

# Bayesian inference of environmental and biotic factors determining the occurrence of the grapevine disease ‘bois noir’

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**Abstract.** Insect-vectorized plant diseases often create complex epidemiological systems that are challenging to understand, predict, and manage. An example is ‘bois noir’ (BN), a phytoplasma-associated grapevine disease commonly found in European vineyards. Although BN has the potential to cause substantial economic damage, the factors that contribute to BN prevalence in vineyards are still not well understood.

We used Bayesian inference with generalized linear mixed-effect models to test the hypotheses that (1) grapevine varieties exhibit different BN susceptibility; (2) environment drivers influence prevalence of the disease and occurrence of the vector; and (3) the presence of the main vector is a major determinant of BN occurrence.

We found that the presence of the vector *Hyalesthes obsoletus* increased with increasing isothermality, minimum temperatures during the coldest period, soil erosion, and natural vegetation in close proximity to the vineyards. Presence of the BN disease increased with presence of the vector as well as increasing altitudes and mean annual temperatures. After accounting for those factors, Chardonnay and Riesling showed higher disease prevalence than Müller-Thurgau, Silvaner, and Merlot. Although the vector had an overall positive effect on the disease prevalence, disease and vector occurrence show distinct spatial patterns.

In conclusion, our analysis suggests that vector presence is not the only, and maybe not the most important factor for BN disease prevalence. Environment and grape cultivar also play important roles. Hence, area-wide predictions of both environmental disease risk and vector presence, together with information about the susceptibility of grape cultivars, will enable a more targeted disease management. Our modelling framework could easily be applied to other diseases of concern, such as apple proliferation or flavescence dorée.

**Key words:** aetiology; bacterial disease; Bayesian inference; grapevine; *Hyalesthes obsoletus*; insect pest; landscape epidemiology; phytoplasmosis; planthopper; species distribution model.

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## INTRODUCTION

Bacterial diseases of agricultural crops are of considerable economic importance. They are also interesting systems from an ecological perspective, given the frequent complexity of interactions between hosts, vectors, and pathogens. Examples include vector-pathogen symbiosis, plant-pathogen interactions, such as the manipulation of non-hosts to become host plants (Purcell 1988), or disease cycles and multiple pathogens (Nault 1980). Understanding such agricultural epidemiological systems is methodologically challenging, because a variety of factors introduce uncertainties in different stages of the modelling process. One particularly important problem is the frequent absence of good data on the distribution, population size, and prevalence of the disease in the vector, the potential presence of unknown alternative vectors, as well as latency period between infection and disease symptoms. The latter camouflages severity of signs can often only be addressed by pathogen detection using molecular methods.

One example of such a system is 'bois noir' (BN), a grapevine yellow disease that is widespread in European vineyards (Caudwell 1961, Lessio et al. 2007). In some regions, disease prevalence has been reported to exceed 50%, leading to serious yield loss (Maixner et al. 2006, Johannesen et al. 2008). Disease symptoms include discolored leaves with downward-rolled margins, vein chlorosis, absence of shoot lignification in the fall, and stunted berries. The aetiology of grapevine yellow diseases is attributed to cell-wall-less bacteria, known as phytoplasma. BN-associated phytoplasma belong to the stolbur (16SrXII-A) group (Daire et al. 1992, Maixner et al. 1994) and can be detected in a wide range of plants using biomolecular methods (Fos et al. 1992, Maixner et al. 1995, Marcone et al. 1997). In their host plants, phytoplasma are limited to the sieve tubes and are transmitted by phloem-sucking insects (Weintraub and Beanland 2006). Stolbur phytoplasma are harbored by several leaf- and planthoppers, such as *Anaceratagallia ribauti*, *Aphrodes bicincta*, *Dictyophara europaea*, *Macrosteles laevis*, *Euscelis incisus*, *Hyalesthes obsoletus*, *Reptalus panzeri*, and *R. quinquecostatus* (Batlle et al. 2000, Cvrković et al. 2013).

The epidemiology of BN is still poorly under-

stood and is the subject of ongoing research. Until recently, the planthopper *H. obsoletus* was considered to be the main vector of BN disease (Maixner 1994, Sforza et al. 1998, Panassiti et al. 2013). However, discrepancies in disease prevalence and *H. obsoletus* abundances in Serbian vineyards prompted experiments that confirmed the ability of *R. panzeri* to transmit BN disease to grapevines (Cvrković et al. 2013). Therefore, the possibility of further disease vectors cannot be excluded.

In Germany, the known BN epidemiology is characterized by two distinct disease cycles involving either stinging nettle (*Urtica dioica*) or bindweeds (*Convolvulus arvensis* and *Calystegia sepium*) as host plants, two genotypes of the stolbur phytoplasma (tuf a and b) as pathogens, and different host races of *H. obsoletus* as vectors (Langer and Maixner 2004, Johannesen et al. 2008, Imo et al. 2013). In this system, grapevine is a dead-end host because the vector cannot acquire stolbur phytoplasma from diseased vines again (Sforza 1998). The susceptibility and disease severity of a plant is determined by several factors including environmental conditions, rootstock, vector activity, and the type of pathogen (Weintraub and Jones 2010, Guerra and Steenwerth 2012, Andrade et al. 2013). For example, Waring and Cobb (1992) found that the water content in the soil can change the chemical composition of the plant defences thus affecting the pest populations. The interplay of many factors that may affect vector, host, and disease makes the study of such an epidemiological system extremely difficult.

Habitat models, also called species distribution or niche models, allow us to determine the environmental factors that correlate with species or disease occurrence. In a recent study, Panassiti et al. (2013) used habitat models to investigate the habitat requirements of the BN disease vector *H. obsoletus*. The study showed that the ecological niche of *H. obsoletus* in the Baden region (Southwest Germany) is mainly determined by soil properties and the amount of average annual precipitation; however, it did not test whether this presence actually correlates to 'bois noir' prevalence at the respective sites.

There are a number of reasons why BN disease prevalence might differ from the presence/absence of *H. obsoletus*: (1) other insect vectors

might be responsible for pathogen transmission (Cvrković et al. 2013); (2) the vector infestation rate may vary between spatially distinct populations and according to the environmental factors that control the host plants; and (3) grapevine cultivars may exhibit different susceptibility and symptom severity (Riedle-Bauer and Brader 2013, Roggia et al. 2013). For research and management, it is therefore important to understand better if the vector or other factors are the main determinants of BN occurrence in vineyards.

To address these questions, we investigated the correlation of BN prevalence with the predicted distribution of the main vector in the Baden region as well as with other environmental factors and with the grape cultivar. Disease prevalence was obtained by inspecting 123,703 grapevine plants in 438 vineyard parcels at 85 locations across southern Germany. The purpose of this biomonitoring of *H. obsoletus* was to identify the main ecological drivers for its occurrence (Panassiti et al. 2013). We analyzed these data together with environmental and biotic covariates derived from the WorldClim database (Hijmans et al. 2005), federal databases, and a previous biomonitoring campaign of the insect vector in a generalized linear mixed model, evaluated in a Bayesian framework. We hypothesize that (1) grapevine varieties exhibit different BN susceptibility, (2) environment influences disease prevalence, and (3) the presence of the main vector is an important predictor for BN occurrence.

## MATERIAL AND METHODS

### Study sites

Disease prevalence was monitored at 85 locations in the Baden region of southwestern Germany. These locations formed part of a previous study on the habitat requirements of *H. obsoletus* and are described in Panassiti et al. (2013).

### Data collection

At the 85 study sites, a planthopper survey was conducted between June and August in 2011 (Panassiti et al. 2013) at the center of the site, and all grapevine plants within a 50-m buffer around the location of the previous planthopper survey

were visually examined for ‘bois noir’ (BN) symptoms in the period from October to November 2012, resulting in a sample of 123,703 grapevine plants in 438 vineyard parcels. The 50-m buffer was chosen based on the estimated active dispersal range of a single *H. obsoletus* individual per year. Vine plants were classified as BN-infected when their leaves and shoots showed characteristic disease symptoms. Parcels with young vine plants and parcels with the grapevine cultivar Cabernet Mitos were excluded from our survey because for those, BN disease symptoms can be difficult to detect.

As variables of interest that could affect the presence of the disease or the planthopper, we identified for the disease the planthopper itself, environment, and grape variety and for the grasshopper its environment. Moreover, we conjectured that effects may be different in different regions and also in different parcels, the latter due to the fact that management is usually determined per parcel.

To obtain grape varieties and ownership, we linked plant individuals to data obtained from the State Office of Land Consolidation and Land Development, Baden-Württemberg (LGL) with information found in the viticulture registry maintained by the State Institute for Viticulture and Oenology, Freiburg (accessed 28 March 2013). In 34 of the 371 grapevine parcels, several vine cultivars were listed (26 with two varieties, six with three varieties, and two with four varieties). In these cases, we assigned the reported fraction per parcel to all plant individuals in the parcels. In rare cases where there were different owners within the same land parcel, we treated these owner combinations as a new owner in the analysis.

As a proxy for the likely presence of the main vector *H. obsoletus* at the sites, we used predictions of a habitat model that correlated *H. obsoletus* presence with fine soil, the average annual precipitation, precipitation seasonality, and shade as environmental predictors (see Panassiti et al. 2013:6; model ID 13465, AUC = 0.92). We judged these predictions that implicitly average over multiple observations as more accurate than the number of *H. obsoletus* catches on each site, because the latter can be expected to show significant variability, for example due to variability in weather conditions during sam-

pling. The reason to use the model results from Panassiti et al. (2013) and not the results from the *H. obsoletus* model developed in this study was that Panassiti et al. (2013) used a larger range of sites that were sampled for presence, partly outside vineyards, and the predictions from this model were therefore considered more reliable. Additionally to this existing model, we developed a new habitat model for *H. obsoletus* in this study. The reason is that the existing model from Panassiti et al. (2013) used different environmental variables as well as a slightly different statistical setup than the BN model developed in this study. A direct comparison of the habitat preferences of the BN disease inferred in this study with the habitat preferences of *H. obsoletus* would otherwise not have been possible.

We derived environmental predictors from several data sources. From the WorldClim database, we obtained 19 bioclimatic variables with a spatial resolution of 30 arc minutes (Hijmans et al. 2005; <http://www.worldclim.org>). These data summarize climate conditions over a time interval of 50 years (1950–2000). Edaphic parameters were obtained from interpolated soil data (scale 1:50,000) provided by the Federal State Office for Geology Resources and Mining, Freiburg Regional Board (LGRB). Topographic data (altitude a.s.l. and exposition) was derived from digital elevation maps (Michalak 2004; <http://netgis.geo.uw.edu.pl/srtm/Europe/>).

The final dataset included the disease observations of 105,489 grapevine plants of different varieties from 398 parcels on 74 sites (Fig. 1a), together with environmental predictors as well as predicted (from a previous study) and observed vector presence in the center of the site.

### Statistical analyses

Environmental predictors were scaled and centered (i.e., mean subtracted and divided by the standard deviation) before further analysis. Grape varieties were by definition already between 0 and 1 and neither scaled nor centered. To avoid multicollinearity problems, we removed predictors when the pairwise Spearman's correlation coefficient  $|r_s| \geq 0.7$  (Dormann et al. 2013). Although slightly below  $|r_s| = 0.7$ , we also removed the predictor temporal annular range because it showed strong correlations with several other environmental factors. The selection

amongst highly correlated variables was based on ecological proximity, i.e., resource, direct, indirect predictors (Austin 2002, Guisan and Thuiller 2005, Dormann 2011), or on ecological expertise. The final set of environmental predictors included in the analysis is shown in Table 1.

To decide whether to include quadratic terms for those predictors, we performed a pre-analysis with a multivariate GLM including linear and quadratic terms for all environmental predictors (Austin 2002). We postulated that quadratic terms were ecologically sensible only when they led to unimodal response-curves to the individual predictors. As we did not find any significant support for such responses, we considered only linear relationships in the subsequent analysis.

We used a generalized linear mixed-model using a binomial error distribution and a logit link function (GLMM; Gelman and Hill 2007, Bolker et al. 2009) to test the correlation of the remaining predictors with BN infection of plant individuals. Wine growing regions and owners were included as random effects to account for spatial autocorrelation and different management practices, respectively.

To be able to directly compare disease and vector predictions across the Baden region, we used the identical GLMM structure to model presence/absence of *H. obsoletus* on the same sites and with the same climate and soil predictor variables as for BN. The variables *H. obsoletus* predictions, grapes, exposition, and the random effect owners were excluded.

The GLMMs were evaluated in a Bayesian framework using Markov chain Monte Carlo (MCMC) sampling. Bayesian inference is becoming increasingly popular in ecological research (Ellison 2004, Cressie et al. 2009, Hartig et al. 2012). Bayesian inference has a number of advantages over the more traditional method of inference via maximum likelihood estimation. One main feature of Bayesian inference is the possibility to include prior knowledge about parameters. Another advantage is that MCMC sampling covers the parameter space globally, which allows a better analysis of uncertainty and interactions between parameters, especially for random effect structures. Moreover, the algorithms used for Bayesian inference allow higher flexibility in the model specification. Models can be easily extended to include observation accura-

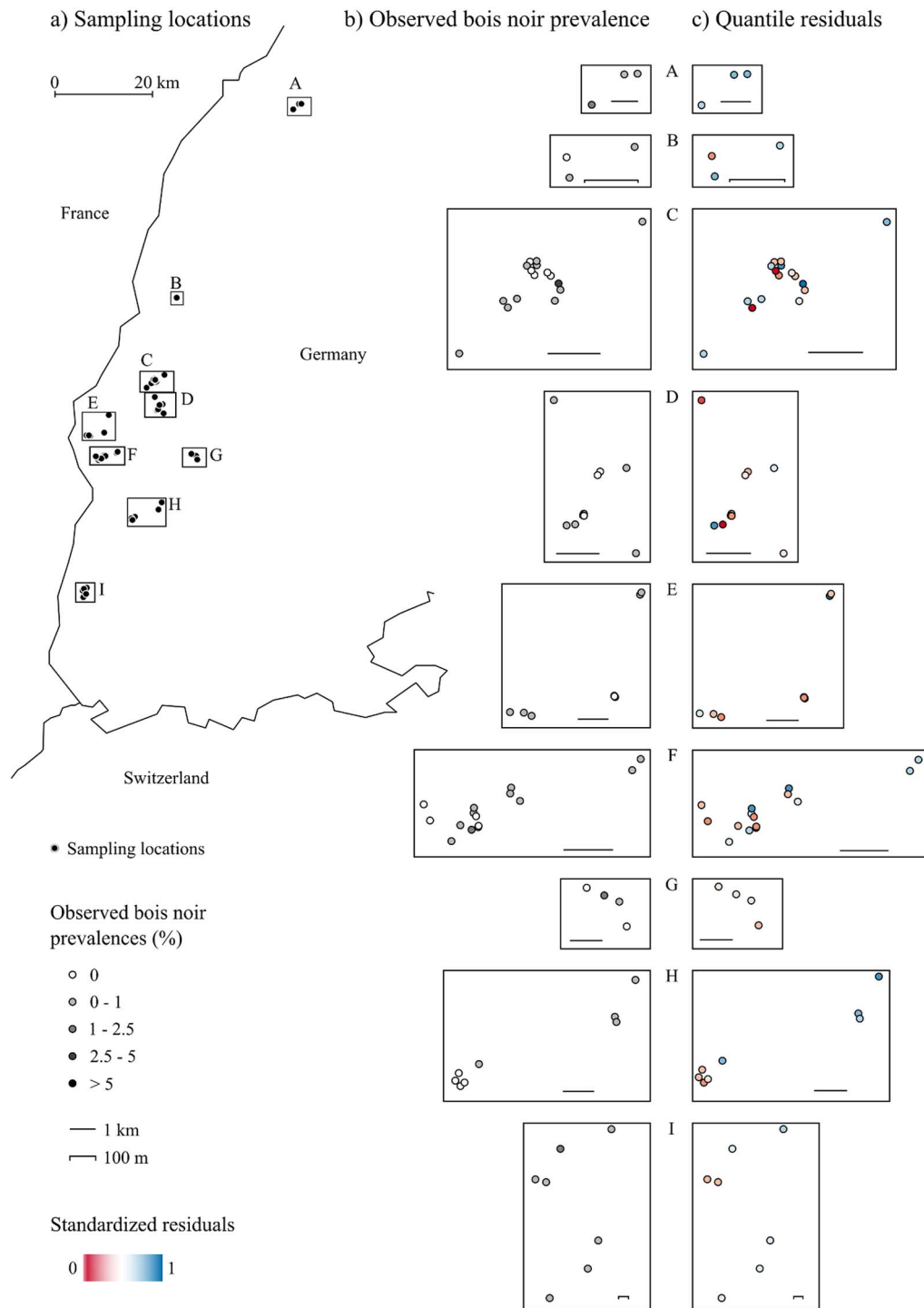


Fig. 1. Observed prevalence of 'bois noir' in the Baden region, southwest Germany, and model residuals for these observations. (a) Sampling locations of the phytoplasma disease 'bois noir' in the Baden region, SW Germany. (b) Detailed view of the sampling locations with observed 'bois noir' prevalences in 2012. (c) Residuals of the sampling locations as quantiles of the distribution expected from the fitted model at the value that was observed.



Table 1. Environmental variables used to fit habitat models for 'bois noir' disease and the vector *Hyalesthes obsoletus*.

Data type and variable	Unit	Source description
Disease vector		
<i>Hyalesthes obsoletus</i> predictions†	...	occurrence probabilities from habitat model ID 13465, Panassiti et al. (2013); only used for 'bois noir' model
Topographic variables		
Altitude a.s.l.	m	digital elevation models, <a href="http://netgis.geo.uw.edu.pl/srtm/Europe/">http://netgis.geo.uw.edu.pl/srtm/Europe/</a>
Exposition	°	digital elevation models, <a href="http://netgis.geo.uw.edu.pl/srtm/Europe/">http://netgis.geo.uw.edu.pl/srtm/Europe/</a>
Bioclimatic variables		
Mean annual temperature	°C	WorldClim database
Isothermality 2/7		WorldClim database
Min temperature of coldest period	°C	WorldClim database
Mean temperature of driest quarter	°C	WorldClim database
Precipitation seasonality	mm	WorldClim database
Effective field capacity	...	digital soil map by LGRB
Cation exchange capacity	...	digital soil map by LGRB
Erosion	...	k-factor as a measure for soil erosion, digital soil map by LGRB
Soil pH	...	soil functions as a buffer for acids, digital soil map by LGRB
Natural vegetation	...	soils as habitat for natural vegetation, digital soil map by LGRB
Vine data		
Grapevine cultivars†	...	relative area within land parcel, LGL vine database
Land parcel owner†	...	random factor, LGL vine database
Vine regions	...	random factor

Note: LGRB is Federal State Office for Geology Resources and Mining, Freiburg Regional Board; LGL is State Office of Land Consolidation and Land Development, Baden-Württemberg.

† Variables excluded in the *H. obsoletus* model.

cy, zero-inflation, or overdispersion (Wikle 2003, Clark 2005, Zuur et al. 2012). Finally, the results of Bayesian inference (posterior distributions and credibility intervals) are often considered more intuitive and provide a straightforward way to forecast predictive uncertainty also for fairly complex models.

To estimate the model, we used mildly informative normal priors centered around zero for the fixed effects, which corresponds to a mild regularization of the model similar to a ridge-regression (see, e.g., Park and Casella 2008). For the hyperpriors on the random effect variance, we used the common choice of inverse gamma distributions. These relatively uninformative prior specification should yield results very similar to a standard maximum-likelihood estimation. MCMC sampling was performed with the software STAN version 1.3.0 in combination with R version 2.15 (R Development Core Team 2011, Stan Development Team 2013). A value of the potential scale reduction factor  $\hat{R} < 1.05$  was used as an indication of chain convergence (Gelman et al. 1995). To assess model fit (posterior predictive check), we calculated the distribution of infected individuals expected under the posterior (posterior predictive distribution) for each site and compared this to

observed infected individuals by calculating the quantile at the observed value. The resulting value can be interpreted as a scaled residual, with 0.5 indicating that the observed value is in the median of the model expectations, 0 indicating maximal overestimation of the model (all simulated values higher than observed), and 1 indicating maximal underestimation of the model (all simulated values are lower than the observed value). Fig. 1c shows that these scaled residuals indicate no major discrepancies or spatial autocorrelation.

## RESULTS

### Effects of the environment on 'bois noir' prevalence

Average 'bois noir' (BN) disease prevalence in the studied vineyards was 0.4% (Fig. 1b). Of 74 vineyards, 53 had diseased grapevines. The disease in these 53 vineyards with symptomatic grapevines ranged from 0.004% to 9.53% (mean = 0.65%, standard deviation = 1.38%). The proportions of the BN disease in areas where the planthopper occurred ranged from 0 to 9.53% (mean = 0.97%, standard deviation = 2.06%).

In the raw data, the cultivars Chardonnay, Chasselas, Riesling, Pinot gris, Pinot blanc, and Pinot noir showed higher BN prevalence than

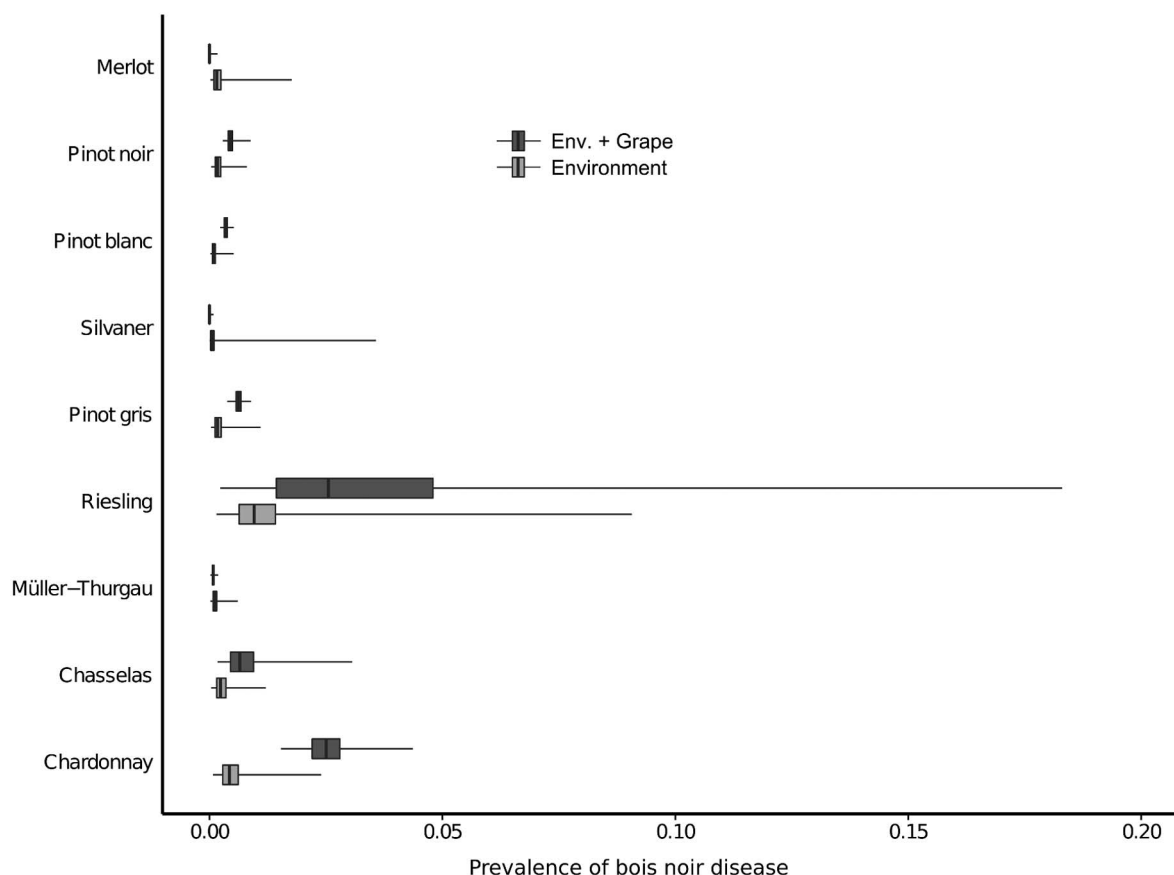


Fig. 2. 'Bois noir' (BN) susceptibility of the studied grape varieties. Posterior predictions and uncertainty for the average environment of a particular grape cultivar without accounting for differences in susceptibility (lower, lighter boxes) and for this environment together with the susceptibility effect fitted for the respective grape cultivar (upper, darker boxes).

Müller-Thurgau, Silvaner, and Merlot. However, as grape cultivars are planted with consideration of the environment, there is a high probability of confounding effects between the cultivar and environmental predictors. The GLMM results, which account for such confounding environmental effects, show that a part of this pattern is indeed likely due to environmental covariates. To demonstrate this, we plotted the disease prevalence predicted by the GLMM for each grape cultivar under the prevailing conditions for all other environmental predictors. Chardonnay and Riesling are now identified as having the highest predisposition to BN disease (Fig. 2).

Regarding the influence of environmental covariates on disease prevalence, we find the strongest positive correlations with mean annual

temperature, altitude a.s.l., and *H. obsoletus* occurrence predictions, the latter having the lowest credible interval. The strongest negative correlations are found for cation exchange capacity of the soil and minimum temperature of coldest period. The credible intervals of the marginal posterior distributions for these variables are displayed in Fig. 3a.

#### Effects of environment on the vector presence

*Hyalesthes obsoletus* was found in 24% of the sampled locations. Fig. 3b shows that environmental variables with the highest influence on planthopper occurrence in vineyards are temperature-related bioclimatic variables (the minimum temperature of coldest period and isothermality) and the amount of natural vegetation in the

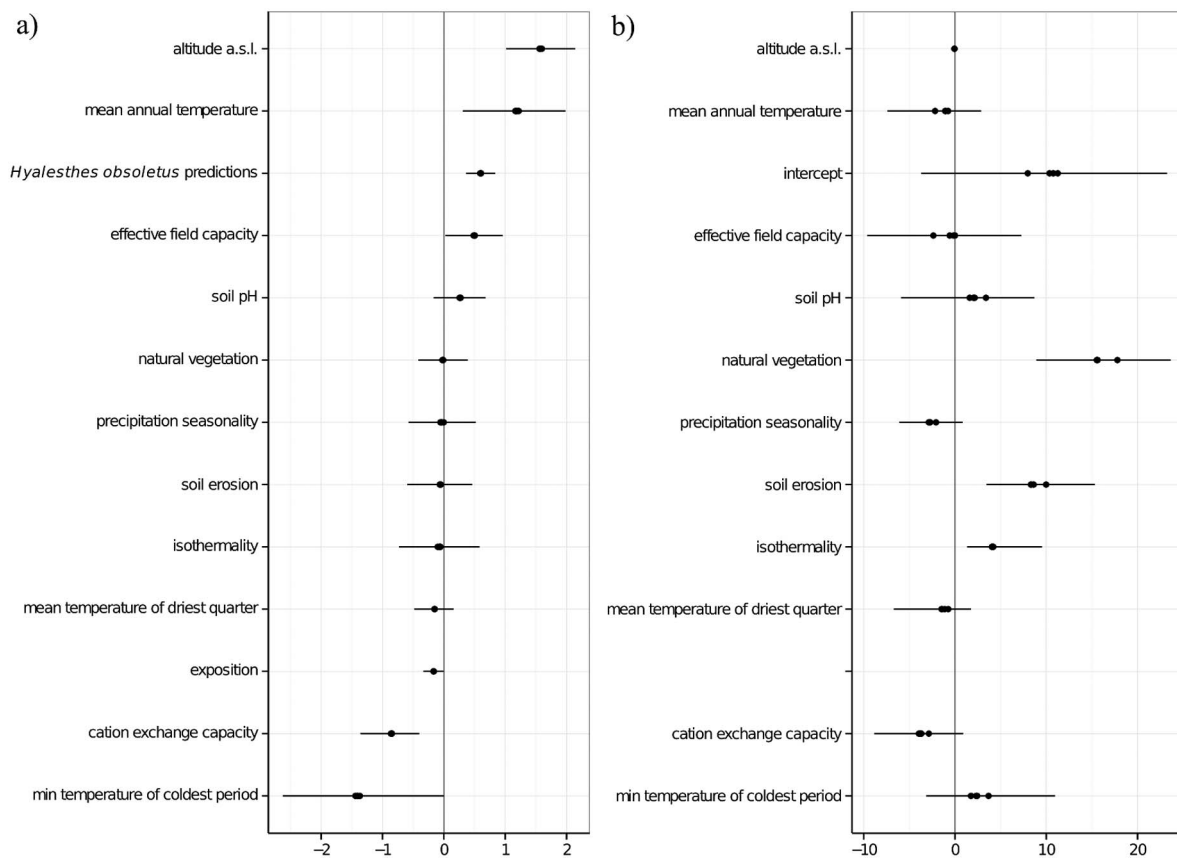


Fig. 3. Marginal posterior distributions of the environmental predictors from (a) the 'bois noir' and (b) the *Hyalesthes obsoletus* model. For each parameter, bullets denote the medians of the four MCMC chains and the line denotes the overall 80% credibility interval.

surroundings of vineyards and soil erosion, while mean temperature of the driest quarter, mean annual temperature, precipitation seasonality, and cation exchange capacity negatively affect *H. obsoletus* presence. In general, the environmental conditions that correlate with *H. obsoletus* presence are notably different from the environmental conditions that correlate with BN prevalence.

#### Predictive maps of disease and vector

We created probabilistic predictions to visualize our results in geographical space. The predictions are based on 1000 model runs, with parameters drawn from the respective posterior distributions, projected onto our study area (Fig. 4).

BN disease predictions were, on average, higher in the eastern part of the study region, with higher uncertainty in areas of high disease

prevalence. *H. obsoletus* occurrence probabilities were high across the entire study area and overall highest in the southern part of the Baden region. Uncertainties of *H. obsoletus* prevalence coincide with occurrence probabilities.

## DISCUSSION

We used a Bayesian modelling framework to identify abiotic and biotic environmental factors that correlate with the presence of 'bois noir' (BN) disease and its vector *H. obsoletus*.

#### Influence of environment on 'bois noir'

BN prevalence was found to correlate with various environmental conditions, predicted presence of the vector, and grapevine cultivar. Of the environmental and biotic variables, mean annual temperature, altitude a.s.l., and predicted



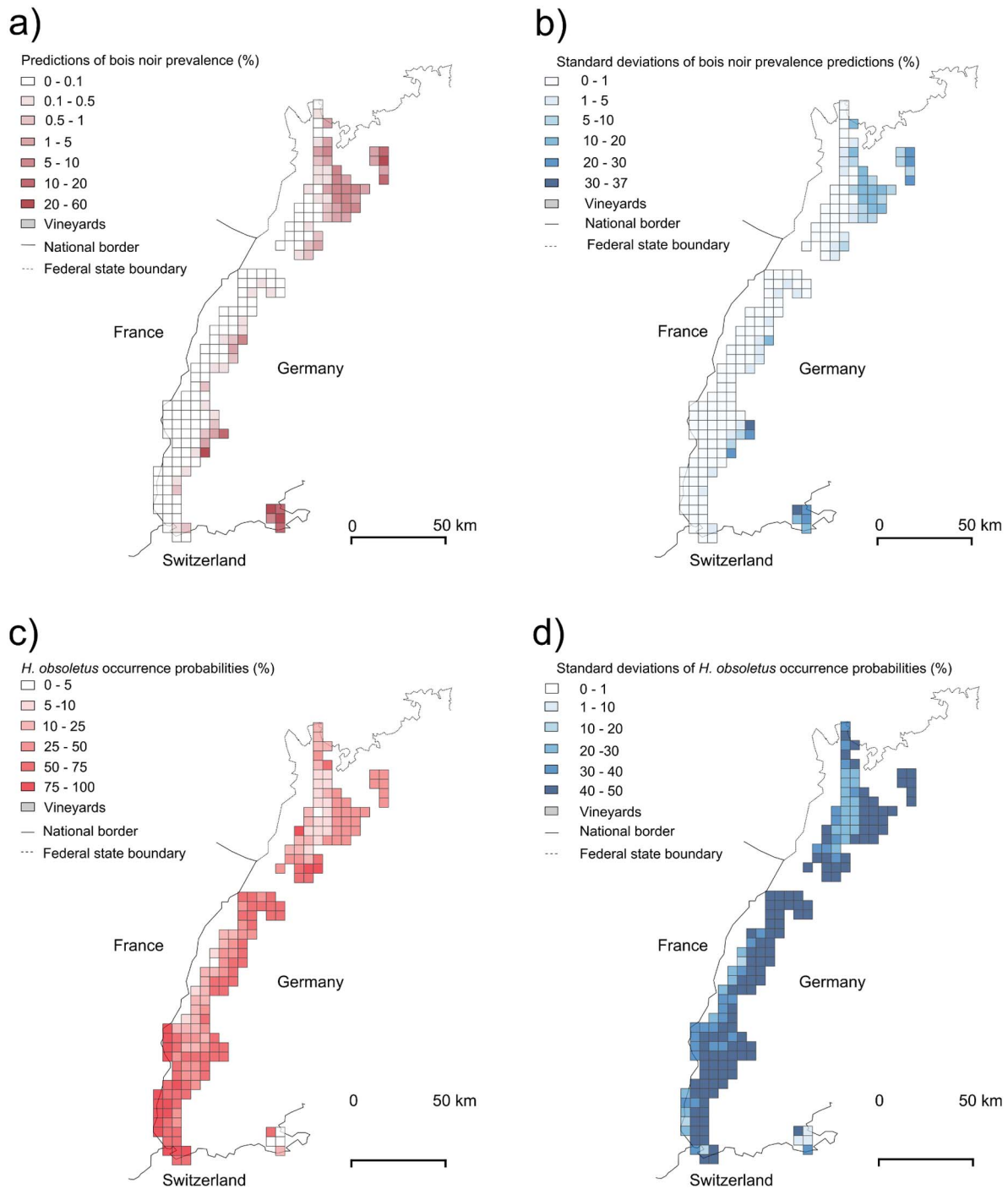


Fig. 4. Posterior predictions of 'bois noir' (BN) disease and *H. obsoletus* in SW Germany: (a) BN average predictions; (b) standard deviations of BN predictions; (c) *H. obsoletus* average predictions; and (d) standard deviations of *H. obsoletus* average predictions.

*H. obsoletus* presence showed the strongest correlation with BN prevalence. Interestingly, while there is clear support for a positive correlation of BN prevalence with its vector, predictions based solely on the vector were found to be insufficient to explain a large share of the BN pattern. This is evidenced by the habitat model for the vector, which identified different environmental variables than the habitat model of the disease, as well as by the fact that various factors other than the vector were identified as important predictors for the disease prevalence. Obviously, the understanding of the distribution of the vector alone does not seem sufficient to understand the distribution of the disease. We discuss this point in more detail below.

#### *Disentangling the influence of grape vs. environment on 'bois noir'*

Our results indicate that some grape varieties are more strongly affected by BN than others. Specifically, we could show that, accounting for all other covariates, predicted disease prevalence is highest in Chardonnay and Riesling. This is in agreement with other authors' reports that Chardonnay and Riesling are highly susceptible to BN (Mohr 2005, Riedle-Bauer and Brader 2013) or to grapevine yellow in general (Weintraub and Jones 2010). However, as grape varieties are typically planted under consideration of environmental conditions, there is an inherent danger that such a pattern could also arise from environmental factors that were not accounted for in any of the previous studies. Experimental verification of these results would therefore be a valuable task for further research.

#### *Comparing patterns of disease and vector*

One of the results of this study is that BN disease prevalence is only weakly correlated with the predictions of *H. obsoletus* presence derived from a previously developed habitat model. The AUC values from this previous model do not suggest that this is due to low discriminatory power. The fact that there is a true mismatch in environmental conditions that correlate with vector and disease is further supported by our results from refitting *H. obsoletus* presence data with exactly the same model that was used for BN prevalence. The results, which are visualized

in Fig. 3a and b, as well as in the area-wide predictions of disease and vector (Fig. 4), show that vector and disease seem to have different environmental preferences that are spatially separated, except in the northeastern part of the study area.

#### *Implications for disease management*

The management of phytoplasmoses in commercial agriculture currently focuses mainly on controlling the vector. In the case of BN, this means the removal of the host plants of *H. obsoletus* nearby vineyards or the use of insecticides. We know that the driving force of phytoplasmoses is the phytoplasma, which can manipulate insects as well as plants as reported for the Aster Yellows phytoplasma strain 'Witches' Broom' (Hogenhout et al. 2008). The direct combat of the pathogen is, however, not a feasible solution. For example, the application of tetracycline antibiotics does not lead to a full eradication of the pathogen and is of high controversy in agricultural food production (Weintraub and Jones 2010).

The positive correlation between vector occurrence probabilities and disease prevalences found in the present study broadly supports the strategy of insect pest management. However, our results (e.g., Fig. 4) also clearly indicate that disease prevalence is affected by factors other than the presence of the insect, which suggests additional management options.

First of all, our results support previous findings that vine cultivars differ in their disease susceptibility. This knowledge can be used when planning new vineyards. It also opens an avenue for plant-breeding by the selection of less susceptible crop varieties.

Secondly, we found that the environment has a substantial impact on BN prevalence, apparently independent of the vector. At the moment, it is unclear to us whether environmental conditions directly affect the disease susceptibility of plants or whether they modify the disease prevalence or the behavior of the vector, potentially via modifying host plant availability. It may well be that a reduction of the host plant density could indeed have adverse effect, because it may lead to a higher rate of infected host plants. There are very few studies on this topic so far. In a recent study, Johannesen et al. (2011) found a preva-

lence of the bacterium in 28% in *H. obsoletus* caught on bindweed compared to 15% in insects originating from stinging nettle. In the present study, we did not consider the host plant, but *H. obsoletus* catches on bindweed occurred only in the northeastern part of the study region (B. Panassiti, *personal observation*), which is a possible explanation for the observed spatial pattern. Additional studies are needed to examine this questions in more detail.

Finally, a further possibility for the observed mismatch, and a potential concern for management, is the presence of other, currently unknown disease vectors, as reported from southeastern Europe (Cvrković et al. 2013). More effort in biomonitoring and transmission trials is needed to identify alternative vectors and adjust insect pest management.

### Conclusions

Our study showed that BN disease incidence is correlated with the main vector *Hyalesthes obsoletus*, altitude a.s.l., and mean annual temperature. Somewhat surprising, however, was the effect of *H. obsoletus* presence, although positive, was relatively weak and seemed to vary across the study region. We suggest that environmental effects, disease dynamics, different host plants, or alternative vectors may be responsible for this pattern. Further studies are needed to shed light upon this question.

Of all the grapevine cultivars, Chardonnay and Riesling showed the highest correlation with BN infections. Although caution should be applied when interpreting this correlation as causal, the pattern is in agreement with previous studies and suggests that disease management is particularly important for those cultivars.

The Bayesian framework applied in this study provides a flexible and scalable tool for inference in situations such as those present in this study. It can be easily expanded to include overdispersion or observation models, and it provides a straightforward way to map the predictive uncertainty of the fitted model across study regions, which is an important consideration for practitioners when applying insect pest management.

It would be interesting to extend the present study to similar existing cases of phytoplasma-associated diseases, such as the grapevine yellow

disease flavescence dorée transmitted by the leafhopper *Scaphoideus titanus*.

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## SUPPLEMENTAL MATERIAL

### SUPPLEMENT

Data and Stan code specifying the statistical model used to analyze prevalences of a phytoplasma disease in grapevines ('bois noir') in the Baden region (southwest Germany) in a Bayesian framework (*Ecological Archives*, <http://dx.doi.org/10.1890/ES14-00439.1.sm>).