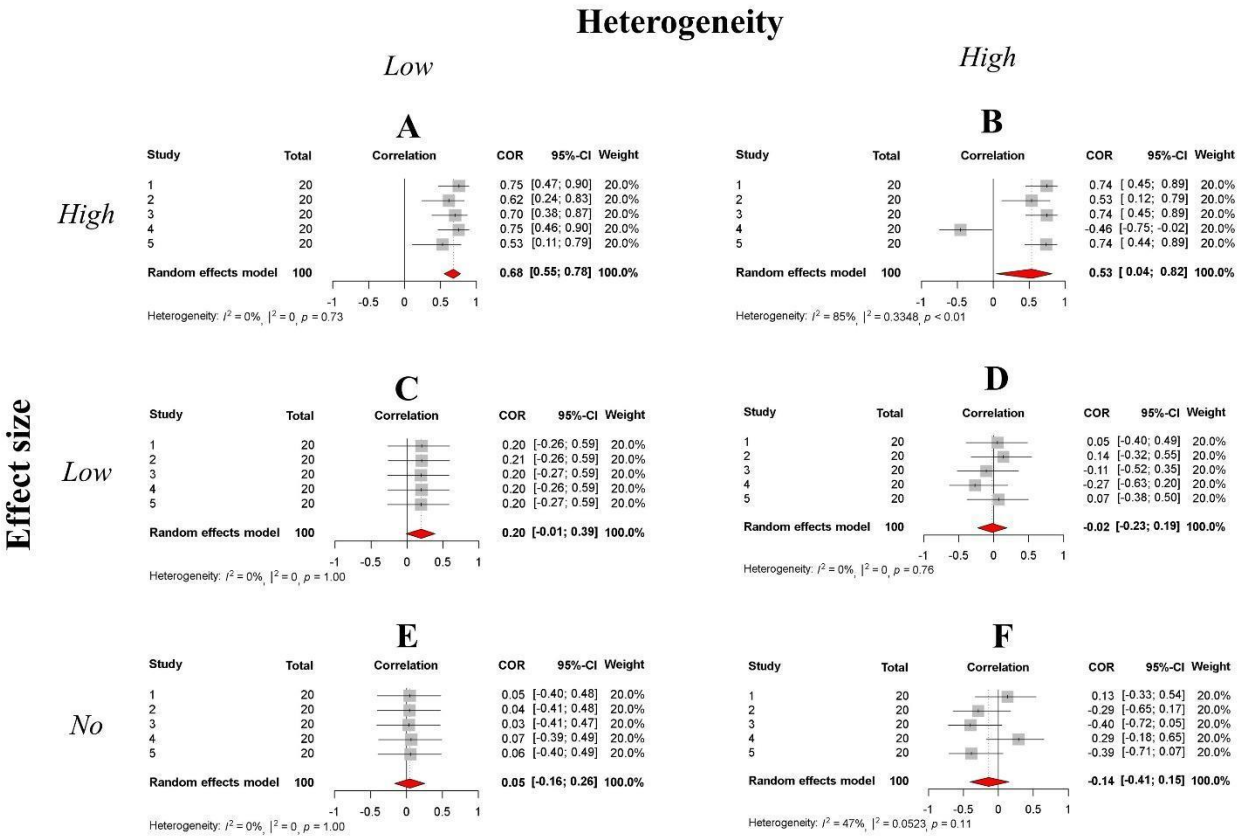


Figure 14 *A visual representation of our predictions regarding various effect sizes and their heterogeneity is illustrated by mini-forest plots*

Heterogeneity can arise from various environmental factors and from the way these variables are measured or assessed. The measurement process and associated errors can be specific to a group, and environmental factors within the same group (i.e., 'within-group') may exhibit more similarities than those in different groups (i.e., 'between-group'). Therefore, understanding the heterogeneity of a correlation structure within a group reflects the consistency of the included variables. Low heterogeneity indicates a consistent pattern, where individual variables exhibit similar directions and magnitudes of effect, while high heterogeneity could result from substantial biological and environmental differences or spatiotemporal patterns (e.g., population and temporal variations become more evident). Consequently, the biological interpretation of Effect Size depends on the level of heterogeneity; from this, six fundamental predictions can be made with varying biological implications. **A) high effect size with low heterogeneity:** The given set of correlations represents a consistent and strong effect. The within-group variables affect the pathogen in the same direction, and there is no high variance in their effects. Therefore, a shift in the same direction for each environmental variable leads to a corresponding and systematic shift in the pathogen's direction. Thus, the role of environmental variables is high. **B) high effect size with high heterogeneity:** There could be meaningful differences between the specific

environmental varieties, but the main direction (combined effect) of each factor is predominantly parallel (directional), producing a systematic effect. **C) low effect size with low heterogeneity:** Although the average overall effect is small, it is consistent across the environmental variables. The role of each environmental variable is small individually, but they could counterbalance each other's effects in the long term. **D) low effect size with high heterogeneity:** The results are less reliable, making it challenging to analyse the effect of variables independently or the overall correlation structure. Due to the high heterogeneity, it is more likely that effects in opposing directions could offset each other. From this pattern, we can conclude that a specific variable represents a spatial or variety-dependent response (potentially more meaningful), while other variables display an inconsistent pattern. **E) no significant effect size with low heterogeneity:** There is no detectable effect of environmental variables on long-term infection occurrence. Low heterogeneity represents consistency without a detectable direction and the magnitude of the individual variables, suggesting that systematic biological effects are probably due to an insufficient sample size or the selection of focal associations. **F) no significant effect size with high heterogeneity (null hypothesis):** The environmental variables exhibit no detectable directional effect on the long-term occurrence of pathogens. The tested environmental variables may fluctuate frequently, hindering the establishment of clear, systematic and directional effects.

5.3 Material and methods

Data collection

To accomplish the analyses, we collected data from each domain using different methods and approaches based on the following general framework. Data about the Infection severity and variables regarding the Vineyard and Technology domains were collected from grape growers using a citizen science research approach via questionnaire, while for the variables related to the Soil domain, we gathered data from a national database. The following sections provide detailed descriptions.

Citizen science approach

To explore the effect of a complex growing environment, a citizen science approach was used based on the research design of previous studies (KOCSIS et al. 2024). For more details see Chapter 3.3 Material and methods, Data collection section (Figure 7). Framers provided data on the average plant health conditions of vineyards based on the preceding five years, average cultivation technology, the most relevant growing environment properties (KOCSIS et al. 2024) and vineyard position (i.e., GPS coordinates of the vineyard or its nearest location). Consequently, the overall multi-year crop protection effects and trends could be quantified, and the long-term

relationships between factors influencing pathogen infestation could be explored. Within the citizen science method, the surveyed variables belonged to three main sections: infection evaluation, Vineyard and Technology domains. The surveyed variables are described briefly in the following.

Infection evaluation

Volunteers provided data on the overall plant health conditions. We surveyed two infection variables to describe the long-term infection status over the last five years, following the guidelines established in our previous citizen science study (KOCSIS et al. 2024). For more details see Chapter 3.3 Material and methods, Infection evaluation section (Table 2).

Before the statistical analyses, first, we created a general infection occurrence index based on the average of the two infection variables, such as infection ratio and infection severity in each pathogen separately, then we applied a min-max normalisation method on these pathogen-specific infection occurrence indices in each year separately. For this procedure, we used the following transformation formula: $x' = (x - x_{min})/(x_{max} - x_{min})$, where x represented the general infection occurrence index, and the x_{min} and x_{max} were the yearly minimum and maximum infection values, respectively. Consequently, all infection data were brought to a standard, continuous range between 0 and 1, where 0 means no infection occurrence, and 1 represents a heavy infection event. These pathogen-specific infection occurrence (hereafter infection occurrence) variables were used in further statistical analyses.

Tested variables

Variables for the Vineyard domain, volunteers provided data on the most relevant vineyard properties such as: ripening, plantation age, slope of the vineyard, orientation, surrounding vineyards, for more details see Chapter 3.3 Material and methods, Vineyard features section (Table 3).

The growers shared information on the technology applied, which belongs to the Technology domain as: number of pesticide applications, inter-row management, leaf removal and height of the canopy wall. For more details see Chapter 3.3 Material and methods, Vineyard features and Crop management sections (Table 3-4).

Finally, regarding the Soil domain, we obtained properties to characterise the corresponding soil condition that were collected from HUN-REN Centre for Agricultural Research Institute for Soil Sciences, Department of Soil Mapping and Environmental Informatics, using an open-sourced Soil Database (https://dosoremi.hu/en/) for each vineyard position following the descriptions of

previous studies (PÁSZTOR et al. 2020; TANÁCS et al. 2022). We gathered site-specific soil quality data as the mean of rootable depth ('Rootable depth', numeric-continuous), organic matter content ('Organic matter', numeric-continuous), lime content ('Lime content', numeric-continuous), pH ('pH', numeric-continuous), clay ('Clay content', numeric-continuous), silt ('Silt content', numeric-continuous), and sand ('Sand content', numeric-continuous). Estimated soil parameters, such as organic matter content, lime content, pH, and the fraction of sand-silt-clay, were available from different soil layers (0-30 cm, 30-60 cm, 60-100 cm, and 100-200 cm). However, the soil quality can be highly varied among the vertical soil profiles, and the root biomass is also unevenly distributed across the different vertical layers of soil (LINSENMEIER et al. 2010; STEENWERTH et al. 2008). So, we calculated a weighted mean for each soil parameter, considering the weights (0.15, 0.55, 0.25, and 0.05, respectively) based on the biomass proportion of the root system among the soil vertical profile provided by previous studies (LINSENMEIER et al. 2010; STEENWERTH et al. 2008). Moreover, the estimation accuracy of the provided soil properties could vary based on the size of the corresponding vineyard (i.e. data from a smaller vineyard is more accurate). Therefore, we provided data regarding the size of the area for further statistical analyses to incorporate this variable into the models as a statistical correction.

Statistical analysis

All statistical analyses were run in the R environment (version 4.4.3., R Development CoreTeam 2019).

Calculating effect-size

An effect size value (ES, hereafter) describes the direction and magnitude of the corresponding relationship, providing opportunities for meta-analytic comparisons. In the present study, we applied two different approaches for calculating effect sizes that describe the focal relationships between infection occurrence and environmental variables. In both approaches, we conducted full pairwise comparisons, where the dependent variable was always the infection, and the explanatory variable was one of the environmental variables.

First, we used Spearman's rank correlation, a robust non-parametric test. Second, we applied a more sophisticated approach, using a parametric Generalized Linear Mixed Model. The application of different approaches required getting a more comprehensive picture of the infection patterns driven by environmental factors. However, both statistical methods are suitable for analysing the magnitude and direction of the relationship between two variables, and they are based on different methodological foundations, assuming divergences in the calculation of ES between the two statistical approaches. Regarding the diversity of tested variables, their data can

have different types and resolutions, and an integrated analysis may not be able to deal with them uniformly. An important addition is that a mixed model can account for random and non-independent systematic effects (e.g., repeated sampling, Variety), can handle differences in non-normal distributions, incorporate statistical corrections for different data quality by weighting (e.g., size of vineyard), and allow spatial autocorrelation for spatial non-independence. A possible disadvantage of mixed models is that the application of excessive statistical corrections can obscure existing biological correlations, which is not the case with Spearman's correlations.

- Spearman's rank correlation

In Spearman's rank correlation, the effect sizes were directly converted from the deterministic coefficients (i.e., the rho of Spearman's correlation), identifying the relationships between pathogen-specific infection indexes and the domain variables.

- Generalized Mixed-Effect Model

To analyse the relationships between the pathogen-specific infection occurrence index and the environmental factors (regarding the leading domains), we applied a Generalized Linear Mixed Model (GLMM) using Template Model Builder (TMB) ('glmmTMB', hereafter) implemented by the 'glmmTMB' package (BROOKS et al. 2017; KOCSIS et al. 2024). The glmmTMB models were run using the following general frameworks. The constructed mixed models were run separately for BC, PV and EN, where the response variable was the pathogen severity, while the predictor variable was the single focal domain variable that was tested separately. Models incorporated their domain-specific adjustments, which were applied constantly along variables belonging to the same domain. The random effects were incorporated to account for non-independence in the data. In all models, the dependent variable was log-transformed to improve normality and stabilize the variance, and the explanatory variables were scaled (by the 'scale' function) before running the model to facilitate standard comparison of the calculated effect sizes. The response variable was modelled using a gaussian family distribution ('gaussian'). The model was weighted by the plantation age to give older plants more influence (KOCSIS et al. 2024). Model assumptions were assessed through residual diagnostics and goodness-of-fit measures. The glmmTMB models were run using the following model specifications outlined in Table 11.

Table 11 *General descriptive table of the glmmTMB model structures for the Vineyard, Technology, and Soil domain variables to analyse the relationships between the infection and specific domain variables.*

Domain	Dependent Variables*	Explanatory Variables*	Mixed model approach (glmmTMB)			
			Type	Random factor**	Weights***	Spatial correction
Vineyard	BC PV EN	*Inclination*, *Orientation*, *Surrounding vineyards*, *Plant age*, *Ripening*	glmmTMB	User + Variety	Vineyard age	no
Technology	BC PV EN	*Treatments*, *Distance*, *Inter-row*, *Leaf removal*	glmmTMB	User + Variety	Vineyard age	no
Soil	BC PV EN	*Rootable depth*, *Organic matter*, *Lime content*, *pH*, *Clay content*, *Silt content*, *Sand content*	glmmTMB	Locality	Vineyard size	yes (Locality)

*Note: * In the model, only one variable was selected from this column at a time in each domain. In each domain, we provided all combinations of dependent and explanatory variables.*

***Random factor: The random factors were included in the models to account for potential systematic variation among observations from individual farmers (i.e., 'User') and grape varieties ('Variety'), identifying data points sourced from the exact same location or grower and grape variety, respectively. Thus, we were able to address repeated observations from the same location in the statistical analyses due to their statistical non-independence.*

****Vineyard age: If the vineyard is 5 years old or older, the weight is set to 1. For vineyards younger than 5 years, the weight is calculated by dividing the plant's age by 5 (KOCSIS et al. 2024).*

Vineyard size: The soil properties of smaller vineyards are estimated with greater accuracy than those of larger ones. This calculation method normalizes the weight data by setting the minimum value (80 hectares) to 1 and progressively down-weighting larger values using a logarithmic scale (log (min (area size)) / log(area size)).

Calculating the effect size of a given relationship from a mixed model structure is challenging due to the random structures. Therefore, we calculated the marginal R2 (R-squared) value that quantifies the proportion of variance only of the fixed effects (without the random effects) in the corresponding mixed-effects models. The marginal R2 explains the magnitude of the variance attributed to the fixed effects alone, on a scale between 0 and 1, where higher values reflect a greater proportion of variance. We applied the function of 'r2_nakagawa' from the 'performance' package.

The marginal R^2 values were considered as effect sizes (ES) for each focal relationship based on the theoretical framework of (COHEN 1988). To preserve the correct direction of the relationship described by marginal R^2, we signed the calculated marginal R^2 values according to the sign of the t-values of the corresponding focal variable (signed marginal R^2, hereafter)

Moderator variables

The domain concept organises environmental factors into three classes based on viticulture disciplines. The vineyard group is a collective category that describes the biological and environmental context of the vineyard. The technology group includes production-related variables that refer to cultivation and management interventions in the vineyard. The soil group encompasses variables that describe the physical, chemical, and biological properties of the soil, which are largely determined by natural conditions. Due to the robust and artificial nature of the domain classification, we created four additional moderator variables, including 'Temporal dynamics', 'Spatial scale', 'Plant health', and 'Pathogen appearance', which consider other relevant aspects. A comprehensive summary of environmental variables and their corresponding scores for each moderator variable is presented in Table 12.

The 'Temporal dynamics' refer to the temporal stability of an environmental factor in a vineyard, and the extent to which it can be flexibly changed through direct farming interventions. These levels were scored on a scale of 0 to 3. Stable (0): Factors that remain constant and fixed during the cultivation period, showing no temporal variation. These factors determine the cultivation process and cannot be altered at the farmer level. Limited flexibility (1): Change can be expressed on a decadal scale. Factors associated with plantation establishment, the extent of which is not entirely constant. The potential for change exists, but it requires strong intervention to achieve modest improvements. Moderate flexibility (2): Change is detectable over the years, influenced by growers' decisions or occurring steadily due to natural processes. Fully flexible (3): Change occurs quickly and flexibly within a year during the growing season, often linked to direct operational management decisions.

The ‘Spatial scale’ indicates the geospatial level at which an environmental factor is present and how its effects can be observed in the vineyard. Vine (0): This level is related to individual plants or small groups of plants. Plantation (1): This level reflects the properties or other differences within a plantation (i.e., blocks or parts of the plantation). Landscape (2): This factor level determines the entire area or region, which includes several plantations.

The ‘Plant health’ reveals the production-related factors that directly and immediately impact the overall health condition of the vine. No or weak indirect (0): There is no direct effect, or the effect is weak and only indirect, influenced by multiple factors. Conditionally indirect (1): The effect is mostly indirect but can become significant under extreme environmental conditions or threshold situations. Moderate direct (2): It has a direct and moderate effect on the health of the plant occurring within the season. Strong direct (3): It has an immediate, direct effect on the plant condition or on the pressure of plant pathogens.

The ‘Pathogen appearance’ indicates how much an environmental factor contributes to the potential for infection and the spread of pathogens in viticulture. No or mild (0): The related environmental factors cannot directly influence the appearance of pathogens. Their effects are only indirect, long-term, or highly influenced by other factors. Moderate (1): This level includes factors which may contribute to the risk of infection but are less important on their own. Their effects are indirect and moderately influence the living conditions of pathogens. Strong (2): This level incorporates factors which effectively modify the living conditions of pathogens or the circumstances of infection. While their effects are more direct and significant, they are not sufficient on their own, so they usually contribute to the emergence of pathogens in combination with other factors. Critical (3): The factors at this level play a key role in the emergence of pathogens. Their effect is immediate, direct, and influential, and they are often capable of either causing or preventing an epidemic on their own.

Table 12 *Comprehensive table of the environmental factors for each moderator variable.*

See text for the detailed description of each moderator variable and its factor levels. Numbers in parentheses indicate the scores used for performing meta-regressions.

Environmental factors	**Moderator variables**				
	Domain	***Temporal dynamics***	***Spatial scale***	***Plant health***	***Pathogen appearance***
Inclination	Vineyard	Stable (0)	Landscape (2)	No or weak indirect (0)	Strong (2)
Orientation	Vineyard	Limited flexibility (1)	Plantation (1)	Moderate direct (2)	Strong (2)
Surrounding vineyards	Vineyard	Stable (0)	Landscape (2)	No or weak indirect (0)	Critical (3)
Age	Vineyard	Moderate flexibility (2)	Vine (0)	Conditionally indirect (1)	Moderate (1)
Ripening	Vineyard	Limited flexibility (1)	Vine (0)	Moderate direct (2)	Critical (3)
Treatments	Technology	Fully flexible (3)	Plantation (1)	Strong direct (3)	Critical (3)
Distance	Technology	Limited flexibility (1)	Plantation (1)	Moderate direct (2)	Strong (2)
Inter-row	Technology	Moderate flexibility (2)	Plantation (1)	Conditionally indirect (1)	Strong (2)
Leaf removal	Technology	Fully flexible (3)	Vine (0)	Strong direct (3)	Critical (3)
Rootable depth	Soil	Stable (0)	Plantation (1)	No or weak indirect (0)	No or mild (0)
Organic matter	Soil	Limited flexibility (1)	Plantation (1)	Conditionally indirect (1)	Moderate (1)
Lime content	Soil	Stable (0)	Landscape (2)	Conditionally indirect (1)	No or mild (0)
pH	Soil	Limited flexibility (1)	Plantation (1)	Conditionally indirect (1)	Moderate (1)
Clay content	Soil	Stable (0)	Landscape (2)	No or weak indirect (0)	Strong (2)
Silt content	Soil	Stable (0)	Landscape (2)	No or weak indirect (0)	Moderate (1)
Sand content	Soil	Stable (0)	Landscape (2)	No or weak indirect (0)	No or mild (0)

Meta regression and testing heterogeneity

We used a meta-analytic approach using '*meta*' (BALDUZZI et al. 2019) and '*metafor*' (VIECHTBAUER 2010) packages. We applied the '*rma.mv*' function to provide meta-regression models and '*metacor*' function to deliver heterogeneity statistics and visualizations. In all meta-analytic random-effects models, effect size estimates were transformed using Fisher's z transformation ('*escalc*' function) before conducting the analyses. During model fitting, we used restricted maximum-likelihood estimator methods ('REML'). For each research objective, we utilized the same model structure and database subsets for both types of ES estimates, which were calculated by Spearman's rank correlation or glmmTMB, and these models were tested separately during the meta-analyses.

First, to calculate the average effect size across the ES estimates and quantify the total heterogeneity (Obj. 1), we fitted a meta-analytic random-effects model, including all pathogens (k = 48) without entering any moderator variables *[(mod.mv2=rma.mv(yi, vi, struct="CS", data=xdata))]*.

Second, to identify the pathogen-specific differences in the overall effect and assess the level of heterogeneity (Obj. 2), we made slight modifications to the initial model. We created a pathogen-specific subset of the ES estimates and ran separate analyses for each pathogen species (k = 16 for each species). *[e.g., (mod.mv2=rma.mv(yi, vi, struct="CS", data=xdata[xdata$pathogen=="BC",])); (met<-metacor(yi, N, data=xdata[xdata$pathogen=="BC",], studlab=VAR2a, sm="zcor", print.byvar=F, comb.fixed=F, comb.random=T, backtransf=T, method.tau="REML", keepdata=T))]*.

Third, to investigate how different moderators influence the relationships between disease occurrence and environmental factors (Obj. 3), we fitted multivariate meta-analytic random-effects models, each including a single moderator variable. We tested each moderator individually, applying separate analyses for each pathogen species (k = 16 for each species). [e.g., (mod.mv2=rma.mv(yi, vi, mods = ~ Domain, struct="CS", data=xdata[xdata$pathogen=="BC",])); met<-metacor(yi, N, data=xdata[xdata$pathogen=="BC",], studlab=VAR2a, sm="zcor", byvar=factor(Domain), print.byvar=F, comb.fixed=F, comb.random=T, backtransf=T, method.tau="REML", keepdata=T)].

This study interpreted the magnitude of the overall effect size and heterogeneity values based on the following benchmarks. The effect sizes, calculated by both Spearman's rank correlation or glmmTMB approaches, for a given environmental factor, such as r < 0.05, 0.05–0.1, 0.1–0.2, 0.2–

0.3, 0.3–0.4, 0.4<, were considered ‘Tiny’, ‘Very small’, ‘Small’, ‘Medium’, ‘Large’, and ‘Very large’ effect categories, respectively (COHEN 1988; FUNDER and OZER 2019). The degree of heterogeneity was described by Cochran’s Q, I^2, τ^2 and τ. An I^2-value reflects the proportion of total variation due to heterogeneity attributed, which can be estimated within a range between 0 and 100, using the traditional benchmarks for interpretation as follows: 25%, 50%, and 75% values referred to as low, moderate and high heterogeneity, respectively (NAKAGAWA and SANTOS 2012). We also tested the statistical difference of the heterogeneity from being zero. To calculate the amount of true heterogeneity, we calculated τ^2 and τ (the square root of τ^2), which indicate the variance of the effect size parameters across the correlation structures tested and describe the variance of the true effect sizes (BORENSTEIN et al. 2009).

5.4 Results

Overall patterns (Obj 1)

The overall ES of all pathogens was found to be tiny, similarly in both ES calculation approaches (Table 13). However, ES estimates calculated by Spearman's rank correlation revealed significant effects, while the GLMM approach was slightly below the detection threshold. The heterogeneity estimates associated with both calculation methods showed consistently moderate levels.

Pathogen-specific effects (Obj 2)

To identify the role of each pathogen species in the variations of the overall effect, we assessed the pathogen-specific overall effect sizes separately for each species (Table 14). The pathogen-specific overall ES values were tiny and positive, but only PV (Spearman) showed a significant difference from zero. The associated heterogeneity estimates varied considerably across pathogens, ranging from low to high levels, indicating high pathogen-specific variances. The BC exhibited the highest heterogeneity, the PV showed a moderate level, but only in the case of the Spearman calculation. Furthermore, the heterogeneity of EN was negligibly low.

Regardless of the type, the ES calculation procedure yielded highly consistent results across the model statistics for the meta-regressions and their associated heterogeneity tests. However, the Spearman approach provided stronger ES estimates and indicated stronger effects than the GLMM approach.

The effects of moderators (Obj 3)

We found high variations in the effects of moderators among the pathogen species (Figures 15-17, Table 15, Table 16, Table 17).

In BC, we found that all moderator variables significantly or marginally contributed to explaining the observed heterogeneity. However, none of them could completely account for the residual heterogeneity (i.e., QE values). Additionally, based on the model estimates and the model fit statistics (i.e., BIC values) of the meta-regressions, it was indicated that Pathogen appearance (increase) and Domain were the most informative predictors with the strongest impact. The pathogen's appearance or risk of infection increased the ES estimates. Within the Domain, the soil-related variables showed a detectably lower association compared to vineyard factors, which increased the ES estimates. Technological factors had similarly marginally lower, yet still positive, effects than vineyard factors. Consequently, we identified significant differences among the Domain subgroups in their within-group heterogeneities. Soil and vineyard groups exhibited moderate and high levels, respectively, while the technology group reflected a moderate amount, but only in the GLMM type of ES calculation. Furthermore, Temporal dynamics showed a modestly significant positive effect on the occurrence of disease through environmental factors. Plant health showed a significant positive effect, suggesting that more direct interventions against plant pathogens or enhancements to plant health conditions could have a greater impact on the relationship between disease and environmental factors. In contrast, Spatial scale had limited explanatory power, showing a negative, marginally significant trend that indicated increasing spatial scales reduced the impact on the ES estimates.

In PV, we were unable to detect any significant moderator variables that could explain the variance in the ES estimates. Accordingly, the associated heterogeneity estimates were insignificant in both the Spearman and GLMM approaches. However, in the Spearman ES calculation, we observed detectable residual heterogeneity in all models that the moderators could not account for. When testing the within-group heterogeneity of the Domain moderator, only the soil (in Spearman-type) and the vineyard (in GLMM-type) groups showed high and moderate levels of heterogeneity, respectively.

Regarding EN, we found that Spatial scale completely explains the observed heterogeneity by demonstrating a significantly negative impact on the relationships between disease occurrence and environmental factors. Temporal dynamics could also contribute to understanding this heterogeneity, showing a significant positive impact (i.e., insignificant QE, significant QM values). This effect was visible in the Spearman approach; the same trend was only partially

detectable using the GLMM approach. We observed a marginally significant positive impact of Plant health. Moreover, domain moderators also exhibited a marginally detectable impact on the ES estimates. Only the Technology subgroup exhibited moderate within-group heterogeneity in the Domain moderator.

Table 13 *The overall and pathogen-specific effects on the relationship between long-term disease occurrence and production-related environmental factors in vineyards*

*The table presents a summary of the fitted meta-regressions to estimate the overall effects for both overall and pathogen-specific null models. The statistical tests were run separately for each model. Abbreviations: ES calculation refers to the method of the calculation of effect size estimates, parameter estimates (β) with their standard errors (SE), z-values, 95% confidence intervals (CI) and p-values. Significant results are highlighted in bold. The asterisks indicate the level of significance of the given predictor (*p < 0.05, **p < 0.01, ***p < 0.001). Each model is based on 16 effect sizes.*

ES calculation	**Predictor**	**ß**	**CI (lower; upper)**	**SE**	**z-value**	**p-value**
ALL pathogen						
Spearman	**Intercept**	**0.029**	**0.010; 0.047**	**0.009**	**3.030**	**0.002 ****
GLMM	Intercept	0.013	-0.006; 0.031	0.009	1.355	0.175
BC						
Spearman	Intercept	0.022	-0.01; 0.054	0.016	1.345	0.179
GLMM	Intercept	0.006	-0.026; 0.038	0.016	0.366	0.715
PV						
Spearman	**Intercept**	**0.038**	**0.006; 0.07**	**0.016**	**2.327**	**0.020 ***
GLMM	Intercept	0.019	-0.013; 0.051	0.016	1.172	0.241
EN						
Spearman	Intercept	0.026	-0.006; 0.058	0.016	1.575	0.115
GLMM	Intercept	0.013	-0.019; 0.045	0.016	0.809	0.419

Table 14 *Heterogeneity estimates for meta-analytic models: overall and pathogen models*

The table presents the relevant heterogeneity estimates calculated from the meta-analytic random-effects models without moderator variables, for all pathogens and for each pathogen separately

*Abbreviations: ES calculation refers to the method of the calculation of effect size estimates, Q: Cochran's Q statistics for assessing heterogeneity, τ^2: estimated amount of total heterogeneity, τ: the square root of the τ^2, I^2: degree of heterogeneity expressed in percent, df: corresponding degree of freedom, CI: corresponding confidence intervals, p-value: corresponding p-value. Significant results are highlighted in bold. The asterisks indicate the level of significance of the given predictor (*p < 0.05, **p < 0.01, ***p < 0.001).*

ES calculation	**Predictor**	**BIC**	**Q (df) p-value**	**tau2 CI (lower; upper)**	**tau CI (lower; upper)**	**I2 (%) [CI lower; upper]**
ALL pathogen						
Spearman	**Intercept**	-50.56	**115.70 (47) <0.001 *****	**0.006 [0.003; 0.012]**	**0.079 [0.055; 0.111]**	**59.4 [44.2; 70.4]**
GLMM	**Intercept**	-67.00	**99.72 (47) <0.001 *****	**0.005 [0.002; 0.010]**	**0.069 [0.045; 0.100]**	**52.9 [34.5; 66.1]**
BC						
Spearman	**Intercept**	21.96	**73.50 (15) <0.001 *****	**0.017 [0.007; 0.047]**	**0.131 [0.086; 0.217]**	**80 [68.4; 87.4]**
GLMM	**Intercept**	16.41	**68.15 (15) <0.001 *****	**0.015 [0.006; 0.043]**	**0.124 [0.08; 0.207]**	**78.3 [65.3; 86.5]**
PV						
Spearman	**Intercept**	-23.32	**28.29 (15) 0.0198 ***	**0.004 [0; 0.015]**	**0.062 [0.013; 0.123]**	**47.5 [6.2; 70.6]**
GLMM	Intercept	-37.18	14.58 (15) 0.482	0 [0; 0.006]	0 [0; 0.075]	0 [0; 52.3]
EN						
Spearman	Intercept	-38.22	13.39 (15) 0.5724	0 [0; 0.005]	0 [0; 0.071]	0 [0; 52.3]
GLMM	Intercept	-36.02	15.74 (15) 0.400	0 [0; 0.006]	0.014 [0; 0.08]	4.5 [0; 54.5]

Table 15 *The effect of moderator variables on the relationship between long-term disease occurrence and production-related environmental factors in vineyards*

*The table presents a summary of the fitted meta-regressions to test the effect of moderator variables on the relationship between long-term infection occurrence and environmental factors (Predictor). The statistical tests were run separately for moderator variables in each pathogen (*Botrytis cinerea, Plasmopara viticola, Erysiphe necator*). We report parameter estimates (β) with their standard errors (SE), z-values, 95% confidence intervals (CI) and p-values. Significant results are highlighted in bold, while the marginally significant effects (0.05 < p ≤ 0.1) are in italics. The asterisks indicate the level of significance of the given predictor (*p < 0.05, **p < 0.01, ***p < 0.001). Each model is based on 16 effect sizes.*

Model	Predictor	**Spearman**						**GLMM**					
		ß	**CI_lb**	**CI_ub**	**SE**	**z-value**	**p-value**	**ß**	**CI_lb**	**CI_ub**	**SE**	**z-value**	**p-value**
Botrytis cinerea													
Domain	**Intercept (Domain: Vineyard)**	**0.132**	**0.074**	**0.189**	**0.029**	**4.5**	**<0.001*** **	**0.084**	**0.027**	**0.141**	**0.029**	**2.882**	**0.004** **
	Domain: Technology	-0.074	-0.16	0.012	0.044	-1.688	0.0915	-0.025	-0.111	0.06	0.044	-0.577	0.564
	Domain: Soil	**-0.208**	**-0.283**	**-0.133**	**0.038**	**-5.438**	**<0.001*** **	**-0.164**	**-0.238**	**-0.089**	**0.038**	**-4.296**	**<0.001*** **
Temporal dynamics	Intercept	-0.01	-0.053	0.034	0.022	-0.435	0.6639	-0.025	-0.068	0.018	0.022	-1.124	0.261
	Temporal dynamics	**0.034**	**0.003**	**0.065**	**0.016**	**2.122**	**0.0339***	**0.033**	**0.002**	**0.064**	**0.016**	**2.07**	**0.038***
Spatial scale	Intercept	0.065	0.003	0.126	0.031	2.066	0.0388*	0.054	-0.008	0.115	0.031	1.716	0.086.
	Spatial scale	*-0.036*	*-0.08*	*0.008*	*0.023*	*-1.6*	*0.1097*	*-0.04*	*-0.084*	*0.004*	*0.022*	*-1.788*	*0.074.*
Plant health	Intercept	-0.004	-0.05	0.042	0.023	-0.179	0.8576	-0.044	-0.09	0.002	0.023	-1.885	0.059.
	Plant health	0.025	-0.006	0.056	0.016	1.553	0.1204	**0.047**	**0.016**	**0.078**	**0.016**	**2.979**	**0.003** **
Pathogen appearance	**Intercept**	**-0.123**	**-0.182**	**-0.064**	**0.03**	**-4.094**	**<0.001*** **	**-0.135**	**-0.193**	**-0.076**	**0.03**	**-4.505**	**<0.001*** **
	Pathogen appearance	**0.089**	**0.059**	**0.12**	**0.016**	**5.751**	**<0.001*** **	**0.086**	**0.056**	**0.117**	**0.015**	**5.606**	**<0.001*** **

Plasmopara viticola													
Domain	Intercept (Domain: Vineyard)	0.023	-0.034	0.08	0.029	0.795	0.4267	0.032	-0.025	0.089	0.029	1.088	0.277
	Domain: Technology	0.061	-0.025	0.146	0.044	1.386	0.1659	0.016	-0.069	0.101	0.044	0.366	0.714
	Domain: Soil	-0.001	-0.076	0.074	0.038	-0.026	0.9793	-0.038	-0.112	0.037	0.038	-0.995	0.32
Temporal dynamics	Intercept	0.022	-0.021	0.065	0.022	0.995	0.3197	0.009	-0.034	0.052	0.022	0.412	0.68
	Temporal dynamics	0.017	-0.014	0.048	0.016	1.077	0.2815	0.011	-0.02	0.042	0.016	0.676	0.499
Spatial scale	Intercept	0.074	0.013	0.135	0.031	2.364	0.0181*	0.047	-0.014	0.108	0.031	1.496	0.135
	Spatial scale	-0.03	-0.074	0.014	0.022	-1.349	0.1775	-0.023	-0.067	0.021	0.022	-1.037	0.3
Plant health	Intercept	0.015	-0.031	0.061	0.023	0.651	0.5148	0.016	-0.03	0.062	0.023	0.679	0.497
	Plant health	0.021	-0.01	0.052	0.016	1.348	0.1777	0.003	-0.028	0.034	0.016	0.191	0.848
Pathogen appearance	Intercept	0.07	0.011	0.129	0.03	2.332	0.0197*	0.032	-0.027	0.09	0.03	1.069	0.285
	Pathogen appearance	-0.02	-0.05	0.011	0.015	-1.27	0.2039	-0.008	-0.038	0.022	0.015	-0.514	0.607

Erysiphe necator													
Domain	Intercept (Domain: Vineyard)	0.043	-0.015	0.1	0.029	1.461	0.144	0.047	-0.01	0.104	0.029	1.605	0.108
	Domain: Technology	0.029	-0.057	0.114	0.044	0.654	0.5128	-0.011	-0.096	0.075	0.044	-0.25	0.802
	Domain: Soil	-0.055	-0.13	0.02	0.038	-1.443	0.1489	-0.07	-0.145	0.004	0.038	-1.848	0.065.
Temporal dynamics	Intercept	-0.005	-0.049	0.038	0.022	-0.241	0.8095	-0.011	-0.054	0.032	0.022	-0.479	0.632
	Temporal dynamics	**0.033**	**0.002**	**0.064**	**0.016**	**2.087**	**0.0369***	0.025	-0.006	0.056	0.016	1.601	0.109
Spatial scale	**Intercept**	**0.088**	**0.027**	**0.149**	**0.031**	**2.811**	**0.0049****	**0.077**	**0.016**	**0.138**	**0.031**	**2.471**	**0.013***
	Spatial scale	**-0.052**	**-0.096**	**-0.008**	**0.022**	**-2.332**	**0.0197***	**-0.054**	**-0.098**	**-0.01**	**0.022**	**-2.401**	**0.016***
Plant health	Intercept	-0.006	-0.052	0.04	0.023	-0.26	0.795	-0.006	-0.051	0.04	0.023	-0.24	0.81
	Plant health	*0.03*	*-0.001*	*0.061*	*0.016*	*1.888*	*0.059.*	0.018	-0.013	0.049	0.016	1.118	0.263
Pathogen appearance	Intercept	-0.011	-0.069	0.048	0.03	-0.353	0.7242	-0.014	-0.073	0.044	0.03	-0.473	0.636
	Pathogen appearance	0.022	-0.008	0.053	0.015	1.442	0.1494	0.017	-0.013	0.047	0.015	1.089	0.276

Table 16 *Summary of heterogeneity estimates for all meta-analytic models with moderators*

*The table presents the relevant heterogeneity estimates calculated from the meta-analytic random-effects models with moderator variables provided for each pathogen separately. The statistical tests were run separately for moderator variables in each pathogen (*Botrytis cinerea, Plasmopara viticola, Erysiphe necator*). Abbreviations: Spearman and GLMM terms refer to the method of the calculation of effect sizes, BIC: Bayesian Information Criterion, QE: degree of residual heterogeneity, QM: degree of moderator heterogeneity, df: corresponding degree of freedom, p-value: corresponding p-value. Significant results are highlighted in bold, while the marginally significant effects (0.05 < p ≤ 0.1) are in italics. The asterisks indicate the level of significance of the given predictor (*p < 0.05, **p < 0.01, ***p < 0.001). Each model is based on 16 effect sizes.*

Model	Spearman			GLMM		
	BIC	**QE (df) p-value**	**QM (df) p-value**	**BIC**	**QE (df) p-value**	**QM (df) p-value**
BC						
Null	21.96			16.41		
Domain	3.02	**42.34 (13) <0.001 *****	**31.17 (2) <0.001 *****	6.69	**46.17 (13) <0.001 *****	**21.97 (2) <0.001 *****
Temporal dynamics	23.65	**69 (14) <0.001 *****	**4.5 (1) 0.034 ***	18.33	**63.86 (14) <0.001 *****	**4.29 (1) 0.038 ***
Spatial scale	25.59	**70.94 (14) <0.001 *****	2.56 (1) 0.110	19.42	**64.95 (14) <0.001 *****	*3.2 (1) 0.074* .
Plant health	25.74	**71.09 (14) <0.001 *****	2.41 (1) 0.12 0	13.74	**59.27 (14) <0.001 *****	**8.87 (1) 0.003 ****
Pathogen appearance	-4.93	**40.42 (14) <0.001 *****	**33.08 (1) <0.001 *****	-8.81	**36.72 (14) 0.001 ****	**31.43 (1) <0.001 *****
PV						
Null	-23.32			-37.18		
Domain	-13.73	**25.64 (13) 0.019 ***	2.64 (2) 0.267	-26.96	12.56 (13) 0.483	2.02 (2) 0.364
Temporal dynamics	-18.28	**27.13 (14) 0.019 ***	1.16 (1) 0.282	-31.44	14.12 (14) 0.441	0.46 (1) 0.499
Spatial scale	-18.95	**26.47 (14) 0.023 ***	1.82 (1) 0.177	-32.06	13.5 (14) 0.487	1.08 (1) 0.3
Plant health	-18.94	**26.47 (14) 0.023 ***	1.82 (1) 0.178	-31.02	14.54 (14) 0.410	0.04 (1) 0.848
Pathogen appearance	-18.74	**26.68 (14) 0.021 ***	1.61 (1) 0.204	-31.24	14.31 (14) 0.427	0.26 (1) 0.607
EN						
Null	-38.22			-36.02		
Domain	-30.68	8.69 (13) 0.796	*4.7 (2) 0.096* .	-27.83	11.68 (13) 0.554	4.06 (2) 0.131
Temporal dynamics	-36.38	9.03 (14) 0.829	**4.36 (1) 0.037 ***	-32.38	13.18 (14) 0.513	2.56 (1) 0.109
Spatial scale	-37.46	7.95 (14) 0.892	**5.44 (1) 0.020 ***	-35.58	9.98 (14) 0.764	**5.76 (1) 0.016 ***
Plant health	-35.59	9.82 (14) 0.775	*3.56 (1) 0.059* .	-31.07	14.49 (14) 0.414	1.25 (1) 0.263
Pathogen appearance	-34.11	11.31 (14) 0.662	2.08 (1) 0.149	-31	14.55 (14) 0.409	1.19 (1) 0.276

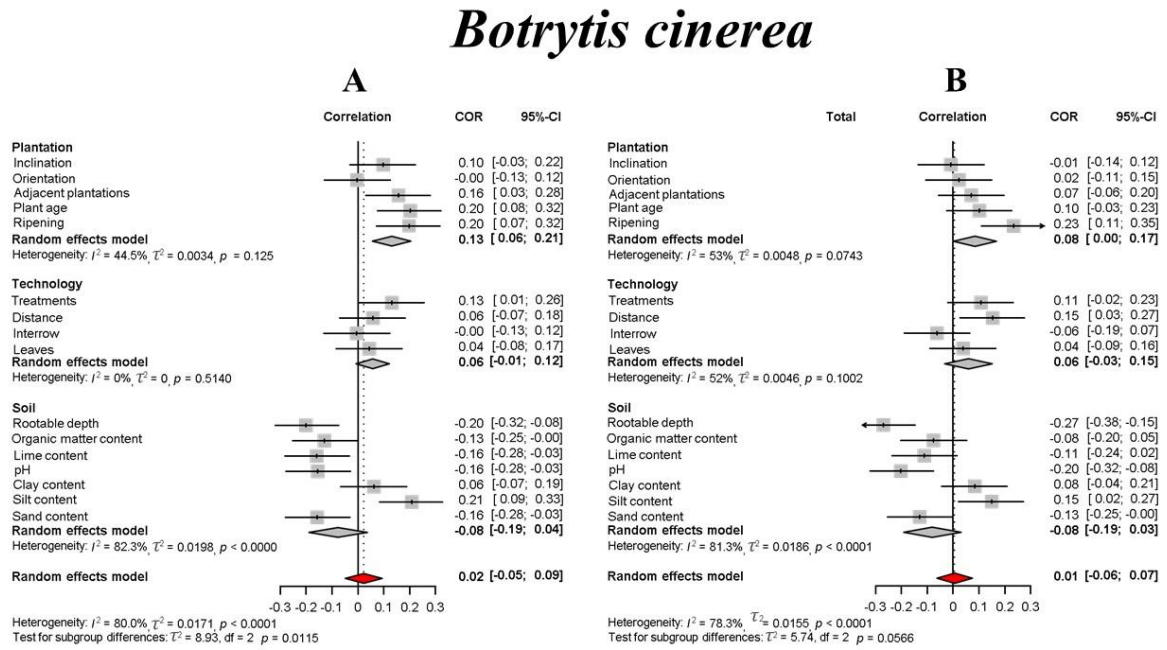


Figure 15 *The overall effects of tested domains in Botrytis cinerea*

The figure shows the overall effect sizes of tested domains (Vineyard, Technology, Soil) from Spearman's rank correlation (A) and Generalized Linear Mixed Model (B) on Botrytis cinerea *(N=237). A grey square indicates the effect size (based on Fisher's z transformation) within moderator variables with the associated confidence intervals (CI 95%, horizontal line). The distance from zero reflects the magnitude of the effect size, while the corresponding effect size was considered significant when the corresponding CI did not include zero. The grey diamonds represent the ES values for the corresponding domain, while the red diamond indicates the overall ES value calculated by the Random effects model.*

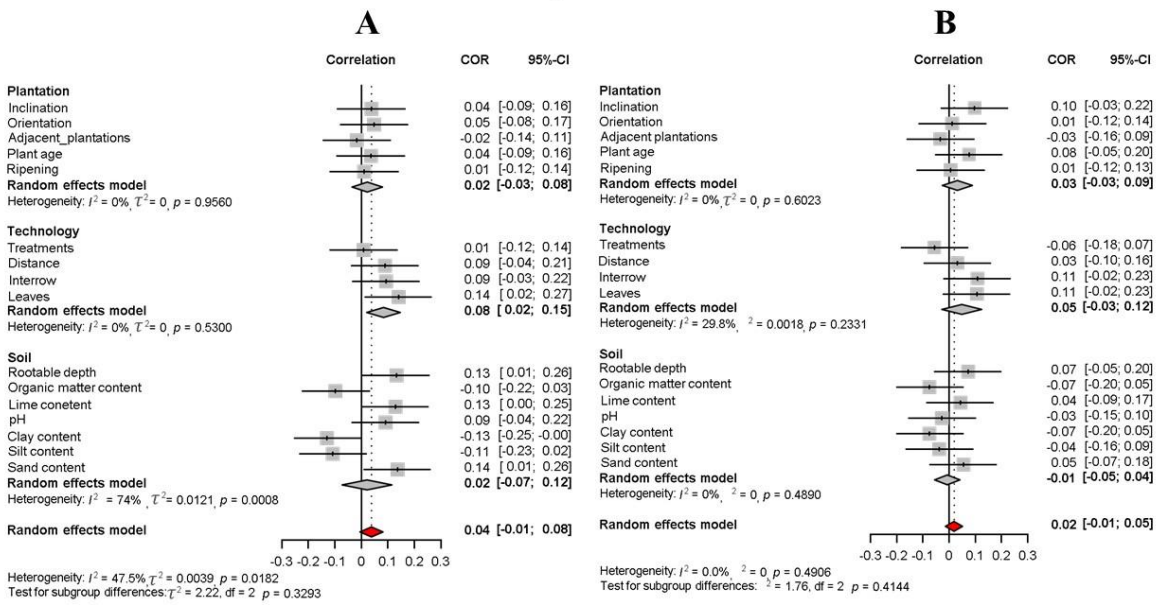


Figure 16 *The overall effects of tested domains in* Plasmopara viticola

The figure shows the overall effect sizes of tested domains (Vineyard, Technology, Soil) from Spearman's rank correlation (A) and Generalized Linear Mixed Model (B) Plasmopara viticola *(N=238). A grey square indicates the effect size (based on Fisher's z transformation) within moderator variables with the associated confidence intervals (CI 95%, horizontal line). The distance from zero reflects the magnitude of the effect size, while the corresponding effect size was considered significant when the corresponding CI did not include zero. The grey diamonds represent the ES values for the corresponding domain, while the red diamond indicates the overall ES value calculated by the Random effects model.*

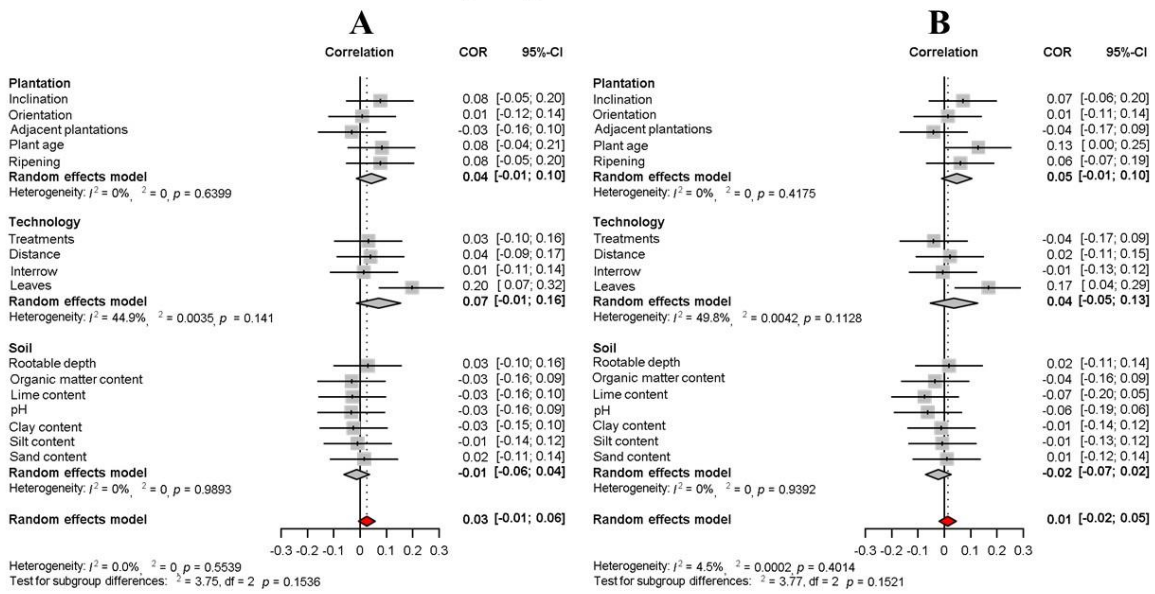


Figure 17 *The overall effects of tested domains in* Erysiphe necator

The figure shows the overall effect sizes of tested domains (Vineyard, Technology, Soil) from Spearman's rank correlation (A) and Generalized Linear Mixed Model (B) Erysiphe necator *(N=237). A grey square indicates the effect size (based on Fisher's z transformation) within moderator variables with the associated confidence intervals (CI 95%, horizontal line). The distance from zero reflects the magnitude of the effect size, while the corresponding effect size was considered significant when the corresponding CI did not include zero. The grey diamonds represent the ES values for the corresponding domain, while the red diamond indicates the overall ES value calculated by the Random effects model.*

Table 17 *Estimates of the subgroup heterogeneity within Domain moderator for each pathogen*

*The table presents the relevant heterogeneity estimates of the subgroups within the Domain moderator calculated from the meta-analytic random-effects models provided for each pathogen separately. The statistical tests were run separately for each pathogen (*Botrytis cinerea, Plasmopara viticola, Erysiphe necator*). Abbreviations: Spearman and GLMM terms refer to the method of the calculation of effect sizes, k: number of the tests combined in the current meta-analysis, τ^2: estimated amount of total heterogeneity, τ: the square root of the $\tau 2$, Q: Cochran's Q statistics for assessing heterogeneity, I^2: degree of heterogeneity in percent.*

Pathogen	ES calculation	Domain subgroups	k	τ^2	τ	Q	I^2(%)
Botrytis cinerea	Spearman	Vineyard	5	0.003	0.059	7.21	44.5
		Technology	4	0	0.000	2.29	0
		Soil	7	0.020	0.141	33.86	82.3
	GLMM	Vineyard	5	0.005	0.070	8.52	53.0
		Technology	4	0.005	0.068	6.25	52.0
		Soil	7	0.019	0.136	32.14	81.3
Plasmopara viticola	Spearman	Vineyard	5	0	0.000	0.66	0
		Technology	4	0	0.000	2.21	0
		Soil	7	0.012	0.110	23.04	74.0
	GLMM	Vineyard	5	0	0.000	2.74	0
		Technology	4	0.002	0.043	4.28	29.8
		Soil	7	0	0.000	5.44	0
Erysiphe necator	Spearman	Vineyard	5	0	0.000	2.53	0
		Technology	4	0.004	0.059	5.45	44.9
		Soil	7	0	0.000	0.89	0
	GLMM	Vineyard	5	0	0.000	3.92	0
		Technology	4	0.004	0.065	5.97	49.8
		Soil	7	0	0.000	1.78	0

5.4 Discussion

General patterns

Overall ES & heterogeneity

In this study, we report a large-scale citizen science project that examined the relationships between complex growing conditions and plant health in vineyards through a meta-analytical approach. Although the overall effect of environmental factors on pathogen occurrence was generally weak, the actual effect size varied significantly among different focal plant pathogens and moderators, with both positive and negative effects repeatedly recorded, which generates a considerable amount of heterogeneity.

For all pathogen species, the overall ES values consistently displayed tiny, positive values. However, the associated heterogeneity values obtained very significant species-specific effects, indicating high, moderate, and low heterogeneity levels in BC, PV, and EN, respectively. The degree of heterogeneity in the strength of the relationships between disease occurrence and environmental variables reflects the degree of exposure of the given pathogen to the combined effects of environmental factors. High heterogeneity, as assessed in BC, suggests that environmental variables have the most complex effect on the pathogen's infection processes, making them the most difficult to understand. In contrast, pathogens with medium or low heterogeneity (in PV and EN, respectively) are only partially influenced by the growing environment concerning their infection processes and long-term prevalence, so their infection risk varies depending on one or a few specific factors.

The low overall ES, along with the varied pathogen-specific heterogeneity, may be attributed to specific environmental variables having either small positive or negative impacts on disease occurrence when considered individually. These opposing factors can counterbalance each other’s effects over time, leading to a low overall ES. Furthermore, when ES remains low despite increasing heterogeneity, it suggests that potentially more meaningful factors may be acting in opposing directions, reducing or neutralising the overall impact. In such cases, identifying one or more specific moderator variables that account for the variance in the total heterogeneity can help us better understand the pathogen-specific patterns of disease occurrence in relation to environmental factors.

As a final remarks regarding the general patterns, we should highlight how critical is the calculation of ES estimates in a meta-analytic study. To avoid potential bias and ensure consistency of the results, we applied two different approaches. We found that the procedure for ES calculation

yielded highly consistent results across model statistics for the meta-regressions and their associated heterogeneity tests, regardless of the type of calculation used. However, the ES estimates calculated from Spearman's rank correlation were more robust and indicated stronger effects in the meta-regressions, whereas the estimates from the GLMM approach yielded moderate effects. A possible explanation for this variance is that a GLMM model is highly adjusted statistically, considering more parameters than the calculation of Spearman's rank correlation. Moreover, the GLMM approach is a parametric test, calculated with the original raw data. Thus, we can take into account differences in data distributions, and every tested relationship can be corrected sophisticatedly for different parameters (e.g., as random factors); however, the effects may be enhanced, but they can also be reduced due to the possible overfitting of multiple parameters. In contrast, Spearman's correlation is a non-parametric test, where only two variables are considered simultaneously; thus, the additional sources of variation in the raw data are neglected and remain hidden.

Effects of moderators

By testing moderator variables in meta-analytic analyses, we can gain a deeper understanding of the role of biological or other functional mechanisms responsible for the heterogeneity observed in ES estimate values (BORENSTEIN et al. 2009). Each environmental factor has distinct and unique properties on the pathogen pressures, but these are act as a combined effect (KOCSIS et al. 2024); therefore, it is necessary to fragment the complex impact of a growing environment into distinct domains or along moderators. Our results revealed high pathogen-specific heterogeneity in the ES estimates, which complexity was explained by moderators that varied significantly in terms of degree and explanatory power. These findings supported our hypothesis that the same or similar regulating factors shift the strength of relationships on disease occurrence in the same direction, thereby shaping the overall impact. However, the domain concept (i.e., grouping of the production-related factors into discipline categories) offers a suitable approach, but it cannot fully explain the within-domain heterogeneity patterns. This is because the environmental variables within the domain groups differ in several aspects, such as acting on different spatial or temporal scales (Table 12) and influencing the long-term appearance of pathogens while modifying their effects in a manner characteristic of the specific pathogen species.

We found that BC showed the most complex and heterogeneous picture regarding the moderator variables among the pathogens tested. Both the domain and the other numeric moderators played a significant or partial role in explaining the observed heterogeneity; nevertheless, none were able to fully account for the residual heterogeneity, as indicated by the QE values. Our results demonstrated the high relevance of the Domain concept, as we identified it as a strong moderator,

but the relevance of subgroups showed high variability, producing a counterbalancing effect. Vineyard and Technology-related factors tended to increase the positive impact on BC occurrence via environmental factors, while soil factors contributed to a reduction. These opposing effects explain the low overall ES values. Our findings illustrate how the effects of domain groups neutralise each other's opposing effects, although strong effects are evident when environmental factors are tested individually on disease occurrence. Supplementing the general results regarding the Domain, other moderators helped to better understand the heterogeneity associated with BC.

Among the numeric moderators, **Pathogen appearance** was one of the strongest moderators, describing a positive gradient along environmental factors that contributed to the potential for infection and the spread of BC in vineyards. This indicates that environmental factors, which have a greater direct and more immediate impact on the living conditions of pathogens or the circumstances of infection, and cause or prevent an epidemic (i.e., 'strong', 'critical' classes), have a stronger influence on the long-term occurrence in BC, while opposing factors with zero or less direct impacts ('No or mild' or 'Moderate') tended to reduce the BC occurrence.

According to our findings, the pathogen occurrence in BC is primarily influenced by factors related to cultivation technology and specific plantation characteristics. Among the factors we examined, several are particularly relevant to pathogen appearance. Fungicide treatments are essential in grape production (LIERE et al. 2017) due to the short incubation period of BC, which allows infection to progress rapidly (CORIO-COSTET et al. 2010; GADOURY et al. 2012; NAIR and ALLEN 1993). These treatments also help prevent infection following unfavourable climatic events (ROMANAZZI et al. 2016). However, resistance to chemical fungicides could compromise the effectiveness of these implementations, regardless of the treatment frequency (HAHN 2014). Additionally, pathogen appearance can depend on the susceptible phenological stage, which is determined by the timing of ripening based on the variety selection (COERTZE et al. 2001; KELLER et al. 2003; WOLFE 2000). Furthermore, other key factors also contribute, particularly the conidial pressure from surrounding vineyards (ELLIS 2008; STAPLETON et al. 1995; WARREN et al. 1999), and climatic conditions affecting the plantation, such as solar exposition and air circulation within the canopy (MUNDY and BERESFORD 2007). In contrast, soil properties that promote the removal of excess water, such as sandy soils (FINCH et al. 2014), contribute to reducing pathogen occurrence. Thus, the technologies applied in viticulture directly impact infection potential by reducing the presence of conidia and preventing early infections during susceptible phenological stages, while plantation-related factors indirectly affect the growing environment, shaping the infection processes by modifying the environmental requirements to be less ideal for the pathogen.

The temporal dimension plays a crucial role in viticulture. Our study emphasised that accounting for these temporal dynamics is essential for understanding the relationship between disease occurrence and environmental factors, making it a critical aspect to consider. We found that temporal dynamics showed a modestly significant positive effect on the occurrence of disease through environmental factors, which indicates that systematic modifications to the plantation environment can create changes that have a cumulative impact over a longer timescale. On one hand, there is a strong need for flexible and responsive management decisions to mitigate damage caused by plant pathogens or other undesirable events (OLIVER et al. 2024; THIESSEN et al. 2017).

On the other hand, current plant management can influence the long-term presence and severity of pathogens through decisions that modify specific environmental and technological factors, which have different temporal consequences and can affect outcomes within a single season or over the span of years or decades. For instance, at the establishment of a plantation, vineyard structure and landscape can determine several environmental conditions that can be advantageous or not (JAYARAMAN et al. 2021; KOCSIS et al. 2024; VAN LEEUWEN et al. 2018).

These results also emphasise the importance of timing and the effectiveness of the management decisions over time. Addressing these aspects is crucial for shaping viticulture to adapt to a climate-resilient growing environment, such as mitigating unwanted abiotic stresses and the increasing emergence of pathogens (MURRAY-WATSON and CUNNIFFE 2022).

Traditional grape and wine production relies on regional quality specifications and standards, highlighting its unique characteristics tied to a specific terroir brand (VAN LEEUWEN et al. 2018). Systematic spatial differences in grape infections may suggest a possible role for large-scale background mechanisms, along with variations related to macroclimatic, topographic, and soil conditions (FINCH et al. 2014; LI, S. et al. 2017; MATESE et al. 2014). In contrast, our large-scale study found that spatial scale had limited explanatory power of spatial scale. Specifically, we revealed a negative, marginally significant trend that indicated increasing spatial scales reduced the impact on the ES estimates. This may indicate that larger scales can compensate for local variability, making spatial scale less relevant in predicting disease occurrence at the landscape level.

A healthier plant has a more effective defence system against pathogens compared to plants that have deteriorated physiological condition as a consequence of exposure to biotic and abiotic stressors (DENANCÉ et al. 2013). Therefore, establishing and maintaining an optimal growing environment for grapes is crucial, not only for producing a higher quality product but also for

ensuring effective plant protection (FAGERIA et al. 2008; GAUNT 1995). More direct interventions against plant pathogens or improvements to plant health could have a greater impact on the relationship between disease and environmental factors (EVERS et al. 2010). Aligning with this, we identified a significant positive effect of the Plant health moderator. Moreover, these results are consistent with studies that have revealed that BC is more likely to infect weakened or stressed tissues rather than healthy ones (EDLICH et al. 1989; ELAD and EVENSEN 1995). Therefore, management practices aimed at maintaining or enhancing ideal growth conditions, such as balanced soil nutrient compositions and other properties (DE NEVE 2017; HARTEMINK and BARROW 2023; NDUWUMUREMYI 2013; NEWMAN 1985) and structural factors of the vineyard landscapes (JACOMETTI et al. 2007a, 2007b; KOCSIS et al. 2024; VAN LEEUWEN et al. 2018), can help reduce abiotic stresses to indirectly lower the risk of pathogen infections.

Although most moderators contributed significantly to clarifying the sources of heterogeneity, none could fully explain the total heterogeneity observed. This pattern indicates that the infection and epidemic spread of BC are regulated by complex, multifactorial processes. These processes are primarily determined by environmental factors related to vineyard properties and soil, and only secondarily by the technological components of grape production.

Identifying the combined effect of environmental factors on disease occurrence through the domain variables is especially challenging due to their complex interactions, which vary across temporal and spatial scales. However, future research that utilizes a comprehensive transdisciplinary approach could enhance our understanding of this complexity.

In the case of PV, explaining the role of moderators is challenging because none of them had a detectable effect. Additionally, the heterogeneity of the ES estimates was particularly low and showed a consistent pattern. The only exceptions to this were detected within certain domain subgroups, such as soil and vineyard (in Spearman and GLMM, respectively), which suggests that some technology-related features may have an impact on the disease occurrence. Although some specific fungicide treatments can control or mitigate the severity of damage (VERCESI et al. 2002), rather than the other plantation-related factors examined, it is more likely that the occurrence of PV is better determined by current climatic and microclimatic conditions (KHATAL et al. 2023). Moreover, these environmental factors provide a stable background with only minimal or indirect influence on climatic conditions, which exhibit little to no fluctuation during the season or over the years, thereby, only the current climatic conditions can limit the spread of PV (CAFFI et al. 2016). In this study, climatic factors were not examined and therefore cannot be captured by the moderators examined. However, the tested environmental factors may directly or moderately impact the microclimatic conditions within the plantation. For instance, applying leaf removal in

the cluster zone promotes solar exposure and reduces humidity (MUNDY et al. 2012; ROMANAZZI and FELIZIANI 2014), while the use of cover plants in the inter-row can increase humidity (BAU and CHASSAING 2025; QUDSI et al. 2021). Additionally, other studies have demonstrated that other species-specific features of PV, such as genetic adaptation, wide tolerance to environmental conditions, and other life-history traits, can also promote the widespread occurrence in vineyards (DELMOTTE et al. 2014; FRANCESCA et al. 2006). Our results indicate that predicting the long-term PV occurrence is less effective when relying solely on simple environmental or cultivation technology variables. Therefore, future comprehensive studies should consider factors that directly affect microclimatic conditions within the environment, with an emphasis on more flexible, climate-dependent predictors, as static variables provided a limited contribution to reducing infections.

The overall heterogeneity of EN was very low. However, this was only fully explained by moderators related to spatial and temporal scales. Concerning spatial scale, factors with extensive spatial representation tend to weaken the identified relationships between disease occurrence and environmental factors. This suggests that processes occurring at the vine level primarily drive the long-term emergence of the pathogen. Conversely, the positive effect of Temporal dynamics indicates that more rapidly and flexibly controllable environmental factors had the greatest influence on the emergence of ES estimates through environmental factors. The impact of other axes, described by the Domain and Plant health moderators, was minimal, but the Technology subgroup displayed moderate internal heterogeneity. This aligns with earlier observations that spatiotemporal aspects show the most flexibly controllable factors are mainly linked to grape production technologies, such as defoliation of the cluster zone and fungicide applications. In addition to fungicide treatments, defoliation effectively reduces humidity and enhances UV exposure, creating a less favourable microenvironment for EN infection (MUNDY et al. 2012; ROMANAZZI and FELIZIANI 2014). Therefore, our findings indicate that EN damage is mainly regulated by rapid and flexible technological applications at the vine level, rather than by less affected static or slowly changing soil or plantation characteristics. The results are consistent with the fact that EN infection and epidemic spread mainly originate from inoculum accumulating on the vine and its microenvironment (REDL et al. 2021), rather than the lesser influence of surrounding plantations. Both EN and PV are mainly affected by climatic conditions, which may similarly shape their infection and spread (KHATAL et al. 2023; REDL et al. 2021). However, most tested environmental factors had little or no direct impact on microclimate regulation. We observed a less pronounced effect on long-term EN occurrence, indicating that the widespread presence of EN in vineyards is likely to persist, emphasising the importance of regular fungicide

management. Future research should focus on environmental variables that significantly influence the microclimate of grapevines and on factors reducing inoculum sources.

Our Citizen science study, employing a meta-analytical approach, highlights that vineya rds, as a production environment, are shaped by a complex interaction of vineyard features, management practices, and soil properties, which collectively establish the plant health and the potential risk of infection by pathogens. The pathogen's occurrence showed a species-specific variance according to the environmental conditions. Environmental factors play distinct functional roles and impacts; however, similar factors may lead to similar pathogen responses through their impacts on similar functional roles in the pathogen's life cycle. Treating the impact of unique environmental traits separately can be misleading, as grapevine health emerges from the complex interactions of multiple factors within the growing environment. Using moderator variables provided a valuable framework to distinguish these traits and better understand their roles within a broader production context. The present study demonstrated that the responses of the three pathogens to the moderators differed significantly, reflecting their specific ecological requirements and the environmental factors that influence infection. BC was shaped by a complex, multicausal set of factors, with no single moderator fully explaining the variance. In contrast, PV was less predictable based on static environmental factors, indicating a stronger influence of microclimate and current climatic events. In EN, spatial and temporal environmental patterns were evident and could be better incorporated comprehensively into large-scale studies in the future.

These pathogen-specific differences emphasise that grapevine diseases cannot be controlled according to uniform schemes, but management decisions require pathogen-specific strategies that reflect their ecological and environmental embeddedness. Practically, identifying moderators also allows for targeted plant protection interventions and identifying environmental factors that predict damage caused by particular pathogens. For example, in BC, more sophisticated data collection and multivariate models could improve prediction accuracy by accounting for ecological variables and plantation structure. For PV, models that include weather-dependent and microclimatic factors are necessary, while for EN, appropriate spatial monitoring and defoliation decisions require further attention. Ignoring this complexity risks underestimating or overemphasising certain factors, whereas recognising their combined effects allows for more precise and adaptive plant protection.

Beyond these pathogen-specific insights, our study also demonstrates the value of large-scale observation obtained from real growing conditions, which complements previous studies. Citizen science is a particularly useful methodological approach when combining the valuable experience of vine growers with scientific methodology, offering partial benefits from the results of scientific

knowledge. With the increasing availability of autonomous sensors and IT platforms, collecting environmental data is becoming less challenging; however, comprehensive analysis and validation of these data will be critical for supporting evidence-based vineyard management. Future studies should pay more attention to analysing these data comprehensively for model validation supporting decision-making of vineyard management. Overall, our findings emphasise that grapevine diseases exhibit varying ecological and technological embeddedness, underscoring the need for differentiated, adaptive, and pathogen-specific management strategies in viticulture.

Vineyards are permanently extended to various environmental factors in the shared biophysical context. These factors encompass vineyard features, soil characteristics and crop management practices, which collectively establish the plant health. The separate interpretation of the impact of the unique characteristics could lead to erroneous conclusions, as the vine health is the result of a dynamic synergism given by the growing context. As an agricultural outcome of the neglected effect of a complex growing environment, the role of some environmental factors could be underestimated, while others could be overemphasised. These results highlighted how different results could be retrieved by examining variables within complex systems instead of testing them independently. Our study revealed that the long-term occurrence of grape primary pathogens originated in the cooperation of various interdisciplinary variable groups, called domains. We detected vineyard and soil domains as the main drivers of long-term disease occurrence, while in a complex analysis, the crop management domain did not have a determining role. Moreover, our large-scale research is based on observation of real growers from real growing conditions, thus in vivo testing the concepts of previous research. We are committed to benefit more from the Citizen science research approach, which enables combining the valuable experience of vine growers with the methodological knowledge of researchers. This offers an excellent opportunity for further research to complement the knowledge gap on the role of climatic conditions in a complex growing context.

8. NEW SCIENTIFIC RESULTS

8.1 Pollen-spore interaction

1. Using the Generalised Mixed Effect Model, I have proved that the aqueous extracts of pollen grains have a general stimulating effect on the germination of *Botrytis cinerea* conidia. The ratio of spore germination increases with time, along with the concentration gradient.
2. Species-specific functional attributes, such as host compatibility, cultivation and pollen size, highly affect the germination ratio of *Botrytis cinerea:* the efficiency of host pollen, non-crop plants and larger pollen grains is improved.

8.2 Vineyard, management and variety characteristics influence disease prevalence

3. Analysing the citizen science data using multivariate statistical models, I found that specific vineyard properties influence the long-term occurrence of *Botrytis cinerea* and *Plasmopara viticola*, but not *Erysiphe necator*. *Botrytis cinerea* infection is increased by the Northeast-Southwest row orientation, a higher proportion of adjacent plantations, a higher canopy wall, an increased number of chemical treatments and spatial variation. *Plasmopara viticola* infection is more severe in areas with a higher inclination, row orientation, a higher proportion of adjacent plantations, and spatial variation.
4. Specific features of grape varieties influence the long-term occurrence of *Botrytis cinerea*: the occurrence of infection is increased by the delay in ripening periods, finer berry skin, and blanc berry colour.

8.3 Impact of vineyard properties on shifting grape phenology and its implications for plant diseases

5. Using a large-scale Citizen science survey, I revealed that the row orientation increased the grapevine phenological shifts along with the systematic deviation from the northern direction.
6. In *Erysiphe necator*, the infection occurrence is decreased with the increased phenological shift over the long-term.

8.4 Long-term influences on disease occurrence: a meta-analytic comparison of vineyard, technology and soil features.

7. Using a meta-analytical statistical approach on Citizen science data, I found that the complex growing context in viticulture, including environmental factors related to vineyard, soil, and technology domains, has a pathogen-specific impact on overall effect sizes, which show consistently low overall effect sizes for each tested pathogen (*Botrytis cinerea, Plasmopara viticola, Erysiphe necator*) with low to high heterogeneity. These results suggest that the ongoing environmental factors' counterbalancing effects neutralise the opposing impacts, shaping the long-term presence of pathogens.

9. SUMMARY

Agricultural systems are constantly under pressure by various environmental factors that create a complex production environment. Living organisms are not simple receivers of these environmental impacts, but they influenced and shaped according to the magnitude and the direction of the selection forces perceived from the environment adapting to their habitat in the most efficient way, thus the lifecycle of living organisms formed by the synergetic effect of the environment (CORRIS 2020). These interactions are the main drivers of the adaptation processes of species living in natural habitats and also in agroecosystems. Therefore, crops and their pathogens are under similar adaptation processes, which are located within the same growing conditions over a long period as vineyards. Grape's primary pathogens, such as grey mould (*Botrytis cinerea*), downy mildew (*Plasmopara viticola*) and powdery mildew (*Erysiphe necator*), linked tightly to their host and the local growing conditions, including crop management and plant protection. These complex interactions provide an accelerated adaptation process to the changes of the host plant and the environment at the same time. Environmental variables, rather than acting independently, operate simultaneously within the same environmental regimes, causing an integral effect on crop production, including disease occurrence and severity. Therefore, there is a rising need for a complex and empirical revision of the interfering effects between grape infection and other external factors, such as environmental conditions and management practices. In our cross-disciplinary research series, we aimed to identify the most meaningful factors of complex growing environments which define the long-term disease prevalence of grape primary pathogens. To reveal the complex effect of the growing environment, we always applied multivariate approaches and tested their contribution at the wide spatial scales from the microscopic environment, focusing on the phyllosphere processes, and to the country-level scales, investigating the effects of large-scale global patterns on the sector of grape production.

At the dimension of micro-environment, plant pathogens are exposed to a wide range of organic mass, such as diverse airborne plant pollen grains and fungal spores, whose microbial interaction could take place on the surface of the grape (HENNEBERT 1973; KOCSIS et al. 2022). Thus, this could increase the variation of the pathogen infection risk in certain plants due to selection mechanisms, such as host–pathogen coevolution, crop breeding or pollination type. To detect the germination stimulation effect, we performed a multispecies experimental comparison (including 20 plant species) to test the role of the taxon–specific attributes (i.e., host–pathogen compatibility, cultivation, pollination type and pollen size) in the dose and temporal response of the spore germination in *Botrytis cinerea*. We found a strong pollen-stimulating effect on spore germination; however, the triggering effect highly varied among plant species and differed between specific

functional categories across temporal and concentration gradients. Specifically, the *Botrytis cinerea* hosts, the non-cultivated plants and species with larger pollen size, increased the spore stimulation effects, but not the pollination type. The systematic taxonomic and functional differences might reflect indirectly the diversity of the pollens' chemical profile (i.e. composition matrix or specific trigger molecules), which different selection mechanisms might shape. In conclusion, the pollen-stimulation effect could play an essential role in early fungal development. A publication representing the research: **Ivett Kocsi, Marietta Petróczy, Kolos Zoltán Takács, Gábor Markó (2022): Stimulation role of pollen grains in the initial development of *Botrytis cinerea*: The importance of host compatibility, cultivation status and pollen size, in: Journal of Phytopathology, Q2, IF: 1.1 (2023)**

To detect a more complex effect of the growing environment, we turned to the large-scale dimensions. At this level, the environment-induced selection pressures could modify the occurrence of grape pathogen agents. With this aim, we applied citizen science research approaches. We gathered data from active grape growers about their vineyard properties and the occurrence of grape primary diseases, such as grey mould, downy mildew and powdery mildew, across Hungary. After building a massive dataset across Hungary, including the traditional grape producer regions, containing time- and georeferenced data, we examined the effects of complex environments on the long-term disease occurrence from the following aspects: (1) Vineyard environment and crop management practices; (2) Climate- and variety-specific roles, and their impact on the phenological shift; and (3) Comparing leading environmental domains regarding soil, vineyard properties and crop management.

1. 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. The present study revealed that specific plantation features influence the long-term occurrence of *Botrytis cinerea* and *Plasmopara viticola* but not *Erysiphe necator*. Long-term occurrence of *Botrytis cinerea* was increased by NorthEast–SouthWest row orientation, higher proportion of adjacent plantations, higher canopy wall and increased number of chemical treatments, while SouthWest- NorthEast row orientation decreased the long-term disease severity. *Plasmopara vitcola* infection was more enhanced along with the magnitude of the inclination of the vineyard, NorthEast–SouthWest and SouthWest- NorthEast row orientation, higher proportion of adjacent plantations. Furthermore, regions reflected significant spatial variation in *Botrytis cinerea* and *Plamopara viticola* long-term infection. Furthermore, specific variety features influenced the long-term occurrence of *Botrytis cinerea*. The observed infection occurrence increased with the delay of the ripening

periods, finer berry skin and berry colour: blanc varieties suffered more from BC infections, while noir varieties enjoyed a relatively higher defense. Consequently, 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. A publication representing the research: **Ivett Kocsis, Marietta Petróczy, Gábor Markó (2024): Bridging boundaries: Exploring vineyard, management and variety characteristics influencing long-term infection of grapevine pathogens, in: OENO One, Q1, IF: 2.2 (2024)**

2. Viticulture is forced to adapt to global climatic changes, which can be expressed via more frequent and extreme climatic events. These effects could generate shifts in grape phenological development, since vine phenology aligns with suboptimal growing conditions generated by climate change. The less understood environment-driven grape phenological shift could make production even more challenging, since monitoring grapevine phenology is crucial for professional grape and wine producers due to phenology-specific management decisions. Hence, there was an increasing need for a thorough review of the phenological development based on existing Growing Degree Days (GDD) approaches, while also considering climatic factors and other environmental cues that affect vineyard management. We found that the single threshold GDD approach at an 8°C base temperature described the most accurate grape development between the stages fruit set and harvest. Among the vineyard properties, only the row orientation played a role in modifying grape phenology and caused the phenological shift. When studying the long-term occurrence of grape diseases, we found that various production-related factors influenced disease prevalence, but the climate and variety-driven grape development determined only the prevalence of powdery mildew disease. **A revised and resubmitted manuscript: Ivett Kocsis, Marietta Petróczy, Gábor Markó: Unveiling grape phenology dynamics through large-scale citizen science: Insights on variety, climate, vineyard features, and diseases (resubmitted: Aug 2025).**

3. Vineyards are constantly exposed to a variety of environmental factors, including soil characteristics, vineyard features, and crop management practices, which work together to influence and shape physiological conditions and plant health. Using an unconventional methodological approach, we attempt to test them in the same study, breaking up their potential relevances and testing their role in disease development.

   Our meta-analytical study revealed that the long-term occurrence of grape primary pathogens originated in the cooperation of various variable groups, called domains, which represented

different disciplines. We detected the vineyard and soil domains as the main drivers in long-term disease occurrence, while the crop management domain showed a less determining role. This could be explained by the fact that crop management interventions could rapidly and flexibly shape the production environment according to current problems, even at a within-year level. **A manuscript under the final preparation before the first submission: Ivett Kocsis, Marietta Petróczy, László Pásztor, Annamária Laborczi, Gábor Markó: Long-term influences on disease occurrence: a meta-analytic comparison of vineyard features, soil, and technology in a citizen science study (expected submission: September 2025).**

This transdisciplinary research series provided comprehensive insights into the role of the production environment in the plant protection strategy of the grapevine. We are committed to benefiting more from citizen science as a research and methodological approach, which enables us to combine the valuable experience of vine growers with the methodological knowledge of researchers and could increase the civil engagement and awareness of new scientific aspects. This offers an excellent opportunity to complete the dynamic evolving knowledge gap in plant-pathogen-environment interaction.

10. CONTRIBUTION

The authors provided the following contributions during the study and along with the publication process:

1. **Stimulation role of pollen grains in the initial development of *Botrytis cinerea*: The importance of host compatibility, cultivation status and pollen size, in: Journal of Phytopathology, Q2, IF: 1.1 (2023)** https://doi.org/10.1111/jph.13149

Ivett Kocsis: methodology, formal analysis and investigation, writing the first draft, review and editing

Marietta Petróczy: conceptualization, methodology, review and editing

Kolos Zoltán Takács: formal analysis and investigation

Gábor Markó: methodology, formal analysis and investigation, writing the first draft, review and editing, supervision

2. **Bridging boundaries: Exploring vineyard, management and variety characteristics influencing long-term infection of grapevine pathogens, in: OENO One, Q1, IF: 2.2 (2024**) https://doi.org/10.20870/oeno-one.2024.58.1.7677

Ivett Kocsis: methodology, formal analysis and investigation, writing the first draft, review and editing

Marietta Petróczy: methodology, review and editing

Gábor Markó: conceptualization, methodology, formal analysis and investigation, writing the first draft, review and editing, supervision

3. **Unveiling Grape Phenology Dynamics Through Large-Scale Citizen Science: Insights on Variety, Climate, Vineyard Features, and Diseases** (manuscript, resubmission: August 2025)

Ivett Kocsis: methodology, formal analysis and investigation, writing the first draft, review and editing

Marietta Petróczy: methodology, review and editing

Gábor Markó: conceptualization, methodology, formal analysis and investigation, writing the first draft, review and editing, supervision

4. **Long-term influences on disease occurrence: a meta-analytic comparison of technology, soil, and vineyard features in a citizen science study** (expected submission: September 2025)

Ivett Kocsis: methodology, formal analysis and investigation, writing the first draft, review and editing

Marietta Petróczy: conceptualization, methodology, review and editing

László Pásztor: data collection, methodology, review and editing

Annamária Laborczi: data collection, methodology, review and editing

Gábor Markó: conceptualization, methodology, formal analysis and investigation, writing the first draft, review and editing, supervision

ACKNOWLEDGMENT

'Nothing in life is to be feared, it is only to be understood. Now is the time to understand more, so that we may fear less.' -Marie Curie-

This thesis is the Milestone of years of hard work, professional and personal development, but it would not have been possible without the ongoing support and encouragement of many exceptional individuals.

First and foremost, I am extraordinarily grateful to my supervisor, Gábor Markó. You taught me to seek for the mechanisms of the world around us and always encouraged me to think critically. Your constructive thinking has always helped me through challenges that seemed impossible. I would like to express my profound gratitude to my former supervisor, Marietta Petróczy, also. Thank you for always seeing what I needed, teaching, supporting and encouraging, you were there beyond strength. I appreciate for giving me professional knowledge and human values at the same time. Working in our team of three has always been an inspiring process. I would start again with you anytime. I will be eternally grateful to you for teaching me to believe in myself and get from the 'Am I able to do?' to a 'How can I do?' mindset.

My heartfelt gratitude goes to the former and current colleagues of the Plant Pathology Department. Thank you for the supportive environment you created, the inspiring conversations and the countless shared experiences. I will always look back with pleasure on the years we spent together. I would also like to thank every member of the 'PhD room' ever, glad to share this journey with you. Special thanks go to Lilla Szendrei and Attila Fodor, thank you for your ongoing support in the most challenging situations.

I would like to express my sincere appreciation for the inspiring conversations about plant protection of grape with Terézia Dula, István Füzi, Péter Hoffmann and András Sebestyén. Special thanks for the professional support to Donát Magyar in the pollen project, Annamária Laborczi and László Pásztor in the soil project. I would like to thank the volunteers who participated in the citizen science research and contributed valuable data to support the project.

Last but not least, I am grateful to my family for the unconditional support. To my parents, thank you for teaching me perseverance, humility and for providing the opportunity for learning over and above your strength. I am grateful for my sister, Otília, for being a role model of diligence and her family for supporting me with their love. To my forever co-author in soul and life in the field of private life, Tamás, thank you for your patience and for the emotional support during the long hours of writing and research.

SUPPLEMENTARY

Supplementary 1 *Summary of the taxonomic and biological differences of the tested plant species, including the sampling events*

** Multiple dates indicate multiple events for sampling (date format: dd/mm/yyyy).*

Plant species (family)	**Pollination**	**Cultivation**	**Host-plant of *Botrytis cinerea***	**Pollen diameter (mean, µm)**	**Sample collection (site; date) ***
Ambrosia artemisiifolia (Asteraceae)	anemophilous	non-crop	no	18.25	Dömsöd; 04/08/2018
Artemisia vulgaris (Asteraceae)	anemophilous	non-crop	no	19.90	Dömsöd; 17/09/2018
Bellis perennis (Asteraceae)	entomophilous	non-crop	no	18.23	Szekszárd; 21/04/2019
Brassica napus (Asteraceae)	entomophilous	crop	yes	31.80	Bónifok; 14/04/2018, 21/04/2019
Cannabis sativa (Cannabaceae)	anemophilous	non-crop	yes	22.78	Dömsöd; 24/07/2018
Chenopodium album (Chenopodiaceae)	anemophilous	non-crop	no	36.25	Szekszárd; 13/07/2019, 14/07/2019
Chenopodium hybridum (Chenopodiaceae)	anemophilous	non-crop	no	19.25	Szekszárd; 25/07/2019
Convolvulus arvensis (Convolvulaceae)	entomophilous	non-crop	no	54.15	Etyek; 17/07/2018

Cupressocyparis leylandii (Cupressaceae)	anemophilous	crop	no	20.75	Budapest; 10/07/2019
Elymus repens (Poaceae)	anemophilous	non-crop	no	24.40	Szekszárd; 29/06/2019
Fragaria x ananassa (Rosaceae)	entomophilous	crop	yes	28.08	Szekszárd; 04/05/2019
Helianthus anuus (Asteraceae)	entomophilous	crop	yes	39.38	Etyek; 20/06/2018
Medicago sativa (Fabaceae)	entomophilous	crop	yes	19.98	Etyek; 24/07/2018
Plantago lanceolata (Plantaginaceae)	anemophilous	non-crop	no	24.28	Szekszárd; 06/07/2019
Popolus alba (Salicaceae)	anemophilous	crop	no	26.70	Szekszárd; 04/05/2019
Rubus idaeus (Rosaceae)	entomophilous	crop	yes	21.55	Lengyel; 27/05/2018, 04/05/2019
Sambucus nigra (Adoxaceae)	entomophilous	crop	yes	11.10	Szekszárd; 02/06/2019
Taraxacum officinale (Asteraceae)	entomophilous	non-crop	no	26.95	Szekszárd; 16/06/2018
Triticum aestivum (Poaceae)	anemophilous	crop	no	56.65	Bónifok; 09/06/2018,

					10/06/2018, 13/06/2019
Vitis vinifera (Vitaceae)	entomophilous	crop	yes	24.23	Etyek; 17/05/2018

Supplementary 2 *The associations between conidia germination of* Botrytis cinerea *and a set of predictors: temporal, concentration, species and their interactions*

*Results of the Generalized Mixed Effect Model with a negative binomial error structure (GLMM-nb) ('species model'). The table summarizes the associations between conidia germination (response variable) and a set of predictors: temporal, concentration, species (*Ambrosia artemisiifolia, Artemisia vulgaris, Bellis perennis, Brassica napus, Cannabis sativa, Chenopodium album, Chenopodium hybridum, Convolvulus arvensis, Cupressocyparis leylandii, Elymus repens, Fragaria x ananassa, Helianthus anuus, Medicago sativa, Plantago lanceolata, Populus alba, Rubus idaeus, Sambucus nigra, Taraxacum officinale, Triticum aestivum, Vitis vinifera*), and their interactions. The model incorporated the slide identification number, the family, and the order as statistical control for taxonomical dependence. We report parameter estimates (β) with their standard errors (SE) and 95% confidence intervals (CI). Significant results are highlighted in bold. (Model statistics: R2(fixed)=0.68, R2(total)=0.95).*

Predictor variable	β	CI (lower; upper)	SE	z-value	p-value
intercept	1.28	0.81; 1.74	0.24	5.37	<0.001
time	**0.28**	**0.22; 0.34**	**0.03**	**9.35**	**<0.001**
concentration	**1.53**	**1.35; 1.70**	**0.09**	**17.12**	**<0.001**
time × concentration	**0.10**	**0.04; 0.17**	**0.03**	**3.02**	**0.002**
intercept	1.22	0.59; 1.85	0.32	3.82	<0.001
time	**0.72**	**0.45; 0.99**	**0.14**	**5.22**	**<0.001**
concentration	**1.47**	**0.84; 2.10**	**0.32**	**4.57**	**<0.001**
species (*Artemisia vulgaris*)	**1.14**	**0.28; 2.01**	**0.44**	**2.59**	**0.009**
species (*Bellis perennis*)	**-1.12**	**-2.05; -0.18**	**0.47**	**-2.35**	**0.019**
species (*Brassica napus*)	0.15	-0.75; 1.06	0.46	0.33	0.739
species (*Cannabis sativa*)	**1.23**	**0.36; 2.09**	**0.44**	**2.78**	**0.005**
species (*Chenopodium album*)	-0.17	-0.97; 0.63	0.41	-0.42	0.675
species (*Chenopodium hybridum*)	0.13	-0.74; 1.00	0.44	0.30	0.766
species (*Convolvulus arvensis*)	-0.15	-1.04; 0.74	0.45	-0.33	0.738
species (*Cupressocyparis leylandii*)	**0.93**	**0.00; 1.85**	**0.47**	**1.96**	**0.049**
species (*Elymus repens*)	**-2.15**	**-3.18; -1.13**	**0.52**	**-4.12**	**<0.001**
species (*Fragaria x ananassa*)	-0.36	-1.27; 0.55	0.46	-0.78	0.435
species (*Helianthus anuus*)	**1.06**	**0.19; 1.93**	**0.44**	**2.39**	**0.017**
species (*Medicago sativa)*	**-1.40**	**-2.31; -0.48**	**0.47**	**-2.99**	**0.003**
species (*Plantago lanceolata*)	-0.12	-1.08; 0.83	0.49	-0.25	0.799
species (*Populus alba*)	0.35	-0.53; 1.23	0.45	0.78	0.438
species (*Rubus idaeus)*	-0.63	-1.49; 0.23	0.44	-1.43	0.151
species (*Sambucus nigra*)	0.09	-1.18; 1.36	0.65	0.14	0.885

species (*Taraxacum officinale*)	-0.37	-1.70; 0.96	0.68	-0.55	0.584
species (*Triticum aestivum*)	-0.82	-1.68; 0.04	0.44	-1.86	0.063
species (*Vitis vinifera*)	**1.30**	**0.43; 2.16**	**0.44**	**2.92**	**0.003**
time × concentration	**0.11**	**0.05; 0.17**	**0.03**	**3.35**	**<0.001**
concentration × species (*Artemisia vulgaris*)	-0.47	-1.34; 0.40	0.44	-1.05	0.294
concentration × species (*Bellis perennis*)	-0.21	-1.17; 0.75	0.49	-0.43	0.669
concentration × species (*Brassica napus*)	**0.96**	**0.01; 1.90**	**0.48**	**1.99**	**0.046**
concentration × species (*Cannabis sativa*)	-0.45	-1.32; 0.42	0.44	-1.01	0.313
concentration × species (*Chenopodium album*)	-0.28	-1.11; 0.55	0.42	-0.65	0.514
concentration × species (*Chenopodium hybridum*)	**-0.98**	**-1.86; -0.11**	**0.45**	**-2.19**	**0.028**
concentration × species (*Convolvulus arvensis*)	0.12	-0.77; 1.01	0.45	0.27	0.787
concentration × species (*Cupressocyparis leylandii*)	**1.18**	**0.22; 2.14**	**0.49**	**2.40**	**0.016**
concentration × species (*Elymus repens*)	-0.11	-1.17; 0.95	0.54	-0.21	0.835
concentration × species (*Fragaria x ananassa*)	0.42	-0.52; 1.36	0.48	0.87	0.382
concentration × species (*Helianthus anuus*)	-0.15	-1.02; 0.73	0.44	-0.33	0.743
concentration × species (*Medicago sativa*)	**-0.94**	**-1.84; -0.04**	**0.46**	**-2.04**	**0.041**
concentration × species (*Plantago lanceolata*)	0.83	-0.16; 1.82	0.50	1.64	0.102
concentration × species (*Populus alba*)	0.32	-0.58; 1.22	0.46	0.69	0.490
concentration × species (*Rubus idaeus*)	0.13	-0.76; 1.02	0.45	0.28	0.776
concentration × species (*Sambucus nigra*)	0.21	-1.09; 1.51	0.66	0.32	0.751
concentration × species (*Taraxacum officinale*)	0.40	-0.99; 1.79	0.71	0.56	0.574
concentration × species (*Triticum aestivum*)	0.28	-0.60; 1.17	0.45	0.62	0.533
concentration × species (*Vitis vinifera*)	0.02	-0.86; 0.90	0.45	0.04	0.965

time × species (*Artemisia vulgaris*)	-0.28	-0.63; 0.08	0.18	-1.53	0.125
time × species (*Bellis perennis*)	-0.27	-0.67; 0.12	0.20	-1.36	0.174
time × species (*Brassica napus*)	**-0.61**	**-0.93; -0.29**	**0.16**	**-3.75**	**<0.001**
time × species (*Cannabis sativa*)	**-0.36**	**-0.71; -0.01**	**0.18**	**-2.02**	**0.044**
time × species (*Chenopodium album*)	**-0.60**	**-0.92; -0.28**	**0.16**	**-3.64**	**<0.001**
time × species (*Chenopodium hybridum*)	**-0.44**	**-0.81; -0.07**	**0.19**	**-2.35**	**0.019**
time × species (*Convolvulus arvensis*)	**-0.46**	**-0.84; -0.09**	**0.19**	**-2.44**	**0.015**
time × species (*Cupressocyparis leylandii*)	**-0.69**	**-1.04; -0.33**	**0.18**	**-3.75**	**<0.001**
time × species (*Elymus repens*)	**-0.41**	**-0.87; 0.04**	**0.23**	**-1.79**	**0.074**
time × species (*Fragaria x ananassa*)	**-0.45**	**-0.77; -0.12**	**0.17**	**-2.68**	**0.007**
time × species (*Helianthus anuus*)	-0.26	-0.62; 0.09	0.18	-1.47	0.141
time × species (*Medicago sativa*)	**-0.78**	**-1.20; -0.35**	**0.22**	**-3.56**	**<0.001**
time × species (*Plantago lanceolata*)	**-0.75**	**-1.12; -0.38**	**0.19**	**-3.99**	**<0.001**
time × species (*Populus alba*)	**-0.40**	**-0.72; -0.07**	**0.16**	**-2.41**	**0.016**
time × species (*Rubus idaeus*)	-0.27	-0.64; 0.10	0.19	-1.43	0.152
time × species (*Sambucus nigra*)	0.12	-0.43; 0.67	0.28	0.43	0.666
time × species (*Taraxacum officinale*)	-0.31	-0.85; 0.23	0.27	-1.14	0.255
time × species (*Triticum aestivum*)	**-0.50**	**-0.82; -0.19**	**0.16**	**-3.11**	**0.002**
time × species (*Vitis vinifera*)	-0.25	-0.60; 0.11	0.18	-1.37	0.172

Supplementary 3 *The associations between conidia germination of* Botrytis cinerea *and a set of predictors: temporal, concentration, host compatibility (host, non-host) and their interactions*

Results of the Generalized Mixed Effect Model with a negative binomial error structure (GLMM-nb) ('compatibility model'). The table summarizes the associations between conidia germination (response variable) and a set of predictors: temporal, concentration, host compatibility (host, non-host), and their interactions. The model incorporated the slide identification number, the family, and the order as statistical control for taxonomical dependence. We report parameter estimates (β) with their standard errors (SE) and 95% confidence intervals (CI). Significant results are highlighted in bold. (Model statistics: R2(fixed)=0.48, R2(total)=0.95).

Predictor variable	β	CI (lower; upper)	SE	z-value	p-value
intercept	1.01	0.47; 1.55	0.28	3.66	<0.001
time	**0.24**	**0.17; 0.31**	**0.04**	**6.72**	**<0.001**
concentration	**1.62**	**1.40; 1.84**	**0.11**	**14.71**	**<0.001**
host compatibility (host)	**0.69**	**0.05; 1.33**	**0.33**	**2.11**	**0.035**
time × concentration	**0.10**	**0.04; 0.17**	**0.03**	**3.16**	**0.002**
concentration × host compatibility (host)	-0.27	-0.62; 0.08	0.18	-1.50	0.134
time × host compatibility (host)	**0.13**	**0.01; 0.24**	**0.06**	**2.17**	**0.03**

Supplementary 4 *The associations between conidia germination of* Botrytis cinerea *and a set of predictors: temporal, pollen concentration, cultivation (crop, non-crop) and their interactions*

Results of the Generalized Mixed Effect Model with a negative binomial error structure (GLMM-nb) ('cultivation model'). The table summarizes the associations between conidia germination (response variable) and a set of predictors: temporal, concentration, cultivation (crop, non-crop), and their interactions. The model incorporated the slide identification number, the family, and the order as statistical control for taxonomical dependence. We report parameter estimates (β) with their standard errors (SE) and 95% confidence intervals (CI). Significant results are highlighted in bold. (Model statistics: R^2(fixed)=0.48, R^2(total)=0.95)

Predictor variable	β	CI (lower; upper)	SE	z-value	p-value
intercept	0.87	0.26; 1.47	0.31	2.81	0.005
time	**0.31**	**0.23; 0.38**	**0.04**	**7.53**	**<0.001**
concentration	**1.34**	**1.12; 1.56**	**0.11**	**11.79**	**<0.001**
cultivation (crop)	**0.81**	**0.24; 1.39**	**0.29**	**2.76**	**0.006**
time × concentration	**0.10**	**0.04; 0.17**	**0.03**	**3.08**	**0.002**
concentration × cultivation (crop)	**0.39**	**0.06; 0.72**	**0.17**	**2.31**	**0.021**
time × cultivation (crop)	-0.04	-0.15; 0.07	0.05	-0.78	0.438

Supplementary 5 *The associations between conidia germination of* Botrytis cinerea *and a set of predictors: temporal, concentration, pollen volume and their interactions*

Results of the Generalized Mixed Effect Model with a negative binomial error structure (GLMM-nb) ('pollen volume model'). The table summarizes the associations between conidia germination (response variable) and a set of predictors: temporal, concentration, pollen volume and their interactions. The model incorporated the slide identification number, the family, and the order as statistical control for taxonomical dependence. We report parameter estimates (β) with their standard errors (SE) and 95% confidence intervals (CI). Significant results are highlighted in bold. (Model statistics: R2(fixed)=0.23, R2(total)=0.96)

Predictor variable	**β**	**CI (lower; upper)**	**SE**	**z-value**	**p-value**
intercept	1.34	0.61; 2,07	0.37	3.58	<0.001
time	**0.33**	**0.28; 0.39**	**0.03**	**11.72**	**<0.001**
volume	**1.20**	**0.92; 1.49**	**0.14**	**8.31**	**<0.001**
time×	-0.00	-0.5; 0.05	0.025	-0.07	0.940

Supplementary 6 *The association between grape disease occurrence and vineyard features, crop management, and grape variety features*

The table briefly introduces the tested hypotheses, the relevance in the infection of plant pathogens, the predicted directions of the main effect and the applied variables.

Tested variables	**Tested hypotheses**			**Reference**
	Main effect	**Predicted direction or effect on variance**	**Short description and relevance with infection**	
Vineyard features				
Slope of the plantation (‘*Inclination*’)	gradient variation in climatic and soil conditions	-	Vineyards are often established in sloping areas owing to favourable climatic conditions (e.g., air ventilation, solar radiation), which could modify (reduce) the infection severity.	VAN LEEUWEN et al. (2004)
Row orientation (‘*Orientation*’)	prevailing wind direction	+	The row orientation could be linked to the prevailing wind direction, promoting air ventilation along the rows and increasing the spatial dispersion of the airborne spores.	MEZŐSI (2017)
Ratio of the surrounding vineyards (‘*Surrounding vineyard*’)	amount of inoculum sources	+	Large-scale cultivation of crops facilitates the multiplication of culture-specific plant pathogens over a wider area.	WOLFE (2000)
Plantation age (‘*Age*’)	plant condition and infection status	+	The accumulation of endophytic parasites (i.e., viruses, trunk diseases) can increase over time. Such vines are more likely to be infected by other pathogens.	KOVÁCS et al. (2017)

Height of the canopy wall (‘*Distance*’)	isolation distance from the soil surface (i.e., infection source)	-	Leaves closer to the soil surface are more exposed to the infection pressure by the pathogens overwintering on the fallen plant parts.	ROSSI CAFFI (2012)
Counties of Hungary (‘*Region*’)	heterogeneous climatic and soil conditions	increase the variance	The traditional grape and wine-producing regions (i.e., terroir) are based on their environmental characteristics as a source of heterogeneity in pathogen infections among areas.	VAN LEEUWEN et al. (2018)
Crop management				
Inter-row management: application of cover plants or organic materials (‘*Inter-row’*)	microclimatic conditions	+	Inter-row crops and organic mulch could favour the microclimatic conditions in grape production, reducing the infection severity.	GUERRA STEENWERTH (2012)
Number of pesticide applications (‘*Treatments*’)	fungicide application	-	An increased level of chemical plant protection could effectively reduce the general occurrence and symptom severity of fungal pathogen infection.	POOLE ARNAUDIN (2014), HAHN (2014)
Removing the grape leaves from the cluster zone (‘*Leaf removal*’)	microclimatic conditions within the canopy, fungicide coverage	-	Opening the foliage in the cluster zone facilitates less optimal microclimatic conditions for the pathogen infection (i.e., shorter wetness duration and humidity reduction). This facilitates ideal coverage of the pesticide during treatment.	EVERS et al. (2010), ROMANAZZI FELIZIANI (2014)

Supplementary 7 *The association between* Botrytis cinerea *infection occurrence and plantation and crop management characteristics*

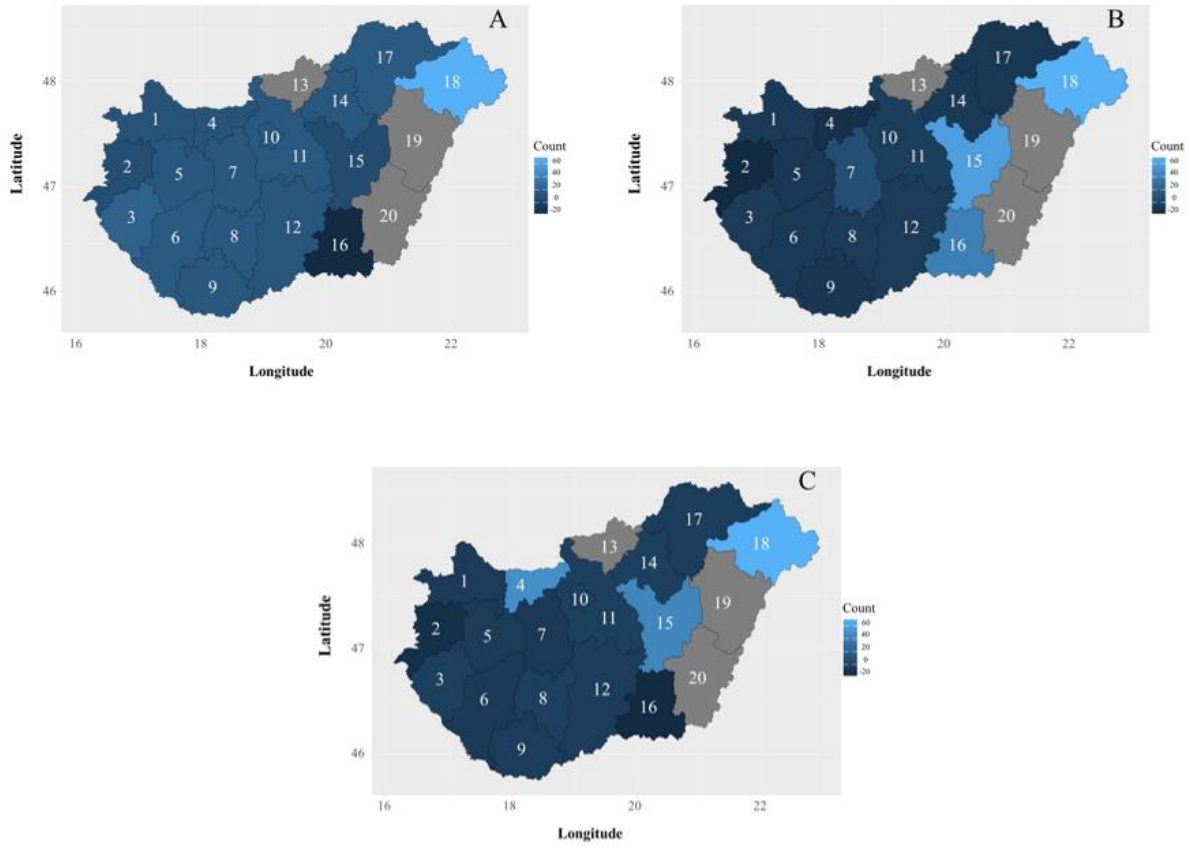
The table summarises the associations between Botrytis cinerea *infection occurrence and plantation and crop management characteristics (Predictors) fitted by the Generalized Mixed Effect Model with a negative binomial error structure (GLMM-nb). We report parameter estimates (β) with their standard errors (SE) and 95% Confidence Intervals (CI). Significant results are highlighted in bold. The asterisks indicate the level of significance of the given predictor (*p < 0.05, **p < 0.01, ***p < 0 .001). Model statistics: R2(fixed) = 0.89, R2(total) = 0.90.*

Predictor	**ß**	**CI** (lower; upper)	**SE**	**z-value**	**p-value**
Intercept	-0.82	-2.46; 0.82	0.84	-0.98	0.328
Inclination	0.33	-0.17; 0.82	0.25	1.30	0.195
Orientation: N-S	1.14	-0.18; 2.46	0.67	1.69	0.092
Orientation: NE-SW	**3.19**	**1.37; 5.01**	**0.93**	**3.44**	**0.001*** **
Orientation: E-W	**1.56**	**0.15; 2.97**	**0.72**	**2.17**	**0.030***
Surrounding vineyards	**0.63**	**0.08; 1.18**	**0.28**	**2.26**	**0.024***
Survey year	**-0.51**	**-1.01; -0.01**	**0.26**	**-2.01**	**0.045***
Age	0.26	-0.24; 0.76	0.25	1.02	0.310
Distance	**0.86**	**0.30; 1.43**	**0.29**	**3.00**	**0.003****
Inter-row: yes	0.43	-0.60; 1.47	0.53	0.82	0.410
Treatments	**0.80**	**0.28; 1.31**	**0.26**	**3.01**	**0.003****
Leaf removal	-0.64	-1.64; 0.36	0.51	-1.26	0.208
Region: Baranya	0.35	-2.06; 2.75	1.23	0.28	0.778
Region: Borsod-Abaúj-Zemplén	1.56	-0.42; 3.55	1.01	1.54	0.123

Region: Budapest	-2.74	-6.07; 0.59	1.70	-1.61	0.107
Region: Csongrád	-30.41	-13778188.26; 13778127.43	7030000	0.00	1.000
Region: Fejér	0.37	-1.84; 2.58	1.13	0.33	0.745
Region: Győr-Moson-Sopron	-3.11	-6.57; 0.35	1.77	-1.76	0.078
Region: Heves	0.15	-1.64; 1.93	0.91	0.16	0.873
Region: Jász-Nagykun-Szolnok	-4.96	-49.04; 39.12	22.49	-0.22	0.825
Region: Komárom-Esztergom	-3.23	-6.75; 0.29	1.80	-1.80	0.072
Region: Nitra (Sk)	-6.59	-18.60; 5.41	6.13	-1.08	0.282
Region: Pest	1.32	-0.82; 3.47	1.10	1.21	0.228
Region: Somogy	1.21	-1.53; 3.96	1.40	0.87	0.386
Region: Szabolcs-Szatmár-Bereg	10.06	-60.08; 80.20	35.79	0.28	0.779
Region: Tolna	0.93	-1.11; 2.97	1.04	0.90	0.371
Region: Vas	-6.32	-13.98; 1.34	3.91	-1.62	0.106
Region: Veszprém	-0.34	-2.26; 1.57	0.98	-0.35	0.726
Region: Vojvodina (Srb)	-65.64	-131531022.12; 131530890.84	67110000	0.00	1.000
Region: Zala	5.96	-1.73; 13.65	3.92	1.52	0.129

Supplementary 8 *The spatial variations of grape disease occurrence among regions*

The figures show the model estimates (β) in each Hungarian county ('Region'), reflecting the spatial variation among regions in the grape diseases' occurrence, such as Botrytis cinerea *(A),* Plasmopara viticola *(B) and* Erysiphe necator *(C). The x and y axes represent the longitude and latitude coordinate scales, respectively. The numbers indicate the following counties: 1: Győr-Moson-Sopron, 2: Vas, 3: Zala, 4: Komáron-Esztergom, 5: Veszprém, 6: Somogy, 7: Fejér, 8: Tolna, 9: Baranya, 10: Budapest, 11: Pest, 12: Bács-Kiskun, 13: Nógrád, 14: Heves, 15: Jász-Nagykun-Szolnok, 16: Csongrád, 17: Borsod-Abaúj-Zemplén, 18: Szabolcs-Szatmár Bereg, 19: Hajdú-Bihar, 20: Békés. A lighter blue shade indicates higher model estimates (i.e., more likely disease occurrence), while a darker blue shade reflects lower ones (i.e., less likely disease occurrence). The grey colour reflects Counties without relevant information due to a lack of observations. These spatial differences may suggest a possible role of large-scale background mechanisms and their variations related to the macroclimatic, topographic and soil conditions.*



Supplementary 9 *The association between* Plasmopara viticola *infection occurrence and plantation and crop management characteristics*

The table summarises the associations between Plasmopara viticola *infection occurrence and plantation and crop management characteristics (Predictors) fitted by the Generalized Mixed Effect Model with a negative binomial error structure (GLMM-nb). We report parameter estimates (β) with their standard errors (SE) and 95% Confidence Intervals (CI). Significant results are highlighted in bold. The asterisks indicate the level of significance of the given predictor (*p < 0.05, **p < 0.01, ***p < 0.001). Model statistics: R2(fixed) = 0.98, R2(total) = 0.99.*

Predictor	**ß**	**CI** (lower; upper)	**SE**	**z-value**	**p-value**
Intercept	**2.14**	**0.18; 4.09**	**1.00**	**2.14**	**0.033**
Inclination	**0.53**	**0.07; 1.00**	**0.24**	**2.26**	**0.024***
Orientation: N-S	-0.90	-2.39; 0.60	0.76	-1.17	0.240
Orientation: NE-SW	1.33	-0.69; 3.35	1.03	1.29	0.197
Orientation: E-W	0.06	-1.55; 1.68	0.83	0.08	0.937
Surrounding vineyards	**0.68**	**0.17; 1.20**	**0.26**	**2.63**	**0.009****
Survey year	**-0.77**	**-1.30; -0.25**	**0.27**	**-2.90**	**0.004****
Age	-0.03	-0.46; 0.41	0.22	-0.12	0.904
Distance	0.27	-0.34; 0.88	0.31	0.88	0.381
Inter-row: yes	0.95	-0.02; 1.92	0.49	1.92	0.054
Treatments	-0.28	-0.74; 0.18	0.24	-1.18	0.237
Leaf removal	0.04	-0.93; 1.01	0.50	0.08	0.935
Region: Baranya	-2.07	-4.39; 0.26	1.19	-1.74	0.082
Region: Borsod-Abaúj-Zemplén	**-1.98**	**-3.87; -0.10**	**0.96**	**-2.06**	**0.039***

Region: Budapest	**-3.70**	**-6.94; -0.46**	**1.65**	**-2.24**	**0.025***
Region: Csongrád	50.84	-169805683.82; 169805785.49	86640000.00	0.00	1.000
Region: Fejér	72.19	-49713956.46; 49714100.85	25360000.00	0.00	1.000
Region: Győr-Moson-Sopron	-1.10	-4.19; 1.99	1.58	-0.70	0.486
Region: Heves	-1.11	-3.00; 0.79	0.97	-1.15	0.252
Region: Jász-Nagykun-Szolnok	37.36	-131530919.12; 131530993.85	67110000.00	0.00	1.000
Region: Komárom-Esztergom	**-4.75**	**-8.37; -1.12**	**1.85**	**-2.57**	**0.010***
Region: Nitra (Sk)	**-5.55**	**-10.80; -0.31**	**2.68**	**-2.07**	**0.038***
Region: Pest	0.88	-1.77; 3.52	1.35	0.65	0.516
Region: Somogy	-0.87	-3.45; 1.71	1.32	-0.66	0.510
Region: Szabolcs-Szatmár-Bereg	25.34	-502207.29; 502257.97	256200.00	0.00	1.000
Region: Tolna	-0.31	-2.63; 44958	1.18	-0.26	0.793
Region: Vas	-7.27	-15.37; 0.82	4.13	-1.76	0.078
Region: Veszprém	-1.83	-3.84; 0.17	1.02	-1.79	0.073
Region: Vojvodina (Srb)	6.09	-68.92; 29860	38.27	0.16	0.874
Region: Zala	-1.75	-4.42; 0.92	1.36	-1.29	0.198

Supplementary 10 *The association between* Erysiphe necator *infection occurrence and plantation and crop management characteristics*

The table summarises the associations between Erysiphe necator *infection occurrence and plantation and crop management characteristics (Predictors) fitted by the Generalized Mixed Effect Model with a negative binomial error structure (GLMM-nb). We report parameter estimates (β) with their standard errors (SE) and 95% Confidence Intervals (CI). Significant results are highlighted in bold. The asterisks indicate the level of significance of the given predictor (*p < 0.05, **p < 0.01, ***p < 0 .001). Model statistics: R2(fixed) = 0.87, R2(total) = 0.87.*

Predictor	**ß**	**CI** (lower; upper)	**SE**	**z-value**	**p-value**
Intercept	-0.08	-1.57; 1.41	0.76	-0.11	0.916
Inclination	0.25	-0.15; 0.65	0.20	1.21	0.227
Orientation: N-S	-0.36	-1.56; 0.83	0.61	-0.60	0.549
Orientation: NE-SW	1.07	-0.40; 2.54	0.75	1.42	0.155
Orientation: E-W	-0.49	-1.74; 0.77	0.64	-0.76	0.449
Surrounding vineyards	0.33	-0.09; 0.74	0.21	1.55	0.121
Survey year	-0.04	-0.42; 0.35	0.20	-0.20	0.843
Age	-0.08	-0.46; 0.30	0.19	-0.41	0.681
Distance	0.47	0.06; 0.87	0.21	2.26	**0.024***
Inter-row: yes	0.34	-0.45; 1.13	0.40	0.83	0.404
Treatments	0.26	-0.11; 0.63	0.19	1.37	0.170
Leaf removal	0.77	-0.04; 1.58	0.41	1.87	0.061
Region: Baranya	-0.53	-2.55; 1.49	1.03	-0.52	0.604
Region: Borsod-Abaúj-Zemplén	-0.39	-1.93; 1.15	0.79	-0.49	0.622

Region: Budapest	-1.57	-4.43; 1.29	1.46	-1.07	0.283
Region: Csongrád	-17.67	-10939.16; 10903.82	5572.00	0.00	0.998
Region: Fejér	-1.16	-3.27; 0.96	1.08	-1.07	0.283
Region: Győr-Moson-Sopron	-0.89	-3.46; 1.69	1.31	-0.68	0.499
Region: Heves	0.83	-0.72; 2.38	0.79	1.05	0.293
Region: Jász-Nagykun-Szolnok	22.48	-125656.56; 125701.51	64120.00	0.00	1.000
Region: Komárom-Esztergom	18.28	-12387.82; 12424.39	6330.00	0.00	0.998
Region: Nitra (Sk)	-3.62	-9.93; 2.69	3.22	-1.13	0.261
Region: Pest	0.47	-1.21; 2.15	0.86	0.55	0.585
Region: Somogy	-1.09	-3.32; 1.14	1.14	-0.95	0.340
Region: Szabolcs-Szatmár-Bereg	24.68	-145453.09; 145502.45	74220.00	0.00	1.000
Region: Tolna	0.71	-1.14; 2.57	0.95	0.75	0.452
Region: Vas	-5.38	-19.44; 8.68	7.17	-0.75	0.453
Region: Veszprém	-0.76	-2.35; 0.83	0.81	-0.94	0.350
Region:Vojvodina (Srb)	41.54	-131530914.94; 131530998.03	67110000.00	0.00	1.000
Region: Zala	0.21	-2.15; 2.58	1.21	0.18	0.860

Supplementary 11 *The association between the infection occurrence and the grape variety-specific characteristics*

*The table details the fitted General Linear Model summary to test the association (highlighted in bold) of the infection occurrence and the grape variety-specific characteristics (Predictor). The statistical tests were run separately in each pathogen (*Botrytis cinerea, Plasmopara viticola, Erysiphe necator*). In* Botrytis cinerea*, we run two models based on the complete database (including all grape varieties) and the reduced database (excluding the noble rot varieties). We report parameter estimates (β) with their standard errors (SE) and 95% confidence intervals (CI). Significant results are highlighted in bold. The asterisks indicate the level of significance of the given predictor (*p < 0.05, **p < 0.01, ***p < 0.001).*

Predictor	**ß**	**CI** (lower; upper)	**SE**	**t-value**	**p-value**
		Botrytis cinerea (Complete database)			
Intercept	**0.24**	**0.09; 0.38**	**0.07**	**3.53**	**0.003****
Susceptibility	**0.05**	**0.00; 0.09**	**0.02**	**2.32**	**0.036***
Ripening	**0.09**	**0.05; 0.13**	**0.02**	**4.87**	**<0.001*****
Bunch compactness	**-0.05**	**-0.10; -0.01**	**0.02**	**-2.38**	**0.032***
Berry skin thickness	**0.08**	**0.04; 0.12**	**0.02**	**3.96**	**0.001****
Berry colour: noir	**-0.18**	**-0.28; -0.08**	**0.05**	**-4.02**	**0.001****
Berry colour: rouge	0.02	-0.25; 0.28	0.12	0.13	0.902
Utilisation: wine	0.09	-0.06; 0.24	0.07	1.27	0.224
		Botrytis cinerea (Reduced database)			
Intercept	0.15	-0.09; 0.39	0.11	1.40	0.188
Susceptibility	0.04	-0.02; 0.10	0.03	1.42	0.184
Ripening	**0.07**	**0.00; 0.14**	**0.03**	**2.32**	**0.041***
Bunch compactness	-0.04	-0.13; 0.05	0.04	-1.07	0.307
Berry skin thickness	**0.08**	**0.02; 0.14**	**0.03**	**2.84**	**0.016***
Berry colour: noir	**-0.18**	**-0.32; -0.05**	**0.06**	**-3.10**	**0.010***
Berry colour: rouge	-0.01	-0.32; 0.30	0.14	-0.05	0.958
Utilisation: wine	0.15	-0.12; 0.41	0.12	1.23	0.243

Plasmopara viticola					
Intercept	0.25	0.05; 0.44	0.09	2.75	0.016
Susceptibility	0.02	-0.04; 0.09	0.03	0.72	0.484
Ripening	-0.01	-0.06; 0.05	0.02	-0.29	0.776
Bunch compactness	0.02	-0.04; 0.08	0.03	0.82	0.426
Berry skin thickness	0.03	-0.02; 0.08	0.02	1.29	0.217
Berry colour: noir	-0.03	-0.14; 0.09	0.05	-0.53	0.606
Berry colour: rouge	0.07	-0.27; 0.40	0.16	0.42	0.682
Utilisation: wine	0.02	-0.18; 0.23	0.10	0.24	0.812
Erysiphe necator					
Intercept	0.32	0.16; 0.48	0.07	4.29	0.001
Susceptibility	0.01	-0.10; 0.11	0.05	0.14	0.893
Ripening	0.01	-0.03; 0.05	0.02	0.55	0.589
Bunch compactness	0.03	-0.03; 0.08	0.03	1.07	0.302
Berry skin thickness	0.02	-0.03; 0.07	0.02	0.84	0.416
Berry colour: noir	-0.04	-0.14; 0.07	0.05	-0.75	0.465
Berry colour: rouge	0.04	-0.47; 0.54	0.24	0.15	0.883
Utilisation: wine	-0.01	-0.19; 0.17	0.08	-0.15	0.883

Supplementary 12 *Summary of the formal grape variety name based on the VIVC database, the reference variety number and the common name used in Hungarian.*

VIVC name	VIVC number	Hungarian name
Bianca	1321	Bianka
Blauburger	1457	Blauburger
Cabernet franc	1927	Cabernet franc
Chardonnay	2455	Chardonnay
Cserszegi fueszeres	3277	Cserszegi fűszeres
Furmint	4292	Furmint
Harslevelu	5314	Hárslevelű
Irsai oliver	5557	Irsai Olivér
Kekfrankos	1459	Kékfrankos
Kiralyleanyka	4121	Királyleaányka
Olasz rizling	13217	Olaszrizling
Othello	8838	Othello
Sarga muskotaly	8193	Sárgamuskotály
Sauvignon blanc	10790	Sauvignon blanc
Szurkebarat	9275	Szürkebarát
Zalagyoengye	13374	Zalagyöngye
Zweigelt	13484	Zweigelt
Cabernet sauvignon	1929	Cabernet sauvignon
Merlot	7657	Merlot
Ottonel muscotaly	8243	Ottonel muskotály
Zoeld veltelini	12930	Zöld veltelini
Rajnai rizling	0077	Rajnai rizling

Supplementary 13 *Summary of grape varieties based on VIVC database*

The table summarises the formal grape variety name based on the VIVC database, the reference variety number, the common name used in Hungarian, the ripening category based on validated open-source international databases or breeders' manuals, the sample size and the percentage from total variety.

Hungarian name	VIVC name	VIVC number	Ripening	N	Percent (%)
Adriana			early	2	0.17
Afuz ali	Afus ali	122	medium	2	0.17
Akademik	Professor Maltabar	24443	early	1	0.08
Alvika			early	1	0.08
Anita	Anita	16288	early	1	0.08
Anjuta	Anjuta	25387	early	4	0.34
Aracsnij			early	1	0.08
Árkádia	Arkadia	17380	early	22	1.84
Árkádia rozowa	Arkadia rozowa	25382	medium	1	0.08
Aszja			early	2	0.17
Atosz	Athos	15736	early	2	0.17
Attila	Attila	756	medium	4	0.34
Bajkonur			early	1	0.08
Bako	Bako Noir	870	medium	5	0.42
Bazsena	Baschena	26340	early	1	0.08
Belgrádi magtalan	Beogradska besemena	1143	early	5	0.42
Beluj original	Originalnuej beluej	40741	late	2	0.17
Bianca	Bianca	1321	early	44	3.69
Blauburger	Blauburger	1457	medium	14	1.17
Bolgár rezi			early	4	0.34
Budai zöld	Budai zoeld	881	late	1	0.08
Cabernet franc	Cabernet franc	1927	late	11	0.92
Cabernet sauvignon	Cabernet sauvignon	1929	late	13	1.09
Cardinal	Cardinal	2091	early	21	1.76
Chardonnay	Chardonnay Blanc	2455	early	27	2.26
Chasselas	Chasselas	3678	early	9	0.75
Concord	Concord	2801	medium	8	0.67

Conegliano	Conegliano/Cove	16281	early	2	0.17
Crimson seedless	Crimson seedless	16019	medium	2	0.17
Csaba gyöngye	Csaba gyoengye	9166	early	10	0.84
Cserszegi fűszeres	Cserszegi fueszeres	3277	early	21	1.76
Csillám	Csillam	14317	medium	3	0.25
Csiri	Admirable de courtiller	68	medium	1	0.08
Danam	Danam	3418	late	1	0.08
Darja			early	1	0.08
Delaware	Delaware	3498	early	1	0.08
Diamant	Diamant	15753	early	2	0.17
Dixon			early	1	0.08
Dornfelder	Dornfelder	3659	medium	3	0.25
Dubovszkij rozovii	Dubovskii	3700	early	5	0.42
Dunagyöngye	Duna Gyoengye	23137	late	4	0.34
Dunav	Dunav	16239	early	6	0.50
Eszter	Esther	20341	early	6	0.50
Éva	Eva	16187	early	4	0.34
Ezerfürtű	Ezerfuertue	4026	early	6	0.50
Ezerjó	Ezerjó	4027	medium	11	0.92
Faeton			early	3	0.25
Fanny	Fanny	20346	medium	2	0.17
Favorit	Favorit	4062	early	7	0.59
Fehér delaware	Delaware white	3499	early	3	0.25
Fekete leányka	Feteasca neagra	4120	medium	1	0.08
Feri	Aurore	784	early	1	0.08
Furmint	Furmint	4292	late	19	1.59
Gála			early	3	0.25
Generosa	Generosa	23776	medium	6	0.50
Gloria Hungariae	Gloria hungariae	4830	medium	3	0.25
Golden muscat	Golden muscat	4881	early	1	0.08
Hamburgi muskotály	Muscat Hamburg	8226	late	10	0.84

Hárslevelű	Harslevelu	5314	late	15	1.26
Helikon szépe	Helikon szepe	27119	early	3	0.25
Irsai Olivér	Irsai oliver	5557	early	40	3.35
Italia	Italia	5582	late	8	0.67
Izabella	Isabella	5560	medium	12	1.01
Ján Izabella			early	1	0.08
Jázmin	Jazmin	26255	early	1	0.08
Jubilej novocserkaszka	Ovocherkasskii Chernyi	8617	early	3	0.25
Juhfark	Juhfark	5852	medium	3	0.25
Julian			early	1	0.08
Jupiter	Jupiter	23947	medium	2	0.17
Kadarka	Kadarka kek	5898	late	4	0.34
Kardinal	Cardinal	2091	early	1	0.08
Kármin	Karmin	5999	late	1	0.08
Kékfrankos	Blaufraenkisch	1459	late	87	7.29
Kékoportó	Portugieser blau	9620	early	6	0.50
Királyleányka	Feteasca regala	4121	medium	8	0.67
Kismis lucsusztuj	Kishmish luchistyi	15517	medium	1	0.08
Kismis moldovaszkij	Kishmish moldavskii	14053	medium	3	0.25
Kocsis Irma	Kocsis Irma	6325	medium	2	0.17
Kodrianka	Kodryanka	7569	early	2	0.17
Kósa	Kosa	23153	early	1	0.08
Kozma Pálné muskotály	Kozma Palne muskotaly	15732	early	5	0.42
Kövidinka	Koevidinka	13727	late	12	1.01
Kunleány	Kunleany	6560	late	5	0.42
Kurucvér	Kurucver	6573	medium	2	0.17
Landis			early	2	0.17
Laura	Laurana	6774	early	1	0.08
Leányka	Feteasca alba	4119	early	4	0.34
Lidi	Lidi	22350	early	2	0.17
Lívia	Liwia	25335	early	4	0.34

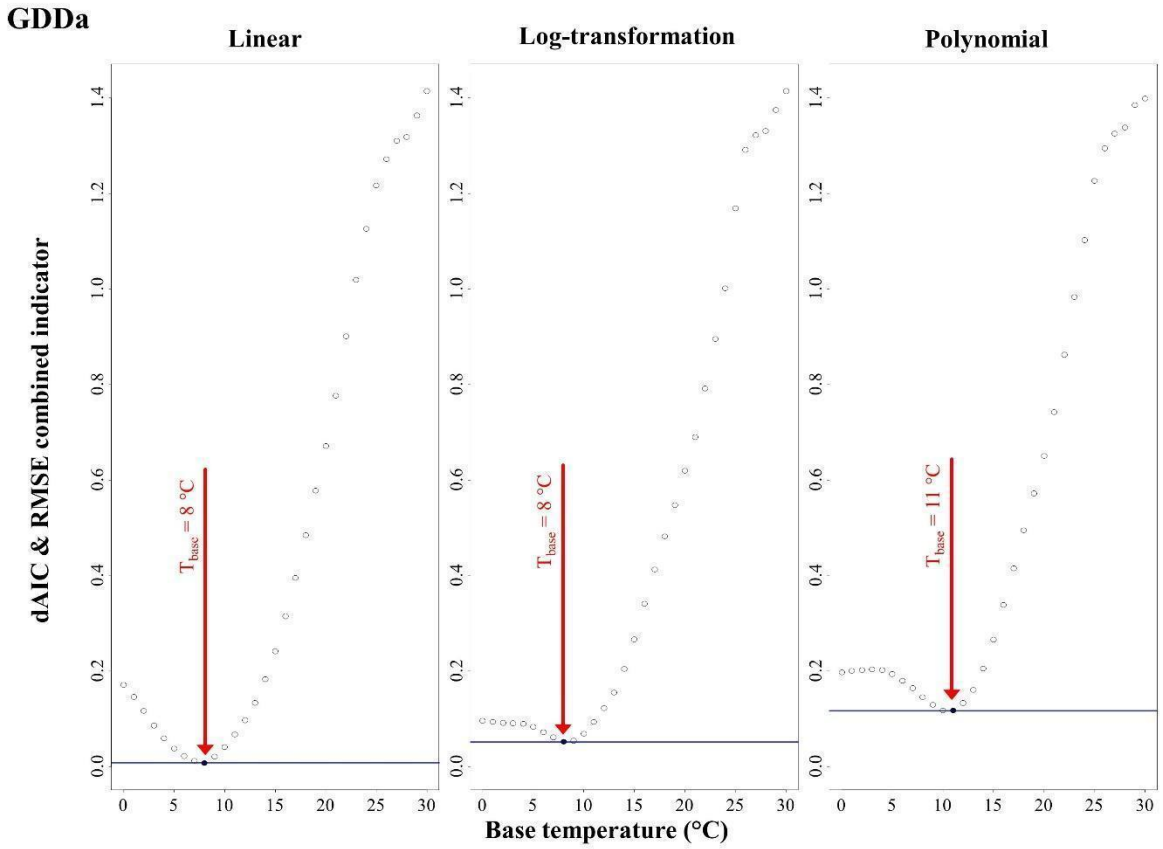
Lubik	Lubik piros	23160	early	1	0.08
Manikur finger	Manicure finger	19819	early	3	0.25
Mathiasz Jánosne muskotály	Mathiasz Janosne	7503	early	2	0.17
Matilda	Matilde	7512	early	1	0.08
Medina	Medina	7583	early	2	0.17
Medoc	Medoc noir	17316	early	2	0.17
Merlot	Merlot noir	7657	late	22	1.84
Moldova	Monarch	7914	early	17	1.42
Monarch	Moldova	7896	early	1	0.08
Monte cristo			early	1	0.08
Morva muskotály			early	1	0.08
Muskotály	Muscat a petits grains blancs	8193	late	4	0.34
Nagyezsda azosz	Nadezhda azos	17744	early	1	0.08
Narancsizű	Narancsizue	8350	early	3	0.25
Nelson			early	1	0.08
Néro	Nero	14013	early	60	5.03
Nina	Nina	8564	early	2	0.17
Nizina			early	4	0.34
Noah	Noah	8573	medium	4	0.34
Olaszrizling	Welschriesling	13217	late	60	5.03
Onyx	Onyx	8779	early	2	0.17
Oportó	Oporto	8785	late	6	0.50
Oszkár			early	2	0.17
Othello	Othello	8838	medium	53	4.44
Ottonel muskotály	Muscat ottonel	8243	early	9	0.75
Palatina	Palatina	14012	early	7	0.59
Pannonia kincse	Pannonia kincse	8915	early	13	1.09
Patria	Patria	23185	late	1	0.08
Pinot blanc	Pinot blanc	9272	medium	1	0.08
Pinot noir	Pinot noir	9279	medium	4	0.34
Piros bakator	Bakator roz	905	late	1	0.08

Piros delaware	Delaware	3498	early	2	0.17
Piros saszla	Chasselas rose	2493	early	2	0.17
Piros szlanka	Pamid	8899	medium	18	1.51
Piros tramini	Gewuerztraminer	12609	medium	1	0.08
Piros veltelini	Veltliner rot	12931	medium	1	0.08
Piroska	Piroska	17520	early	1	0.08
Portugieser	Portugieser blau	9620	early	3	0.25
Pozsonyi fehér	Pozsonyi	9653	late	1	0.08
Pölöskei muskotály	Poeloeske muskotaly	8207	medium	37	3.10
Premier	Premier	15714	early	1	0.08
Preobrazsenyie	Preobrazhenie	25528	early	6	0.50
Purcsin	Purcsin	9822	late	10	0.84
Rajnai rizling	Rajnai rizling	77	late	6	0.50
Reliance	Reliance	10010	early	1	0.08
Rizamat	Rizamat	10114	medium	4	0.34
Rizling	Riesling Weiss	10077	late	1	0.08
Rizlingszilváni	Mueller Thurgau Weiss	8141	early	12	1.01
Rosa menna di Vacca	Parmak cerven	8945	early	4	0.34
Rubiking	Ruby seedless	10314	medium	1	0.08
Sárgamuskotály	Muscat a petitis grains blancs	8193	late	8	0.67
Saszla	Chasselas blanc	2473	early	1	0.08
Sauvignon blanc	Sauvignon blanc	10790	medium	12	1.01
Sultana			medium	1	0.08
Szenátor	Fruehgipfler	4269	early	2	0.17
Szenzácija			early	1	0.08
Szőlőskertek királynője	Koenigin der Weingarten	6350	early	5	0.42
Szponzor			early	1	0.08
Szultán	Sultanina	12051	medium	5	0.42
Szuvenir	Souvenir D'Odessa	12111	early	21	1.76
Szürkebarát	Pinot gris	9275	early	11	0.92
Talizmán	Talisman	25356	medium	1	0.08

Teréz	Terez	14323	medium	20	1.68
Tonia			early	1	0.08
Tramini	Savagnin Blanc	17636	medium	1	0.08
Turan	Turan	15834	early	5	0.42
Valentina	Valentina	26664	early	1	0.08
Velesz	Veles	25345	medium	4	0.34
Velika	Velika	17754	early	2	0.17
Vénusz	Venus	12937	early	5	0.42
Viktor	Viktor	16351	medium	2	0.17
Viktória	Victoria	13031	early	2	0.17
Viktoria gyöngye	Viktoria gyoengye	14318	medium	4	0.34
Vinna reva			early	1	0.08
Zalagyöngye	Zalagyoengye	13374	early	22	1.84
Zengő	Zengoe	13423	early	2	0.17
Zenit	Zenit	13424	early	7	0.59
Zéta	Zeta	23225	medium	5	0.42
Zeusz	Zeusz	16038	late	2	0.17
Zöld veltelini	Veltliner gruen	12930	medium	14	1.17
Zweigelt	Zweigeltrebe blau	13484	medium	22	1.84
Early				**98**	**58%**
Late				**27**	**16%**
Medium				**45**	**26%**
Total				**170**	**100%**

Supplementary 14 *The plot shows combined indicator values for dAIC and RMSE at different base temperatures using the GDDa approach*

This combined indicator assesses how well the model fits the data for each GDDa predictor. The best model, with the most accurate GDDa predictor, is indicated by the lowest value on the horizontal blue line. The indicator values are plotted separately for different model types: linear, log-transformation, and polynomial. In the plots, the open circle dots represent the combined dAIC and RMSE indicator values, and the black dots indicate the lowest value for each model type, indicating the best model.



Supplementary 15 *Growing Degree Days: Scientific Relevance, Explanations and Methodical Implications*

Scientific context and relevance

The Growing Degree Days (GDD) approach is widely used in various scientific studies and agricultural practice. However, the calculation methods are rather inconsistent in the literature due to the varying recommendations for base temperatures and methods for calculating heat accumulations (e.g., calculating only base temperature or adding upper-lower and heat threshold) (AMERINE and WINKLER 1944; FERRINI et al. 1995; GLADSTONES 1992). In the present study, we assumed high local- and variety-specific differences in grapevine development due to the high heterogeneity of local climatic conditions (BAHUGUNA and JAGADISH 2014). Additionally, there was conflicting or insufficient information regarding the different GDD calculation methods for predicting grape phenology across different varieties, especially during

the ripening period. To address these issues, our initial methodical step was to test a wide range of temperature settings to identify the most appropriate GDD model by conducting a comprehensive series of statistical simulations. Subsequently, we investigated the role of the most relevant climatic factors, including GDD and precipitation.

Calculation of GGD predictors

The relationship between grape phenological development and the different GDD calculation methods was calculated according to the detailed description of MOLITOR et al. (2014). Thus, we calculated the cumulative GDD from January 1 to the observation day using the temperature values corresponding to the GPS coordinates of the location. The calculation of GDD values was implemented using three different methodological approaches:

1. *Single threshold model (GDDa)*: Only a base temperature was considered for GDD calculation at the temperature range: T_{base}=0-40°C, one value for each T_{base} temperature. Therefore, we generated 41 GDDa variables.
2. *Lower-upper threshold model (GDDb):* A lower and an upper limit were introduced to maximise the development of the vine at temperature ranges: T_{lower}=0-15°C, T_{upper}=16-40°C. Accordingly, we generated 400 GDDb variables (16 lower value T_{lower} × 25 upper value T_{upper}).
3. *Heat threshold model (GDDc):* A heat stress threshold was introduced into the GDDb model to complete the calculations. Consequently, the lower, upper, and heat temperature limits were established, along with the following temperature ranges: T_{lower}=0-15°C, T_{upper}=16-30°C, T_{heat}=20-40°C. We excluded the GDDc variables that had threshold combinations with overlapping ranges. For instance, GDDc_14_26_20 (T_{lower}=14°C, T_{upper}=26°C, T_{heat}=20°C) was excluded because T_{heat}<T_{upper}, due to the threshold of T_{heat} having an overlapped temperature range with T_{upper}. After excluding the variables with overlapping threshold ranges, we generated 3984 GDDc variables (full combinations: 16 value T_{lower} × 15 value T_{upper} × 21 value T_{heat} = 5040; overlapping combinations: 1056).

We systematically calculated the GDD variables according to each set of temperatures within the given temperature ranges, providing separate GDD predictors. Each predictor was calculated for all phenological observations by providing observation-specific (i.e., vineyard-, spatial- and temporal-specific) climatic data and used for further statistical analyses.

Selection of the GDD predictor

Linear Mixed-Effect Models (LMMs) were applied to identify the most predictive GDD variable, describing the relationship between grape development and accumulated temperature. In the

model, the dependent variable was the BBCH value, and the predictors were the focal GDD variable and the day of the year (DOY) as covariates. The random factor was entered as the identifier, labelling the farmer (or observer) with the corresponding year of the observation individually. The random factor provided statistical control for the non-independent observations gained from the repeated sampling provided by the same observer within the same year. All GDD variables were tested and entered separately into the model. The model output parameters were recorded, which reflected the goodness of model fitting (i.e., Akaike Information Criterion: AIC, Root-Mean-Squared-Error: RMSE).

We also considered the possibility of nonlinear features of grapevine growth. Consequently, we explored testing the focal GDD variables using modified LMMs that applied log-transformation (i.e., log(GDD+1)) and polynomial (i.e., $GDD+GDD^2$) model structures. To improve the model performance and accuracy, the continuous variables were centred and scaled in all models. Thus, 4425 models were run in each model structure.

After that, we aimed to identify the best model, specifically the GDD predictor, that most accurately describes the relationship between BBCH and the specified GDD variable, considering widely applied model indicators such as AIC and RMSE, which describe the goodness of fit. However, AIC and RMSE are two common key model indicators; the best model based on dAIC values was not the same as the one selected by RMSE. Furthermore, when comparing different model types, we found significant differences in both AIC and RMSE values, making direct comparison between models (e.g., log versus polynomial) impossible. Therefore, our goal was to identify the best GDD predictor by evaluating both values together, which can address these issues and allow for standardised model comparison. Unfortunately, the literature lacks any other indicator or procedure that considers the parameters describing the model's goodness collectively. For these reasons, we were forced to develop an intuitive solution.

A brief, step-by-step description of the applied calculation approach:

1. Calculation of the AIC value of the null model was performed for each model type.
2. AIC values were calculated for each model.
3. The difference between the AIC of the null model and that of the observed model (dAIC) was calculated for each model type.
4. The dAIC values were normalized between 0 and 1, based on the minimum and maximum dAIC values, ensuring that a value of 0 represented the worst model, while a value of 1 represented the best.
5. The same procedure was applied to the RMSE values.

6. The smallest Euclidean distance was determined, approximating the models with the best AIC and RMSE values.

This composite indicator was suitable for comparing different model types, thus making it possible to select the absolute best model. The selected model provided realistic and professionally relevant results.

Calculation of the Phenological shifts: Considering the roles of the variety and ripening features

In grapes, phenological development is strongly linked to variety-specific growth, the timing of ripening, and other variety-specific features, which should be considered when calculating phenological shifts. Therefore, to address these issues, we developed two similar Generalised Linear Mixed Model using Template Model Builder ('glmmTMB') models, namely the Ripening model (described in the main text) and the Variety model. This is because we could not enter the ripening and the variety together as fixed variables in the same model.

Similarly to the Ripening model, in the Variety model, we tested the variety-specific effect on the relationship between phenological shift and climate. We applied the same model as described previously after making some modifications, such as entering the variety ('Variety') as a factor. In the Variety model, the BBCH value was the response variable, while the predictor variables were the following covariates: GDD ST8 and the precipitation ('Precipitation') as continuous numeric variables, and the grape variety ('Leading sort') entered as a factor. The random factors were entered as the observation year (numeric, discrete) and the observation identifier ('Observation ID', factor).

Although both models were suitable for calculating residuals (phenological shifts) and showed a strong link with grape development (BBCH), we chose the Ripening model due to its easier interpretability (i.e., Ripening: 3 factor levels, Variety: 182 factor levels).

Results and Experiences

In our systematic model comparison of the three different threshold approaches (i.e., single, upper-lower, heat threshold) for calculating GDD with three model structures (i.e., linear, log-transformed, polynomial), we found that the best model for predicting grapevine phenological development in Hungary is the GDDa method with an 8°C base temperature ('GDD ST8', hereafter). This method involves accumulating heat units that reach or exceed a daily mean temperature of 8°C and using this cumulative heat in a linear model structure.

Summarising the Methodological Implications

Before running the statistical analyses, as part of the Materials and Methods section, we extensively tested the impact of temperature on grape phenological development to identify the best GDD predictor. After selecting the best GDD variable, we calculated the phenological shift using local climatic parameters, such as precipitation, GDD base temperature, and grape variety or ripening category (with separate models for each), considering variety-specific variability in grape growth.

Generally, the estimation accuracy relies on the appropriate GDD calculation approach, the model's structure, and the correct temperature thresholds set. For these reasons, we systematically tested the goodness of the GDD predictors using different GDD calculation approaches and model structures across a wide range of threshold temperatures. We revealed that the single threshold approach (GDDa) described grape growth most accurately by using the linear model structure, with a base temperature set at 8°C. Our findings were consistent with previous studies (PARKER et al. 2011; PRATS-LLINÀS et al. 2020; ZAPATA et al. 2015), which found that the base temperature ranged between 0 and 12.8°C, predicting late phenological development throughout the growing season. Due to the relatively wide base temperature range, providing an accurate estimate through an exact temperature threshold within this range is challenging, particularly when considering different varieties with specific traits and development patterns. In this study, the base temperature was estimated using a new approach that involved monitoring 170 varieties of phenological development from fruit set to harvest. These results suggested that the grapevine phenological development generally begins at lower, relatively narrow temperature ranges. While temperature is a key factor, plant growth should be considered as an integrated thermal response to the complex interaction with other environmental variables (BAHUGUNA and JAGADISH 2014). These environmental cues could indirectly shape the growth patterns via the thermal environment, both within and among growing regions. Consequently, the spatial, vineyard- and variety-specific differences could have a special role in shaping the environmental and biological conditions in production.

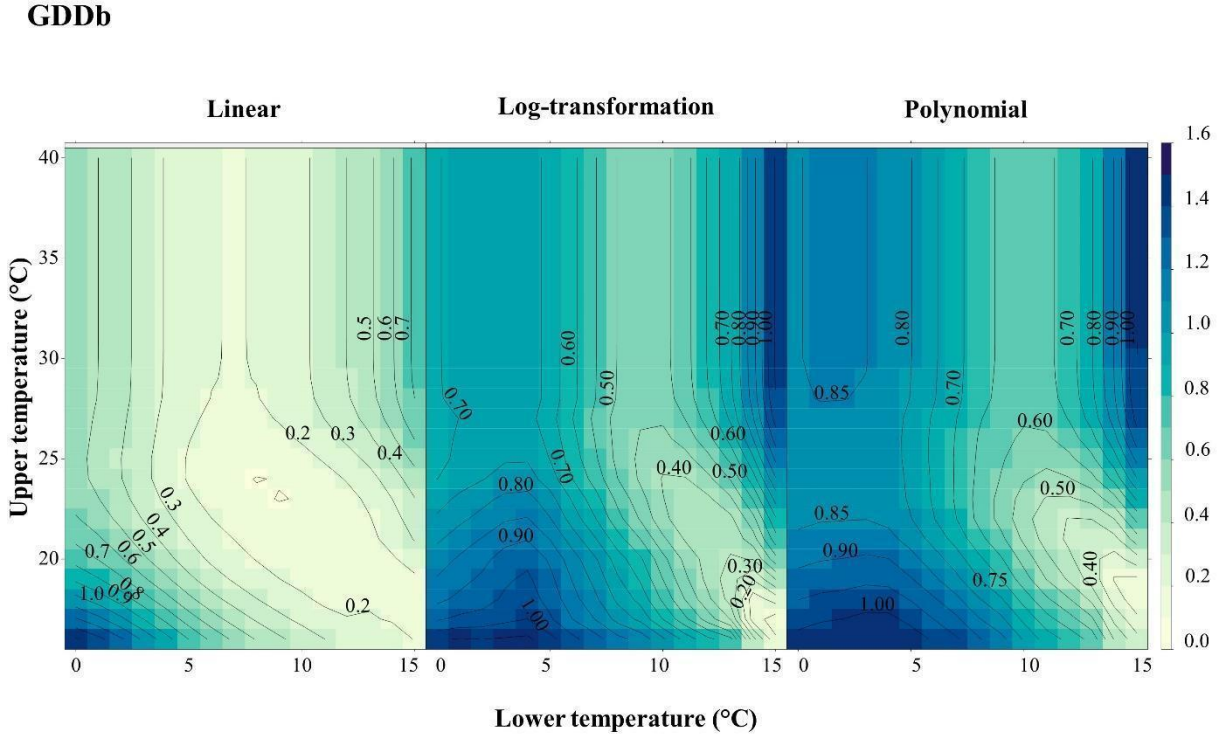
Finding the best GDD predictor is challenging; however, this study has several practical implications for calculating and selecting GDD predictors. GDD predictors were highly correlated depending on the level of threshold differences. This high correlation caused challenges when comparing the relative impact of the predictors in models, due to the minimal differences among the tested variables. Consequently, the model parameters that indicate the goodness of model fitting, such as dAIC and RMSE, also exhibited low variance. Considering the combination of these model parameters proved to be beneficial. Otherwise, relying on a single goodness parameter could mislead the model selection, resulting in incorrect indications of high model fitting in

models, including GDD predictors with zero or low variances. Low variation in GDD predictors could be generated in GDDb when the temperature differences were narrow between the lower and upper thresholds (e.g., GDDb_12_14). Comparing the calculation approaches, GDDc could not provide substantially larger benefits in GDD prediction than the other two approaches. During the present study, it's important to note that the highest daily temperature mean was around 30°C. At this temperature, the grapes were not exposed to heat stress, which could lead to irreversible tissue damage or reduced growth. As a result, the full potential benefits of the GDDc approach were not realised completely.

In conclusion, our findings suggest that the most effective method for calculating Growing Degree Days (GDD) is the straightforward threshold approach, which has significant implications for vineyard management. We developed a model that outlines the phenological shifts, taking into account factors such as grape variety and climate. This study presents a methodological approach grounded in multivariate statistical analysis. This approach can be valuable for analysing grape development in viticulture and for identifying the environmental and climatic factors that may influence phenological shifts.

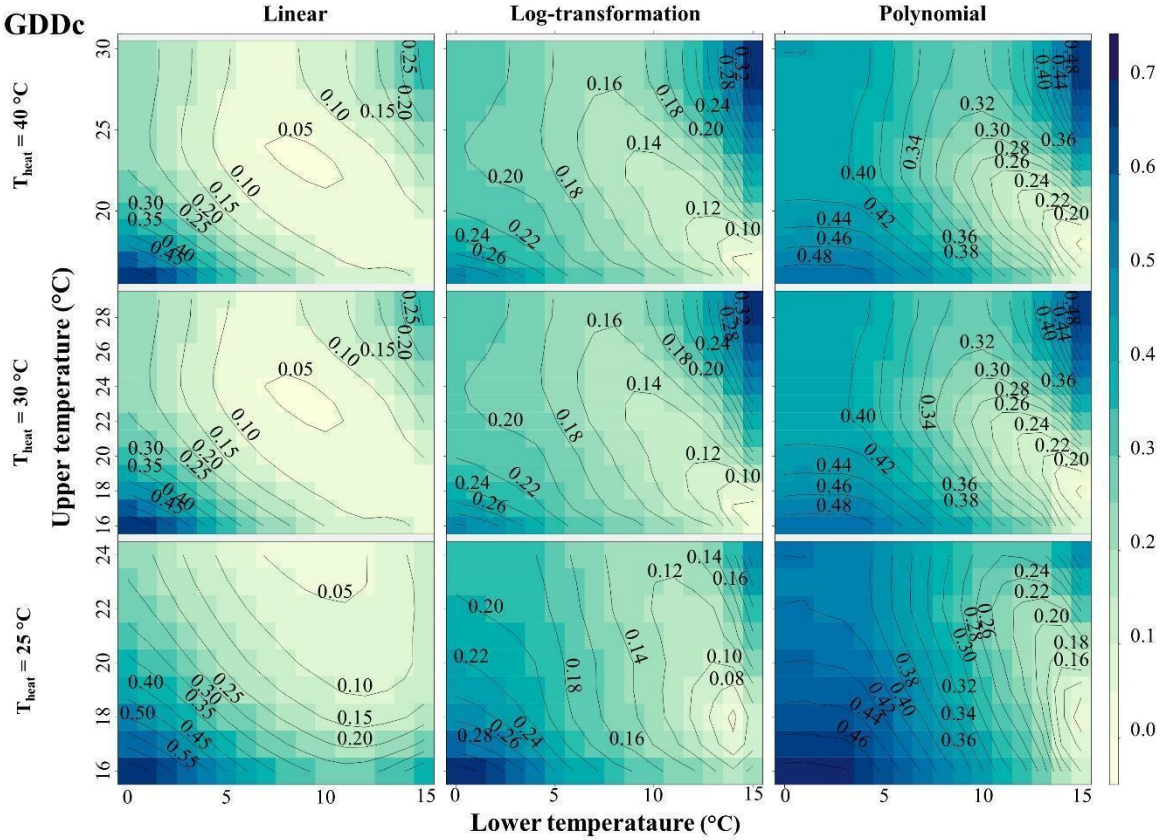
Supplementary 16 *The heat map plot provides a graphical representation of the combined indicator values for dAIC and RMSE at various lower and upper temperature ranges, using the GDDb approach.*

The indicator values are displayed separately for different model types: linear, log-transformation, and polynomial. This combined indicator assesses how well the model fits the data for each GDDb predictor. The best model, with the most accurate GDDb predictor, is indicated by the light yellow areas, which represent the lowest values



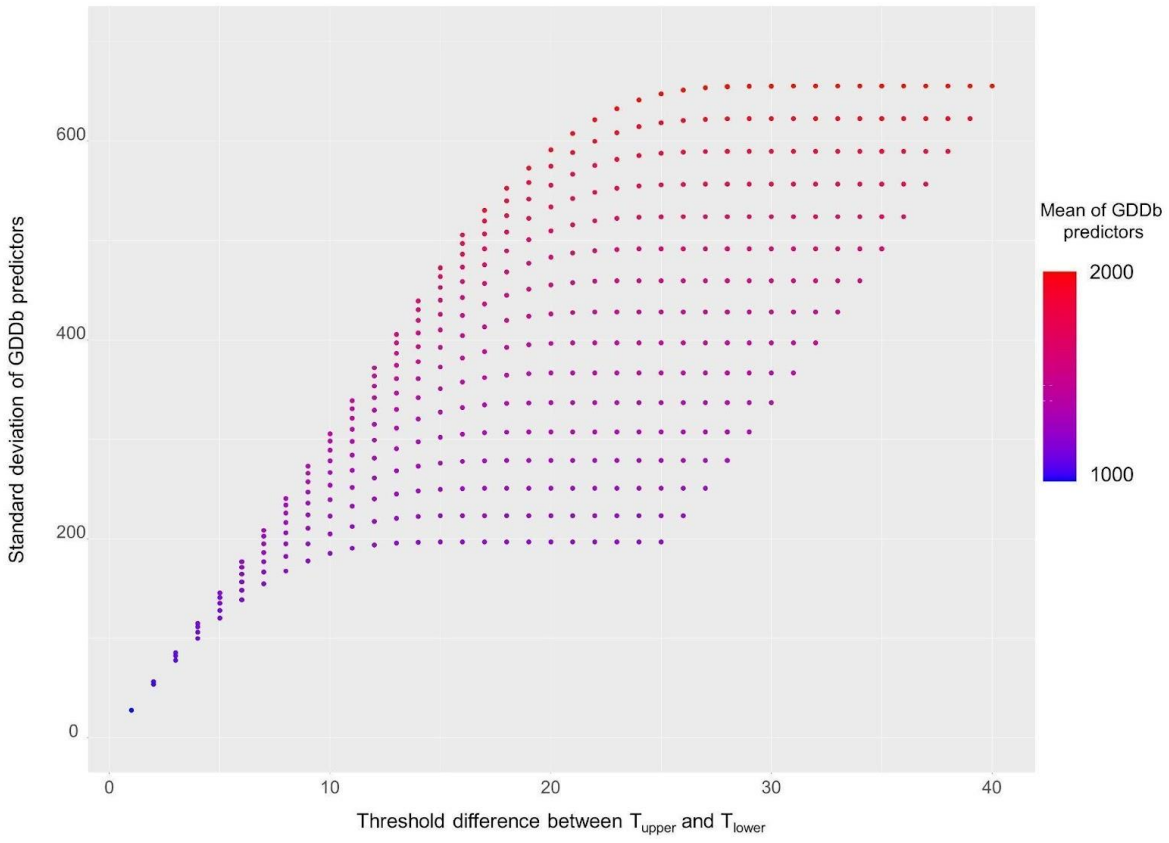
Supplementary 17 *The heat map plot provides a graphical representation of the combined indicator values for dAIC and RMSE at various lower and upper temperature ranges at different heat threshold levels, using the GDDc approach*

The indicator values are displayed separately for different model types: linear, log-transformation, and polynomial. This combined indicator assesses how well the model fits the data for each GDDc predictor. The best model, with the most accurate GDDc predictor, is indicated by the light-yellow areas, which represent the lowest values.



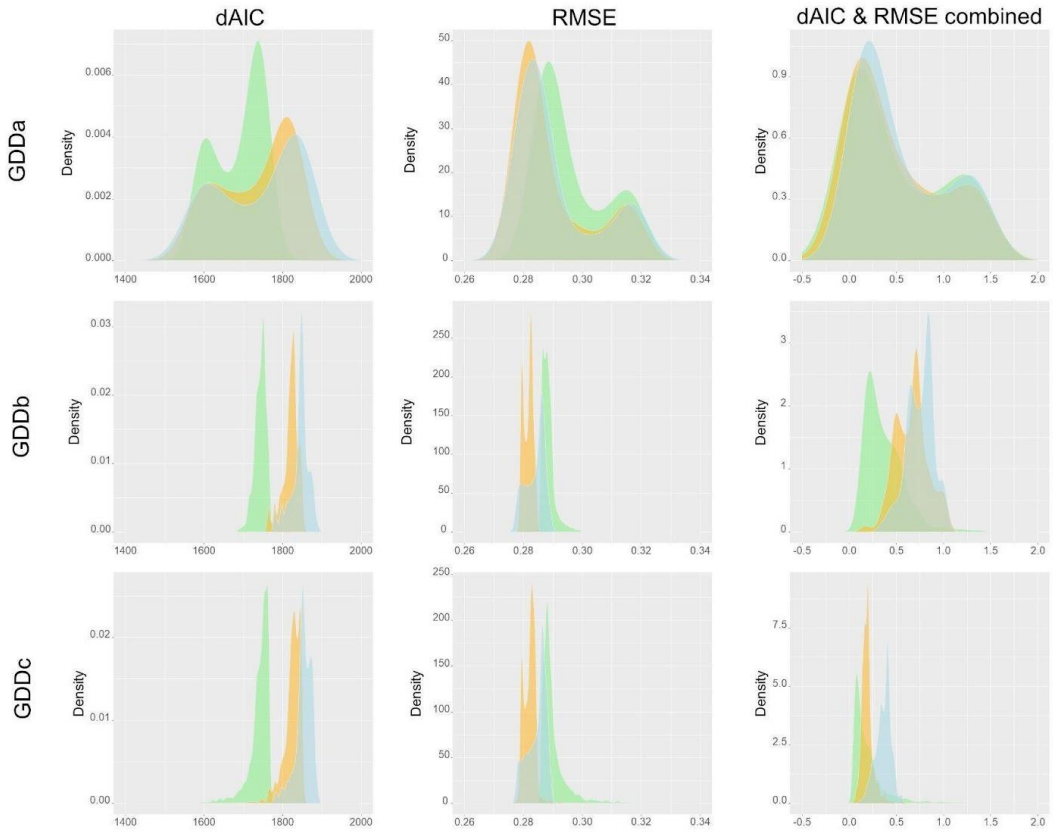
Supplementary 18 *The plot shows the association between the standard deviation and the threshold differences (i.e., T_{upper} - T_{lower}) in the GDDb predictors*

The plot shows increasing variance between lower and upper temperature thresholds and their standard deviations. The different colours of the dots represent the mean of the GDDb predictors. In statistical analyses, selecting a GDDb predictor with an extremely low threshold difference, which has low variance, may cause only the most robust effects, leaving smaller biological differences (e.g., phenological) hidden. Conversely, selecting a GDD predictor with a significantly large threshold difference, the high variance might obscure the spatio-temporal differences among the locations, potentially leading to an underestimation of the importance of climatic effects. This issue is especially noticeable when the threshold difference exceeds 10°C. Furthermore, if an upper threshold approximates the extremely high daily mean temperatures, it will also decrease the variance of the GDDb predictors. These patterns suggest a non-independent feature that is important to consider when selecting the best predictors for the GDDb approach. Similarly, the GDDc approach may also exhibit similar errors. Thus, focusing on a single goodness-of-fit measure (e.g., the dAIC and RSME) can be misleading because of the varying variance levels among the GDD predictors



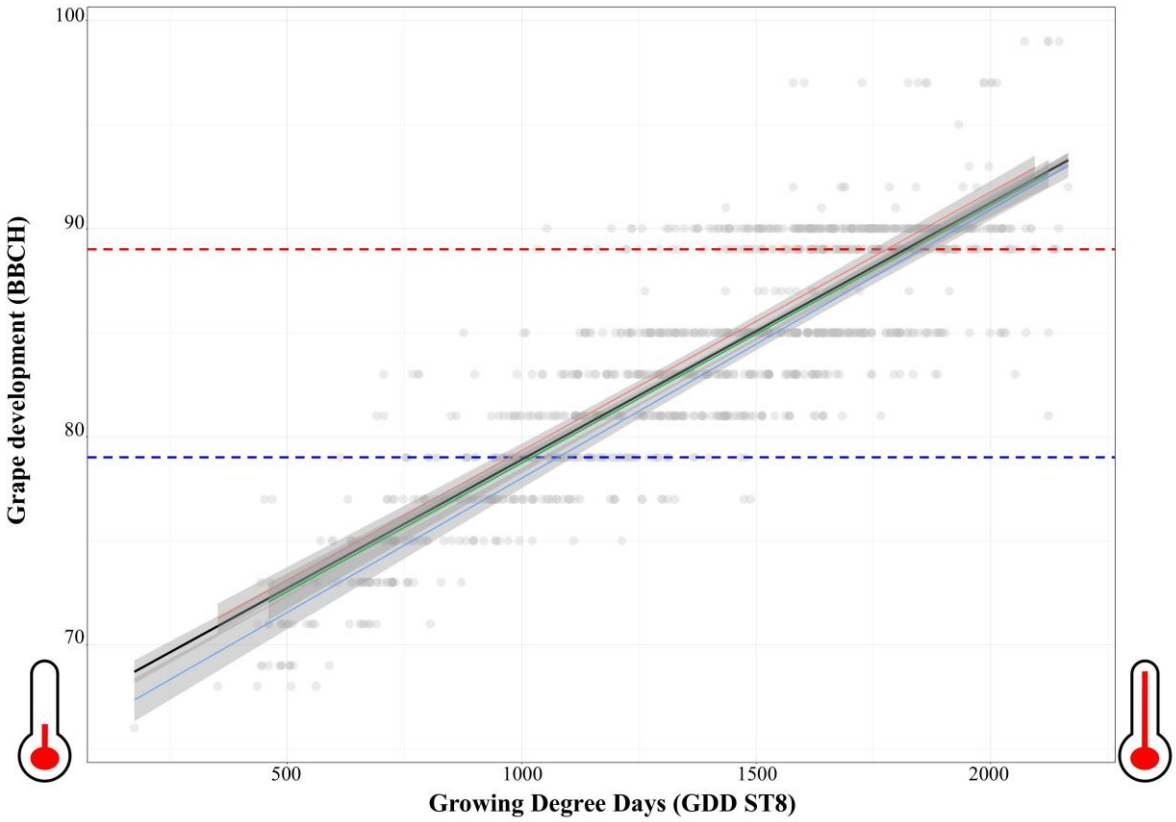
Supplementary 19 *The multiple plots compare the density distribution of the model fits regarding the GDD predictors and their relative positions*

Horizontally, the plots display the same GDD calculator approach, such as GDDa, GDDb, and GDDc. Vertically, the plots display the different statistical model parameters related to goodness-of-fit, such as dAIC, RMSE, and the combined indicator of dAIC & RMSE. The colour of the density functions represents the different model structures, such as Linear (green), Log-transformed (orange) and Polynomial (blue). The plots reveal extremely small differences in model goodness among the calculation approaches and model structures (i.e., narrow ranges and high overlap), which is probably due to the high correlation among the numerous GDD predictors. Thus, this plot also highlights the importance of using a combined indicator, rather than focusing solely on one goodness-of-fit parameter, such as dAIC or RSME. Relying on a single parameter could be misleading due to the varying variance levels among the GDD predictors.



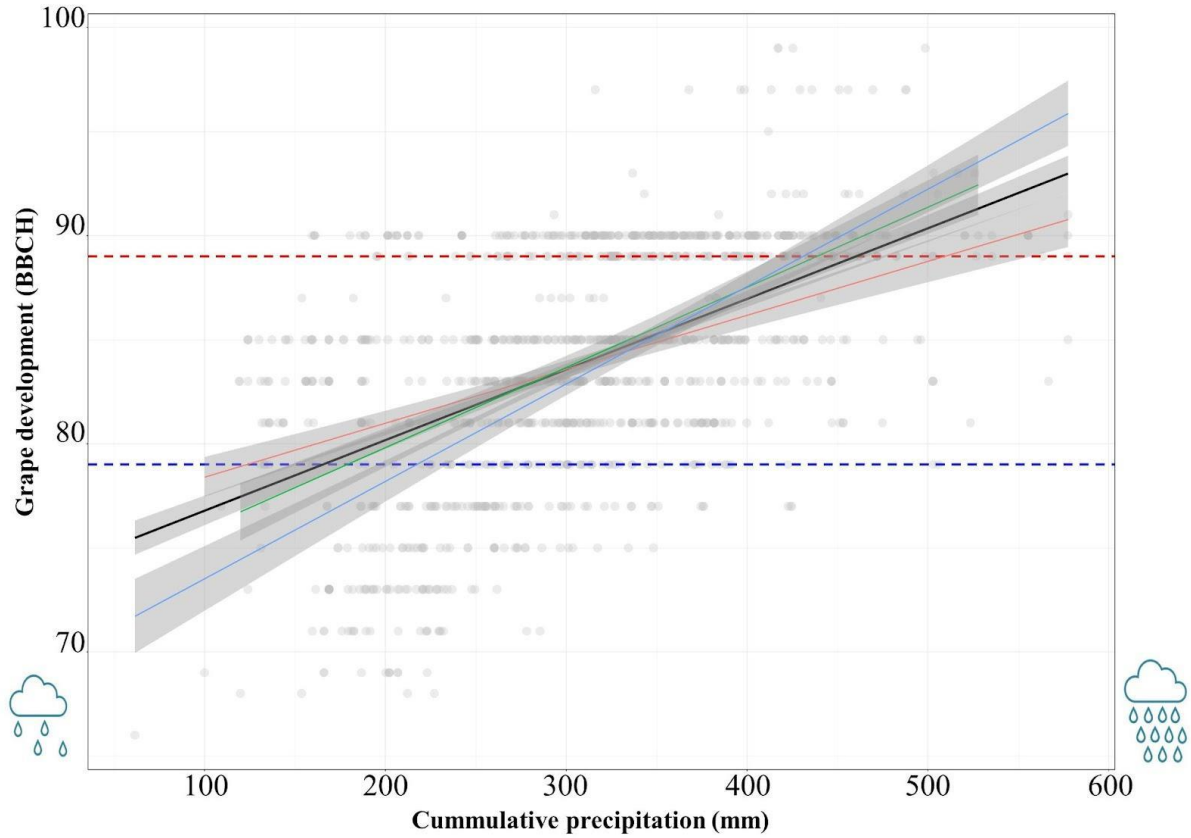
Supplementary 20 *The relationship between the grape development and growing degree days (GDDa, Tbase=8°C, 'GDD ST8')*

The lines represent the regression lines along with their confidence intervals (corresponding grey areas) for the estimated grapevine development. The overall regression line is shown in black, while the regression lines for different ripening categories are represented by different colours: Early (red), Medium (green), and Late (blue). The dashed horizontal lines represent the initial (blue) and the end (red) of susceptible phenological phases to Botrytis cinerea *(BBCH 79 and 89, respectively).*



Supplementary 21 *The relationship between grape development and cumulative precipitation*

The lines represent the regression lines along with their confidence intervals (corresponding grey areas) for the estimated grapevine development. The overall regression line is shown in black, while the regression lines for different ripening categories are represented by different colours: Early (red), Medium (green), and Late (blue). The dashed horizontal lines represent the initial (blue) and the end (red) of susceptible phenological phases to Botrytis cinerea *(BBCH 79 and 89, respectively).*



Supplementary 22 *The relationship between grape phenological shift and other plantation-related factors, such as vineyard and crop management features*

The table summarizes the statistical analyses of the fitted Linear Model testing the relationship between grape phenological shift and other plantation-related factors, such as vineyard and crop management features (Predictor). The table shows the parameter estimates (β) with their standard errors (SE). Significant results are highlighted in bold. The asterisks indicate the level of significance of the given predictor (p < 0.05, ** p < 0.01, *** p < 0.001).*

Predictor	ß	SE	t-value	p-value
Intercept	**0.15**	**0.05**	**2.69**	**0.008****
Orientation	**0.13**	**0.04**	**3.32**	**0.001****
Inclination	0.07	0.51	1.28	0.203
Treatments	0.07	0.05	1.39	0.166
Distance	-0.01	0.04	-0.25	0.804
Plant age	-0.01	0.04	-0.16	0.874
Inter-row: yes	-0.08	0.09	-0.87	0.384
Adjacent plantation	0.07	0.04	1.60	0.112

Supplementary 23 *The relative importance of climate-corrected grape phenological shift, plantation features, and crop management characteristics in the long-term occurrence of diseases*

The table summarises the statistical analyses of the fitted Generalised Linear Models with quasibinomial error structure (GLM-qb). The table shows the relative importance of climate-corrected grape phenological shift, plantation features, and crop management characteristics (Predictors) in the long-term occurrence of grapevine diseases (i.e., Botrytis cinerea, Plasmopara viticola, Erysiphe necator*). The statistical tests were run separately on each pathogen. We report parameter estimates (β) with their standard errors (SE). Significant results are highlighted in bold, while the marginally significant effects (0.05 < p ≤ 0.1) are in italics. The asterisks indicate the level of significance of the given predictor (* p < 0.05, ** p < 0.01, *** p < 0.001).*

Predictor	ß	SE	t-value	p-value
		Botrytis cinerea		
Intercept	**-2.86**	**0.65**	**-4.39**	**<0.001*** **
Phenological shift	-0.14	0.17	-0.79	0.429
Ripening: medium	**1.64**	**0.67**	**2.45**	**0.016***
Ripening: late	**1.99**	**0.58**	**3.40**	**0.001****
Orientation	**0.45**	**0.21**	**2.31**	**0.036***
Inclination	**0.77**	**0.24**	**3.16**	**0.002****
Treatments	-0.03	0.25	-0.12	0.906
Distance	**1.32**	**0.27**	**4.87**	**<0.001*** **
Plant age	**0.72**	**0.20**	**3.52**	**<0.001*** **
Inter-row: yes	**0.90**	**0.44**	**2.05**	**0.044***
Adjacent plantation	0.35	0.27	1.30	0.197

Plasmopara viticola				
Intercept	-0.59	0.39	-1.54	0.127
Phenological shift	-0.14	0.14	-1.05	0.297
Ripening: medium	-0.38	0.47	-0.80	0.425
Ripening: late	0.17	0.39	0.44	0.737
Orientation	*0.29*	*0.17*	*1.79*	*0.077*
Inclination	0.25	0.20	1.30	0.199
Treatments	-0.28	0.19	-1.43	0.156
Distance	*0.30*	*0.16*	*1.89*	*0.062*
Plant age	0.12	0.15	0.80	0.423
Inter-row: yes	-0.39	0.32	-1.21	0.215
Adjacent plantation	**0.95**	**0.21**	**4.62**	**<0.001*****
Erysiphe necator				
Intercept	**-0.78**	**0.35**	**-2.20**	**0.030***
Phenological shift	**-0.28**	**0.14**	**-2.09**	**0.039***
Ripening: medium	-0.28	0.41	-0.68	0.500
Ripening: late	0.60	0.37	1.60	0.112
Orientation	0.17	0.15	1.15	0.254
Inclination	0.11	0.18	0.59	0.560
Treatments	-0.28	0.18	-1.53	0.130

Distance	0.06	0.15	0.41	0.683
Plant age	0.16	0.14	1.14	0.257
Inter-row: yes	-0.00	0.30	-0.01	0.992
Adjacent plantation	0.04	0.16	0.27	0.786

Supplementary 24 *The roles of variety, ripening classes and local climate*

The effect of climate on grape development (i.e., BBCH) was statistically analysed in two different statistical models (i.e., Variety model and Ripening model), considering the effects of variety and ripening separately (see Figures S6 and S7, and Tables S4, S5, and S6 for more details). The models showed similar and consistent results regarding the climatic parameters. In both models, the GDD ST8 and grape development increased significantly along with precipitation, and the variety and ripening highly affected the development dynamics.

In the Variety model, the grape development rate exhibited a strong, variety-specific pattern, which was considered in subsequent statistical analyses. In the Ripening model, the early- and middle-ripening classes exhibited similar development rates, whereas the late-ripening classes were significantly delayed.

Supplementary 25 *The association between grape development (i.e., BBCH) and the climatic characteristics, testing the effects of Ripening and Variety*

*The table summarises the statistical analyses of the fitted Generalised Linear Mixed Model using Template Model Builder ('glmmTMB') to test the association between grape phenological shift and climatic characteristics, using different model structures with the addition of Ripening and Variety predictors, separately. The relevant statistical outputs were calculated from the corresponding ANOVA test (Type II) combined with Wald Chi^2. Significant results are highlighted in bold. The asterisks indicate the level of significance of the given predictor (*p<0.05, **p<0.01, ***p<0.001).*

Predictor	X^2	Df	p-value
Variety model			
GDD ST8	**2582.13**	**1**	**<0.001*** **
Precipitation	**130.88**	**1**	**<0.001*** **
Variety	**509.10**	**182**	**<0.001*** **
Ripening model			
GDD ST8	**2246.35**	**1**	**<0.001*** **
Precipitation	**121.62**	**1**	**<0.001*** **
Ripening	**44.68**	**2**	**<0.001*** **

Supplementary 26 *Effects of climatic characteristics and variety on grape phenological shift*

*The table summarises the statistical analyses of the fitted Generalized Linear Mixed Model using Template Model Builder ('glmmTMB'), which model (i.e., 'Variety model') tested the effects of climatic characteristics and variety on grape phenological shift (Predictor). The table shows the parameter estimates (β) with their standard errors (SE), t-values and p-values. Significant results are highlighted in bold, while the marginally significant effects (0.05 < p ≤ 0.1) are in italics. The asterisks indicate the level of significance of the given predictor (*p < 0.05, **p < 0.01, ***p < 0.001). (The dispersion estimates for sigma^2 in the t family: 0.118, N=1196)*

Predictor	ß	SE	t-value	p-value
Intercept	**0.77**	**0.29**	**2.62**	**0.009****
GDDa 8°C	**0.83**	**0.02**	**50.81**	**<0.001*****
Precipitation	**0.20**	**0.02**	**11.44**	**<0.001*****
Variety: Afuz ali	*-1.06*	*0.58*	*-1.85*	*0.064*
Variety: Akademik	-0.62	0.47	-1.32	0.187
Variety: Alvika	**-0.93**	**0.47**	**-1.97**	**0.049***

Variety: Anita	-0.63	0.47	-1.34	0.180
Variety: Anjuta	*-0.66*	*0.36*	*-1.85*	*0.065*
Variety: Aracsnij	**-1.58**	**0.47**	**-3.32**	**<0.001*****
Variety: Arkadia	**-0.70**	**0.31**	**-2.28**	**0.023***
Variety: Arkadia rozowa	**-1.25**	**0.47**	**-2.63**	**0.009****
Variety: Aszja	*-0.7*	*0.42*	*-1.65*	*0.099*
Variety: Atosz	0.14	0.41	0.35	0.727
Variety: Attila	*-0.65*	*0.36*	*-1.80*	*0.072*
Variety: Bajkonur	-0.48	047	-1.02	0.301
Variety: Bako	**-0.84**	**0.34**	**-2.50**	**0.013***
Variety: Bazsena	**-0.97**	**0.47**	**-2.06**	**0.040***
Variety: Belgrad seedless	*-0.60*	*0.35*	*-1.69*	*0.090*
Variety: Beluj original	**-1.33**	**0.35**	**-3.27**	**0.001****
Variety: Bianca	**-0.8**	**0.30**	**-2.69**	**0.007****
Variety: Blauburger	**-0.66**	**0.31**	**-2.10**	**0.036***
Variety: Bolgar Rezi	-039	0.36	-1.09	0.275
Variety: Budai zöld	-0.64	0.47	-1.35	0.177
Variety: Bukovics Dora	**-0.95**	**0.48**	**-2.00**	**0.046***
Variety: Cabernet franc	**-1.2**	**0.32**	**-3.65**	**<0.001*****
Variety: Cabernet sauvignon	**-0.98**	**0.31**	**-3.10**	**0.002****
Variety: Cardinal	***-0.66***	***0.30***	***-2.16***	***0.031****
Variety: Cetatuia	**-0.97**	**0.47**	**-2.06**	**0.040***
Variety: Chardonnay	**-0.7**	**0.30**	**-2.27**	**0.023***
Variety: Chasselas	*-0.62*	*0.32*	*-1.90*	*0.058*
Variety: Concord	**-0.89**	**0.33**	**-2.74**	**0.006****
Variety: Conegliano	-0.02	0.40	-0.05	0.961
Variety: Crimson seedless	*-0.67*	*040*	*-1.67*	*0.095*
Variety: Csabagyöngye	-0.38	0.32	-1.19	0.233
Variety: Cserszegi fűszeres	-0.47	0.31	-1.55	0.122
Variety: Csillám	**-0.87**	**0.40**	**-219**	**0.028***
Variety: Csiri	**-1.17**	**0.47**	**-2.46**	**0.014***
Variety: Danam	*-0.83*	*0.47*	*-1.75*	*0.080*
Variety: Darja	**-0.93**	**0.47**	**-1.97**	**0.049***
Variety: Delaware	-0.63	0.47	-1.33	0.184

Variety: Diamant	*-0.80*	*040*	*-1.93*	*0.053*
Variety: Dixon	-0.62	0.47	-1.32	0.187
Variety: Dornfelder	*-0.67*	*0.37*	*-1.80*	*0.072*
Variety: Dubovszkij rozovij	**-0.75**	**0.35**	**-2.17**	**0.030***
Variety: Duna gyöngye	**-0.98**	**0.38**	**-2.60**	**0.009****
Variety: Dunav	-0.41	0.33	-1.21	0.225
Variety: Elvira	**-1.31**	**0.47**	**-2.75**	**0.006****
Variety: Eperízű	**-1.05**	**0.47**	**-2.22**	**0.026***
Variety: Eszter	-0.36	0.40	-0.92	0.358
Variety: Éva	-0.36	0.36	-1.01	0.310
Variety: Ezerfürtű	-0.50	0.34	-1.49	0.135
Variety: Ezerjó	-0.51	0.32	-1.60	0.110
Variety: Faeton	**-1.00**	**0.38**	**-2.66**	**0.008****
Variety: Fanny	**-0.81**	**0.39**	**-2.04**	**0.041***
Variety: Favorit	**-0.44**	**0.34**	**-1.30**	**0.193**
Variety: Fehér delaware	**-1.22**	**0.37**	**-3.34**	**<0.001***
Variety: Fekete leányka	-0.40	0.48	-0.83	0.401
Variety: Feri	0.40	0.48	0.85	0.397
Variety: Furmint	**-0.83**	**0.31**	**-2.69**	**0.007****
Variety: Gala	-0.38	0.36	-1.06	0.290
Variety: Generosa	**-0.87**	**0.33**	**-2.57**	**0.010***
Variety: Gloria hungariae	*-0.66*	*0.39*	*-1.70*	*0.089*
Variety: Golden muscat	**-1.17**	**0.48**	**-2.45**	**0.014***
Variety: Hamburgi muskotály	**-1.22**	**0.32**	**-3.78**	**<0.001*****
Variety: Hárslevelű	**-0.72**	**0.32**	**-2.26**	**0.024***
Variety: Helikon szépe	**-0.78**	**0.36**	**-2.15**	**0.031***
Variety: Irsai Olivér	-0.36	0.30	-1.23	0.219
Variety: Italia	**-1.03**	**0.34**	**-3.07**	**0.002****
Variety: Izabella	**-1.20**	**0.32**	**-3.77**	**<0.001*****
Variety: Japán Izabella	**-1.29**	**0.48**	**-2.71**	**0.007****
Variety: Jázmin	0.11	0.47	0.24	0.811
Variety: Jubilej novocserkaszka	-0.37	0.40	-0.94	0.345
Variety: Juhfark	-0.67	0.43	-1.56	0.118
Variety: Julian	**-0.93**	**0.47**	**-1.97**	**0.049***

Variety: Juliannna	**-1.13**	**0.47**	**-2.38**	**0.017***
Variety: Jupiter	**-1.43**	**0.40**	**-3.62**	**<0.001*****
Variety: Kadarka	**-1.20**	**0.37**	**-3.25**	**0.001****
Variety: Kardinal	0.08	0.47	0.17	0.866
Variety: Karmin	-0.78	0.48	-1.64	0.101
Variety: Kecskeméti rizling	**-1.06**	**0.47**	**-2.25**	**0.024***
Variety: Kékfrankos	**-0.84**	**0.29**	**-2.88**	**0.04****
Variety: Kékoportó	**-0.9**	**0.34**	**-2.70**	**0.007****
Variety: Királyleányka	**-0.86**	**0.32**	**-2.65**	**0.008****
Variety: Kismis lucsüsztüj	**-1.56**	**0.48**	**-3.28**	**0.001****
Variety: Kismis moldovaszkij	**-1.29**	**0.38**	**-3.46**	**<0.001****
Variety: Kocsis Irma	*-0.80*	*0.42*	*-1.92*	*0.055*
Variety: Kodrianka	**-0.89**	**0.45**	**-1.97**	**0.049***
Variety: Kosa	**-1.43**	**0.48**	**-3.01**	**0.003****
Variety: Kövidinka	**-1.17**	**0.32**	**-3.67**	**<0.001****
Variety: Kozma Pálné muskotály	-0.32	0.35	-0.90	0.371
Variety: Kunleány	**-1.09**	**0.36**	**-3.07**	**0.002****
Variety: Kurucvér	*-0.68*	*0.39*	*-1.72*	*0.086*
Variety: Landis	-0.37	0.42	-0.88	0.381
Variety: Laura	-0.20	0.48	-0.42	0.674
Variety: Leányka	**-1.13**	**0.37**	**-3.07**	**0.020****
Variety: Lidi	**-1.54**	**0.40**	**-3.86**	**<0.001*****
Variety: Livia	**-0.75**	**0.35**	**-2.15**	**0.032***
Variety: Ljubumuj	**-1.03**	**0.39**	**-2.61**	**0.001****
Variety: Lubik	***-1.13***	***0.48***	***-2.36***	***0.018****
Variety: Manikur finger	**-0.92**	**0.37**	**-2.47**	**0.014***
Variety: Mathiász Jánosné muskotály	**-1.05**	**0.40**	**-2.63**	**0.008****
Variety: Matilda	-0.16	0.47	-0.33	0.739
Variety: Matrai muskotaly	0.44	0.47	0.92	0.358
Variety: Medina	*-0.81*	*0.43*	*-1.88*	*0.060*
Variety: Medoc	***-0.86***	***0.5***	***-1.72***	***0.087****
Variety: Merlot	**-0.91**	**0.30**	**-3.00**	**0.003****
Variety: Monarch	*-0.83*	*0.47*	*-1.77*	*0.077*
Variety: Moldova	**-1.14**	**0.31**	**-3.67**	**<0.001****

Variety: Monte Cristo	*-0.84*	*0.47*	*-1.77*	*0.077*
Variety: Muskotály	**-1.04**	**0.36**	**-2.85**	**0.004****
Variety: Nagyezsda azosz	*-0.87*	*0.48*	*-1.84*	*0.066*
Variety: Narancsizű	**-0.8**	**0.39**	**-2.05**	**0.040***
Variety: Negruja	**-0.97**	**0.47**	**-2.06**	**0.040***
Variety: Nelson	0.10	0.47	0.21	0.831
Variety: Néró	-0.41	0.30	-1.38	0.168
Variety: Nina	-0.13	0.41	-0.315	0.753
Variety: Nizina	*-0.63*	*0.36*	*-1.73*	*0.083*
Variety: Noah	**-0.76**	**0.35**	**-2.18**	**0.030***
Variety: Nova	**-1.08**	**0.48**	**-2.26**	**0.024***
Variety: Olaszrizling	**-0.99**	**0.30**	**-3.34**	**<0.001*****
Variety: Onyx	-0.54	0.40	-1.36	0.174
Variety: Oporto	**-0.88**	**0.34**	**-2.55**	**0.011***
Variety: Original	**-1.65**	**0.48**	**-3.47**	**<0.001*****
Variety: Oszkár	*-0.68*	*0.40*	*-1.70*	*0.089*
Variety: Othello	**-0.89**	**0.30**	**-2.98**	**0.003****
Variety: Ottonel muskotály	-0.42	0.32	-1.32	0.188
Variety: Palatina	-0.43	0.33	-1.31	0.191
Variety: Pannonia kincse	**-0.65**	**0.31**	**-2.10**	**0.036***
Variety: Patria	-0.25	0.47	-0.52	0.603
Variety: Pinot blanc	-0.41	0.48	-0.86	0.39
Variety: Pinot noir	**-0.82**	**0.36**	**-2.25**	**0.025***
Variety: Piros bakator	**-1.45**	**0.48**	**-3.05**	**0.0020****
Variety: Piros delaware	**-0.86**	**0.41**	**-2.12**	**0.034***
Variety: Piros dinka	**-1.29**	**0.47**	**-2.72**	**0.007****
Variety: Piros saszla	-0.57	0.40	-1.43	0.152
Variety: Piros szlanka	**-0.96**	**0.31**	**-3.09**	**0.002****
Variety: Piros tramini	-0.13	0.47	-0.29	0.774
Variety: Piros veltelini	-0.24	0.47	-0.51	0.612
Variety: Piroska	**-1.17**	**0.47**	**-2.46**	**0.014***
Variety: Pobeda	**-0.95**	**0.48**	**-2.0**	**0.046***
Variety: Pölöskei muskotály	**-0.78**	**0.30**	**-2.61**	**0.009****
Variety: Portugieser	**-1.12**	**0.36**	**-3.06**	**0.002****

Variety: Pozsonyi fehér	*-0.89*	*0.47*	*-1.87*	*0.061*
Variety: Prekoc	**-2.25**	**0.48**	**-4.73**	**<0.001*****
Variety: Premier	-0.61	0.48	-1.28	0.200
Variety: Preobrazsenyie	**-0.83**	**0.34**	**-2.45**	**0.014***
Variety: Purcsin	**-0.83**	**0.34**	**-2.47**	**0.014***
Variety: Rajnai rizling	**-0.90**	**0.34**	**-2.64**	**0.008****
Variety: Reliance	**-1.16**	**0.48**	**-2.43**	**0.015***
Variety: Rizamat	**-1.28**	**0.35**	**-3.64**	**<0.001*****
Variety: Rizling	**-1.16**	**0.48**	**-2.43**	**0.015***
Variety: Rizlingszilváni	**-0.84**	**0.32**	**-2.64**	**0.008****
Variety: Rosa menna di vacca	**-1.7**	**0.36**	**-4.73**	**<0.001*****
Variety: Rubiking	**-1.65**	**0.48**	**-3.47**	**<0.001*****
Variety: Sárga muskotály	**-0.7**	**0.33**	**-2.05**	**0.040***
Variety: Saszla	-0.7	0.47	-1.50	0.134
Variety: Sauvignon blanc	**-0.70**	**0.32**	**-2.18**	**0.030***
Variety: Szenator	0.15	0.41	0.37	0.713
Variety: Szenzacija	**-1.67**	**0.48**	**-3.52**	**<0.001****
Variety: Szőlőskertek királynője	*-0.58*	*0.35*	*-1.65*	*0.099*
Variety: Szponzor	*-0.83*	*0.47*	*-1.75*	*0.079*
Variety: Szultán	*-0.59*	*0.35*	*-1.69*	*0.6091*
Variety: Szürkebarát	**-1.04**	**0.32**	**-3.21**	**0.001****
Variety: Szuvenir	**-1.07**	**0.30**	**-3.48**	**<0.001****
Variety: Talizman	-0.14	0.47	-0.30	0.765
Variety: Teréz	**-0.85**	**0.31**	**-2.74**	**0.006****
Variety: Tonia	-0.71	0.48	-1.49	0.137
Variety: Tramini	-0.29	0.47	-0.62	0.538
Variety: Turán	-0.36	0.34	-1.06	0.291
Variety: Valentina	-0.72	0.48	-1.51	0.131
Variety: Vecsési piros	*-0.82*	*0.48*	*-1.72*	*0.085*
Variety: Velesz	-0.13	0.38	-0.35	0.727
Variety: Velika	**-1.60**	**0.40**	**-4.04**	**<0.001****
Variety: Vénusz	-0.31	0.35	-0.89	0.374
Variety: Viktor	-0.12	0.32	-0.39	0.761
Variety: Viktória	-0.63	0.40	-1.59	0.111

Variety: Viktória gyöngye	**-0.93**	**0.37**	**-2.55**	**0.011***
Variety: Vinna réva	-0.6	0.47	-1.20	0.229
Variety: Zalagyöngye	**-0.76**	**0.31**	**-2.43**	**0.015***
Variety: Zengő	-0.48	0.41	-1.16	1.248
Variety: Zenit	-0.50	0.33	-1.52	0.128
Variety: Zéta	**-0.86**	**0.35**	**-2.43**	**0.015***
Variety: Zeusz	*-0.71*	*0.40*	*-1.80*	*0.072*
Variety: Zöld veltelini	-0.33	0.31	-1.07	0.289
Variety: Zweigelt	**-0.74**	**0.30**	**-2.44**	**0.015***

Supplementary 27 *Effects of the climatic characteristics and variety-specific ripening categories on grape phenological shift*

The table summarises the statistical analyses of the fitted Generalized Linear Mixed Model using Template Model Builder ('glmmTMB'), which model (i.e., 'Ripening model') tested the effects of the climatic characteristics and variety-specific ripening categories on grape phenological shift (Predictor). The table shows the parameter estimates (β) with their standard errors (SE), t-values and p-values. Significant results are highlighted in bold. The asterisks indicate the level of significance of the given predictor (p < 0.05, ** p < 0.01, *** p < 0.001). (The dispersion estimates sigma^2 in the t family: 0.145, N=1180)*

Predictor	ß	SE	t-value	p-value
Intercept	**0.11**	**0.02**	**4.79**	**<0.001*** **
GDDa 8°C	**0.80**	**0.02**	**47.40**	**<0.001*** **
Precipitation	**0.20**	**0.02**	**11.03**	**<0.001*** **
Ripening: medium	**-0.14**	**0.04**	**-3.62**	**<0.001*** **
Ripening: late	**-0.26**	**0.04**	**-6.55**	**<0.001*** **

REFERENCES

ADRIAN, M. et al. (1997). Biological Activity of Resveratrol, a Stilbenic Compound from Grapevines, Against *Botrytis cinerea*, the Causal Agent for Gray Mold. *Journal of Chemical Ecology*, 23 (7), 1689-1702 p. doi: https://doi.org/10.1023/B:JOEC.0000006444.79951.75

ANDERSON, J. and SONG, B. H. (2020). Plant adaptation to climate change - Where are we? *Journal of Systematics and Evolution*, 58 (5), 533-545 p. doi: https://doi.org/10.1111/jse.12649

ARORA, N. K. (2019). Impact of climate change on agriculture production and its sustainable solutions. *Environmental Sustainability*, 2 (2), 95-96 p. doi: https://doi.org/10.1007/s42398-019-00078-w

ATKINSON, N. J. and URWIN, P. E. (2012). The interaction of plant biotic and abiotic stresses: from genes to the field. *Journal of Experimental Botany*, 63 (10), 3523-3543 p. doi: https://doi.org/10.1093/jxb/ers100

AZHAR KHAN, M. et al. (2014). Global estimates of energy consumption and greenhouse gas emissions. *Renewable and Sustainable Energy Reviews*, 29, 336-344 p. doi: https://doi.org/10.1016/j.rser.2013.08.091

BACHELDER, S. and ORTON, E. E. (1962). *Botrytis* Inflorescence blight on American Holly in New Jersey. *Plant Disease Reporter*, 46 (5), 320 p.

BAHUGUNA, R. and JAGADISH, K. (2014). Temperature regulation of plant phenological development. *Environmental and Experimental Botany*, 111, 83-90 p. doi: https://doi.org/10.1016/j.envexpbot.2014.10.007

BALDUZZI, S., RÜCKER, G. and SCHWARZER, G. (2019). How to perform a meta-analysis with R: a practical tutorial. *Evid Based Ment Health*, 22 (4), 153-160 p. doi: 10.1136/ebmental-2019-300117

BATES, D. et al. (2014a). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67 (1), 1 - 48 p. doi: https://doi.org/10.18637/jss.v067.i01

BATES, D. et al. (2014b). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67 (1), 1-48 p. doi: https://doi.org/10.18637/jss.v067.i01

BAU, L. and CHASSAING, T. (2025). Impact assessment of cover crops on the risk of frost in the Anjou vineyard: Original language of the article: English. *IVES Technical Reviews, vine and wine* p. doi: https://doi.org/10.20870/IVES-TR.2025.8467

BAVARESCO, L., GATTI, M. and FREGONI, M. (2010). Nutritional Deficiencies. In S. DELROT, H. MEDRANO, E. OR, L. BAVARESCO, & S. GRANDO (Eds.),

Methodologies and Results in Grapevine Research (p. 165-191). Dordrecht: Springer Netherlands. https://doi.org/10.1007/978-90-481-9283-0_12

BÉKÉSI, P. (1977). The influence of sunfower pollen on the germination of *Botrytis cinerea* (In Hungarian: A napraforgó- virágpor hatása a *Botrytis cinerea* konídiumainak csírázására). *Növényvédelem*, 13, 5 p.

BENJAMIN, J. G., NIELSEN, D. C. and VIGIL, M. F. (2003). Quantifying effects of soil conditions on plant growth and crop production. *Geoderma*, 116 (1), 137-148 p. doi: https://doi.org/10.1016/S0016-7061(03)00098-3

BEZA, E. et al. (2018). Exploring farmers' intentions to adopt mobile Short Message Service (SMS) for citizen science in agriculture. *Computers and Electronics in Agriculture*, 151, 295-310 p. doi: https://doi.org/10.1016/j.compag.2018.06.015

BORENSTEIN, M. et al. (2009). *Introduction to Meta-Analysis*: John Wiley & Sons, Ltd. 10.1002/9780470743386

BOYER, J. S. (1982). Plant Productivity and Environment. *Science*, 218 (4571), 443-448 p. doi: http://dx.doi.org/10.1126/science.218.4571.443

BROOKS, M. et al. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9 (2), 378-400 p. doi: 10.32614/RJ-2017-066

BURDON, J. J., JAROSZ, A. M. and KIRBY, G. C. (1989). Pattern and Patchiness in Plant-Pathogen Interactions—Causes and Consequences. *Annual Review of Ecology, Evolution, and Systematics*, 20, 119-136 p. doi: https://doi.org/10.1146/annurev.es.20.110189.001003

CABAS, J., WEERSINK, A. and OLALE, E. (2010). Crop yield response to economic, site and climatic variables. *Climatic Change*, 101 (3), 599-616 p. doi: https://doi.org/10.1007/s10584-009-9754-4

CAFFARRA, A. et al. (2012). Modelling the impact of climate change on the interaction between grapevine and its pests and pathogens: European grapevine moth and *Powdery mildew*. *Agriculture, Ecosystems & Environment*, 148, 89-101 p. doi: https://doi.org/10.1016/j.agee.2011.11.017

CAFFI, T. et al. (2016). Effect of temperature and wetness duration on infection by *Plasmopara viticola* and on post-inoculation efficacy of copper. *European Journal of Plant Pathology*, 144 (4), 737-750 p. doi: https://doi.org/10.1007/s10658-015-0802-9

CAMERON, W., PETRIE, P. R. and BONADA, M. (2024). Effects of Vineyard Management Practices on Winegrape Yield Components. A Review Using Meta-analysis. *American Journal of Enology and Viticulture*, 75 (1), 0750007 p. doi: 10.5344/ajev.2024.23046

CHAKRABORTY, S. (2013). Migrate or evolve: options for plant pathogens under climate change. *Global Change Biology*, 19 (7), 1985-2000 p. doi: https://doi.org/10.1111/gcb.12205

CHEN, Y. et al. (2024). Rootstocks for Grapevines Now and into the Future: Selection of Rootstocks Based on Drought Tolerance, Soil Nutrient Availability, and Soil pH. *Australian Journal of Grape and Wine Research*, 2024 (1), 6704238 p. doi: https://doi.org/10.1155/2024/6704238

CHOU, M. C. and PREECE, T. F. (1968). The effect of pollen grains on infections caused by *Botrytis cinerea* Fr. *Annals of Applied Biology*, 62 (1), 11-22 p. doi: https://doi.org/10.1111/j.1744-7348.1968.tb03846.x

CILIBERTI, N. et al. (2015). Influence of Fungal Strain, Temperature, and Wetness Duration on Infection of Grapevine Inflorescences and Young Berry Clusters by *Botrytis cinerea*. *Phytopathology*, 105 (3), 325-333 p. doi: 10.1094/phyto-05-14-0152-r

CILIBERTI, N. et al. (2016). Environmental effects on the production of *Botrytis cinerea* conidia on different media, grape bunch trash, and mature berries. *Australian Journal of Grape and Wine Research*, 22 (2), 262-270 p. doi: https://doi.org/10.1111/ajgw.12217

CLEMENTS, H. F. (1964). Interaction of Factors Affecting Yield. *Annual Review of Plant Biology*, 15 (Volume 15, 1964), 409-442 p. doi: https://doi.org/10.1146/annurev.pp.15.060164.002205

COERTZE, S., HOLZ, G. and SADIE, A. (2001). Germination and Establishment of Infection on Grape Berries by Single Airborne Conidia of *Botrytis cinerea*. *Plant Disease Journal*, 85 (0191-2917 (Print)), 668-677 p. doi: 10.1094/PDIS.2001.85.6.668

COHEN, J. (1988). Set Correlation and Contingency Tables. *Applied Psychological Measurement*, 12 (4), 425-434 p. doi: https://doi.org/10.1177/014662168801200410

COLEY- SMITH, J. R., JARVIS, W. R., & VERHOEFF, K. . (1980). *The biology of Botrytis* (J. R. COLEY- SMITH Ed.): Academic Press.

COMMENIL, P., LOÏC, B. and AUDRAN, J.-C. (1997). The development of the grape berry cuticle in relation to bunch rot disease. *Journal of Experimental Botany*, 48 (313), 1599-1607 p. doi: https://doi.org/10.1093/jxb/48.8.1599

CORIO-COSTET, M.-F. et al. (2010). Diversity and fitness of *Plasmopara viticola* isolates resistant to QoI fungicides. *European Journal of Plant Pathology*, 129 (2), 315-329 p. doi: https://doi.org/10.1007/s10658-010-9711-0

CORRIS, A. (2020). Defining the Environment in Organism–Environment Systems. *Frontiers in Psychology*, 11 p. doi: https://doi.org/10.3389/fpls.2015.00352

CSEPREGI, P. and ZILAI, J. (1988). *Knowledge and useage of grape varieties (In Hungarian: Szőlőfajta-ismeret és -használat)*.

DAI, Z., Z. et al. (2011). Ecophysiological, genetic, and molecular causes of variation in grape berry weight and composition : a review. *American Journal of Enology and Viticulture*, 62 (4), 413-425 p. doi: 10.5344/ajev.2011.10116

DARRIAUT, R. et al. (2022). Grapevine rootstock and soil microbiome interactions: Keys for a resilient viticulture. *Horticulture Research*, 9 p. doi: https://doi.org/10.1093/hr/uhac019

DE NEVE, S. (2017). Organic Matter Mineralization as a Source of Nitrogen. In F. TEI, S. NICOLA, & P. BENINCASA (Eds.), *Advances in Research on Fertilization Management of Vegetable Crops* (p. 65-83). Cham: Springer International Publishing. https://doi.org/10.1007/978-3-319-53626-2_3

DELMOTTE, F. et al. (2014). Rapid and multiregional adaptation to host partial resistance in a plant pathogenic oomycete: evidence from European populations of *Plasmopara viticola*, the causal agent of grapevine downy mildew. *Infect Genet Evol*, 27, 500-508 p. doi: 10.1016/j.meegid.2013.10.017

DENANCÉ, N. et al. (2013). Disease resistance or growth: the role of plant hormones in balancing immune responses and fitness costs. *Frontiers in Plant Science*, Volume 4 - 2013 p. doi: https://doi.org/10.3389/fpls.2013.00155

DESPREZ-LOUSTAU, M. L. et al. (2010). Are plant pathogen populations adapted for encounter with their host? A case study of phenological synchrony between oak and an obligate fungal parasite along an altitudinal gradient. *Journal of Evolutionary Biology*, 23 (1), 87-97 p. doi: https://doi.org/10.1111/j.1420-9101.2009.01881.x

DEYTIEUX-BELLEAU, C. et al. (2009). Grape berry skin features related to ontogenic resistance to *Botrytis cinerea*. *European Journal of Plant Pathology*, 125 (4), 551-563 p. doi: https://doi.org/10.1007/s10658-009-9503-6

DIMOU, M. et al. (2020). The effect of pollen grain morphology on sugars content of bee-collected pollen: the significance of size and exine ornamentation. *Grana*, 59 (5), 389-395 p. doi: https://doi.org/10.1080/00173134.2020.1734651

DOBSON, H. E. M. (1988). Survey of Pollen and Pollenkitt Lipids-chemical cues to flower visitors? *American Journal of Botany*, 75 (2), 170-182 p. doi: https://doi.org/10.1002/j.1537-2197.1988.tb13429.x

EDLICH, W. et al. (1989). New aspects on the infection mechanism of *Botrytis cinerea* Pers. *Netherlands Journal of Plant Pathology*, 95 (1), 53-62 p. doi: https://doi.org/10.1007/BF01974284

EFTIMOVÁ, J. and BACIGÁLOVÁ, K. (2012). The susceptibility of Tokay vine varieties to *Erysiphe necator* Schwein., and *Plasmopara viticola* (Berk. & M.A.Curtis) Berl. & De Toni. *Journal of Central European Agriculture*, 13 (3), 560-578 p. doi: https://doi.org/10.5513/JCEA01/13.3.1092

ELAD, Y. and EVENSEN, K. (1995). Physiological Aspects of Resistance to *Botrytis cinerea*. *Phytopathology*, 85 p. doi: 10.1094/Phyto-85-637

ELLIS, M. A. (2008). *Downy mildew of grape-Fact Sheet*

The Ohio State University Extension-Agriculture and Natural Resources 1-3 p.

ELMER, P. and MICHAILIDES, T. (2007). Epidemiology of Botrytis cinerea in Orchard and Vine Crops. In *Botrytis: Biology, Pathology and Control* (p. 243-272). https://doi.org/10.1007/978-1-4020-2626-3_14

ELMER, P. and REGLINSKI, T. (2006). Biosuppression of *Botrytis cinerea* in grapes. *Plant Pathology*, 55 (2), 155-177 p. doi: https://doi.org/10.1111/j.1365-3059.2006.01348.x

EVERS, D. et al. (2010). Efficiency of different strategies for the control of grey mold on grapes including gibberellic acid (Gibb3), leaf removal and/or botrycide treatments. *OENO One*, 44, 151-159 p. doi: https://doi.org/10.20870/oeno-one.2010.44.3.1469

FÆGRI, K., KALAND, P. E. and KRZYWINSKI, K. (1989). *Textbook of pollen analysis*: Blackwell Scientific Publications.

FAGERIA, N. K., BALIGAR, V. C. and LI, Y. C. (2008). The Role of Nutrient Efficient Plants in Improving Crop Yields in the Twenty First Century. *Journal of Plant Nutrition*, 31 (6), 1121-1157 p. doi: https://doi.org/10.1080/01904160802116068

FERMAUD, M. (1998). Cultivar Susceptibility of Grape Berry Clusters to Larvae of *Lobesia botrana* (*Lepidoptera*: *Tortricidae*). *Journal of Economic Entomology*, 91 (4), 974-980 p. doi: https://doi.org/10.1093/jee/91.4.974

FERNÁNDEZ-GONZÁLEZ, M. et al. (2013). Optimization of integrated pest management for powdery mildew (*Unincula necator*) control in a vineyard based on a combination of phenological, meteorological and aerobiological data. *The Journal of Agricultural Science*, 151 (5), 648-658 p. doi: https://doi.org/10.1017/S0021859612000743

FINCH, H. J. S., SAMUEL, A. M. and LANE, G. P. F. (2014). 3 - Soils and soil management. In H. J. S. FINCH, A. M. SAMUEL, & G. P. F. LANE (Eds.), *Lockhart & Wiseman's Crop Husbandry Including Grassland (Ninth Edition)* (p. 37-62): Woodhead Publishing. https://doi.org/10.1533/9781782423928.1.37

FOKKEMA, N. J. (1971). The effect of pollen in the phyllosphere of rye on colonization by saprophytic fungi and on infection by *Helminthosporium sativum* and other leaf pathogens.

Netherlands Journal of Plant Pathology, 77 (1), 1-60 p. doi: https://doi.org/10.1007/BF01977600

FOURNIER, E., GLADIEUX, P. and GIRAUD, T. (2013). The 'Dr Jekyll and Mr Hyde fungus': Noble rot versus gray mold symptoms of *Botrytis cinerea* on grapes. *Evolutionary Applications*, 6, 960-969 p. doi: https://doi.org/10.1111/eva.12079

FRAGA, H. et al. (2017). Viticulture in Portugal: A review of recent trends and climate change projections. *OENO One*, 51 (2), 61-69 p. doi: https://doi.org/10.20870/oeno-one.2017.51.2.1621

FRAISSE, C., BELLOW, J. and BROWN, C. (2018). Degree Days: Heating, Cooling, and Growing1. *EDIS*, 2018 (2), 1-5 p. doi: https://doi.org/10.32473/edis-ae428-2018

FRANCESCA, S. et al. (2006). Downy mildew (*Plasmopara viticola*) epidemics on grapevine under climate change. *Global Change Biology*, 12 (7), 1299-1307 p. doi: https://doi.org/10.1111/j.1365-2486.2006.01175.x

FUNDER, D. C. and OZER, D. J. (2019). Evaluating Effect Size in Psychological Research: Sense and Nonsense. *Advances in Methods and Practices in Psychological Science*, 2 (2), 156-168 p. doi: https://doi.org/10.1177/2515245919847202

GABLER, M. F. et al. (2003). Correlations of Morphological, Anatomical, and Chemical Features of Grape Berries with Resistance to *Botrytis cinerea*. *Genetics and Resistance*, 93 (10), 1263-1273 p. doi: 10.1094/PHYTO.2003.93.10.1263

GADOURY, D. M. et al. (2012). Effects of prior vegetative growth, inoculum density, light, and mating on conidiation of *Erysiphe necator*. *Phytopathology*, 102, 65-72 p. doi: http://dx.doi.org/10.1094/PHYTO-03-11-0085

GAUNT, R. E. (1995). The Relationship Between Plant Disease Severity and Yield. *Annual Review of Phytopathology*, 33 (Volume 33, 1995), 119-144 p. doi: https://doi.org/10.1146/annurev.py.33.090195.001003

GHORBANI, R. et al. (2008). Soil management for sustainable crop disease control: a review. *Environmental Chemistry Letters*, 6 (3), 149-162 p. doi: https://doi.org/10.1007/s10311-008-0147-0

GRAY, S. B. and BRADY, S. M. (2016). Plant developmental responses to climate change. *Developmental Biology*, 419 (1), 64-77 p. doi: https://doi.org/10.1016/j.ydbio.2016.07.023

GREEN, B. J. et al. (2006). Measurement of personal exposure to outdoor aeromycota in northern New South Wales, Australia. *Annals of Agricultural and Environmental Medicine*, 13 (2), 225-234 p. doi: https://doi.org/10.18637/jss.v067.i01

GRIESSER, M. et al. (2022). General trends of different inter-row vegetation management affecting vine vigor and grape quality across European vineyards. *Agriculture Ecosystems & Environment*, 338 (56), 1-11 p. doi: https://doi.org/10.1016/j.agee.2022.108073

GRIS, E. et al. (2010). Phenology and ripening of *Vitis vinifera* grape varieties in São Joaquim, southern Brazil: a new South American wine growing region. *Ciencia e Investigacion Agraria*, 37 (2), 61-75 p. doi: http://dx.doi.org/10.4067/S0718-16202010000200007.

GROENMAN-VAN WAATERINGE, W. (1998). Bark as a natural pollen trap. *Review of Palaeobotany and Palynology*, 103 (3), 289-294 p. doi: https://doi.org/10.1016/S0034-6667(98)00040-2

GUERRA, B. and STEENWERTH, K. (2012). Influence of Floor Management Technique on Grapevine Growth, Disease Pressure, and Juice and Wine Composition: A Review. *American Journal of Enology and Viticulture*, 63 (2), 149-164 p. doi: 10.5344/ajev.2011.10001

GUPTA, N., SLAWSON, D. D. and MOFFAT, A. J. (2021). Using citizen science for early detection of tree pests and diseases: perceptions of professional and public participants. *Biological Invasions*, 24 (1), 123-138 p. doi: https://doi.org/10.1007/s10530-021-02631-3

GUPTA, N., SLAWSON, D. D. and MOFFAT, A. J. (2022). Using citizen science for early detection of tree pests and diseases: perceptions of professional and public participants. *Biological Invasions*, 24 (1), 123-138 p. doi: https://doi.org/10.1007/s10530-021-02631-3

HADFIELD, J. D. (2010). MCMC Methods for Multi-Response Generalized Linear Mixed Models: The MCMCglmm R Package. *Journal of Statistical Software*, 33 (2), 1-22 p. doi: https://doi.org/10.18637/jss.v033.i02

HAHN, M. (2014). The rising threat of fungicide resistance in plant pathogenic fungi: *Botrytis* as a case study. *Journal of Biological Chemistry*, 7, 133–141 p. doi: https://doi.org/10.1007/s12154-014-0113-1

HAJDU, E. (2018). Viticulture of Hungary. *Acta Agraria Debreceniensis* (150), 175-182 p. doi: https://doi.org/10.34101/actaagrar/150/1713

HALL, A. and BLACKMAN, J. (2019). Modelling within-region spatiotemporal variability in grapevine phenology with high resolution temperature data: This article is published in cooperation with the 21th GIESCO International Meeting, June 23-28 2019, Thessaloniki, Greece. Guests editors : Stefanos Koundouras and Laurent Torregrosa. *OENO One*, 53 (2), 147-159 p. doi: https://doi.org/10.20870/oeno-one.2019.53.2.2450

HARDY, R. J. and THOMPSON, S. G. (1998). Detecting and describing heterogeneity in meta-analysis. *Statistics in Medicine*, 17 (8), 841-856 p. doi: https://doi.org/10.1002/(SICI)1097-0258(19980430)17:8<841::AID-SIM781>3.0.CO;2-D

HARTEMINK, A. E. and BARROW, N. J. (2023). Soil pH - nutrient relationships: the diagram. *Plant and Soil*, 486 (1), 209-215 p. doi: https://doi.org/10.1007/s11104-022-05861-z

HENNEBERT, G. L. (1973). *Botrytis* and *Botrytis*-like genera. *Persoonia - Molecular Phylogeny and Evolution of Fungi*, 7 (2), 183-204 p.

HERMS, D. A. and MATTSON, W. J. (1992). The Dilemma of Plants: To Grow or Defend. *The Quarterly Review of Biology*, 67 (3), 283-335 p. doi: http://dx.doi.org/10.1086/417659

HESSE, M. (1981). The fine structure of the exine in relation to the stickiness of angiosperm pollen. *Review of Palaeobotany and Palynology*, 35 (1), 81-92 p. doi: https://doi.org/10.1016/0034-6667(81)90015-4

ILAND, P. et al. (2009). *A taste of the world of wine*: Board & Bench Pub.

IZSÁK, B. (2023). Homogenization and interpolation of relative humidity hourly values with MASH and MISH software. *International Journal of Climatology*, 43 (13), 6285-6299 p. doi: 10.1002/joc.8205

JACOMETTI, M. A., WRATTEN, S. D. and WALTER, M. (2007a). Enhancing ecosystem services in vineyards: using cover crops to decrease *botrytis* bunch rot severity. *International Journal of Agricultural Sustainability*, 5 (4), 305-314 p. doi: https://doi.org/10.1080/14735903.2007.9684830

JACOMETTI, M. A., WRATTEN, S. D. and WALTER, M. (2007b). Management of understorey to reduce the primary inoculum of *Botrytis cinerea*: Enhancing ecosystem services in vineyards. *Biological Control*, 40 (1), 57-64 p. doi: https://doi.org/10.1016/j.biocontrol.2006.10.001

JAYARAMAN, S. et al. (2021). Disease-Suppressive Soils—Beyond Food Production: a Critical Review. *Journal of Soil Science and Plant Nutrition*, 21 (2), 1437-1465 p. doi: https://doi.org/10.1007/s42729-021-00451-x

JOGAIAH, S. (2023). Vineyard management strategies in scenario of climate change–A review. *Grape Insight*, 11-22 p. doi: https://doi.org/10.59904/gi.v1.i1.2023.7

JONES, G. V. (2015). Grapevines in a changing environment. In *Grapevine in a Changing Environment* (p. 1-17). https://doi.org/10.1002/9781118735985.ch1

JONES, G. V. (2018). Spatial variability in climate, phenology, and fruit composition across a reference vineyard network in Southern Oregon. *E3S Web of Conferences*, 50, 1-6 p. doi: https://doi.org/10.1051/e3sconf/20185001018

JONES, G. V. et al. (2005). Climate Change and Global Wine Quality. *Climatic Change*, 73 (3), 319-343 p. doi: https://doi.org/10.1007/s10584-005-4704-2

JORGENSON, A. K. et al. (2019). Social science perspectives on drivers of and responses to global climate change. *Wiley Interdiscip Rev Clim Change*, 10 (1), 1-17 p. doi: 10.1002/wcc.554

JUNGERS, J. et al. (2023). Adapting perennial grain and oilseed crops for climate resiliency. *Crop Science*, 63 (4), 1701-1721 p. doi: https://doi.org/10.1002/csc2.20972

JUNKER, R. R. and KELLER, A. (2015). Microhabitat heterogeneity across leaves and flower organs promotes bacterial diversity. *FEMS Microbiology Ecology*, 91 (9), 1-9 p. doi: https://doi.org/10.1093/femsec/fiv097

KASSEMEYER, H.-H. and BERKELMANN-LÖHNERTZ, B. (2009). Fungi of Grapes. In H. KÖNIG, G. UNDEN, & J. FRÖHLICH (Eds.), *Biology of Microorganisms on Grapes, in Must and in Wine* (p. 61-87). Berlin, Heidelberg: Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-319-60021-5_4

KAST, W. K. and STARK-URNAU, M. (1999). Survival of sporangia from *Plasmopara viticola*, the downy mildew of grapevine. *Vitis*, 38 (4), 185-186 p. doi: https://doi.org/10.5073/vitis.1999.38.185-186

KELLER, M., ROGIERS, S. Y. and SCHULTZ, H. (2003). Nitrogen and ultraviolet radiation modify grapevines' susceptibility to *Powdery mildew. Vitis: Journal of Grapevine Research*, 42 (2), 87-94 p. doi: https://doi.org/10.5073/vitis.2003.42.87-94

KENNELLY, M. M. et al. (2005). Seasonal Development of Ontogenic Resistance to *Downy Mildew* in Grape Berries and Rachises. *Phytopathology*, 95 (12), 1445-1452 p. doi: https://doi.org/10.1094/PHYTO-95-1445

KHAN, N. A. et al. (2020). Grape Production Critical Review in the World. *Social Science Research Network*, 1-55 p. doi: http://dx.doi.org/10.2139/ssrn.3595842

KHATAL, M. P. et al. (2023). Effect of weather parameters on the growth and development of downy mildew of grape caused by *Plasmopara viticola*. *Journal of Agrometeorology*, 25 (4), 610-612 p. doi: https://doi.org/10.54386/jam.v25i4.2063

KOCSIS, I., PETRÓCZY, M. and MARKÓ, G. (2024). Bridging boundaries: Exploring vineyard, management and variety characteristics influencing long-term infection of grapevine pathogens. *OENO One*, 58 (1), 1-17 p. doi: https://doi.org/10.20870/oeno-one.2024.58.1.7677

KOCSIS, I. et al. (2022). Stimulation role of pollen grains in the initial development of *Botrytis cinerea*: The importance of host compatibility, cultivation status and pollen size. *Journal of Phytopathology*, 170 (11-12), 828-837 p. doi: https://doi.org/10.1111/jph.13149

KOK, D. (2014). A Review on Grape Growing in Tropical Regions. *Turkish Journal of Agricultural and Natural Sciences*, 1 p.

KOSTIĆ, A. Ž. et al. (2017). Fatty acids of maize pollen – Quantification, nutritional and morphological evaluation. *Journal of Cereal Science*, 77, 180-185 p. doi: https://doi.org/10.1016/j.jcs.2017.08.004

KOVÁCS, C. et al. (2017). Incidence of grapevine trunk diseases is influenced by soil, topology and vineyard age, but not by *Diplodia seriata* infection rate in the Tokaj Wine Region, Hungary. *Phytoparasitica*, 45 (1), 21-32 p. doi: https://doi.org/10.1007/s12600-017-0570-5

KÖNIG, H., UNDEN, G. and FRÖHLICH, J. (2017). *Biology of Microorganisms on Grapes, in Must and in Wine*: Springer International Publishing. https://doi.org/10.1007/978-3-540-85463-0

KÖSE, B. (2014). Phenology and Ripening of *Vitis vinifera* L. and *Vitis Labrusca* L. Varieties in The Maritime Climate of Samsun in The Black Sea Region of Turkey. *South African Journal for Enology and Viticulture*, 35, 90-102 p. doi: https://doi.org/10.21548/35-1-988

KRETSCHMER, M., KASSEMEYER, H.-H. and HAHN, M. (2007). Age-dependent grey mould susceptibility and tissue-specific defence gene activation of grapevine berry skins after infection by *Botrytis cinerea*. *Journal of Phytopathology*, 155 (5), 258-263 p. doi: https://doi.org/10.1111/j.1439-0434.2007.01216.x

KRON, W., LÖW, P. and KUNDZEWICZ, Z. W. (2019). Changes in risk of extreme weather events in Europe. *Environmental Science & Policy*, 100, 74-83 p. doi: https://doi.org/10.1016/j.envsci.2019.06.007

LAL, R. (2012). Climate Change and Soil Degradation Mitigation by Sustainable Management of Soils and Other Natural Resources. *Agricultural Research*, 1 (3), 199-212 p. doi: https://doi.org/10.1007/s40003-012-0031-9

LANYON, D. M., HANSEN, D. and CASS, A. (2004). *The effect of soil properties on vine performance*: CSIRO Land and Water Australia.

LAWRENCE, R., MATTSON, W. and HAACK, R. (1997). White spruce and the spruce budworm: Defining the phenological window of susceptibility. *Canadian Entomologist*, 129, 291-318 p. doi: 10.4039/Ent129291-2

LI, Q. et al. (2024). Responses of grape yield and quality, soil physicochemical and microbial properties to different planting years. *European Journal of Soil Biology*, 120, 103587 p. doi: https://doi.org/10.1016/j.ejsobi.2023.103587

LI, S. et al. (2017). Spatial and Temporal Pattern Analyses of Esca Grapevine Disease in Vineyards in France. *Phytopathology®*, 107 (1), 59-69 p. doi: https://doi.org/10.1094/PHYTO-07-15-0154-R

LIERE, H., JHA, S. and PHILPOTT, S. M. (2017). Intersection between biodiversity conservation, agroecology, and ecosystem services. *Agroecology and Sustainable Food Systems,* 41 (7), 723-760 p. doi: https://doi.org/10.1080/21683565.2017.1330796

LILIANE, T. N. and CHARLES, M. S. (2020). Factors affecting yield of crops. *Agronomy-climate change & food security,* 9, 9-24 p. doi: 10.5772/intechopen.90672

LINSENMEIER, A. et al. (2010). Investigation of grapevine root distribution by in situ minirhizotron observation. *VITIS - Journal of Grapevine Research,* 49 (1), 1-6 p. doi: https://doi.org/10.5073/vitis.2010.49.1-6

LORENZ, D. H. et al. (1995). Growth Stages of the Grapevine: Phenological growth stages of the grapevine (*Vitis vinifera* L. ssp. vinifera)—Codes and descriptions according to the extended BBCH scale. *Australian Journal of Grape and Wine Research,* 1, 100-103 p. doi: https://doi.org/10.1111/j.1755-0238.1995.tb00085.x

LYU, D. et al. (2021). The Coevolution of Plants and Microbes Underpins Sustainable Agriculture. *Microorganisms,* 9 (5), 1036 p. doi: https://doi.org/10.3390/microorganisms9051036

MAGYAR, D. (2008). The tree bark: a natural spore trap. *Aspects of Applied Biology,* 89, 7-16. p. doi: https://doi.org/10.1016/S0034-6667(98)00040-2

MAHATO, A. (2014). Climate Change and its Impact on Agriculture. *International Journal of Scientific and Research Publications,* 4 (4)p.

MANIRAJAN, B. A. et al. (2018). Diversity, specificity, co-occurrence and hub taxa of the bacterial–fungal pollen microbiome. *FEMS Microbiology Ecology*, 94 (8)p. doi: https://doi.org/10.1093/femsec/fiy112

MANTEAU, S. et al. (2003). Differential regulation by ambient pH of putative virulence factor secretion by the phytopathogenic fungus *Botrytis cinerea*. *FEMS Microbiology Ecology*, 43 (3), 359-366 p. doi: https://doi.org/10.1111/j.1574-6941.2003.tb01076.x

MATESE, A. et al. (2014). Spatial variability of meteorological conditions at different scales in viticulture. *Agricultural and Forest Meteorology*, 189-190, 159-167 p. doi: https://doi.org/10.1016/j.agrformet.2014.01.020

MAUL, E. et al. (2015). The European Vitis Database (www.eu-vitis.de) – a technical innovation through an online uploading and interactive modification system. *VITIS - Journal of Grapevine Research,* 51 (2), 79 p. doi: https://doi.org/10.5073/vitis.2012.51.79-85

MAUL, E. and TÖPFER, R. (2015). Vitis International Variety Catalogue (VIVC): A cultivar database referenced by genetic profiles and morphology. *BIO Web of Conferences,* 5, 01009 p. doi: https://doi.org/10.1051/bioconf/20150501009

MEZŐSI, G. (2017a). Climate of Hungary. In G. MEZŐSI (Ed.), *The Physical Geography of Hungary* (p. 101-119). Cham: Springer International Publishing. 10.1007/978-3-319-45183-1_2

MEZŐSI, G. (2017b). Soils of Hungary. In G. MEZŐSI (Ed.), *The Physical Geography of Hungary* (p. 165-174). Cham: Springer International Publishing. https://doi.org/10.1007/978-3-319-45183-1_4

MILLER, P., LANIER, W. and BRANDT, S. (2001). *Using Growing Degree Days to Predict Plant Stages* p.

MOLITOR, D. and BERKELMANN-LOEHNERTZ, B. (2011). Simulating the susceptibility of clusters to grape black rot infections depending on their phenological development. *Crop Protection,* 30 (12), 1649-1654 p. doi: https://doi.org/10.1016/j.cropro.2011.07.020

MOLITOR, D. et al. (2014). A high resolution cumulative degree day based model to simulate the phenological development of grapevine. *American Journal of Enology and Viticulture,* 65 (1), 72-80 p. doi: 10.5344/ajev.2013.13066

MOSEDALE, J. R. et al. (2016). Climate change impacts and adaptive strategies: lessons from the grapevine. *Global Change Biology,* 22 (11), 3814-3828 p. doi: https://doi.org/10.1111/gcb.13406

MSIMBIRA, L. A. and SMITH, D. L. (2020). The Roles of Plant Growth Promoting Microbes in Enhancing Plant Tolerance to Acidity and Alkalinity Stresses. *Frontiers in Sustainable Food Systems,* Volume 4 - 2020 p. doi: https://doi.org/10.3389/fsufs.2020.00106

MUNDY, D. C., AGNEW, R. H. and WOOD, P. N. (2012). Grape tendrils as an inoculum source of *Botrytis cinerea* in vineyards - A review. *New Zealand Plant Protection,* 65, 218-227 p. doi: https://doi.org/10.30843/nzpp.2012.65.5373

MUNDY, D. C. and BERESFORD, R. M. (2007). Susceptibility of grapes to *Botrytis cinerea* in relation to berry nitrogen and sugar concentration. *New Zealand Plant Protection,* 60 (0), 123-127 p. doi: 10.30843/nzpp.2007.60.4636

MURRAY-WATSON, R. E. and CUNNIFFE, N. J. (2022). How the epidemiology of disease-resistant and disease-tolerant varieties affects grower behaviour. *J R Soc Interface,* 19 (195), 20220517 p. doi: https://doi.org/10.1098/rsif.2022.0517

NAIR, N. G. and ALLEN, R. N. (1993). Infection of grape flowers and berries by B*otrytis cinerea* as a function of time and temperature. *Mycological Research,* 97 (8), 1012-1014 p. doi: https://doi.org/10.1016/S0953-7562(09)80871-X

NAKAGAWA, S. and SANTOS, E. S. A. (2012). Methodological issues and advances in biological meta-analysis. *Evolutionary Ecology,* 26 (5), 1253-1274 p. doi: https://doi.org/10.1007/s10682-012-9555-5

NDUWUMUREMYI, A. (2013). Soil Acidification and Lime Quality: Sources of Soil Acidity, Effects on Plant Nutrients, Efficiency of Lime and Liming Requirements. *Research & Reviews: Journal of Agriculture and Allied Sciences,* 2 (4), 26-34 p.

NEWMAN, E. (1985). *The rhizosphere: carbon sources and microbial populations*. Paper presented at the Ecological interactions in soil: plants, microbes and animals. from Oxford, Blackwell Scientific Publications 107–121 p.

NICOLSON, S. W. et al. (2018). Digestibility and nutritional value of fresh and stored pollen for honey bees (*Apis mellifera* scutellata). *Journal of Insect Physiology,* 107, 302-308 p. doi: https://doi.org/10.1016/j.jinsphys.2017.12.008

NICOLSON, S. W. and HUMAN, H. (2013). Chemical composition of the 'low quality' pollen of sunflower (*Helianthus annuus*, *Asteraceae*). *Apidologie,* 44 (2), 144-152 p. doi: https://doi.org/10.1007/s13592-012-0166-5

OCCHIPINTI, A. (2013). Plant coevolution: evidences and new challenges. *Journal of Plant Interactions,* 8 (3), 188-196 p. doi: https://doi.org/10.1080/17429145.2013.816881

OGAWA, J. M. and ENGLISH, H. (1960). Blossom blight and green fruit rot of Almond, Apricot and Plum caused by *Botrytis cinerea*. *Plant Disease Reporter,* 44 (4), 265–268 p.

OKE, T. et al. (2017). *Urban Climates*: Cambridge University Press. https://doi.org/10.1017/9781139016476

OLIVER, C. et al. (2024). Fungicide Use Patterns in Select United States Wine Grape Production Regions. *Plant Disease,* 108 (1), 104-112 p. doi: https://doi.org/10.1094/PDIS-04-23-0798-RE

OSHUNSANYA, S. (2019). Introductory Chapter: Relevance of Soil pH to Agriculture. In. 10.5772/intechopen.82551

PAREEK, N. (2017). Climate Change Impact on Soils: Adaptation and Mitigation. *MOJ Ecology & Environmental Sciences,* 2 (3), 136-139 p. doi: 10.15406/mojes.2017.02.00026

PARKER, A. K. et al. (2011). General phenological model to characterise the timing of flowering and veraison of *Vitis vinifera* L. *Australian Journal of Grape and Wine Research,* 17, 206-216 p. doi: https://doi.org/10.1111/j.1755-0238.2011.00140.x

PÁSZTOR, L. et al. (2020). Progress in the elaboration of GSM conform DSM products and their functional utilization in Hungary. *Geoderma Regional,* 21, 1-13 p. doi: https://doi.org/10.1016/j.geodrs.2020.e00269

PETIT, A. N. et al. (2012). Fungicide impacts on photosynthesis in crop plants. *Photosynth Res,* 111 (3), 315-326 p. doi: https://doi.org/10.1007/s11120-012-9719-8

PIAO, S. et al. (2019). Plant phenology and global climate change: Current progresses and challenges. *Global Change Biology*, 25 (6), 1922-1940 p. doi: https://doi.org/10.1111/gcb.14619

PISKORSKI, R., KRODER, S. and DORN, S. (2011). Can pollen headspace volatiles and pollenkitt lipids serve as reliable chemical cues for bee pollinators? *Chemistry & Biodiversity*, 8 (4), 577-586 p. doi: https://doi.org/10.1002/cbdv.201100014

PLOETZ, R. C. (2007). Diseases of tropical perennial crops: challenging problems in diverse environments. *Plant Disease*, 91 (6), 644-663 p. doi: https://doi.org/10.1094/PDIS-91-6-0644

POSSINGHAM, J. V. (2004). *On the growing of grapevines in the tropics*.

PRAKASH, S. and VERMA, A. (2022). Anthropogenic activities and Biodiversity threats. *International Journal of Biological Innovations*, 04, 94-103 p. doi: https://doi.org/10.46505/IJBI.2022.4110

QUDSI, Z. et al. (2021). The dynamic effect of air temperature and air humidity toward soil temperature in various lands cover at KHDTK Gunung Bromo, Karanganyar - Indonesia. *IOP Conference Series: Earth and Environmental Science*, 724, 012003 p. doi: 10.1088/1755-1315/724/1/012003

R Development Core Team (2019). *R: A language and environment for statistical computing. R Foundation for Statistical Computing*, R Foundation for Statistical Computing p. doi: https://www.r-project.org/

RANDALL, P. M. (1990). A study of modern pollen deposition, Southern Alps, South Island, New Zealand. *Review of Palaeobotany and Palynology*, 64 (1), 263-272 p. doi: https://doi.org/10.1016/0034-6667(90)90141-5

REDDY, B. V. S. et al. (2003). Crop management factors influencing yield and quality of crop residues. *Field Crops Research*, 84 (1), 57-77 p. doi: https://doi.org/10.1016/S0378-4290(03)00141-2

REDL, M. et al. (2021). Survival and viability of ascospores of *Erysiphe necator* in Austrian vineyards. *European Journal of Plant Pathology*, 159 (3), 615-626 p. doi: https://doi.org/10.1007/s10658-020-02192-6

REISENZEIN, H. et al. (2007). The influence of soil properties on the development of grape *Phylloxera* populations in austrian viticulture. *Acta Horticulturae*, 733, 13-24 p. doi: 10.17660/ActaHortic.2007.733.1

REZZONICO, F., RUPP, O. and FAHRENTRAPP, J. (2017). Pathogen recognition in compatible plant-microbe interactions. *Scientific Reports*, 7 (1), 6383 p. doi: https://doi.org/10.1038/s41598-017-04792-5

RICCIARDI, R. et al. (2024). The European grape berry moth, *Eupoecilia ambiguella* (*Lepidoptera*: *Tortricidae*): Current knowledge and management challenges. *Crop Protection*, 180, 106641 p. doi: https://doi.org/10.1016/j.cropro.2024.106641

RIFFLE, V. L. et al. (2022). Vine Age Affects Vine Performance, Grape and Wine Chemical and Sensory Composition of cv. Zinfandel from California. *American Journal of Enology and Viticulture*, 73 (4), 277-293 p. doi: 10.5344/ajev.2022.22014

RIPOCHE, A. et al. (2011). Changing the soil surface management in vineyards: immediate and delayed effects on the growth and yield of grapevine. *Plant and Soil*, 339 (1), 259-271 p. doi: https://doi.org/10.1007/s11104-010-0573-1

ROBINSON, G. (2014). *Geographies of agriculture: Globalisation, restructuring and sustainability*. London: Taylor and Frances Group. https://doi.org/10.4324/9781315839509

ROMANAZZI, G. and FELIZIANI, E. (2014). *Botrytis cinerea*. In S. BAUTISTA-BAÑOS (Ed.), *Postharvest decay: Control strategies* (p. 131-146): Elsevier. https://doi.org/10.1016/B978-0-12-411552-1.00004-1

ROMANAZZI, G. et al. (2016). Integrated management of postharvest gray mold on fruit crops. *Postharvest Biology and Technology*, 113, 69-76 p. doi: https://doi.org/10.1016/j.postharvbio.2015.11.003

ROSSI, V. and CAFFI, T. (2012). The role of rain in dispersal of the primary inoculum of *Plasmopara viticola*. *Phytopathology*, 102, 158-165 p. doi: http://dx.doi.org/10.1094/PHYTO-08-11-0223

ROUPHAEL, Y. et al. (2012). Vegetable quality as affected by genetic, agronomic and environmental factors. *J. Food Agric. Environ*, 10 (3), 680-688 p. doi: https://api.semanticscholar.org/CorpusID:130553297

SAVARY, S. et al. (2012). Crop losses due to diseases and their implications for global food production losses and food security. *Food Security*, 4, 519–537 p. doi: https://doi.org/10.1007/s12571-012-0200-5

SCHERMAN, J. M. et al. (2025). Revisiting the role of pollen-microbiome interactions: new insights into the “One Health-One Biosecurity” concept in changing agroecosystems. *Frontiers in Microbiology*, Volume 16 - 2025 p. doi: https://doi.org/10.3389/fmicb.2025.1620446

SCHOENEWEISS, D. F. (1975). Predisposition, Stress, and Plant Disease. *Annual Review of Phytopathology*, 13, 193-211 p. doi: https://doi.org/10.1146/annurev.py.13.090175.001205

SCHULTZ, H., MATTHEWS, M. and ANDERSON, M. M. (1987). Phenologic and Growth-Responses to Early and Late Season Water Deficits in Cabernet Franc. *Vitis - Geilweilerhof-*, 26, 147-160 p. doi: https://doi.org/10.5073/vitis.1987.26.147-160

SEGUIN, G. (1986). 'Terroirs' and pedology of wine growing. *Experientia,* 42 (8), 861-873 p. doi: https://doi.org/10.1007/BF01941763

SILVERTOWN, J. (2009). A new dawn for citizen science. *Trends in Ecology & Evolution,* 24 (9), 467-471 p. doi: https://doi.org/10.1016/j.tree.2009.03.017

SIRAPPA, M. and TITAHENA, M. (2014). Improvement of Suboptimal Land Productivity Approach by Land and Plant Management. *Tropical Soil,* 19, 10 p. doi: http://dx.doi.org/10.5400/jts.2014.v19i2.99-109

SMART, R. E. et al. (2017). Canopy Management to Improve Grape Yield and Wine Quality - Principles and Practices. *South African Journal of Enology and Viticulture,* 11, 3-17 p. doi: https://doi.org/10.21548/11-1-2232

SONG, X. et al. (2014). Tree barks as a natural trap for airborne spores and pollen grains from China. *Chinese Science Bulletin,* 59 p. doi: https://doi.org/10.1007/s11434-014-0269-7

SOSA-ALVAREZ, M., MADDEN, L. and ELLIS, M. (1995). Effects of temperature and wetness duration on sporulation of *Botrytis cinerea* on strawberry leaf residues. *Plant Disease,* 79, 609-615 p. doi: https://doi.org/10.1094/PD-79-0609

STANLEY, R. G. and LINSKENS, H. F. (1974). *Pollen: Biology biochemistry management*: Springer. https://doi.org/10.1007/978-3-642-65905-8

STAPLETON, J. J., LEAVITT, G. M. and VERDEGAAL, P. S. (1995). Leaf removal improves fungicide control of *Powdery mildew* in SJV grapes. *California Agriculture,* 49 (5), 33-36 p. doi: 10.3733/ca.v049n05p33

STEENWERTH, K. L. et al. (2008). Soil morphology, depth and grapevine root frequency influence microbial communities in a Pinot noir vineyard. *Soil Biology and Biochemistry,* 40 (6), 1330-1340 p. doi: https://doi.org/10.1016/j.soilbio.2007.04.031

SURAMWAD, S. and KOLGANE, B. (2017). A Study of Adoption of Improved Grape Production Technology Followed by Grape Growers. *Indian Research Journal of Extension Education,* 17 (3), 101-104 p.

SZENTIMREY, T., BIHARI, Z. and SZALAI, S. (2005). Meteorological Interpolation based on Surface Homogenized Data Basis (MISH). *Geophysical Research Abstracts,* 7 (07310), 1-2 p.

TANÁCS, E. et al. (2022). Compiling a high-resolution country-level ecosystem map to support environmental policy: methodological challenges and solutions from Hungary. *Geocarto International,* 37 (25), 8746-8769 p. doi: https://doi.org/10.1080/10106049.2021.2005158

TEAM, R. D. C. (2019). R: a language and environment for statistical computing. In R Foundation for Statistical Computing. p.

TELLO, J. and IBÁÑEZ, J. (2018). What do we know about grapevine bunch compactness? A state-of-the-art review. *Australian Journal of Grape and Wine Research,* 24 (1), 6-23 p. doi: https://doi.org/10.1111/ajgw.12310

TENG, J. et al. (2024). Conservation agriculture improves soil health and sustains crop yields after long-term warming. *Nature Communications,* 15 (1), 8785 p. doi: https://doi.org/10.1038/s41467-024-53169-6

THIESSEN, L. D., NEILL, T. M. and MAHAFFEE, W. F. (2017). Timing Fungicide Application Intervals Based on Airborne *Erysiphe necator* Concentrations. *Plant Disease,* 101 (7), 1246-1252 p. doi: https://doi.org/10.1094/PDIS-12-16-1727-RE

THOMAS, C. S., MARIOS, J. J. and ENGLISH, J. T. (1987). The Effects of Wind Speed, Temperature, and Relative Humidity on Development of Aerial Mycelium and Conidia of *Botrytis cinerea* on Grape. *The American Phytopathological Society,* 260-265 p. doi: 10.1094/Phyto-78-260

TŘÍSKA, J. et al. (2017). Variability in the Content of Trans-Resveratrol, Trans-ε-Viniferin and R2-Viniferin in Grape Cane of Seven *Vitis vinifera* L. Varieties during a Three-Year Study. *Molecules,* 22 (6), 1-10 p. doi: https://doi.org/10.3390/molecules22060928

TSIAFOULI, M. A. et al. (2015). Intensive agriculture reduces soil biodiversity across Europe. *Global Change Biology,* 21 (2), 973-985 p. doi: https://doi.org/10.1111/gcb.12752

UDVARDY, O. et al. (2019). *Brochure of the Hungarian aerobiological network 2018 (A magyarországi aerobiológiai hálózat tájékoztatója 2018)*. National Institute of Public Health (Nemzeti Népegészségügyi Központ).

VAN LEEUWEN, C. and DARRIET, P. (2016). The Impact of Climate Change on Viticulture and Wine Quality. *Journal of Wine Economics,* 11 (1), 150-167 p. doi: https://doi.org/10.1017/jwe.2015.21

VAN LEEUWEN , C. et al. (2004). Influence of Climate, Soil, and Cultivar on Terroir. *American Journal of Enology and Viticulture,* 55, 207-217 p. doi: 10.5344/ajev.2004.55.3.207

VAN LEEUWEN, C., ROBY, J. and DE RESSÉGUIER, L. (2018). Soil-related terroir factors: A review. *OENO One,* 52 (2), 173-188 p. doi: https://doi.org/10.20870/oeno-one.2018.52.2.2208

VANDECASTEELE, M. et al. (2018). Species prevalence and disease progression studies demonstrate a seasonal shift in the *Alternaria* population composition on potato. *Plant Pathology,* 67 (2), 327-336 p. doi: https://doi.org/10.1111/ppa.12734

VANDENKOORNHUYSE, P. et al. (2015). The importance of the microbiome of the plant holobiont. *New Phytologist*, 206 (4), 1196-1206 p. doi: https://doi.org/10.1111/nph.13312

VERCESI, A. et al. (2002). Effect of Azoxystrobin on the Oospores of *Plasmopara Viticola*. In P. T. N. SPENCER-PHILLIPS, U. GISI, & A. LEBEDA (Eds.), *Advances in Downy Mildew Research* (p. 195-199). Dordrecht: Springer Netherlands. https://doi.org/10.1007/0-306-47914-1_11

version: 4.1.0, R Development Core Team. (2019). p. doi:

VIECHTBAUER, W. (2010). Conducting Meta-Analyses in R with the metafor Package. *Journal of Statistical Software*, 36 (3), 1-48 p. doi: https://doi.org/10.18637/jss.v036.i03

VOSS, R. E., HANWAY, J. J. and FULLER, W. A. (1970). Influence of Soil, Management, and Climatic Factors on the Yield Response by Corn (*Zea mays* L.) to N, P, and K Fertilizer. *Agronomy Journal*, 62 (6), 736-740 p. doi: https://doi.org/10.2134/agronj1970.00021962006200060015x

WALSH, D. B. et al. (2011). *Drosophila suzukii* (*Diptera*: *Drosophilidae*): Invasive Pest of Ripening Soft Fruit Expanding its Geographic Range and Damage Potential. *Journal of Integrated Pest Management*, 2 (1), G1-G7 p. doi: https://doi.org/10.1603/IPM10010

WARREN, M. A. et al. (1999). The link between spore concentration, flower infection and subsequent bunch rot caused by *Botrytis cinerea* in winegrape. *12th biennial conference, Canberra, 27-30 September 1999 : Asia-Pacific plant pathology for the new millennium : conference handbook.*, 293 p.

WILLOCQUET, L. et al. (1998). Effects of wind, relative humidity, leaf movement and colony age on dispersal of conidia of Uncinula necator, causal agent of grape *Powdery mildew*. *Plant Pathology*, 47 (3), 234-242 p. doi: https://doi.org/10.1046/j.1365-3059.1998.00242.x

WINK, M. (1988). Plant breeding: importance of plant secondary metabolites for protection against pathogens and herbivores. *Theoretical and Applied Genetics*, 75 (2), 225-233 p. doi: https://doi.org/10.1007/BF00303957

WOLFE, M. S. (2000). Crop strength through diversity. *Nature*, 406, 681-682 p. doi: Crop strength through diversity

YANG, T., SIDDIQUE, K. H. M. and LIU, K. (2020). Cropping systems in agriculture and their impact on soil health-A review. *Global Ecology and Conservation*, 23 p. doi: https://doi.org/10.1016/j.gecco.2020.e01118

ZABEL, F. et al. (2019). Global impacts of future cropland expansion and intensification on agricultural markets and biodiversity. *Nature Communications*, 10 (1), 2844 p. doi: https://doi.org/10.1038/s41467-019-10775-z

ZAPATA, D. et al. (2015). Estimation of the base temperature and growth phase duration in terms of thermal time for four grapevine cultivars. *International Journal of Biometeorology*, 59 p. doi: https://doi.org/10.1007/s00484-015-0985-y

ZHANG, Z.-Y. et al. (2019). Comparison between two kinds of natural pollen traps in tropical China: ants' nests on tree branches versus surface soil. *Palynology*, 44 (1), 4-11 p. doi: https://doi.org/10.1080/01916122.2018.1549117