Influence of environment and climate on occurrence of the cixiid planthopper *Hyalesthes obsoletus*, the vector of the grapevine disease 'bois noir'

Bernd Panassiti[1], Michael Breuer[1]*, Stacey Marquardt[1] and Robert Biedermann[2]

[1]State Institute of Viticulture and Oenology, Freiburg, Germany: [2]Institute for Environmental Modelling, Straubing, Germany

Abstract

Species distribution models (SDMs), which are well established in many fields of biological research, are still uncommon in the agricultural risk analysis of pest insects. To exemplify the use of SDMs, we investigated the influence of environmental factors on the occurrence of *Hyalesthes obsoletus* Signoret (Hemiptera: Cixiidae). The planthopper is the only known vector of the grapevine yellows disease 'bois noir'. The study was conducted in 145 locations in the Baden region of southwest Germany. The planthopper was surveyed on host plant patches, consisting of stinging nettle and/or bindweeds. We used a stratified modelling framework where (1) species presence–absence data were related to an extensive environmental dataset using logistic regressions; and (2) different types of average models were developed based on an information theoretic method. The results show that the incidence of *H. obsoletus* is associated to above- as well as below-ground environmental factors, particularly to the amount of fine soil and average annual precipitation. This result was consistent across all average models. The relative importance of other environmental variables was dependent upon the average model under consideration and thus may vary according to their intended use, either the explanation of habitat requirements or the prediction and mapping of occurrence risks. The study showed that SDMs offer a quantification of species' habitat requirements and thus, could represent a valuable tool for pest management purposes. By providing examples of current issues of grapevine pests in viticulture, we discuss the use of SDMs in agricultural risk analysis and highlight their advantages and caveats.

Keywords: *Hyalesthes obsoletus*, species distribution model, average model, *Vitis vinifera*, logistic regression, bois noir, planthopper vector, pest management

(Accepted 4 March 2013; First published online 29 April 2013)

Introduction

The cixiid planthopper *Hyalesthes obsoletus* Signoret (Hemiptera: Cixiidae) is a serious insect pest found in viticulture (e.g., Sforza *et al.*, 1998; Weber & Maixner, 1998; Palermo *et al.*, 2004; Sharon *et al.*, 2005), because the palaearctic planthopper is till now the only known vector of the grapevine yellow disease, bois noir (BN, Maixner, 2010). This yellow

---

*Author for correspondence
Phone: +49 - 761 - 4016579
Fax: +49 - 761 - 4016570
E-mail: Michael.Breuer@wbi.bwl.de

disease is associated with phytoplasma of the stolbur (16SrXII-A) group (Daire *et al.*, 1992; Maixner *et al.*, 1994). Bois noir is widespread in Europe and increasing in many regions (Lessio *et al.*, 2007), causing significant yield losses in viticulture (e.g., Caudwell, 1961; Maixner *et al.*, 2006; Maixner, 2010).

H. obsoletus is known to feed on a wide range of herbaceous plants; however, the complete life cycle depends upon a few host plants (Bressan *et al.*, 2007; Lessio *et al.*, 2007). In Germany, *H. obsoletus* nymphs mainly develop on roots of stinging nettle (*Urtica dioica* L.), field bindweed (*Convolvulus arvensis*) and hedge bindweed (*Calystegia sepium*) (Langer & Maixner, 2004). These host plants also function as inoculum source of stolbur phytoplasma (Maixner, 2010). Owing to the polyphagous feeding behaviour of *H. obsoletus* adults, the pathogen is accidentally transmitted to the grapevine [*Vitis vinifera* L. (Vitaceae)] which is considered a dead-end host in BN epidemiology (Lee *et al.*, 1998).

As an invasive species, *H. obsoletus* was found only in micro-climatic favourable habitats and was considered as a rare species in Germany (Sergel, 1986). Within the last decade, field bindweed (the traditional host plant) was continuously replaced by stinging nettle, promoting a range expansion of the planthopper (Langer & Maixner, 2004). A recent monitoring network of the State Institute of Viticulture and Oenology, Freiburg, Germany, showed that *H. obsoletus* is present in almost all wine-growing districts of the Baden region (Breuer *et al.*, 2008).

Despite considerable foci on BN epidemiology, host plant association and geographic range expansion of *H. obsoletus* (e.g., Sforza *et al.*, 1998; Johannesen *et al.*, 2008), there is limited detailed ecological information about the environmental drivers of the planthopper's population dynamics (Boudon-Padieu & Maixner, 2007). The xerothermic planthopper is repeatedly reported to prefer sparse vegetation on open soil (Langer *et al.*, 2003; Maixner, 2007). However, in order to formulate effective guidelines for action to advisers of vine growers, quantitative information is required. For example, it is not clear which proportion of vegetation cover in vineyards is sufficient to reduce the settlement of the planthopper and therefore, infection pressure (Mori *et al.*, 2011). In addition, several lines of evidence suggest that other environmental factors, specifically those associated with nymphal development, are likely to play an important role in the distribution of the disease vector (Maixner, 2006; Lessio *et al.*, 2007).

Species distribution models (SDMs), also known as habitat suitability models, can be used to identify and quantify species-environment relationships (Guisan & Zimmermann, 2000). In ecology, numerous studies have successfully applied SDMs, e.g., to support conservation planning and wildlife management (for a review see Franklin, 2009). However, SDMs have received little attention in agricultural research. Only a few studies have explicitly studied the underlying mechanisms of biogeographical distribution of pest insects or pathogens using SDMs (Meentemeyer *et al.*, 2004; Beanland *et al.*, 2006; Hamada *et al.*, 2008). Furthermore, most species distribution studies in agriculture rely on a very limited set of environmental predictors, in the case of the above mentioned studies either climate variables or habitat types, potentially obscuring species inherent distribution patterns.

Using presence–absence data of *H. obsoletus* across the Baden region (Germany) and an extensive dataset of potential environmental predictors compiled from multiple sources, we conducted a multiple-scale modelling approach based on logistic regression. From a modelling perspective, leaf- and planthoppers represent an excellent group for habitat suitability models since they are very sensitive to minor habitat changes (Morris, 1981*a*, *b*; Biedermann *et al.*, 2005). Therefore, in this study, we examined whether SDMs can be used to identify and quantify the habitat requirements of the disease vector. Assuming that *H. obsoletus* is a thermophile species and the nymphs develop below ground (Alma, 2002; Johannesen *et al.*, 2008), we expect that the distribution of *H. obsoletus* can be associated with climate and soil-related variables being the main driving forces. Finally, the application of SDMs in pest science as a means of improving current management practices is discussed.

Material and methods

Study area

The study was conducted in the region of Baden, located in south-western Germany. The region extends between the river Neckar in the north, the border of Switzerland in the south and is boarded by the Black Forest and Vosges mountain ranges. The Black Forest acts as a wind shield against strong easterlies, while the French Vosges mountains prevent heavy rainfall. A strong temperature gradient extends from the Black Forest to the Rhine River Plains. The mean annual temperature in the Baden region is approximately 10°C. The average annual rainfall ranges from ∼680 mm in Kaiserstuhl up to ∼950 mm in the area of Lake Constance. Fine loamy soils and deep, limy loess sediments are widely spread across the study area, reaching depths of up to 7 m (Becker & Kannenberg, 1979). Muschelkalk (Tauberfranken), volcanic rocks (Kaiserstuhl) and granite (Ortenau) are the most common bedrocks found in the region (Becker & Kannenberg, 1979).

Species occurrence data

The presence of *H. obsoletus* was surveyed at 145 locations of its host plants (stinging nettle and/or bindweed) within the Baden region, between early June and late August 2011 (fig. 1). As planthopper flight phenology varies between years and host plants (Weintraub & Jones, 2010), yellow sticky traps were placed at host plants in geographically distinct locations to constantly verify flight activity and ensure optimal sampling conditions. In addition, we used the viticulture prediction tool 'Vitimeteo' (www.vitimeteo.de), which estimates the flight period of *H. obsoletus* based on temperature sums (Maixner & Langer, 2006). Insect sampling was performed using a sweep net (diameter 30 cm) or a suction sampler (Stewart, 2002). In each of the 145 locations the selected host plant patch was surveyed only once during the sampling period. The sampling effort was proportional to patch size. Per square meter, a stinging nettle patch was swept five times, e.g., a patch of 2 m^2 was swept ten times. In the presence of bindweeds, suction sampling was applied for 3 min m^{-2} resulting in one sample covering the entire patch. The sampling procedure was repeated after a time interval of approximately 5 min. Collected insects were transported to the laboratory, where adults of *H. obsoletus* were identified according to the identification keys of Biedermann & Niedringhaus (2004).
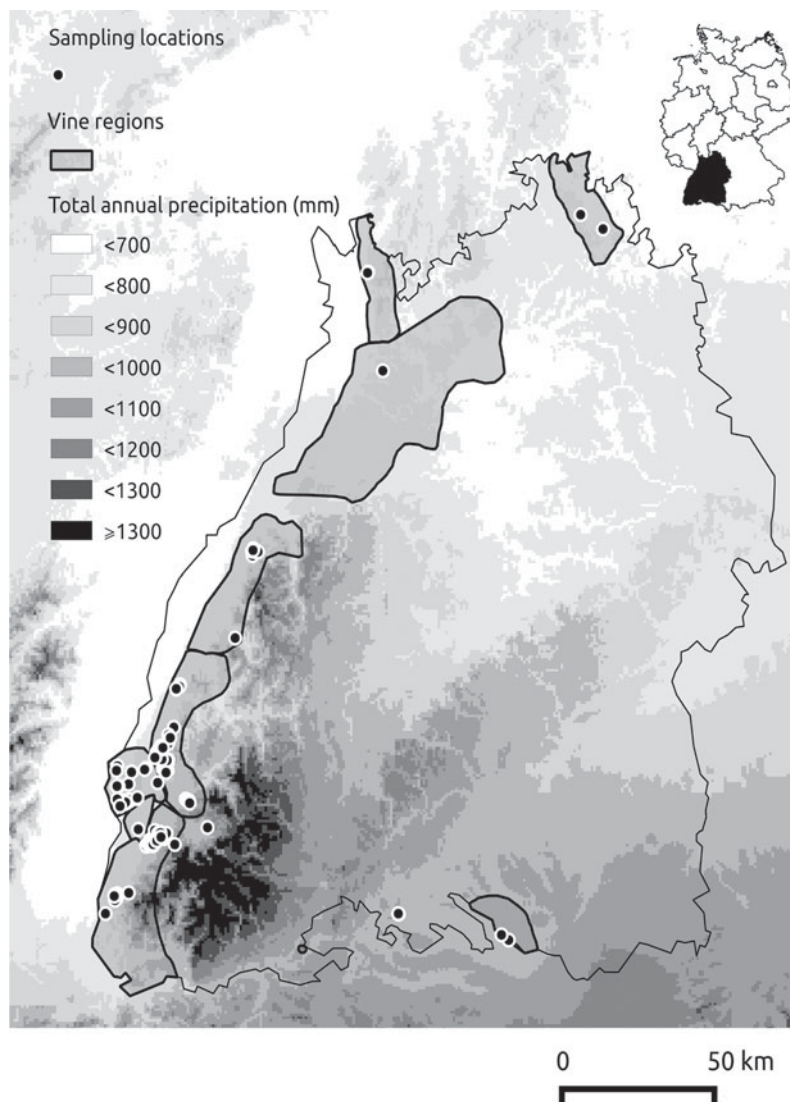
Fig. 1. 145 locations where *H. obsoletus* presence/ absence was surveyed as dots on a chart showing the total annual precipitation in the Baden region. Interpolated average annual precipitation was derived from the WordClim database (original spatial resolution 30 arc seconds).

Environmental predictors

There is little quantitative knowledge about the habitat preferences of cixiid planthopper *H. obsoletus*. Therefore, a large set of environmental parameters (table 1) was chosen as candidate predictor variables, based on preliminary studies and general ecological knowledge. Since most species are influenced by environmental factors on different hierarchical scales (Coudun *et al.*, 2006; Meyer & Thuiller, 2006), predictors operating at different spatial scales were included in this study.

Soil sample analysis

At each location a composite soil sample was obtained by collecting a combination of three sub-samples from the upper soil horizon (10 cm), using the grab sampling method.

Soil texture was determined using the 'Finger test' (Schlichting *et al.*, 1995; Sponagel, 2005). One hundred grams of moist soil was weighed and placed in the oven for a minimum of 12 h at 105°C (VDLUFA, 1991). Differences between moist and dried soils were used to estimate the gravimetric moisture content (gmc) according to Black (1965). Oven-dried soils were sieved (pore size 2 mm) to assess the amount of fine soil. The soil pH (KCl) was measured in a suspension of salt solution of neutral reaction (VDLUFA, 1991). The percentages of total nitrogen and carbon were determined with the 'elementar analyser vario MAX CN' with 850–1150°C following the Dumas combustion methodology (VDLUFA, 1991). In this study, the C:N ratio was calculated using the total carbon instead of C_{org}. In addition, three undisturbed soil samples were collected in 100 ml cylinders at all locations. The volume of the solid state body including water (ssw) was

Table 1. Environmental parameter recorded for all sampling locations.

Terrain parameter
–   Altitude (m.a.s.l.), slope (%), exposition (°)
–   Embankment, wall (each 2 levels): yes/no

Soil factors and geology
●   Laboratory
–   pH (CaCl$_2$), gravimetric water content (gmc,%), pore volume (ml), soil type, fine soil (%), total nitrogen (N,%),
      carbon (C,%) and C:N ratio
●   Digital maps
–   Soil region: crystalline basement, loess landscape, wetlands and other
–   Main soil: silicate rock, hybrid, carbonate rock, other and floodplain
–   Soil morphology: highlands, loamy hills, slopes and wetlands
–   Soil type
–   Subsoil: debris, debris and rock, gravel, rock and unconsolidated rock
–   Bedrock: carbonatic, loam and wetlands
–   Effective field capacity (EFC), erosion (each 4 levels): highly variable, low, medium and high
–   Field capacity (FC), cation exchange capacity (CEC) (each 2 levels): low, high
–   Soil organic matter: humus poor, humus and humus rich

Meteorological data (°C, mm)
–   19 variables for both (a) climate derived from WorldClim database (Hijmans *et al.*, 2005); and (b) weather derived
      from data obtained from www.meteoblue.com
 1 = Annual mean temperature
 2 = Mean diurnal range (Mean of monthly (max temp − min temp))
 3 = Isothermality (BIO2/BIO7) (× 100)
 4 = Temperature seasonality (Standard Deviation × 100)
 5 = Max temperature of warmest month
 6 = Min temperature of coldest month
 7 = Temperature annual range (BIO5–BIO6)
 8 = Mean temperature of wettest quarter
 9 = Mean temperature of driest quarter
10 = Mean temperature of warmest quarter
11 = Mean temperature of coldest quarter
12 = Annual precipitation
13 = Precipitation of wettest month
14 = Precipitation of driest month
15 = Precipitation seasonality (coefficient of variation)
16 = Precipitation of wettest quarter
17 = Precipitation of driest quarter
18 = Precipitation of warmest quarter
19 = Precipitation of coldest quarter
–   Variables coded as follows, e.g. annual mean temperature: (a) climate: bio1_worldclim; (b) weather: bio1
–   Solar radiation (W m^{-2})

Vegetation structure
–   Shade (3 levels): no, marginally, half/totally
–   Name of host plant(s): *U. dioica* (a) or bindweeds (b)
(a) Patch (m^2), patch height (cm), cover (%), density (loose, dense)
(b) Patch (m^2), cover (%)
–   Name and distance (m) of next host plant

Landscape context
–   Proportion (%) and binary classification of habitat types within radii of 25 and 50m
–   Habitat types: vineyard area, field, field path, road, grassland, fallow land, forest, housing, shrub land and water.

Viticulture related parameter
–   Age (years) at 4 levels: ≤10, ≤20, ≤30 and >30
–   Cultivars: proportion (%) and binary classification within a radius of r = 50 m
–   Standard traction vs. cross terracing

---

determined using a pycnometer (Danielson & Sutherland, 1986).

Finally, total pore volume (p) was calculated using the following equation:

$$p = az − (ssw − gmc − cap),$$

where

 az = actual cylinder volume (ml)

ssw = solid state body including water (ml)
gmc = gravimetric moisture content (%)
cap = volume of standardized cylinder cap (ml)

Further edaphic parameters were derived from digital soil maps of Baden-Württemberg (scale 1:200,000) provided by the Federal State Office for Geology Resources and Mining, Freiburg Regional Board (LGRB) (table 1).

Climate and weather variables

In order to obtain biologically meaningful variables that are closely associated with a species' physiological constraints, bioclimatic variables were used to infer the effect of both climate and weather on distribution of *H. obsoletus*. Interpolated climate data with a spatial resolution of 30 arc seconds were derived from the WorldClim dataset (Hijmans *et al.*, 2005, http://www.worldclim.org, downloaded 8 June 2012). This dataset represents weather conditions between 1950 and 2000. Weather variables including air temperature (2 m a.g.°C) and precipitation (mm) were provided by Meteoblue (http://www.meteoblue.com) as gridded data (resolution ∼3 km) for the year 2010. Data points were interpolated using inverse-distance interpolation. In the case of temperature, simple lapse-rate adjustment was performed additionally to account for the effect of elevation in orographically heterogeneous terrain (Dodson & Marks, 1997). Bioclimatic variables were derived from the interpolated climatic data using the 'biovars' function from the R package 'dismo' (Hijmans *et al.*, 2011).

Vegetation structure, habitat types and grapevine varieties

Information about vegetation structure included the names of the host plants, their patch size and cover, and additionally in the case of stinging nettle patch height and the compactness of the stand (loose, dense). A patch was defined as the area including all host plants with a minimum distance of 3 m to the next patch. The distance to the next host plant patch represented an indicator of patch isolation. Moreover, we recorded the potential shade intensity around midday. At each location a set of landscape context parameters were quantified using high-resolution orthophotos. Buffers with radii of 25 m and 50 m were generated within GIS to gauge the proportions of different habitat types surrounding each location (table 1).

In addition, information about the grapevine varieties and their plant years were extracted from the viticulture registry maintained by the State Institute for Viticulture and Oenology on 23rd February 2012. Quantity and expansion of different cultivars as well as the average plant age within a buffer of $r = 50$ m were calculated based on digital information of land parcels. Only grapevine varieties with at least five observations in the data set were considered for subsequent analysis. The orthophotos and the land parcel GIS layer were provided by the State Office of Land Consolidation and Land Development (LGL).

Statistical analysis

Model development

General linear modelling (GLM, McCullagh & Nelder, 1989) was used to develop explanatory species distribution models (SDMs). The patch occupancy of *H. obsoletus* was subjected to logistic GLM's by specifying a binomial error distribution and a logit link function (Hosmer & Lemeshow, 2000).

Model development has previously been described in detail by Strauss & Biedermann (2006). In brief, univariate logistic regression models were first conducted for each environmental variable using all survey data. In order to account for unimodal relationships between species occurrence and environmental predictors, additional univariate

models, including a quadratic term, were constructed in the case of ordinal or metric variables (Austin, 2002). To avoid possible spurious relationships, only univariate models were retained for subsequent analysis if they met the following criteria: (i) a R_N^2 (Nagelkerke, 1991) ≥0.05 (Strauss & Biedermann, 2005); and (ii) being significant at the 0.05 level.

Secondly, multivariate logistic regression models were developed for all possible combinations of candidate predictor variables. We constructed three model types (hereafter referred to as MC, MCW and MCU, respectively). The MC model type included environmental variables and climate data (from the WorldClim dataset). Models with a combination of environmental variables, climate data and weather variables as predictors were termed MCW. The MCU model type included environmental variables, climate data and additionally the height of the stinging nettle patch ('patch_height'). To balance model overfitting and parsimony (Burnham & Anderson, 2002; Franklin, 2009), the maximum number of combined predictors were restricted. According to the size of our data set, this number was set to four (Guisan & Zimmermann, 2000). In order to address the issue of multicollinearity (Neter *et al.*, 1989; Graham, 2003), correlated variables (Spearman's $r > 0.7$; Fielding & Haworth, 1995) were not included in the same multivariate model. Significant multivariate models ($P ≤ 0.05$) were considered for further analysis if they shielded (i) a R_N^2 (Nagelkerke, 1991)≥0.6 and (ii) an 'area under the curve' (AUC) of the receiver-operating curve (ROC)≥0.9. The bioclimatic variable 12 (average annual precipitation, mm) and 13 (precipitation of wettest month, mm) were closely related. Thus, only models with the former variable were considered due to the complementary nature of both. Likelihood ratio tests were calculated for each multivariate model and its corresponding nested models to exclude the possibility of significant deviance reductions (Whittaker, 1984; Ferrier *et al.*, 2002).

Each multivariate model was subjected to an internal validation by applying a bootstrap procedure with 1000 iterations (Verbyla & Litvaitis, 1989). This re-sampling technique ensures unbiased estimates of model performance (Harrell, 2001). Bootstrapped multivariate models were excluded if they did not exhibit an R_N^2 (Nagelkerke, 1991) ≥0.5 and an AUC≥0.85 for at least 95% of the bootstraps.

Spatial autocorrelation (SAC) may lead to biased variable selection or coefficient estimation (Franklin, 2009). The global Moran's I coefficients were computed to examine spatial dependency of model residuals (Dormann *et al.*, 2007). Since we could not detect any spatial pattern in the residuals, there was no further need to take measures to address autocorrelation aspects (table 2).

The remaining models were subjected to model averaging (Burnham & Anderson, 2002; Strauss & Biedermann, 2006). Model averaging calculates averaged coefficients based on the Akaike information criterion (AIC) and Akaike weights. In this study, the second order Akaike information criterion (AIC_c) was applied, as recommended with small datasets (Buckland *et al.*, 1997). In applying the AIC_c, a set of candidate models and their predictors are evaluated to obtain an averaged model that best reflects species habitat requirements. R v. 2.13.1 software (R Development Core Team, 2011, http://www.r-project.org) was used as a simulation platform for statistical analyses.

Table 2. Model performances and Global Moran's I statistics of multiple models which were used to construct average models. All performance measures represent arithmetic means as corrected by bootstrapping. ʼsq indicates a second order term was included to model a unimodal relationship. Model type refers to models that include besides other environmental parameters: (1) climate (MC), (2) climate and weather (MCW) and (3) climate and stinging nettle patch height (MCU). Abbr.: N = number of observations; R^2_N = coefficient of model calibration; AUC (area under the receiver operating characteristic curve) = threshold independent measure for model discrimination; p_{fair} = threshold where sensitivity equals specificity; κ = Cohen's kappa; sensitivity = proportion of correctly predicted presences; specificity = proportion of correctly predicted absences; CCR = correct classification rate; Moran's I = global test to examine spatial structures in model residuals.

Model type	ID	Model parameters	N	Threshold independent		Threshold dependent: p_{fair}					Moran's I
				R^2_N	AUC	p_{fair}	κ	Sensitivity	Specificity	CCR	
MC	11765	fine_soil.sq, subsoil, bio12_worldclim.sq and shade	145	0.66	0.935	0.29	0.68	0.86	0.86	0.86	−0.00707
	11759	fine_soil.sq, subsoil, bio12_worldclim.sq and grape.40.sq	145	0.66	0.923	0.26	0.66	0.85	0.85	0.85	−0.00714
	13465	fine_soil.sq, bio12_worldclim.sq, bio15_worldclim and shade	145	0.65	0.931	0.28	0.66	0.85	0.85	0.85	−0.00705
	11762	fine_soil.sq, subsoil, bio12_worldclim.sq and solar_radiation	145	0.65	0.929	0.29	0.66	0.85	0.85	0.85	−0.00702
MCW	13575	fine_soil.sq, bio12_worldclim.sq and bio11.sq, shade	145	0.68	0.936	0.28	0.67	0.86	0.86	0.86	−0.00710
	13106	fine_soil.sq, bio4.sq, bio12_worldclim.sq and bio11.sq	145	0.64	0.926	0.30	0.63	0.84	0.84	0.84	−0.00730
	13540	fine_soil.sq, bio12_worldclim.sq, solar_radiation and bio11.sq	145	0.64	0.927	0.29	0.62	0.84	0.84	0.84	−0.00739
MCU	13529	fine_soil.sq, bio12_worldclim.sq, main_soil and patch_height.sq	138	0.69	0.941	0.29	0.68	0.86	0.86	0.86	−0.00780
	11770	fine_soil.sq, subsoil, bio12_worldclim.sq and patch_height.sq	138	0.69	0.939	0.27	0.67	0.86	0.86	0.86	−0.00738
	12460	fine_soil.sq, soil_region, bio12_worldclim.sq and patch_height.sq	138	0.68	0.937	0.27	0.67	0.86	0.86	0.86	−0.00783
	11340	fine_soil.sq, soil_type, bio12_worldclim.sq and patch_height.sq	138	0.67	0.936	0.28	0.67	0.86	0.86	0.86	−0.00764
	13510	fine_soil.sq, bio12_worldclim.sq, erosion and patch_height.sq	138	0.67	0.934	0.29	0.67	0.86	0.86	0.86	−0.00776
	13470	fine_soil.sq, bio12_worldclim.sq, bio15_worldclim and patch_height.sq	138	0.66	0.930	0.27	0.65	0.85	0.85	0.85	−0.00749
	13427	fine_soil.sq, bio12_worldclim.sq, CEC and patch_height.sq	138	0.65	0.927	0.28	0.64	0.84	0.84	0.84	−0.00752

Model performance

The degree of model performance was evaluated by using a set of criteria. Nagelkerke's (1991) R^2_N was used as an indicator of model calibration and refinement. Values between 0 and 1 describe the variability explained by the model predictors. To access the rate of prediction error (model discrimination) threshold-dependent measures such as sensitivity (correctly predicted species presences), specificity (correctly predicted species absences) and Cohen's kappa (κ) were calculated (Cohen, 1960; Manel *et al.*, 1999). The threshold was chosen to account for sensitivity and specificity in equal measure (p_{fair}). In addition, the AUC was assessed as a threshold-independent metric of discriminative power (Hanley & McNeil, 1982; Fielding & Bell, 1997).

Results

Prevalence and flight activity

The prevalence of *H. obsoletus* in the studied locations was 28%. The proportion of absences vs. presences was not significantly different between locations with only bindweeds and locations with stinging nettle alone or in combination with bindweeds (prevalence (%): 29:32:21; Fisher's exact test, $P > 0.05$). Flight activity started in the beginning of June and ended in mid August.

Model performance

In total, 51,544 logistic regression models were built. These models consisted of 242 univariate (sigmoid as well as unimodal) and 51,302 multivariate regressions. The occurrence of *H. obsoletus* was explained best by multivariate models containing four environmental parameters. For example, comparison of model *id* = 11,765 with any model with less variables showed that the full model performed best in terms of model calibration and discrimination (table 3). Each time, the LR-test confirmed a significant deviance reduction by using the full model. Satisfying the minimum threshold criteria ($R^2_N ≥ 0.6$ and AUC ≥ 0.9), four multivariate logistic models were found for the model type MC (environmental and climate data) (table 2). The inclusion of weather data from the year before the survey (model type MCW) increases model calibration ($R^2_N = 0.68$). The highest values of model performance (calibration as well as discrimination) were achieved by including the height of stinging nettle patch as an additional parameter (model type MCU, $R^2_N = 0.69$, AUC = 0.941). With regard to the discriminatory abilities using threshold-dependent criteria, all selected multivariate logistic regressions exhibited correct classification rates ranging between 84 and 86% (table 2). Cohen's κ values ranged between 0.62 and 0.68 (table 2).

Relative importance of environmental parameters

Three average models were developed for the following model type combinations: (1) MC; (2) MC + MCW; and (3) MC + MCU. Regardless of different ecological assumptions, all average models demonstrated that the potential habitat of *H. obsoletus* is largely characterized by the amount of both fine soil and average annual precipitation. The percentile weights of both variables remained consistent across all average models (tables 4–6). These two variables are unimodal related to the planthoppers occurrence, whereas occurrence

Table 3. Comparison of a four parameter model with all corresponding nested correspondents. All performance measures represent arithmetic means as corrected by bootstrapping. '.sq' indicates a second order term was included to model a unimodal relationship. Abbr. see table 2.

ID	Model parameters	N	Threshold independent		Threshold dependent: P_{fair}					LR-test	
			R^2_N	AUC	P_{fair}	κ	Sensitivity	Specificity	CCR	Deviance	P
univariate_164	fine_soil.sq	145	0.25	0.759	0.31	0.38	0.72	0.71	0.71	58	<0.001
34	fine_soil.sq_subsoil	145	0.41	0.828	0.27	0.48	0.77	0.77	0.77	41	<0.001
113	fine_soil.sq_subsoil_bio12_worldclim.sq	145	0.60	0.909	0.27	0.62	0.84	0.84	0.84	10	<0.01
11765	fine_soil.sq, subsoil, bio12_worldclim.sq and shade	145	0.66	0.935	0.29	0.68	0.86	0.86	0.86	–	–

Table 4. Model averaging using four multiple models from the MC model type of table 2. Models were ranked in descending order according to their AIC$_c$. For each model weights (w_i) were calculated based on AIC$_c$ differences (Δ) and were used to derive individual coefficients weights (β×w_i) in the next step. Finally, averaged coefficients (averaged β) and variable weights (relative and percentile) were determined.

ID	1 13465	2 11762	3 11765	4 11759			
AIC$_c$	110	111	113	115			
Δ	0	1.64	3.25	5.27	Averaged β	Relative weight	% Weight
w_i	0.585	0.258	0.115	0.042			
fine_soil β	0.28	0.26	0.24	0.24	0.267	1	**25**
fine_soil β+w_i	0.162	0.067	0.028	0.010			
fine_soil.sq β	−0.002	−0.002	−0.002	−0.002	−0.002		
fine_soil.sq β+w_i	−0.001	−0.001	−2.48E-04	−8.64E-05			
bio12_worldclim β	−0.1	0.25	0.27	0.19	0.045	1	**25**
bio12_worldclim β+w_i	−0.059	0.065	0.031	0.008			
bio12_worldclim.sq β	4.66E-05	−1.89E-04	−1.94E-04	−1.40E-04	−4.97E-05		
bio12_worldclim.sq β+w_i	2.73E-05	−4.87E-05	−2.24E-05	−5.87E-06			
Shade							
1 β	−1.05	0	−1.04	0	−0.734	0.701	**18**
1 β+w_i	−0.614	0	−0.120	0			
2 β	−2.77	0	−2.32	0	−1.89		
2 β+w_i	−1.62	0	−0.268	0			
bio15_worldclim β	−0.468	0	0	0	−0.274	0.585	**15**
bio15_worldclim β+w_i	−0.274	0	0	0			
Subsoil							
debris_and_rock β	0	16.4	15.2	13.7	6.55	0.415	**10**
debris_and_rock β+w_i	0	4.22	1.75	0.574			
gravel β	0	0.45	−1.30	0.5	−0.013		
gravel β+w_i	0	0.115	−0.150	0.021			
rock β	0	−1.23	−2.22	−1.14	−0.621		
rock β+w_i	0	−0.317	−0.256	−0.048			
unconsolidated_rock β	0	−1.75	−2.64	−1.19	−0.805		
unconsolidated_rock β+w_i	0	−0.451	−0.305	−0.050			
solar_radiation β	0	−3.43E−05	0	0	−8.83E-06	0.258	**6**
solar_radiation β+w_i	0	−8.83E-06	0	0			
grape.40 β	0	0	0	0.002	9.81E-05	0.042	**1**
grape.40 β+w_i	0	0	0	9.81E-05			
grape.40.sq β	0	0	0	−3.95E-07	−1.66E-08		
grape.40.sq β+w_i	0	0	0	−1.66E-08			
intercept β	55	−44	−95	−67	7.25		
intercept β+w_i	32.3	−11.3	−10.9	−2.81			

probabilities are highest with an intermediate level (∼60%) of fine soil from the upper soil layer and a low amount of average annual precipitation (fig. 2). Furthermore, fig. 2 depicts that *H. obsoletus* preferred marginal or no-shaded host plant patches. The occurrence of the planthopper is also related to soil geology, particularly to the type of subsoil (fig. 2). Shade and the subsoil type together account for 28 and 27% of the total percentile weight (tables 4 and 6). In addition, on including the weather data, the effect of these two variables on species occurrence is replaced by bio11 (mean temperature of the coldest quarter) (table 5). As shown by the coefficients of the average model in table 6, occurrence probabilities of *H. obsoletus* are highest in patches of *U. dioica* with low host plant height. In contrast to edaphic or climate- and weather-related factors, terrain variables as well as the landscape context have no or little impact on species occurrence.

Table 5 Model averaging using multiple models from the "worldclim" model type (MC) combined with models from the "worldclim + weather" model type (MCW) of table 2. Variables with a percental weight lower than one are not shown.

Model parameters	Averaged β	Relative weight	% Weight
fine_soil β	0.278	1	25
fine_soil β+w_i			
fine_soil.sq β	−0.002		
fine_soil.sq β+w_i			
bio12_worldclim β	0.180	1	**25**
bio12_worldclim β+w_i			
bio12_worldclim.sq β	−1.37E-04		
bio12_worldclim.sq β+w_i			
bio11 β	−1.32	0.872	**22**
bio11 β+w_i			
bio11.sq β	1.29		
bio11.sq β+w_i			
Shade			
1 β	−0.536	0.820	**21**
1 β+w_i			
2 β	−2.27		
2 β+w_i			
solar_radiation_β	−3.87E-06	0.105	**2.6**
solar_radiation_β+w_i			
bio15_worldclim β	−0.035	0.075	**1.9**
bio15_worldclim β+w_i			
bio4_β	0.243	0.069	**1.7**
bio4_β+w_i			
bio4.sq β	−1.70E-04		
bio4.sq β+w_i			
Subsoil			
debris_and_rock β	0.838	0.053	**1.3**
debris_and_rock β+w_i			
gravel_β	−0.002		
gravel_β+w_i			
rock β	−0.079		
rock β+w_i			
unconsolidated_rock β	−0.103		
unconsolidated_rock β+w_i			
intercept β	−145		
intercept β+w_i			

Table 6. Model averaging using multiple models from the "worldclim" model type (MC) combined with models from the "worldclim + stinging nettle patch height" – model type (MCU) of table 2. Variables with a percental weight lower than one are not shown.

Model parameters	Averaged β	Relative weight	% Weight
fine_soil β	0.266	1	**25**
fine_soil β+w_i			
fine_soil.sq β	−0.002		
fine_soil.sq β+w_i			
bio12_worldclim β	0.021	1	**25**
bio12_worldclim β+w_i			
bio12_worldclim.sq β	−3.68E-05		
bio12_worldclim.sq β+w_i			
Shade			
1 β	−0.812	0.778	**19**
1 β+w_i			
2 β	−2.27		
2 β+w_i			
bio15_worldclim β	−0.342	0.620	**15**
bio15_worldclim β+w_i			
Subsoil			
debris_and_rock β	5.81	0.321	**8**
debris_and_rock β+w_i			
gravel_β	−0.651		
gravel_β+w_i			
rock β	−0.805		
rock β+w_i			
unconsolidated_rock β	−1.21		
unconsolidated_rock β+w_i			
patch_height β	−0.106	0.155	**4**
patch_height β+w_i			
patch_height.sq β	−0.421		
patch_height.sq β+w_i			
solar_radiation_β	−1.96E-06	0.07	**1.7**
solar_radiation_β+w_i			
intercept β	12		
intercept β+w_i			

Discussion

Multivariate effects of environmental parameters on distribution of H. obsoletus

We were able to build species distribution models (SDMs) including a variety of environmental predictors based on ecological expertise and previous literature studies. Furthermore, three different average models based on multivariate logistic regressions provided multiple lines of evidence identifying and quantifying the habitat preferences of *H. obsoletus*. In agreement with different habitats associated with different life stages of the soil-borne planthopper, our results indicate that (1) *H. obsoletus* occurrence is best characterized by a combination of multiple environmental parameters; and (2) the influence of the main environmental drivers appears to be twofold: above as well as below ground.

Soil conditions are reported to significantly influence leafhopper assemblages (Sanderson *et al.*, 1995; Strauss & Biedermann, 2006). The influence of soil texture on nymphal

development of *H. obsoletus* was already suggested by different authors (Maixner & Langer, 2006; Lessio *et al.*, 2007; Cargnus *et al.*, 2012). With respect to *H. obsoletus*, the modelling results suggest that soil properties related to the pore matrix influence occurrence probabilities. Our analysis identified the amount of fine soil in the upper 10 cm of the soil and the subsoil as highly influential variables, both characterizing the soil pore system. In contrast to argillaceous soils with a dense pore matrix and low pore volume, soils with a coarse pore matrix and low water retention capacity seem to be preferred by *H. obsoletus*.

The dynamics of insect populations are highly influenced by climate and weather variables (Porter *et al.*, 1991; Cammell & Knight, 1992; Cannon, 1998; Huffaker & Gutierrez, 1999; Sforza *et al.*, 1999). Yet, few studies have evaluated the potential effect of temperature and precipitation on Auchenorrhyncha populations (Biedermann *et al.*, 2005). Recent studies including Diptera species revealed that the effect of rainfall and humidity, respectively, is often controversial and species specific (Juliano *et al.*, 2002; Duyck *et al.*, 2006). Our study shows a strong negative relationship between average annual rainfall and occurrence of *H. obsoletus* at the spatial extent of the Baden region. Interestingly,

Subsoil

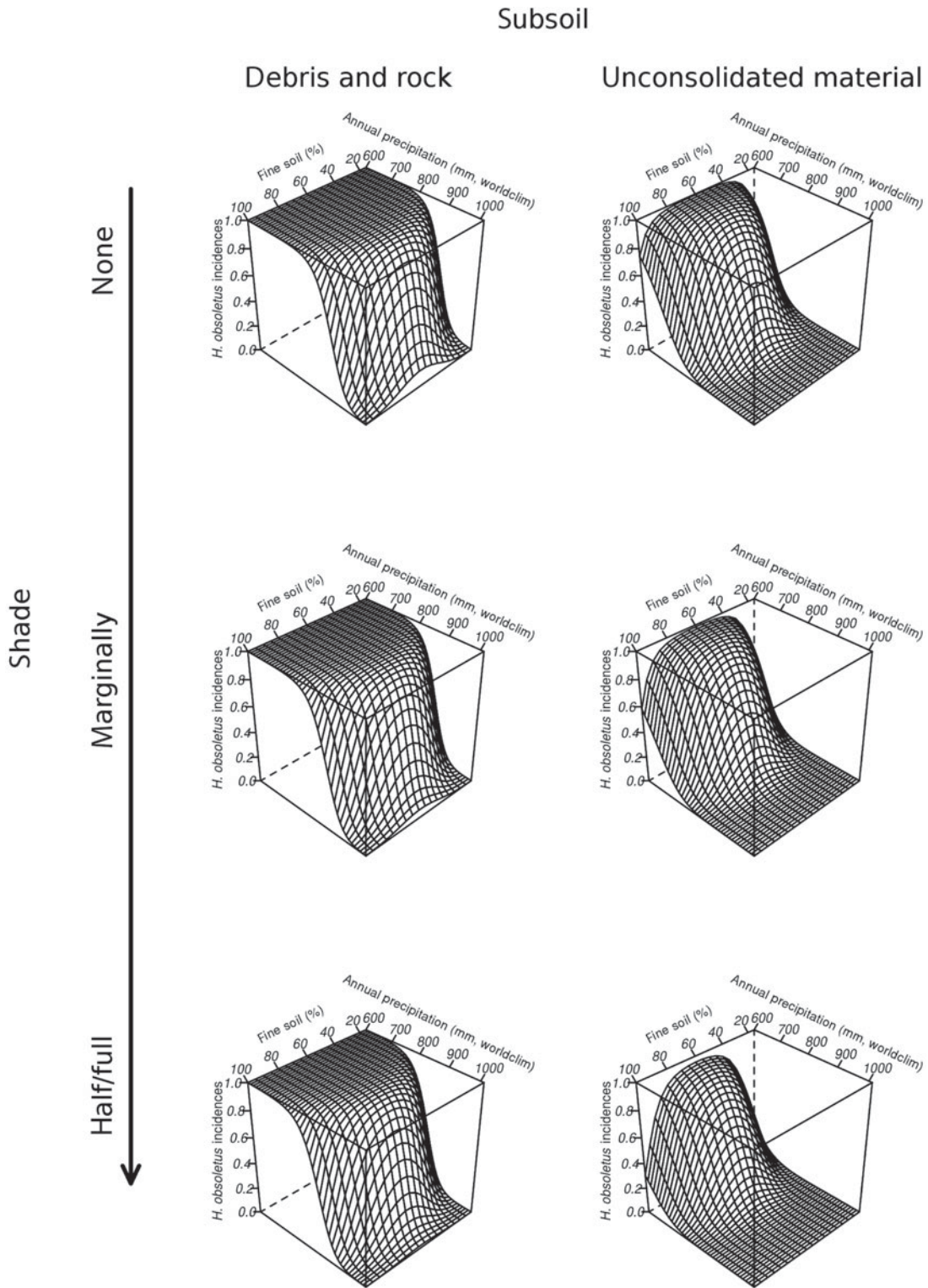### Debris and rock   Unconsolidated material

Fig. 2. Average model MC (environmental and climate data) for *H. obsoletus*. The probability of occurrence of *H. obsoletus* is plotted against the amount of fine soil and average annual precipitation; diagrams represent different levels of shade and two categories of subsoil (other subsoil categories showed a similar trend as 'unconsolidated material' and are, therefore, not shown).

temperature did not represent a main environmental factor driving the occurrence probabilities of *H. obsoletus*. This does not necessarily mean that species occurrence is unrelated to temperature but that temperature probably acts on a different scale or is indirectly represented by other variables. Hence, clear differences of *H. obsoletus* occurrence probabilities between locations, characterized by different degrees of shade, may indicate a high influence of micro-climatic conditions. Factors affecting the micro-climate such as vegetation structure and shade were shown to significantly affect the occurrence of Auchenorrhyncha in a habitat modelling study (Biedermann, 2004). We further assumed that variation in weather conditions in the year preceding the planthopper survey affect species occurrence. This hypothesis is supported by Whittaker & Tribe (1998) stating that the mean minimum temperature of September highly influences the population density of the spittlebug *Neophilaenus lineatus* (L.) (Homoptera, Auchenorrhyncha) in the following year. The average model MC + MCW (model with climate and weather variables) highlights that additional knowledge about habitat preferences can be obtained by not only focusing on long-term climate changes but also incorporating short-term weather events. This way, specific traits of certain species such as feeding or oviposition preferences related to occurrence characteristics might be revealed. In our study, the weather variable bio11 (mean temperature of coldest quarter of the year 2010) received a high percentile weight in the average model MC + MCW, replacing the climate variable bio15_worldclim (precipitation seasonality) and subsoil from the average model MC (model with climate variables only). Denno & Roderick (1990) stated that the survival of planthoppers overwintering as nymphs is negatively correlated with winter severity. In contrast, the high ranking of bio11 suggests that the nymphs are not primarily susceptible to the rigours of a harsh winter. Many overwintering insects tolerate winter severity by migrating into deeper soil layers (Leather *et al.*, 1993). Maixner (2010) found that at the northern range border nymphs of *H. obsoletus* are able to avoid frost damage by escaping into a soil depth of 20–25 cm. Moreover, bio11 is negatively correlated with the occurrence of *H. obsoletus*. We have no straightforward ecological explanation for this phenomenon. The planthoppers' preference for locations with low temperature during the coldest quarter might be related to indirect effects on predators or parasites.

Furthermore, we found that in patches with low host plant height occurrence probabilities of *H. obsoletus* were significantly increased. Thus, stinging nettle patches in managed landscapes with regular mowing of embankments and field margins seem to provide a suitable ecological niche in the Baden region.

Effects of agricultural management practices on interpretation of SDMs

The application of SDMs can be compromised by several limitations in agricultural studies. These are due to the inherent dynamics of these study systems. In addition to natural environmental variation, agricultural management practices introduce high variability in a dataset used to study crop pests (Altieri, 1999; Duyck *et al.*, 2012; Guerra & Steenwerth, 2012). Maps of habitat types used to quantify the surrounding landscape context may differ from one year to another, which is probably due to abandoned farmland or the cultivation of different types of field crops.

With respect to leaf – and planthoppers, the importance of the distribution and structure of the host plant(s) was highlighted by several authors (Denno & Roderick, 1990; Zabel & Tscharntke, 1998; Biedermann, 2002). However, vegetation mowing or the application of herbicides alter host plant related parameters such as patch size or patch height. One solution might be the usage of an extensive data set as demonstrated by Duyck *et al.* (2012). Another approach was presented in this study using different average models. Taking into account a reliable dataset based on a reasonably high number of sampling records, we could identify a possible negative relationship between stinging nettle height and species occurrence probabilities. This average model (MC + MCU), however, is associated with some degree of uncertainty due to the above mentioned reasons. Therefore, for prediction purposes, the use of model types MC and MCW, respectively, would be preferred.

The use of SDMs in agricultural risk analysis – opportunities and limitations

SDMs are well-established tools in many fields of biological research (Dormann *et al.*, 2004; Guisan & Thuiller, 2005). Despite their popularity and their advantages, only few studies have successfully applied SDMs in agricultural risk analysis (e.g., Meentemeyer *et al.*, 2004; Hamada *et al.*, 2008). On the one hand, pest management strategies could highly benefit from increased knowledge about the habitat requirements of many crop pests. In viticulture, detailed ecological information about major grapevine pests such as the grape berry moths *Eupoecilia ambiguella* Hb. and *Lobesia botrana* Schiff. or virus vectoring nematodes is still lacking. On the other hand, SDMs can be used to derive predictions of the potential distribution of crop pests. Such predictive maps may equally help farmers and decision makers to identify areas at high risk and to initiate appropriate plans of action. New avenues of research provide the geographical range prediction of invasive species. An example is the leafhopper *Scaphoideus titanus* Ball., the vector of the grapevine yellows disease Flavescence doreé (Schvester *et al.*, 1963). This species expands its geographical range in Europe towards north at an alarming spread (Boudon-Padieu & Maixner, 2007). Spatial extrapolations of previously developed SDMs could be a useful technique to identify suitable habitats. However, predictive maps of spatial extrapolations should be interpreted with a certain degree of caution and be subjected to a critical analysis as shown by De Meyer *et al.* (2010). Applying two modelling approaches, the authors predicted that suitable habitats of the invasive fruit fly, *Bactrocera invadens* (Diptera: Tephritidae), are characterized by high temperatures and a humid environment. Independent distributional data confirmed the robustness of the model predictions, nevertheless these predictions did not cover all known occurrences. Such discrepancies might be attributable to several factors such as (1) the spatial extrapolation was applied outside the environmental space used to develop the SDM (Franklin, 2009), or (2) a niche shift occurred as demonstrated for some species (Broennimann *et al.*, 2007; Fitzpatrick *et al.*, 2007; Steiner *et al.*, 2008).

SDMs are usually based on the assumption of pseudo-equilibrium (Guisan & Theurillat, 2000), since ecological surveys mostly represent snapshot views of ecological patterns of species-environment relationships. This assumption hampers the straightforward application of SDMs on

species exhibiting range expansions or recently introduced species. An example in the Baden region is *Drosophila suzukii* Matsumura, a recently fast spreading fruit fly (Breuer, unpublished data; Cini *et al.*, 2012). In these cases, the invasive species may not yet be in equilibrium with the environment. However, new methodological frameworks are now proposed to deal with such non-equilibrium dynamics (e.g., De Marco *et al.*, 2008; Gallien *et al.*, 2012).

With respect to *H. obsoletus*, insect pest management is currently based on biomonitoring in combination with a phenological model using temperature sums (Maixner & Langer, 2006). Yet, biomonitoring is laborious and time consuming and thus is limited in practice. Information about flight activity without knowing the species' ecological habitat preferences and occurrence probabilities may result in ineffective pest control measures. Adverse effects on non-target organisms and many aspects of ecosystem functioning due to the inappropriate application of pesticides are well documented (for a review in viticulture see: Guerra & Steenwerth, 2012). In this context, the developed SDMs are of high relevance in viticulture and can be further used to predict the planthoppers potential distribution in the vineyards of the Baden region. In the long term, both the phenological model and the SDMs may provide a complete picture about the spatio-temporal occurrence of *H. obsoletus* and thus, support integrated pest management strategies. Here, we exemplified the analysis of habitat requirements using SDMs for a crop insect in viticulture, an approach that can be easily adopted to other crop pests and diseases.

Acknowledgements

References

Alma, A. (2002) Auchenorrhyncha as pests on grapevine. *Denisia* **4**, 531–538.

Altieri, M.A. (1999) The ecological role of biodiversity in agroecosystems. *Agriculture, Ecosystems and Environment* **74**, 19–31.

Austin, M.P. (2002) Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling* **157**, 101–118.

Beanland, L., Noble, R. & Wolf, T.K. (2006) Spatial and temporal distribution of North American grapevine yellows disease and of potential vectors of the causal phytoplasmas in Virginia. *Environmental Entomology* **35**, 332–344.

Becker, N. & Kannenberg, J. (1979) Das Weinland Baden – sein Klima, seine Landschaft und seine Böden. *Der Badische Winzer* **5**, 170–194.

Biedermann, R. (2002) Leafhoppers (Hemiptera, Auchenorrhyncha) in fragmented habitats. *Denisia* **4**, 523–530.

Biedermann, R. (2004) Patch occupancy of two hemipterans sharing a common host plant. *Journal of Biogeography* **31**, 1179–1184.

Biedermann, R. & Niedringhaus, R. (2004) *The Planthoppers and Leafhoppers of Germany – Identification Key to All Species*. Scheeßel, Germany, WABV-Verlag.

Biedermann, R., Achtziger, R., Nickel, H. & Stewart, A.J.A. (2005) Conservation of grassland leafhoppers: a brief review. *Journal of Insect Conservation* **9**, 229–243.

Black, C.A. (1965) *Methods of Soil Analysis Physical and Mineralogical Properties, Including Statistics of Measurement and Sampling*. Madison, USA, American Society of Agronomy.

Boudon-Padieu, E. & Maixner, M. (2007) Potential effects of climate change on distribution and activity of insect vectors of grapevine pathogens. pp. 1–8 in *Global warming, which potential impacts on the vineyards?*. 28–30 March 2007, Dijon, France, Université de Bourgogne.

Bressan, A., Turata, R., Maixner, M., Spiazzi, S., Boudon-Padieu, E. & Girolami, V. (2007) Vector activity of *Hyalesthes obsoletus* living on nettles and transmitting a stolbur phytoplasma to grapevines: a case study. *Annals of Applied Biology* **150**, 331–339.

Breuer, M., Röcker, J. & Michl, G. (2008) Die Schwarzholzkrankheit kommt per Zikade. *Der Badische Winzer* **1**, 22–24.

Broennimann, O., Treier, U.A., Muller-Scharer, H., Thuiller, W., Peterson, A.T. & Guisan, A. (2007) Evidence of climatic niche shift during biological invasion. *Ecology Letters* **10**, 701–709.

Buckland, S.T., Burnham, K.P. & Augustin, N.H. (1997) Model selection: an integral part of inference. *Biometrics* **53**, 603–618.

Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multi model interference: a practical information-theoretic approach*. New York, USA, Springer-Verlag.

Cammell, M.E. & Knight, J.D. (1992) Effects of climatic-change on the population dynamics of crop pests. *Advances in Ecological Research* **22**, 117–162.

Cannon, R.J.C. (1998) The implications of predicted climate change for insect pests in the UK, with emphasis on non-indigenous species. *Global Change Biology* **4**, 785–796.

Cargnus, E., Pavan, F., Mori, N. & Martini, M. (2012) Identification and phenology of *Hyalesthes obsoletus* (Hemiptera: Auchenorrhyncha: Cixiidae) nymphal instars. *Bulletin of Entomological Research* **102**, 504–514.

Caudwell, A. (1961) Étude sur la maladie du bois noir de la vigne: ses rapports avec la Flavescence dorée. *Annales des Epiphyties* **12**, 241–262.

Cini, A., Ioriatti, C. & Anfora, G. (2012) A review of the invasion of *Drosophila suzukii* in Europe and a draft research agenda for integrated pest management. *Bulletin of Insectology* **65**, 149–160.

Cohen, J. (1960) A coefficient of agreement for nominal scales. *Educational and Psychological Measurement* **30**, 37–46.

Coudun, C., Gegout, J.C., Piedallu, C. & Rameau, J.C. (2006) Soil nutritional factors improve models of plant species distribution: an illustration with *Acer campestre* (L.) in France. *Journal of Biogeography* **33**, 1750–1763.

Danielson, R.E. & Sutherland, P.L. (1986) Porosity. pp. 443–461 *in* Klute, A. (*Ed.*) *Methods of Soil Analysis. Part 1: Physical and Mineralogical Methods*. Madison, USA, Soil Science Society of America.

Daire, X., Boudon-Padieu, E., Berville, A., Schneider, B. & Caudwell, A. (1992) Cloned DNA probes for detection of

grapevine Flavescence dorée mycoplasma-like organism (Mlo). *Annals of Applied Biology* **121**, 95–103.

De Marco, P., Diniz, J.A.F. & Bini, L.M. (2008) Spatial analysis improves species distribution modelling during range expansion. *Biology Letters* **4**, 577–580.

De Meyer, M., Robertson, M.P., Mansell, M.W., Ekesi, S., Tsuruta, K., Mwaiko, W., Vayssières, J.-F. & Peterson, A.T. (2010) Ecological niche and potential geographic distribution of the invasive fruit fly *Bactrocera invadens* (Diptera, Tephritidae). *Bulletin of Entomological Research* **100**, 35–48.

Denno, R.F. & Roderick, G.K. (1990) Population biology of planthoppers. *Annual Review of Entomology* **35**, 489–520.

Dodson, R. & Marks, D. (1997) Daily air temperature interpolated at high spatial resolution over a large mountainous region. *Climate Research* **8**, 1–20.

Dormann, C.F., Blaschke, T., Lausch, A., Schröder, B. & Söndgerath, D. (2004) *Habitatmodelle – Methodik, Anwendung, Nutzen*. Leipzig, Germany, Helmholtz-Zentrum für Umweltforschung UFZ.

Dormann, C.F., McPherson, J.M., Araujo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling, W.D., Kuhn, I., Ohlemuller, R., Peres-Neto, P.R., Reineking, B., Schroder, B., Schurr, F.M. & Wilson, R. (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* **30**, 609–628.

Duyck, P.F., David, P. & Quilici, S. (2006) Climatic niche partitioning following successive invasions by fruit flies in La Réunion. *Journal of Animal Ecology* **75**, 518–526.

Duyck, P.-F., Dortel, E., Vinatier, F., Gaujoux, E., Carval, D. & Tixier, P. (2012) Effect of environment and fallow period on *Cosmopolites sordidus* population dynamics at the landscape scale. *Bulletin of Entomological Research* **102**, 583–588.

Ferrier, S., Drielsma, M., Manion, G. & Watson, G. (2002) Extended statistical approaches to modelling spatial pattern in biodiversity in northeast New South Wales. II. Community-level modelling. *Biodiversity and Conservation* **11**, 2309–2338.

Fielding, A.H. & Bell, J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* **24**, 38–49.

Fielding, A.H. & Haworth, P.F. (1995) Testing the generality of bird-habitat models. *Conservation Biology* **9**, 1466–1481.

Fitzpatrick, M.C., Weltzin, J.F., Sanders, N.J. & Dunn, R.R. (2007) The biogeography of prediction error: why does the introduced range of the fire ant over-predict its native range? *Global Ecology and Biogeography* **16**, 24–33.

Franklin, J. (2009) *Mapping Species Distributions: Spatial Inference and Prediction*. Cambridge, UK, Cambridge University Press.

Gallien, L., Douzet, R., Pratte, S., Zimmermann, N.E. & Thuiller, W. (2012) Invasive species distribution models – how violating the equilibrium assumption can create new insights. *Global Ecology and Biogeography* **21**, 1126–1136.

Graham, M.H. (2003) Confronting multicollinearity in ecological multiple regression. *Ecology* **84**, 2809–2815.

Guerra, B. & 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**, 149–164.

Guisan, A. & Theurillat, J.P. (2000) Equilibrium modeling of alpine plant distribution: how far can we go? *Phytocoenologia* **30**, 353–384.

Guisan, A. & Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters* **8**, 993–1009.

Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling* **135**, 147–186.

Hamada, E., Ghini, R., Rossi, P., Júnior, M.J.P. & Fernandes, J.L. (2008) Climatic risk of grape downy mildew (*Plasmopara viticola*) for the state of São Paulo, Brazil. *Scientia Agricola* **65**, 60–64.

Hanley, J.A. & McNeil, B.J. (1982) The meaning and use of the area under a receiver operating characteristic (ROC) curve. *Radiology* **143**, 29–36.

Harrell, F.E.J. (2001) *Regression Modeling Strategies – with Applications to Linear Models, Logistic Regression, and Survival Analysis*. New York, USA, Springer.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* **25**, 1965–1978.

Hijmans, R.J., Phillips, S., Leathwick, J. & Elith, J. (2011) Dismo: Species Distribution Modeling. R package version 0.7–15. http://cran.r-project.org/web/packages/dismo/index.html.

Hosmer, D.W. & Lemeshow, S. (2000) *Applied Logistic Regression*. New York, USA, John Wiley and Sons.

Huffaker, C.B. & Gutierrez, A.P. (1999) *Ecological Entomology*. New York, USA, John Wiley and Sons.

Johannesen, J., Lux, B., Michel, K., Seitz, A. & Maixner, M. (2008) Invasion biology and host specificity of the grapevine yellows disease vector *Hyalesthes obsoletus* in Europe. *Entomologia experimentalis et applicata* **126**, 217–227.

Juliano, S.A., O'Meara, G.F., Morrill, J.R. & Cutwa, M.M. (2002) Desiccation and thermal tolerance of eggs and the coexistence of competing mosquitoes. *Oecologia* **130**, 458–469.

Langer, M. & Maixner, M. (2004) Molecular characterisation of grapevine yellows associated phytoplasmas of the stolbur-group based on RELP-analysis of non-ribosomal DNA. *Vitis* **43**, 191–199.

Langer, M., Darimont, H. & Maixner, M. (2003) Control of phytoplasma vectors in organic viticulture. *IOBC/WPRS Bulletin* **26**, 197–203.

Leather, S.R., Walters, K.F.A. & Bale, J.S. (1993) *The Ecology of Insect Overwintering*. Cambridge, UK, Cambridge University Press.

Lee, I.M., Gundersen-Rindal, D.E., Davis, R.E. & Bartoszyk, I.M. (1998) Revised classification scheme of phytoplasmas based an RFLP analyses of 16S rRNA and ribosomal protein gene sequences. *International Journal of Systematic Bacteriology* **48**, 1153–1169.

Lessio, F., Tedeschi, R. & Alma, A. (2007) Population dynamics, host plants and infection rate with stolbur phytoplasma of *Hyalesthes obsoletus* Signoret in north-western Italy. *Journal of Plant Pathology* **89**, 97–102.

Maixner, M. (2006) Die Schwarzholzkrankheit der Rebe. *Schweizerische Zeitschrift für Obst – und Weinbau* **17**, 4–7.

Maixner, M. (2007) Biology of *Hyalesthes obsoletus* and approaches to control this soilborne vector of bois noir disease. *IOBC/WPRS Bulletin* **30**, 3–9.

Maixner, M. (2010) Phytoplasma epidemiological systems with multiple plant hosts. pp. 213–232 *in* Weintraub, P.G. & Jones, P. (*Eds*) *Phytoplasmas Genomes, Plant Hosts, and Vectors*. Cambridge, USA, CABI North American Office.

Maixner, M. & Langer, M. (2006) Prediction of the flight of *Hyalesthes obsoletus*, vector of stolbur phytoplasma, using temperature sums. *Integrated Protection in Viticulture, IOBC/wprs Bulletin* **29**, 161–166.

Maixner, M., Ahrens, U. & Seemüller, E. (1994) Detection of mycoplasmalike organisms associated with a yellows disease of grapevine in Germany. *Journal of Phytopathology* **142**, 1–10.

Maixner, M., Langer, M. & Gerhard, Y. (2006) Epidemiological characteristics of bois noir type I. pp. 86–87 in *15th ICVG Conference*, Stellenbosch, South Africa, South African Society for Enology and Viticulture.

Manel, S., Dias, J.M., Buckton, S.T. & Ormerod, S.J. (1999) Alternative methods for predicting species distribution: an illustration with Himalayan river birds. *Journal of Applied Ecology* **36**, 734–747.

McCullagh, P. & Nelder, J.A. (1989) *Generalized Linear Models*. Boca Raton, USA, Chapman and Hall.

Meentemeyer, R., Rizzo, D., Mark, W. & Lotz, E. (2004) Mapping the risk of establishment and spread of sudden oak death in California. *Forest Ecology and Management* **200**, 195–214.

Meyer, C.B. & Thuiller, W. (2006) Accuracy of resource selection functions across spatial scales. *Diversity and Distributions* **12**, 288–297.

Mori, N., Pavan, F., Reggiani, N., Bacchiavini, M., Mazzon, L., Paltrinieri, S. & Bertaccini, A. (2011) Correlation of bois noir disease with nettle and vector abundance in northern Italy vineyards. *Journal of Pest Science* **85**, 1–6.

Morris, M.G. (1981*a*) Responses of grassland invertebrates to management by cutting. III. Adverse effects on Auchenorhyncha. *Journal of Applied Ecology* **18**, 107–123.

Morris, M.G. (1981*b*) Responses of grassland invertebrates to management by cutting: IV positive responses of Auchenorhyncha. *Journal of Applied Ecology* **18**, 763–771.

Nagelkerke, N.J.D. (1991) A note on a general definition of the coefficient of determination. *Biometrika* **78**, 691–692.

Neter, J., Wasserman, W. & Kutner, M.H. (1989) *Applied Linear Regression Models*. Boston, USA, Burr Ridge.

Palermo, S., Elekes, M., Botti, S., Ember, I., Alma, A., Orosz, A., Bertaccini, A. & Kolber, M. (2004) Presence of stolbur phytoplasma in cixiidae in Hungarian vineyards. *Vitis* **43**, 201–203.

Porter, J.H., Parry, M.L. & Carter, T.R. (1991) The potential effects of climatic change on agricultural insect pest. *Agricultural and Forest Meteorology* **57**, 221–240.

R Development Core Team (2011) *R: A Language and Environment for Statistical Computing*. Vienna, Austria, R Foundation for Statistical Computing.

Sanderson, R.A., Rushton, S.P., Cherrill, A.J. & Byrne, J.P. (1995) Soil, vegetation and space: an analysis of their effects on the invertebrate communities of a moorland in north-east England. *Journal of Applied Ecology* **32**, 506–518.

Schlichting, E., Blume, H.-P. & Stahr, K. (1995) *Bodenkundliches Praktikum: eine Einführung in pedologisches Arbeiten für Ökologen, insbesondere Land – und Forstwirte, und für Geowissenschaftler*. Berlin, Germany, Blackwell Wissenschafts-Verlag.

Schvester, D., Carle, P. & Moutous, G. (1963) Transmission de la Flavescence dorée de la vigne par *Scaphoideus littoralis* Ball. *Annales des Epiphyties* **14**, 175–198.

Sergel, R. (1986) Ein weiterer Nachweis der Cixiide *Hyalesthes obsoletus* Signoret in Franken (Homoptera: Auchenorrhyncha: Fulgoroidea). *Abhandlungen des Naturwissenschaftlichen Vereins Würzburg* **25**, 81–82.

Sforza, R., Clair, D., Daire, X., Larrue, J. & Boudon-Padieu, E. (1998) The role of *Hyalesthes obsoletus* (Hemiptera: Cixiidae) on the occurrence of bois noir of grapevines in France. *Journal of Phytopathology – Phytopathologische Zeitschrift* **146**, 549–556.

Sforza, R., Bourgoin, T., Wilson, S.W. & Boudon-Padieu, E. (1999) Field observations, laboratory rearing and description of immatures of the planthopper *Hyalesthes obsoletus* (Hemiptera: Cixiidae). *European Journal of Entomology* **96**, 409–418.

Sharon, R., Soroker, V., Wesley, S.D., Zahavi, T., Harari, A. & Weintraub, P.G. (2005) *Vitex agnus-castus* is a preferred host plant for *Hyalesthes obsoletus*. *Journal of Chemical Ecology* **31**, 1051–1063.

Sponagel, H. (2005) *Bodenkundliche Kartieranleitung*. Bundesanstalt für Geowissenschaften und Rohstoffe in Zusammenarbeit mit den Staatlichen Geologischen Diensten der Bundesrepublik Deutschland (ed.). Stuttgart, Germany, E. Schweizerbart'sche Verlagsbuchhandlung.

Steiner, F.M., Schlick-Steiner, B.C., VanDerWal, J., Reuther, K.D., Christian, E., Stauffer, C., Suarez, A.V., Williams, S.E. & Crozier, R.H. (2008) Combined modelling of distribution and niche in invasion biology: a case study of two invasive *Tetramorium* ant species. *Diversity and Distributions* **14**, 538–545.

Stewart, A.J.A. (2002) Techniques for sampling Auchenorrhyncha in grasslands. *Denisia* **4**, 491–512.

Strauss, B. & Biedermann, R. (2005) The use of habitat models in conservation of rare and endangered leafhopper species (Hemiptera, Auchenorrhyncha). *Journal of Insect Conservation* **9**, 245–259.

Strauss, B. & Biedermann, R. (2006) Urban brownfields as temporary habitats: driving forces for the diversity of phytophagous insects. *Ecography* **29**, 928–940.

VDLUFA (1991) *Methodenbuch*. Darmstadt, Germany, VDLUFA-Verlag.

Verbyla, D.L. & Litvaitis, J.A. (1989) Resampling methods for evaluating classification accuracy of wildlife habitat models. *Environmental Management* **13**, 763–787.

Weber, A. & Maixner, M. (1998) Survey of populations of the planthopper *Hyalesthes obsoletus* Sign. (Auchenorrhyncha, Cixiidae) for infection with the phytoplasma causing grapevine yellows in Germany. *Journal of Applied Entomology – Zeitschrift für Angewandte Entomologie* **122**, 375–381.

Weintraub, P.G. & Jones, P. (2010) *Phytoplasmas Genomes, Plant Hosts, and Vectors*. Cambridge, USA, CABI North American Office.

Whittaker, J. (1984) Model interpretation from the additive elements of the likelihood function. *Applied Statistics-Journal of the Royal Statistical Society Series C* **33**, 52–64.

Whittaker, J.B. & Tribe, N.P. (1998) Predicting numbers of an insect (*Neophilaenus lineatus* : Homoptera) in a changing climate. *Journal of Animal Ecology* **67**, 987–991.

Zabel, J. & Tscharntke, T. (1998) Does fragmentation of *Urtica* habitats affect phytophagous and predatory insects differentially? *Oecologia* **116**, 419–425.