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Title	Abrupt and gradual temperature changes influence on the climatic suitability of Northwestern Alpine grapevine-growing regions for the invasive Grape leafhopper Scaphoideus titanus Ball (Hemiptera, Cicadellidae)
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Abstract

The paper aims to elucidate the influence of abrupt and gradual climate changes on the suitability for colonization of Scaphoideus titanus populations in grapevine-growing areas of the Northwestern Alpine region. This study spans several decades of temperature recordings and is carried out in ten grapevine-growing areas. A time-varying distributed delay with attrition model, linked to a grapevine phenology model, is used to simulate the development of S. titanus populations and produce an annual Climatic Suitability Index (CSI). Area-specific CSI time series were obtained. The Breusch-Godfrey test revealed few significant partial autocorrelations in nine areas and the occurrence of six consecutive - first decreasing and then increasing - partial correlations in one case only. The occurrence of abrupt and gradual changes of the index were studied via multiple least square regression analyses. In general, the climatic suitability of all areas tended to improve through time. However, gradual and abrupt temperature changes were not consistently reflected in gradual and abrupt CSI patterns: abrupt and gradual CSI changes were observed in two areas, abrupt changes were detected in three areas, and exclusively gradual changes in the remaining five. Pest control institution of the region under study may deal with different scenarios of pest status such as long-time presence and increasing risks, high colonization risks or limited colonization risks for the foreseeable future. Institutions charged with pest control elsewhere are advised to use a mechanistic demographic model to study area-specific infestation patterns and colonization risks because the results obtained here cannot be transferred to other areas without site-specific evaluations.

Keywords	climate change; physiologically-based demographic model; climatic suitability; forecast; colonization risk
Corresponding Author	Ivo Ercole Rigamonti
Corresponding Author's Institution	MILANO
Order of Authors	Ivo Ercole Rigamonti, Luigi Mariani, Gabriele Cola, Mauro Jermini, Johann Baumgärtner

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figure two.jpg [Figure]

Figure three.jpg [Figure]

Dear Editor,

we are re-submitting the manuscript ACTOEC_2017_45, revised in accordance with the points raised by reviewer two. Namely, we rewrote the concluding remarks, changing the writing style to improve the narrative flow, and corrected a few typos. Kindly note that the changes in the text have been marked in green colour.

Thank you for your kind consideration of our work
Best regards

Ivo Rigamonti

Climate changes influence the suitability for *S. titanus* in the Northwestern Alps.

The suitability of all areas improved over the period under study.

The areas under study displayed different responses to temperature changes.

Similar analysis may be implemented in regions outside the scope of this paper.

The risk of new viticultural areas to be colonized by *S. titanus* can be specified.

1) REVISED MANUSCRIPT WITH CHANGES MARKED

Abrupt and gradual temperature changes influence on the climatic suitability of Northwestern Alpine grapevine-growing regions for the invasive Grape leafhopper *Scaphoideus titanus* Ball (Hemiptera, Cicadellidae)

Ivo Ercole Rigamonti[a,*], Luigi Mariani[b], Gabriele Cola[b], Mauro Jermini[c], Johann Baumgärtner [d]

[a] DeFENS *Department of Food, Environmental and Nutritional Sciences (DeFENS), Università degli Studi di Milano, Via Celoria 2, I-20133 Milano, Italy. E-mail: ivo.rigamonti@unimi.it*

[b] *Dipartimento di Scienze Agrarie e Ambientali – Produzione, Territorio, Agroenergia (DISAA), Via Celoria 2, I-20133 Milano, Italy. E-mail: luigi.mariani@unimi.it*

[c] *Agroscope, Centro di Cadenazzo (TI). A Ramél, 18, CH-6593 Cadenazzo, Switzerland. E-mail: mauro.jermini@agroscope.admin.ch*

[d] CASAS *Center for the Analysis of Sustainable Agricultural Systems (CASAS), Kensington (CA) 94707 United States of America. E-mail: jbaumgaertner@yahoo.com*

[*]Corresponding author

ABSTRACT

The paper aims to elucidate the influence of abrupt and gradual climate changes on the suitability for colonization of *Scaphoideus titanus* populations in grapevine-growing areas of the Northwestern Alpine region. This study spans several decades of temperature recordings and is carried out in ten grapevine-growing areas. A time-varying distributed delay with attrition model, linked to a grapevine phenology model, is used to simulate the development of *S. titanus* populations and produce an annual Climatic Suitability Index (CSI). Area-specific CSI time series were obtained. The Breusch-Godfrey test revealed few significant partial autocorrelations in nine areas and the occurrence of six consecutive - first decreasing and then increasing - partial correlations in one case only. The occurrence of abrupt and gradual changes of the index were studied via multiple least square regression analyses. In general, the climatic suitability of all areas tended to improve through time. However, gradual and abrupt temperature changes were not consistently reflected in gradual and abrupt CSI patterns: abrupt and gradual CSI changes were observed in two areas, abrupt changes were detected in three areas, and exclusively gradual changes in the remaining five. Pest control institution of the region under study may deal with different scenarios of pest status such as long-time presence and increasing risks, high colonization risks or limited colonization risks for the foreseeable future. Institutions charged with pest control elsewhere are advised to use a mechanistic demographic model to study area-specific infestation patterns and colonization risks because the results obtained here cannot be transferred to other areas without site-specific evaluations.

Key words: climate change, physiologically-based demographic model, climatic suitability, forecast, colonization risk

1. Introduction

Many studies have been undertaken to document changing climates at different spatial and temporal scale extents and resolutions (Anisimov et al., 2013; Anwer, 2015; Portmann et al., 2009; Reiter et al., 2012). According to the global dataset HadCRUT4 (Morice et al., 2012), global temperatures increased by +0.85°C since 1850, while the main part of this increase (about +0.5°C) occurred in the period 1977-1998. During the same period, European temperatures increased by about +1.3°C (Mariani et al., 2012).

Voluminous literatures deal with the effects of changing climates on populations, communities and ecosystems (Graham and Grimm, 1990; Gutierrez et al., 2008; Parmesan, 2006; Yates et al., 2010). The temperature component of climate change is particularly important for poikilothermic organisms whose development depend on body temperatures that vary broadly with environmental temperatures (May, 2005). The methods used to investigate the impact of changing temperatures on population development and geographical distributions of poikilotherms fall broadly into two categories. The first category comprises species distribution models (SDMs) that combine observations of species occurrence or abundance with environmental estimates to characterize climatically the species to gain ecological and evolutionary insights and to predict distributions across landscapes, sometimes requiring extrapolation in space and time (Elith and Leathwick, 2009).

The second category of interest here comprises of physiologically-based demographic models (PBDMs), built on mechanistic representations of poikilothermic population development. PBDMs model the biology of the target species, and, when driven by weather, predict the phenology, age-structured dynamics, and distribution of the species across wide geographic areas independent of the availability of distribution information (Ponti et al., 2015). Since weather is an important driver for PBDMs, they are particularly appropriate for dealing with climate change effects.

In the case of pests and their abundance, the capacity of PBDMs to predict the potential geographic distribution under past, current and future climate change scenarios is fundamental in developing sound policies for their control (Gutierrez and Ponti, 2013; Ponti et al., 2015). Their ability to represent the regional suitability and the spatial distributions of insect pests on explanatory grounds is a complement to the work of international organizations such as the European and Mediterranean Plant Protection Organization (EPPO) that monitors and delineates the spread of pests and provides directions on quarantine pests management (Smith et al., 1996).

The Nearctic leafhopper *Scaphoideus titanus* Ball (Hemiptera, Cicadellidae), vector of the Grapevine Flavescence dorée (FD) phytoplasma, is a key pest of grapevine in Europe. *S. titanus* was accidentally introduced in France in the 1950s (Bonfils and Schvester 1960; Schvester et al. 1961, 1962a, 1962b) and gradually extended its area of distribution. Actually, it is present throughout Western and Southeastern Europe from the Atlantic Ocean to the Black Sea, and the area of distribution is still expanding (Chuche and Thiéry, 2014; Tóthová et al., 2015).

Since the spread of *S. titanus* and FD continues, pest control institutions in regions with high risks of being invaded and colonized should prepare in time for intensive monitoring and expensive control operations. The risk of invasion and colonization depends on the dispersal ability of *S. titanus* and the suitability of the newly-invaded area. After its accidental introduction into Europe, the spread was so fast that most grapevine-growing areas should have been colonized by now. This is not the case, however, and the ongoing expansion suggests that the influence of the high dispersal ability on distribution patterns is constrained by other factors. Empirical and theoretical evidence suggest that climate, undergoing the aforementioned changes since the time of *S. titanus* introduction, plays an important role. In fact, Rigamonti et al. (2014b) found that the climate in two Swiss grapevine-growing areas changed in favor of *S. titanus* and hypothesized that the climatic suitability determines the colonization success and largely explains the changing geographical distribution in Europe.

Since the temperature regime in European grapevine-growing regions has and will undergo changes (IPCC, 1996), a previously-unsuitable region may become suitable through time. Mariani et al. (2012) viewed climate variability as the superimposition of gradual and abrupt changes. Gradual changes can be interpreted as the effect of progressive changes in forcings (IPCC, 2013), while abrupt changes are the result of sharp changes in the frequency and persistence of different circulation patterns (Sneyers et al., 1993). During the period 1977-1998, European temperatures increased by about 1.3°C, while the main part of this increase was observed at the end of the 1980s, where an abrupt change is evident on thermal time series (Mariani et al., 2012).

The paper aims to elucidate the effects of abrupt and gradual climate change on *S. titanus* population development through an analysis of long-term suitability patterns in a geographically-restricted region with high temperature variability among grapevine-growing areas. For each area, a PBDM provides a long-term time series of annual suitability indices whose similarity, depending on time lags, prepares the ground for testing the appearance of abrupt and gradual changes in area-specific patterns of the suitability index.

2. Materials and Methods

2.1. Study sites and temperature recordings

The suitability of grapevine-growing regions for *S. titanus* colonization is assessed in a region referred to as Northwestern Alps (Figure 1, Table 1). This region has been selected because of its location near the northern limits of *S. titanus* distribution and the high climatic variability among grapevine growing areas therein. Both aspects are considered as useful prerequisites for elucidating the effects of climate change on the suitability of the region for colonization by *S. titanus*. Though outside the Alpine zone, we included the Zürich area in the analysis. At meteorological stations located in the different areas, daily temperature maxima and minima were readily available over 54 or 39 years periods (Table 1). To simplify the geographical notations, the location name is used as a name for the area. The locations of all the weather stations except Grenoble, are within or close to the grapevine growing areas.

The temperatures measured at the Swiss locations (Zürich, Lugano, Genève, Aigle, Sion, Chur and Magadino) are referred to as revised data retrieved from the data bank of the Swiss National Weather Service (MeteoSwiss). Namely, during the measuring periods, the position of the temperature sensors was often changed and new equipment were adopted. MeteoSwiss corrected for these changes (Begert et al., 1999, 2003, 2005) and kindly made available a data set referred to as homogenized data. Most of the data for Sondrio were kindly made available by Dr. M. Salvetti (Fondazione Fojanini, Sondrio) and reportedly did not require any correction. In the absence of respective information, the raw data measured at the Aosta and Grenoble stations obtained from Yang et al. (2010) at [https://beaumont.tamu.edu/ClimaticData/] and from the US weather service at [http://www.geodata.us/weather/], respectively, were used in the analyses. The gaps in the Sondrio and Aosta data sets were respectively filled by linear regression of Sondrio data on data measured at the nearby Poschiavo station operated by MeteoSwiss, and linear regression of Aosta data were regressed from data measured at the Torino-Caselle station.

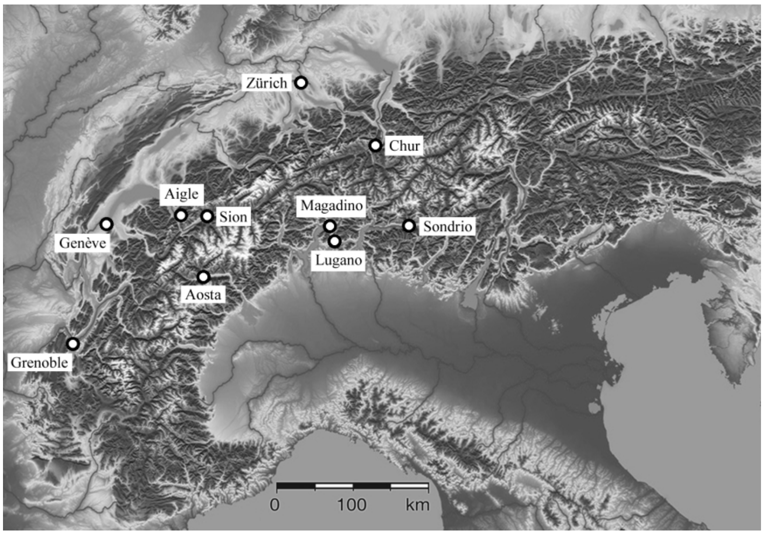

Figure 1. The Northwestern Alpine region with the different areas in that the development of Grape leafhopper *Scaphoideus titanus* populations was simulated.

Table 1. Information on the Northwestern Alpine region with the different areas in that the development of Grape leafhopper *Scaphoideus titanus* populations was simulated. The homogenized daily temperature maxima and minima for the Swiss meteorological stations were kindly made available by MeteoSwiss (National Weather Service of Switzerland). Additional temperature data were retrieved from the Texas A&M University, Beaumont, USA (https://beaumont.tamu.edu/ClimaticData/), the National Climate Data Centre (NCDC), Climate Services Branch (USA) and the Fojanini Foundation (FFS), Sondrio (I). Gaps in the data sets for Aosta and Sondrio were filled by using information from Torino Caselle (I) and Poschiavo (CH), respectively.

Site specification	Area and meteorological station	Beginning of simulations	Latitude N (degrees)	Longitude E (degrees)	Altitude (meters above sea level)	Source for temperatures data
Western and Northern areas	Genève (CH)	1959	46.250	6.133	416	MeteoSwiss
	Aigle (CH)		46.333	6.917	383	
	Sion (CH)		46.217	7.317	428	
	Zürich (CH)		47.383	8.567	569	
	Chur (CH)		46.867	9.533	533	
Western and Southern areas	Grenoble (F)	1973	45.367	5.333	386	NCDC
	Aosta (I)		45.740	7.376	547	Texas A&M
	Magadino (CH)	1959	46.167	8.883	198	MeteoSwiss
	Lugano (CH)		46.000	8.967	276	
	Sondrio (I)	1973	46.168	9.853	323	FFS

2.2. *Model characteristics and computation of the Climatic Suitability Index*

Basic model development. Rigamonti et al. (2011, 2014a) took into account the high variability in development times of nymphs relative to the mean (*cf.* Di Cola et al., 1999) and linked the appropriate "time-varying distributed delay with attrition" variant of the widely used time distributed delay models (Gutierrez, 1996; Gutierrez et al., 2015; Manetsch, 1976; Vansickle, 1977; Welch, 1984; Welch et al., 1978) to the grapevine plant phenology model of Mariani et al. (2013). They noticed that the *S. titanus* population model was appropriate for long-term studies since it allows the representation of multi-cohort and multi-generation poikilothermic population development. The model represents the flow of individuals through diapausing egg, post-diapausing egg, nymph and adult life stages

$$\frac{dr_{ji}(t)}{dt} = \frac{k_j}{DEL_j(t)}\left[r_{ji-1}(t) - r_{ji}(t)\left(1 + AR_j(t)\frac{DEL_j(t)}{k_j} + \frac{d\,DEL_j(t)}{k_j dt} \right) \right] \qquad [1]$$

$j = 1, 2, 3, 4$

$i = 1, 2, \ldots, k_j$

where t is time [days], $r_{ji}(t)$ is the transition rate of the *i-th* substage in the *j-th* life stage, k_j is the number of delay substages in the *j-th* life stage, $DEL_j(t)$ is the time-dependent developmental time (days) in the absence of losses in the *j-th* life stage, and $AR_j(t)$ is the time dependent proportional change or attrition in the *j-th* life stage. The occurrence $Q_j(t)$ of individuals in each life stage can be obtained from

$$Q_j(t) = \sum_{i=1}^{k_j} \frac{DEL_j(t)}{k_j} r_{ji}(t) \qquad [2]$$

Rigamonti et al. (2011, 2014a) discretized model [1] according to Abkin and Wolf (1976) and used a 1-hour time step length.

Model components. The following aspects briefly summarize model components detailed by Rigamonti et al. (2011, 2014a).

i) The stage-specific developmental rate $d_j,[T(t)]$, *i.e.,* the inverse of developmental time $DEL[T(t)]$, is temperature-dependent between lower and upper thresholds, and 0.001 or 0.01, for diapausing and non-diapausing stages respectively, outside this range. The time-dependent temperatures *T(t)* are obtained by forcing a cosine function through daily temperature maxima and minima.

ii) The stage-specific survival rate $s_j[T(t)]$ is composed of a) a temperature-dependent survival, modeled through attrition *AR[T(t)],* operating between lower and upper thresholds, b) a temperature-dependent survival below the lower threshold, and c) mortalities of non-diapausing life stages between the grapevine plant phenological stages BBCH 93 (beginning of leaf fall) and BBCH 11 (first leaf unfolded and spread away from shoot) (Lorenz et al., 1994). Before and after these plant stages, nymphs and adults are suffering from an additional mortality of 0.5 % per day.

iii) The reproduction rate *m[T(t)]* of females becomes the input into the diapausing egg stage. It is the product of the reproductive profile, *i.e.* the relative age-specific fecundity rate and the temperature-dependent reproductive potential *F(T*), *i.e*., the total number of eggs laid by a female (*cf.* Curry and Feldman, 1987) ($m[T(t)]>0$ between the lower and an upper thresholds and $m[T(t)]=0$ outside this range).

iv) The model is initialized with a flow of hatching eggs into the nymphal stage (see below). The use of a single data set for model initialization at other locations may negatively affect the model performance in the first years. Therefore, the subsequent analysis disregards the first computations of the CSI. The simulations are carried out over the time periods specified below.

Model parametrization. The respective temperature-dependent rate functions (i, ii, iii) were developed and parametrized under constant temperatures but used under time-varying temperature regimes. Briefly, temperature-dependent values for the developmental time and mortality of nymphs older than the first stage were obtained from age-specific life tables established under various but constant temperatures (Rigamonti et al., 2011, 2014a). The developmental time of post-diapausing eggs, and the developmental time and mortality of first stage nymphs were obtained from field observations carried out in four vineyards located in Southern Switzerland over a period of three years, whereas data from literature were used to estimate adult female developmental time and associated variability. The respective field data, expert opinions and literature information were used to compute diapause periods. A linear model for first stage nymphs and the non-linear model of Brière et al. (1999) for the remaining stages were used to represent the temperature-dependency of developmental rates. The developmental rate of the widely-cultivated Chardonnay variety, and the phenological stages BBCH 11 and 93, were obtained from the model of Mariani et al. (2007, 2013) and calibrated with information obtained in vineyards located in Southern Switzerland.

Reproduction is composed of the reproductive profile f_i, *i.e*., the relative age-specific fecundity rate in the *i*-th substage, and the temperature-dependent reproductive potential *F*(*T*), *i.e.*, the total number of eggs laid by a female conditioned on her living throughout the oviposition period (Curry and Feldman, 1987). The substage-independent f_i was estimated on the basis of literature data, whereas a Beta function fitted to literature data represented the temperature-dependency of *F*(*T*).

Egg hatching in 2008 was recorded weekly on 20 caged plants in a vineyard. The cumulative proportion of the total number is represented by the cumulative density Weibull function und provided time step-specific inputs (iv) into the delay model.

Model validation is detailed by Rigamonti et al. (2011, 2014a). Over a period of five years, from 2006 to 2010, nymph and adult occurrences were occasionally monitored in five vineyards located in FD-free zones of Western Switzerland (Yvorne, Lutry) and Southern Switzerland (Contone, Biasca, Sessa). Data on nymphs were obtained through the beating tray method, while yellow sticky traps yielded information on adult presence. The plant phenology model was validated with observations made in Southern Switzerland's vineyards,. The model predictions satisfactorily corresponded to field observations and opened the door for the use of the model.

Model use relies on a Climatic Suitability Index calculated as follows. Once the plant has reached the BBCH 11 stage, it is assumed to allow the development of *S. titanus* nymphs. On the day with the first BBCH 11 occurrence, eq. [2] computes, in each year, diapausing and post-diapausing eggs as the only individuals giving rise to the subsequent infestations. The number computed in a particular year is divided by the corresponding number in the previous year to yield a CSI. Population densities are declining, stationary or increasing if CSI<1, CSI=1 or CSI>1, respectively. In a preliminary analysis based on a visual examination of figures depicting the response obtained at two locations, the CSI was found suitable for studying climate change effects (Rigamonti et al, 2014b).

2.3. *Autocorrelation analysis*

To correct for the influence of the abrupt temperature shift occurring in the late 1980s (Mariani et al., 2012), we deducted 1°C from the daily maximum and minimum temperatures, after 1987, in all data sets. Autocorrelation is the similarity between observations as a function of the time lag between them. For visual examination, the partial CSI autocorrelations, as obtained by the SPSS software package (IBM Software Group, 2016) for each area, are depicted in Figure 2. To test whether the autocorrelations of CSI values over differently lagged years are different from zero, the Lagrange multiplier based Breusch-Godfrey test (Breusch, 1978; Godfrey, 1978) is used since Rois et al. (2012) consider it as the most appropriate test for detecting autocorrelation in dynamic models. The number of lags reported is limited to 13 for Swiss locations and 10 for the other locations to limit the analysis to statistically-reliable data series. The statsmodels module of the PYTHON programming language (Seabold and Perktold, 2010) computes the Breusch-Godfrey test statistics for time lags, compares it with the χ^2 distribution and produces lag-specific *p*-values. If the *p*-value exceeds the standard significance level of 0.05, the null hypothesis of no autocorrelation is not rejected.

2.4. Regression analysis

To test the hypothesis that the time series of CSI values undergo gradual and abrupt temperature changes, we evaluated the regression model

$$CSI(t,D) = a_0 + b_1 t + b_2 D \qquad [3]$$

where a_0=intercept, t=time in years beginning with year zero, b_1=regression coefficient reflecting a gradual change through time of CSI values, D=dummy variable representing the temperature shift (D=0 before and D=1 after 1987); b_2 = regression coefficient for the dummy variable that separates the time periods into two sub-groups. Note that $b_1 > 0$ and $b_2 > 0$ at the $P=0.01$ level of significance indicate both gradual and abrupt changes in CSI and confirm the validity of a sloped step model (SSM); if either b_1 or b_2 are not different from 0 at the $P=0.01$ level of significance, CSI was regressed either on time t or D, and the relationship with the higher correlation coefficient was used to express either a gradual ($b_1>0$) or an abrupt ($b_2> 0$) change at the $P=0.01$ level of significance. To represent abrupt and gradual patterns, reference is made to a flat step model (FSM), and linear trend model (LTM), respectively.

3. Results and Discussion

3.1. Analyses of suitability index time series

Model design and multiannual temperature regimes produced few significant autocorrelations (Table 2). After disregarding two rare cases (lag 13 for Chur, lag 1 for Grenoble), in all areas except

Sondrio, the null hypothesis of no autocorrelation cannot be rejected at the standard significance level of *p*=0.05. In Sondrio, however, the null hypothesis of no autocorrelation has to be rejected for the first three decreasing partial autocorrelations and the next three increasing partial autocorrelations (Figure 2). The decreasing positive effect followed by the decreasing negative effect appearing in only 1 out of 10 cases (Table 2) is difficult to explain without detailed studies of demographic processes affecting the long-term dynamics of *S. titanus* populations. Undoubtedly, more cases than considered in this paper are required to ascertain the appearance of few significant autocorrelations in CSI time series and find explanations for distinct pattern as exemplified by the Sondrio case. The rare appearance of significant autocorrelations in most cases and a distinct pattern in one case only are presumably insufficient to sustain a dependency of observations that, in a statistical analysis, would violate the assumptions for statistical inference (Bence, 1995; Boyce et al., 2010; Monserud and Marshall, 2001). Nevertheless, we take into account the restrictions given by Bence (1995) who studied the effects of temporal dependencies on regression analyses and applied high probability requirements to regression analyses.

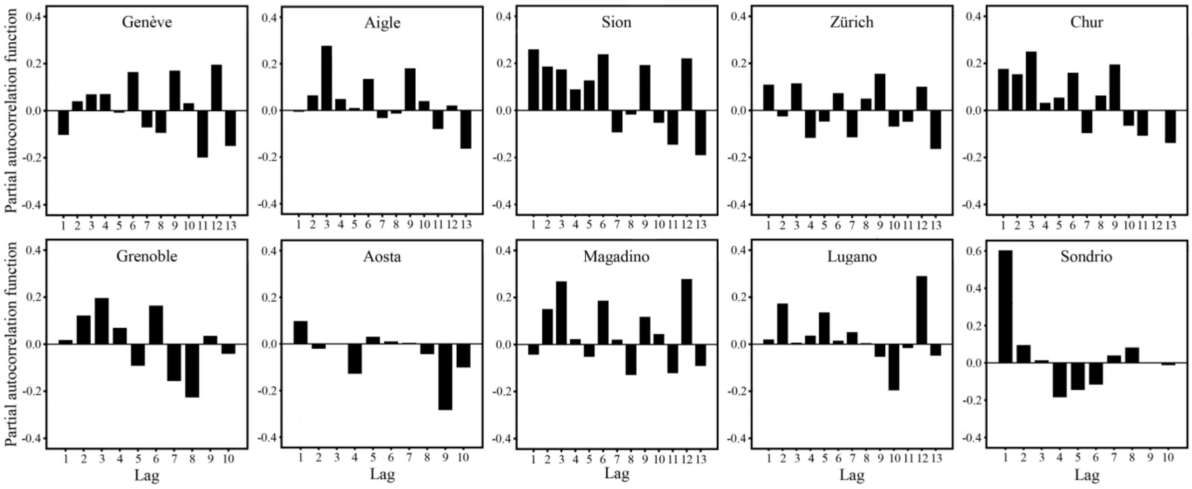

Figure 2. Autocorrelation functions in differently-lagged Climatic Suitability Indices for *S. titanus* in Northwestern Alpine grapevine-growing areas.

Table 2. The *p*-values of the Breusch-Godfrey test for autocorrelation in area-specific Climatic Suitability Indices (CSI) for *S. titanus* in Northwestern Alpine grapevine-growing areas. If the *p*-value is smaller than the standard significance level of 0.05 (numbers in bold), the null hypothesis of no autocorrelation is rejected (n.c. = not computed).

Lag	Genève	Aigle	Sion	Zürich	Chur	Grenoble	Aosta	Magadino	Lugano	Sondrio
1	0.1812	0.4103	0.0904	0.7810	0.8587	**0.0302**	0.1517	0.3404	0.4930	**0.0002**
2	0.3538	0.3972	0.2145	0.8909	0.8900	0.0706	0.2780	0.5163	0.7121	**0.0010**
3	0.5084	0.4321	0.3784	0.9647	0.9341	0.1165	0.4494	0.7112	0.6624	**0.0031**
4	0.6768	0.5330	0.4400	0.8244	0.9782	0.2057	0.4665	0.7062	0.7948	**0.0058**

5	0.6681	0.5900	0.4468	0.7490	0.9547	0.2827	0.2997	0.6894	0.7560	**0.0102**
6	0.7461	0.3884	0.5404	0.7660	0.7344	0.2725	0.2995	0.7588	0.8292	**0.0172**
7	0.6530	0.4388	0.4159	0.4190	0.6790	0.3194	0.4748	0.8252	0.8700	**0.0305**
8	0.4396	0.5432	0.3478	0.5160	0.7569	0.2880	0.4674	0.6484	0.8787	**0.0483**
9	0.5199	0.3368	0.2741	0.4324	0.3854	0.3357	0.1454	0.7372	0.6860	0.0752
10	0.6047	0.4244	0.3448	0.5195	0.4774	0.4184	0.1860	0.7533	0.6624	0.1108
11	0.3544	0.4979	0.4064	0.6090	0.5687	n.c.	n.c.	0.7896	0.7437	n.c.
12	0.3763	0.5788	0.4064	0.2786	0.5694	n.c.	n.c	0.8493	0.7998	n.c.
13	0.2095	0.1355	0.1660	0.0660	**0.0378**	n.c.	n.c.	0.6759	0.8506	n.c.

3.2. Climatic suitability patterns

Table 3 shows a generally-improving climatic suitability through time across areas within the region under study. Regarding the second observation on the reflection of gradual and abrupt temperature changes in gradual and abrupt changes in CSI, however, no generalization across areas is possible. Namely, Table 3 reports significant b_1 and b_2 values that indicate both gradual and abrupt changes of CSI in the Sion and the Magadino areas only. In these areas, a sloped step model (SSM), describing CSI by a linear trend model in the two sub-periods before and after 1988, is adequate. Table 3 also reports significant b_2 but insignificant b_1 values, indicating abrupt changes in the Grenoble, Aosta and Sondrio areas. These changes are adequately represented by an FSM. On the other hand, an LTM is appropriate to describe the patterns of CSI in the remaining regions The differences indicate that predictions of climate change on climatic suitability of grapevine-growing areas should be done carefully.

Table 3. Regression statistics for selecting the adequate model to describe the response of the Climatic Suitability Index in the different regions. The applicability of a sloped step model (SSM) is tested in all regions; for Sion and Magadino, the SSM remained valid, while a flat step model (FSM) is selected for Grenoble, Aosta and Sondrio, and a linear trend model (LTM) is appropriate for Genève, Aigle, Lugano, Zürich and Chur. (n = simulation period in years, R^2 = coefficient of determination, F = F value, a, b_1, b_2 = parameters of regression model [1], t = Student's t, if $t > t_{0.05(2),\,(n-2)}$ then $H_0{:}b_i=0$ is rejected for b_1, and b_2 (marked with *), *cf.* Zar (1974)).

Site	*n*	Model type	R^2, *F*	*A*	b_1	b_2
Genève	53	SSM	0.93E-01 F=2.56	0.19	0.40E-02 t=1.628	-0.47E-01 t=0.627
		LTM	0.86E-01 F=4.77	0.21	0.27E-02* t=2.184	
Zürich	53	SSM	0.47 F=22.30	-0.59E-02	0.61E-02* t=2.719	0.48E-01 t=0.695
		LTM	0.47 F=44.57	-0.18E-01	0.75E-02* t=6.676	
Aigle	53	SSM	0.34	0.77E-01	0.49E-02	0.67E-01

			F=13.08		t=1.819	t=0.815
		LTM	0.33 F=25.66	0.61E-01	0.68E-02* t=5.066	
Sion	53	SSM	0.76 F=80.50	0.97E-01	0.62E-02* t=3.101	0.23* t=3.466
Chur	53	SSM	0.59 F=36.55	-0.45E-01	0.88E-02* t=3.885	0.31E-01 t=0.444
		LTM	0.59 F=74.07	-0.53E-01	0.97E-02* t=8.606	
Grenoble	39	SSM	0.41 F=12.51	0.27	-0.24E-02 t=-0.586	0.99E-01* t=3.344
		FSM	0.40 F=25.12	0.25		0.28* t=5.012
Aosta	39	SSM	0.21 F=4.730	0.52	-0.12E-02 t=-0.170	0.32 t=1.911
		FSM	0.21 F=9.69	0.51		0.30* t=3.113
Magadino	53	SSM	0.57 F=33.78	0.53	0.31E-02* t=2.164	0.20* t=2.091
Lugano	53	SSM	0.18 F=5.43	0.83	0.52E-02 t=1.267	0.53E-01 t=0.424
		LTM	0.18 F=10.86	0.82	0.67E-02* t=3.295	
Sondrio	39	SSM	0.11 F=2.28	0.69	-0.30E-02 t=-0.534	0.22 t=1.622
		FSM	0.11 F=4.37	0.68		0.16* t=2.089

The appropriateness of the area-specific models has to be evaluated under two aspects. First, the temperature recordings have been made at weather stations often located at some distance from the actual vineyards (Genève, Zürich, Chur, Grenoble, Aosta). Since the vineyards have been established in favorable sites inside the areas, the temperatures experienced by *S. titanus* could have been underestimated. However, we do not expect a time effect on the reliability of the temperature measurements and hence, considered the responses to temperature changes as valid. Second, the regions with CSI undergoing only abrupt changes are separated from the other regions by three qualities. i) there was no information on possible changes in the measuring technique available for both Grenoble and Aosta and hence, we used raw data. As previously mentioned, no changes in the measuring procedure occurred at Sondrio. ii) gaps in the data sets for Aosta and Sondrio were filled by modified data from nearby weather stations as explained above. iii) the simulation period at Grenoble, Aosta and Sondrio were restricted to 39 years as opposed to 53 years of other regions. The influence of the reliability of temperature measurements and the influence of the duration (see below) on the patterns of CSI is unknown. Unlikely, however, these influences are responsible for the pattern and hence, the applicability of the FSM.

If we accept an area-specific response of the suitability index, the responses of CSI in Table 3 and Fig. 3, depicting the CSI time series for each of the 10 areas, do not correspond to the responses obtained when using yearly mean temperatures. Namely, Mariani et al. (2012) stated that the yearly temperatures predicted by an LTM are less accurate than the predictions by the equally well-performing SSM and FSM models. Nevertheless, the different performances of the SSM, the FSM and the LTM to describe the patterns of CSI and the analyses of yearly temperatures is not unexpected. This is because the temperature influences CSI through a series of uncorrelated curvilinear functions (Rigamonti et al., 2014a). The influence of these functions on CSI patterns becomes clear in a highly variable temperature environment. Hence, the results support the hypothesis that the selection of a region located at the northern limit of the geographic distribution with areas characterized by high temperature variability facilitates the study of abrupt and gradual climate change effects. It also confirms the utility of weather-driven PBDMs, operating at small-time resolutions, for investigating climate change effects on population dynamics and species distributions.

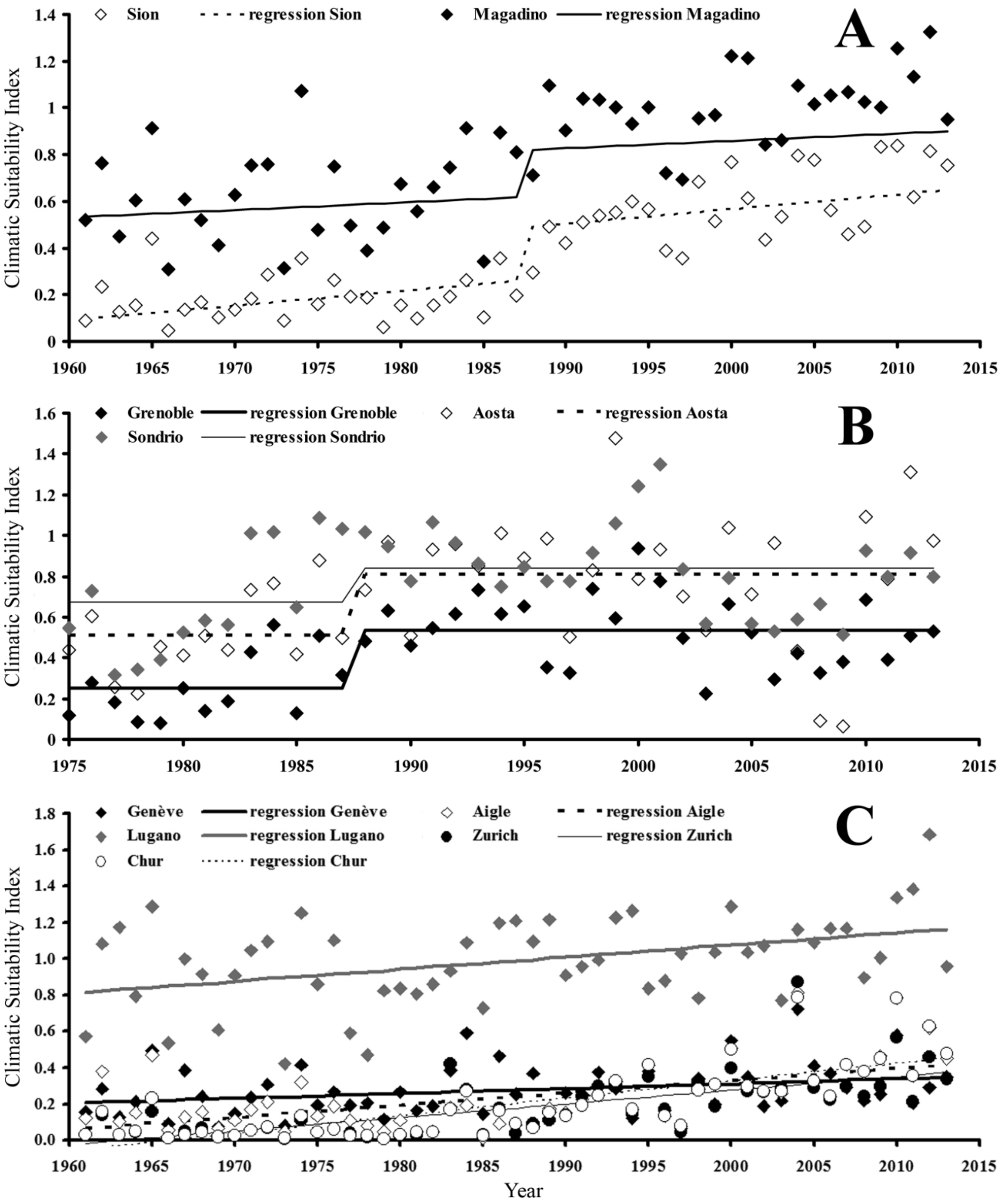

Figure 3. The simulated Climatic Suitability Index (CSI) for Sion and Magadino (A), Grenoble, Aosta and Sondrio (B) and Genève, Aigle, Lugano, Zürich and Chur (C) by a sloped step model (SSM), a flat step model (FSM), and linear trend model (LTM), respectively.

The CSI patterns appear to depend on whether the area was suitable or not for *S. titanus* prior to this investigation. In unsuitable areas with initial values close to zero, the changes were negligible or too small to allow *S. titanus* to settle and reach an economically relevant pest status in the foreseeable future (Zürich, Chur), while in areas characterized by more favorable initial conditions the temperature changes led to continuously-increasing CSIs (Aosta, Sondrio) with favorable conditions appearing in the 1990s.

In areas already suitable in the 1960s, the model predicts a small increase in CSIs (Lugano). There are indications that, in warmer areas located at the southern limits of *S. titanus* distribution, the temperature increase may lead to a decrease in CSIs that indicates negatively-affected population development due by high temperatures.

3.3. Pest management considerations

In the different areas of the region under study, institutions charged with pest control may take into account the following aspects. In the South, the Lugano and Magadino areas have been colonized early and face increasingly favorable conditions for *S. titanus* development and possibly FD transmission. They may represent areas that were colonized early without spreading to other regions because of unfavorable conditions for colonization. The other areas in the South (Aosta and Sondrio) became suitable after the climate shift in 1988 and may represent areas colonized in the second wave of spread (Bertignono et al., 2006; Posenato et al., 2001). The spread will likely lead to the colonization of the neighboring Aigle, Sion and Grenoble areas, if not yet colonized. Institutions charged with pest control in the areas of Zürich and Chur should note that their areas are unlikely to provide suitable climate conditions any time soon.

In other regions, institutions charged with pest control may take note that CSI information complements monitoring efforts by EPPO and local phytosanitary organizations to explain the past, current and future colonization of grapevine-growing areas. However, pest control institutions should take into account that the CSI is derived from a PBDM characterized by thresholds and several non-linear temperature-dependencies, and the extension of the here obtained results to other areas is questionable. Rather, they are advised to run the model with temperatures specific to the areas of interest for representing infestation patterns and assessing the risk of colonization. In doing so, they may acquire a quantitative tool that has been proven useful in supervised pest management in already colonized areas (Jermini et al., 2013; Prevostini et al., 2013).

4. Concluding Remarks

The Northwestern Alpine region, located near the northern limits of the actual geographical distribution of *S. titanus*, with grapevine-growing areas characterized by high temperature variability, was appropriate for studying the effects of gradual and abrupt temperature changes on the suitability of the areas to *S. titanus*. From a methodological standpoint, an annual Climatic Suitability Index (CSI) developed on the basis of a physiologically-based demographic model was useful for providing critical area-specific information on changing pest presence over time periods with changing climates. Furthermore, time series analyses of CSIs were instrumental to obtain the information required for the design and use of regression models aiming at quantifying the effect of temperature changes on CSIs. Thus, the methodology was useful to study the influence of abrupt and gradual temperature changes on the climate suitability of Northwestern Alpine grapevine-growing areas for *S. titanus*.

In general, the climatic suitability of all areas tends to improve during the study period. Across the areas, however, the gradual and abrupt temperature changes are not consistently reflected in gradual and abrupt CSI changes. The different area-specific CSI patterns may be due to the non-linear functions relating *S. titanus* life table parameters to temperature in the simulation model. The respective relationships may be responsible for the CSI patterns arising under variable area-specific temperature regimes. This indicates that the results of this study cannot be generally applied to areas located within other regions and similar studies are required to elucidate respective temperature change effects. Furthermore, it suggests the possibility that climate change may change the area-specific climatic suitability to either the advantage or disadvantage of *S. titanus*.

From a pest management standpoint, the study allows making recommendations to pest management institutions located in the region. Specifically, the methodology allows the assessment of colonization risk and the undertaking of adequate pest control measures. The application of the methodology to areas outside the Northwestern Alpine region holds the promise to provide decision-support to a wider range of institutions charged with *S. titanus* control then considered here.

Author contributions

IE Rigamonti, overall project coordinator with leading role in model parametrization.

L Mariani, developed the plant phenology model, oversaw the linkage to the pest population model and defined spatial scale resolution and extent.

G Cola, participated in crop and pest model implementation, and in definition and use of the Climatic Suitability Index (CSI).

M Jermini, responsible for linking the project team with the viticultural practice, the agricultural research institutions, the extension services and the Swiss Meteorological Service.

J Baumgärtner, responsible for the design of plant and pest population system models.

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Table 1. Information on the Northwestern Alpine region with the different areas in that the development of Grape leafhopper *Scaphoideus titanus* populations was simulated. The homogenized daily temperature maxima and minima for the Swiss meteorological stations were kindly made available by MeteoSwiss (National Weather Service of Switzerland). Additional temperature data were retrieved from the Texas A&M University, Beaumont, USA (https://beaumont.tamu.edu/ClimaticData/), the National Climate Data Centre (NCDC), Climate Services Branch (USA) and the Fojanini Foundation (FFS), Sondrio (I). Gaps in the data sets for Aosta and Sondrio were filled by using information from Torino Caselle (I) and Poschiavo (CH), respectively.

Site specification	Area and meteorological station	Beginning of simulations	Latitude N (degrees)	Longitude E (degrees)	Altitude (meters above sea level)	Source for temperatures data
Western and Northern areas	Genève (CH)	1959	46.250	6.133	416	MeteoSwiss
	Aigle (CH)		46.333	6.917	383	
	Sion (CH)		46.217	7.317	428	
	Zürich (CH)		47.383	8.567	569	
	Chur (CH)		46.867	9.533	533	
Western and Southern areas	Grenoble (F)	1973	45.367	5.333	386	NCDC
	Aosta (I)		45.740	7.376	547	Texas A&M
	Magadino (CH)	1959	46.167	8.883	198	MeteoSwiss
	Lugano (CH)		46.000	8.967	276	
	Sondrio (I)	1973	46.168	9.853	323	FFS

Table 2. The *p*-values of the Breusch-Godfrey test for autocorrelation in area-specific Climatic Suitability Indices (CSI) for *S. titanus* in Northwestern Alpine grapevine growing areas. If the *p*-value is smaller than the standard significance level of 0.05 (numbers in bold), the null hypothesis of no autocorrelation is rejected (n.c. = not computed).

Lag	Genève	Aigle	Sion	Zürich	Chur	Grenoble	Aosta	Magadino	Lugano	Sondrio
1	0.1812	0.4103	0.0904	0.7810	0.8587	**0.0302**	0.1517	0.3404	0.4930	**0.0002**
2	0.3538	0.3972	0.2145	0.8909	0.8900	0.0706	0.2780	0.5163	0.7121	**0.0010**
3	0.5084	0.4321	0.3784	0.9647	0.9341	0.1165	0.4494	0.7112	0.6624	**0.0031**
4	0.6768	0.5330	0.4400	0.8244	0.9782	0.2057	0.4665	0.7062	0.7948	**0.0058**
5	0.6681	0.5900	0.4468	0.7490	0.9547	0.2827	0.2997	0.6894	0.7560	**0.0102**
6	0.7461	0.3884	0.5404	0.7660	0.7344	0.2725	0.2995	0.7588	0.8292	**0.0172**
7	0.6530	0.4388	0.4159	0.4190	0.6790	0.3194	0.4748	0.8252	0.8700	**0.0305**
8	0.4396	0.5432	0.3478	0.5160	0.7569	0.2880	0.4674	0.6484	0.8787	**0.0483**
9	0.5199	0.3368	0.2741	0.4324	0.3854	0.3357	0.1454	0.7372	0.6860	0.0752
10	0.6047	0.4244	0.3448	0.5195	0.4774	0.4184	0.1860	0.7533	0.6624	0.1108
11	0.3544	0.4979	0.4064	0.6090	0.5687	n.c.	n.c.	0.7896	0.7437	n.c.
12	0.3763	0.5788	0.4064	0.2786	0.5694	n.c.	n.c	0.8493	0.7998	n.c.
13	0.2095	0.1355	0.1660	0.0660	**0.0378**	n.c.	n.c.	0.6759	0.8506	n.c.

Table 3. Regression statistics for selecting the adequate model to describe the response of the Climatic Suitability Index in the different regions. The applicability of a sloped step model (SSM) is tested in all regions; for Sion and Magadino, the SSM remained valid, while a flat step model (FSM) is selected for Grenoble, Aosta and Sondrio, and a linear trend model (LTM) is appropriate for Genève, Aigle, Lugano, Zürich and Chur. (*n* = simulation period in years, R^2 = coefficient of determination, F = F value, *a*, b_1, b_2 = parameters of regression model [1], *t* = Student's t, if *t* $>t_{0.05(2),\,(n-2)}$ then $H_0{:}b_i=0$ is rejected for b_1, and b_2 (marked with *), *cf.* Zar (1974)).

Site	*n*	Model type	R^2, *F*	*a*	b_1	b_2
Genève	53	SSM	0.93E-01 F=2.56	0.19	0.40E-02 t=1.628	-0.47E-01 t=0.627
		LTM	0.86E-01 F=4.77	0.21	0.27E-02* t=2.184	
Zürich	53	SSM	0.47 F=22.30	-0.59E-02	0.61E-02* t=2.719	0.48E-01 t=0.695
		LTM	0.47 F=44.57	-0.18E-01	0.75E-02* t=6.676	
Aigle	53	SSM	0.34 F=13.08	0.77E-01	0.49E-02 t=1.819	0.67E-01 t=0.815
		LTM	0.33 F=25.66	0.61E-01	0.68E-02* t=5.066	
Sion	53	SSM	0.76 F=80.50	0.97E-01	0.62E-02* t=3.101	0.23* t=3.466
Chur	53	SSM	0.59 F=36.55	-0.45E-01	0.88E-02* t=3.885	0.31E-01 t=0.444
		LTM	0.59 F=74.07	-0.53E-01	0.97E-02* t=8.606	
Grenoble	39	SSM	0.41 F=12.51	0.27	-0.24E-02 t=-0.586	0.99E-01* t=3.344
		FSM	0.40 F=25.12	0.25		0.28* t=5.012
Aosta	39	SSM	0.21 F=4.730	0.52	-0.12E-02 t=-0.170	0.32 t=1.911
		FSM	0.21 F=9.69	0.51		0.30* t=3.113
Magadino	53	SSM	0.57 F=33.78	0.53	0.31E-02* t=2.164	0.20* t=2.091
Lugano	53	SSM	0.18 F=5.43	0.83	0.52E-02 t=1.267	0.53E-01 t=0.424
		LTM	0.18 F=10.86	0.82	0.67E-02* t=3.295	
Sondrio	39	SSM	0.11 F=2.28	0.69	-0.30E-02 t=-0.534	0.22 t=1.622
		FSM	0.11 F=4.37	0.68		0.16* t=2.089

FIGURE LEGENDS

Figure 1. The Northwestern Alpine region with the different areas in that the development of Grape leafhopper *Scaphoideus titanus* populations was simulated.

Figure 2. Autocorrelation functions in differently-lagged Climatic Suitability Indices for *S. titanus* in Northwestern Alpine grapevine growing areas.

Figure 3. The simulated Climatic Suitability Index (CSI) for Sion and Magadino (A), Grenoble, Aosta and Sondrio (B) and Genève, Aigle, Lugano, Zürich and Chur (C) by a sloped step model (SSM), a flat step model (FSM), and linear trend model (LTM), respectively.

2) REVISED MANUSCRIPT WITHOUT CHANGES MARKED

Abrupt and gradual temperature changes influence on the climatic suitability of Northwestern Alpine grapevine-growing regions for the invasive Grape leafhopper *Scaphoideus titanus* Ball (Hemiptera, Cicadellidae)

Ivo Ercole Rigamonti[a,*], Luigi Mariani[b], Gabriele Cola[b], Mauro Jermini[c], Johann Baumgärtner [d]

[a] DeFENS *Department of Food, Environmental and Nutritional Sciences (DeFENS), Università degli Studi di Milano, Via Celoria 2, I-20133 Milano, Italy. E-mail: ivo.rigamonti@unimi.it*

[b] *Dipartimento di Scienze Agrarie e Ambientali – Produzione, Territorio, Agroenergia (DISAA), Via Celoria 2, I-20133 Milano, Italy. E-mail: luigi.mariani@unimi.it*

[c] *Agroscope, Centro di Cadenazzo (TI). A Ramél, 18, CH-6593 Cadenazzo, Switzerland. E-mail: mauro.jermini@agroscope.admin.ch*

[d] CASAS *Center for the Analysis of Sustainable Agricultural Systems (CASAS), Kensington (CA) 94707 United States of America. E-mail: jbaumgaertner@yahoo.com*

[*] Corresponding author

ABSTRACT

The paper aims to elucidate the influence of abrupt and gradual climate changes on the suitability for colonization of *Scaphoideus titanus* populations in grapevine-growing areas of the Northwestern Alpine region. This study spans several decades of temperature recordings and is carried out in ten grapevine-growing areas. A time-varying distributed delay with attrition model, linked to a grapevine phenology model, is used to simulate the development of *S. titanus* populations and produce an annual Climatic Suitability Index (CSI). Area-specific CSI time series were obtained. The Breusch-Godfrey test revealed few significant partial autocorrelations in nine areas and the occurrence of six consecutive - first decreasing and then increasing - partial correlations in one case only. The occurrence of abrupt and gradual changes of the index were studied via multiple least square regression analyses. In general, the climatic suitability of all areas tended to improve through time. However, gradual and abrupt temperature changes were not consistently reflected in gradual and abrupt CSI patterns: abrupt and gradual CSI changes were observed in two areas, abrupt changes were detected in three areas, and exclusively gradual changes in the remaining five. Pest control institution of the region under study may deal with different scenarios of pest status such as long-time presence and increasing risks, high colonization risks or limited colonization risks for the foreseeable future. Institutions charged with pest control elsewhere are advised to use a mechanistic demographic model to study area-specific infestation patterns and colonization risks because the results obtained here cannot be transferred to other areas without site-specific evaluations.

Key words: climate change, physiologically-based demographic model, climatic suitability, forecast, colonization risk

1. Introduction

Many studies have been undertaken to document changing climates at different spatial and temporal scale extents and resolutions (Anisimov et al., 2013; Anwer, 2015; Portmann et al., 2009; Reiter et al., 2012). According to the global dataset HadCRUT4 (Morice et al., 2012), global temperatures increased by +0.85°C since 1850, while the main part of this increase (about +0.5°C) occurred in the period 1977-1998. During the same period, European temperatures increased by about +1.3°C (Mariani et al., 2012).

Voluminous literatures deal with the effects of changing climates on populations, communities and ecosystems (Graham and Grimm, 1990; Gutierrez et al., 2008; Parmesan, 2006; Yates et al., 2010). The temperature component of climate change is particularly important for poikilothermic organisms whose development depend on body temperatures that vary broadly with environmental temperatures (May, 2005). The methods used to investigate the impact of changing temperatures on population development and geographical distributions of poikilotherms fall broadly into two categories. The first category comprises species distribution models (SDMs) that combine observations of species occurrence or abundance with environmental estimates to characterize climatically the species to gain ecological and evolutionary insights and to predict distributions across landscapes, sometimes requiring extrapolation in space and time (Elith and Leathwick, 2009).

The second category of interest here comprises of physiologically-based demographic models (PBDMs), built on mechanistic representations of poikilothermic population development. PBDMs model the biology of the target species, and, when driven by weather, predict the phenology, age-structured dynamics, and distribution of the species across wide geographic areas independent of the availability of distribution information (Ponti et al., 2015). Since weather is an important driver for PBDMs, they are particularly appropriate for dealing with climate change effects.

In the case of pests and their abundance, the capacity of PBDMs to predict the potential geographic distribution under past, current and future climate change scenarios is fundamental in developing sound policies for their control (Gutierrez and Ponti, 2013; Ponti et al., 2015). Their ability to represent the regional suitability and the spatial distributions of insect pests on explanatory grounds is a complement to the work of international organizations such as the European and Mediterranean Plant Protection Organization (EPPO) that monitors and delineates the spread of pests and provides directions on quarantine pests management (Smith et al., 1996).

The Nearctic leafhopper *Scaphoideus titanus* Ball (Hemiptera, Cicadellidae), vector of the Grapevine Flavescence dorée (FD) phytoplasma, is a key pest of grapevine in Europe. *S. titanus* was accidentally introduced in France in the 1950s (Bonfils and Schvester 1960; Schvester et al. 1961, 1962a, 1962b) and gradually extended its area of distribution. Actually, it is present throughout Western and Southeastern Europe from the Atlantic Ocean to the Black Sea, and the area of distribution is still expanding (Chuche and Thiéry, 2014; Tóthová et al., 2015).

Since the spread of *S. titanus* and FD continues, pest control institutions in regions with high risks of being invaded and colonized should prepare in time for intensive monitoring and expensive control operations. The risk of invasion and colonization depends on the dispersal ability of *S. titanus* and the suitability of the newly-invaded area. After its accidental introduction into Europe, the spread was so fast that most grapevine-growing areas should have been colonized by now. This is not the case, however, and the ongoing expansion suggests that the influence of the high dispersal ability on distribution patterns is constrained by other factors. Empirical and theoretical evidence suggest that climate, undergoing the aforementioned changes since the time of *S. titanus* introduction, plays an important role. In fact, Rigamonti et al. (2014b) found that the climate in two Swiss grapevine-growing areas changed in favor of *S. titanus* and hypothesized that the climatic suitability determines the colonization success and largely explains the changing geographical distribution in Europe.

Since the temperature regime in European grapevine-growing regions has and will undergo changes (IPCC, 1996), a previously-unsuitable region may become suitable through time. Mariani et al. (2012) viewed climate variability as the superimposition of gradual and abrupt changes. Gradual changes can be interpreted as the effect of progressive changes in forcings (IPCC, 2013), while abrupt changes are the result of sharp changes in the frequency and persistence of different circulation patterns (Sneyers et al., 1993). During the period 1977-1998, European temperatures increased by about 1.3°C, while the main part of this increase was observed at the end of the 1980s, where an abrupt change is evident on thermal time series (Mariani et al., 2012).

The paper aims to elucidate the effects of abrupt and gradual climate change on *S. titanus* population development through an analysis of long-term suitability patterns in a geographically-restricted region with high temperature variability among grapevine-growing areas. For each area, a PBDM provides a long-term time series of annual suitability indices whose similarity, depending on time lags, prepares the ground for testing the appearance of abrupt and gradual changes in area-specific patterns of the suitability index.

2. Materials and Methods

2.1. Study sites and temperature recordings

The suitability of grapevine-growing regions for *S. titanus* colonization is assessed in a region referred to as Northwestern Alps (Figure 1, Table 1). This region has been selected because of its location near the northern limits of *S. titanus* distribution and the high climatic variability among grapevine growing areas therein. Both aspects are considered as useful prerequisites for elucidating the effects of climate change on the suitability of the region for colonization by *S. titanus*. Though outside the Alpine zone, we included the Zürich area in the analysis. At meteorological stations located in the different areas, daily temperature maxima and minima were readily available over 54 or 39 years periods (Table 1). To simplify the geographical notations, the location name is used as a name for the area. The locations of all the weather stations except Grenoble, are within or close to the grapevine growing areas.

The temperatures measured at the Swiss locations (Zürich, Lugano, Genève, Aigle, Sion, Chur and Magadino) are referred to as revised data retrieved from the data bank of the Swiss National Weather Service (MeteoSwiss). Namely, during the measuring periods, the position of the temperature sensors was often changed and new equipment were adopted. MeteoSwiss corrected for these changes (Begert et al., 1999, 2003, 2005) and kindly made available a data set referred to as homogenized data. Most of the data for Sondrio were kindly made available by Dr. M. Salvetti (Fondazione Fojanini, Sondrio) and reportedly did not require any correction. In the absence of respective information, the raw data measured at the Aosta and Grenoble stations obtained from Yang et al. (2010) at [https://beaumont.tamu.edu/ClimaticData/] and from the US weather service at [http://www.geodata.us/weather/], respectively, were used in the analyses. The gaps in the Sondrio and Aosta data sets were respectively filled by linear regression of Sondrio data on data measured at the nearby Poschiavo station operated by MeteoSwiss, and linear regression of Aosta data were regressed from data measured at the Torino-Caselle station.

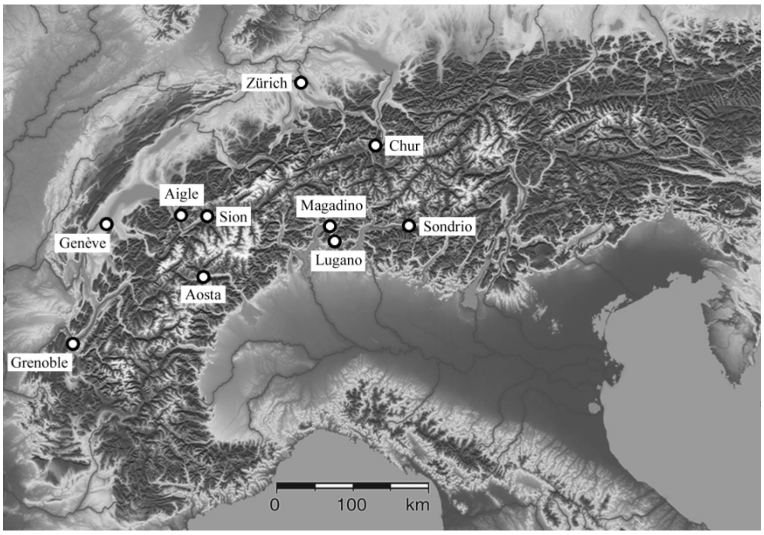

Figure 1. The Northwestern Alpine region with the different areas in that the development of Grape leafhopper *Scaphoideus titanus* populations was simulated.

Table 1. Information on the Northwestern Alpine region with the different areas in that the development of Grape leafhopper *Scaphoideus titanus* populations was simulated. The homogenized daily temperature maxima and minima for the Swiss meteorological stations were kindly made available by MeteoSwiss (National Weather Service of Switzerland). Additional temperature data were retrieved from the Texas A&M University, Beaumont, USA (https://beaumont.tamu.edu/ClimaticData/), the National Climate Data Centre (NCDC), Climate Services Branch (USA) and the Fojanini Foundation (FFS), Sondrio (I). Gaps in the data sets for Aosta and Sondrio were filled by using information from Torino Caselle (I) and Poschiavo (CH), respectively.

Site specification	Area and meteorological station	Beginning of simulations	Latitude N (degrees)	Longitude E (degrees)	Altitude (meters above sea level)	Source for temperatures data
Western and Northern areas	Genève (CH)	1959	46.250	6.133	416	MeteoSwiss
	Aigle (CH)		46.333	6.917	383	
	Sion (CH)		46.217	7.317	428	
	Zürich (CH)		47.383	8.567	569	
	Chur (CH)		46.867	9.533	533	
Western and Southern areas	Grenoble (F)	1973	45.367	5.333	386	NCDC
	Aosta (I)		45.740	7.376	547	Texas A&M
	Magadino (CH)	1959	46.167	8.883	198	MeteoSwiss
	Lugano (CH)		46.000	8.967	276	
	Sondrio (I)	1973	46.168	9.853	323	FFS

2.2. Model characteristics and computation of the Climatic Suitability Index

Basic model development. Rigamonti et al. (2011, 2014a) took into account the high variability in development times of nymphs relative to the mean (*cf.* Di Cola et al., 1999) and linked the appropriate "time-varying distributed delay with attrition" variant of the widely used time distributed delay models (Gutierrez, 1996; Gutierrez et al., 2015; Manetsch, 1976; Vansickle, 1977; Welch, 1984; Welch et al., 1978) to the grapevine plant phenology model of Mariani et al. (2013). They noticed that the *S. titanus* population model was appropriate for long-term studies since it allows the representation of multi-cohort and multi-generation poikilothermic population development. The model represents the flow of individuals through diapausing egg, post-diapausing egg, nymph and adult life stages

$$\frac{dr_{ji}(t)}{dt} = \frac{k_j}{DEL_j(t)}\left[r_{ji-1}(t) - r_{ji}(t)\left(1 + AR_j(t)\frac{DEL_j(t)}{k_j} + \frac{d\,DEL_j(t)}{k_j dt}\right)\right] \qquad [1]$$

$$j = 1, 2, 3, 4$$

$$i = 1, 2, \ldots, k_j$$

where t is time [days], $r_{ji}(t)$ is the transition rate of the *i-th* substage in the *j-th* life stage, k_j is the number of delay substages in the *j-th* life stage, $DEL_j(t)$ is the time-dependent developmental time (days) in the absence of losses in the *j-th* life stage, and $AR_j(t)$ is the time dependent proportional change or attrition in the *j-th* life stage. The occurrence $Q_j(t)$ of individuals in each life stage can be obtained from

$$Q_j(t) = \sum_{i=1}^{k_j} \frac{DEL_j(t)}{k_j} r_{ji}(t) \qquad [2]$$

Rigamonti et al. (2011, 2014a) discretized model [1] according to Abkin and Wolf (1976) and used a 1-hour time step length.

Model components. The following aspects briefly summarize model components detailed by Rigamonti et al. (2011, 2014a).

i) The stage-specific developmental rate $d_j,[T(t)]$, *i.e.,* the inverse of developmental time $DEL[T(t)]$, is temperature-dependent between lower and upper thresholds, and 0.001 or 0.01, for diapausing and non-diapausing stages respectively, outside this range. The time-dependent temperatures $T(t)$ are obtained by forcing a cosine function through daily temperature maxima and minima.

ii) The stage-specific survival rate $s_j[T(t)]$ is composed of a) a temperature-dependent survival, modeled through attrition $AR[T(t)]$, operating between lower and upper thresholds, b) a temperature-dependent survival below the lower threshold, and c) mortalities of non-diapausing life stages between the grapevine plant phenological stages BBCH 93 (beginning of leaf fall) and BBCH 11 (first leaf unfolded and spread away from shoot) (Lorenz et al., 1994). Before and after these plant stages, nymphs and adults are suffering from an additional mortality of 0.5 % per day.

iii) The reproduction rate $m[T(t)]$ of females becomes the input into the diapausing egg stage. It is the product of the reproductive profile, *i.e.* the relative age-specific fecundity rate and the temperature-dependent reproductive potential $F(T)$, *i.e.*, the total number of eggs laid by a female (*cf.* Curry and Feldman, 1987) ($m[T(t)]>0$ between the lower and an upper thresholds and $m[T(t)]=0$ outside this range).

iv) The model is initialized with a flow of hatching eggs into the nymphal stage (see below). The use of a single data set for model initialization at other locations may negatively affect the model performance in the first years. Therefore, the subsequent analysis disregards the first computations of the CSI. The simulations are carried out over the time periods specified below.

Model parametrization. The respective temperature-dependent rate functions (i, ii, iii) were developed and parametrized under constant temperatures but used under time-varying temperature regimes. Briefly, temperature-dependent values for the developmental time and mortality of nymphs older than the first stage were obtained from age-specific life tables established under various but constant temperatures (Rigamonti et al., 2011, 2014a). The developmental time of post-diapausing eggs, and the developmental time and mortality of first stage nymphs were obtained from field observations carried out in four vineyards located in Southern Switzerland over a period of three years, whereas data from literature were used to estimate adult female developmental time and associated variability. The respective field data, expert opinions and literature information were used to compute diapause periods. A linear model for first stage nymphs and the non-linear model of Brière et al. (1999) for the remaining stages were used to represent the temperature-dependency of developmental rates. The developmental rate of the widely-cultivated Chardonnay variety, and the phenological stages BBCH 11 and 93, were obtained from the model of Mariani et al. (2007, 2013) and calibrated with information obtained in vineyards located in Southern Switzerland.

Reproduction is composed of the reproductive profile f_i, *i.e.*, the relative age-specific fecundity rate in the *i*-th substage, and the temperature-dependent reproductive potential $F(T)$, *i.e.*, the total number of eggs laid by a female conditioned on her living throughout the oviposition period (Curry and Feldman, 1987). The substage-independent f_i was estimated on the basis of literature data, whereas a Beta function fitted to literature data represented the temperature-dependency of $F(T)$.

Egg hatching in 2008 was recorded weekly on 20 caged plants in a vineyard. The cumulative proportion of the total number is represented by the cumulative density Weibull function und provided time step-specific inputs (iv) into the delay model.

Model validation is detailed by Rigamonti et al. (2011, 2014a). Over a period of five years, from 2006 to 2010, nymph and adult occurrences were occasionally monitored in five vineyards located in FD-free zones of Western Switzerland (Yvorne, Lutry) and Southern Switzerland (Contone, Biasca, Sessa). Data on nymphs were obtained through the beating tray method, while yellow sticky traps yielded information on adult presence. The plant phenology model was validated with observations made in Southern Switzerland's vineyards,. The model predictions satisfactorily corresponded to field observations and opened the door for the use of the model.

Model use relies on a Climatic Suitability Index calculated as follows. Once the plant has reached the BBCH 11 stage, it is assumed to allow the development of *S. titanus* nymphs. On the day with the first BBCH 11 occurrence, eq. [2] computes, in each year, diapausing and post-diapausing eggs as the only individuals giving rise to the subsequent infestations. The number computed in a particular year is divided by the corresponding number in the previous year to yield a CSI. Population densities are declining, stationary or increasing if CSI<1, CSI=1 or CSI>1, respectively. In a preliminary analysis based on a visual examination of figures depicting the response obtained at two locations, the CSI was found suitable for studying climate change effects (Rigamonti et al, 2014b).

2.3. Autocorrelation analysis

To correct for the influence of the abrupt temperature shift occurring in the late 1980s (Mariani et al., 2012), we deducted 1°C from the daily maximum and minimum temperatures, after 1987, in all data sets. Autocorrelation is the similarity between observations as a function of the time lag between them. For visual examination, the partial CSI autocorrelations, as obtained by the SPSS software package (IBM Software Group, 2016) for each area, are depicted in Figure 2. To test whether the autocorrelations of CSI values over differently lagged years are different from zero, the Lagrange multiplier based Breusch-Godfrey test (Breusch, 1978; Godfrey, 1978) is used since Rois et al. (2012) consider it as the most appropriate test for detecting autocorrelation in dynamic models. The number of lags reported is limited to 13 for Swiss locations and 10 for the other locations to limit the analysis to statistically-reliable data series. The statsmodels module of the PYTHON programming language (Seabold and Perktold, 2010) computes the Breusch-Godfrey test statistics for time lags, compares it with the χ^2 distribution and produces lag-specific *p*-values. If the *p*-value exceeds the standard significance level of 0.05, the null hypothesis of no autocorrelation is not rejected.

2.4. Regression analysis

To test the hypothesis that the time series of CSI values undergo gradual and abrupt temperature changes, we evaluated the regression model

$$CSI(t,D) = a_0 + b_1 t + b_2 D \qquad [3]$$

where a_0=intercept, t=time in years beginning with year zero, b_1=regression coefficient reflecting a gradual change through time of CSI values, D=dummy variable representing the temperature shift (D=0 before and D=1 after 1987); b_2 = regression coefficient for the dummy variable that separates the time periods into two sub-groups. Note that $b_1 > 0$ and $b_2 > 0$ at the $P=0.01$ level of significance indicate both gradual and abrupt changes in CSI and confirm the validity of a sloped step model (SSM); if either b_1 or b_2 are not different from 0 at the $P=0.01$ level of significance, CSI was regressed either on time t or D, and the relationship with the higher correlation coefficient was used to express either a gradual ($b_1>0$) or an abrupt ($b_2> 0$) change at the $P=0.01$ level of significance. To represent abrupt and gradual patterns, reference is made to a flat step model (FSM), and linear trend model (LTM), respectively.

3. Results and Discussion

3.1. Analyses of suitability index time series

Model design and multiannual temperature regimes produced few significant autocorrelations (Table 2). After disregarding two rare cases (lag 13 for Chur, lag 1 for Grenoble), in all areas except

Sondrio, the null hypothesis of no autocorrelation cannot be rejected at the standard significance level of p=0.05. In Sondrio, however, the null hypothesis of no autocorrelation has to be rejected for the first three decreasing partial autocorrelations and the next three increasing partial autocorrelations (Figure 2). The decreasing positive effect followed by the decreasing negative effect appearing in only 1 out of 10 cases (Table 2) is difficult to explain without detailed studies of demographic processes affecting the long-term dynamics of *S. titanus* populations. Undoubtedly, more cases than considered in this paper are required to ascertain the appearance of few significant autocorrelations in CSI time series and find explanations for distinct pattern as exemplified by the Sondrio case. The rare appearance of significant autocorrelations in most cases and a distinct pattern in one case only are presumably insufficient to sustain a dependency of observations that, in a statistical analysis, would violate the assumptions for statistical inference (Bence, 1995; Boyce et al., 2010; Monserud and Marshall, 2001). Nevertheless, we take into account the restrictions given by Bence (1995) who studied the effects of temporal dependencies on regression analyses and applied high probability requirements to regression analyses.

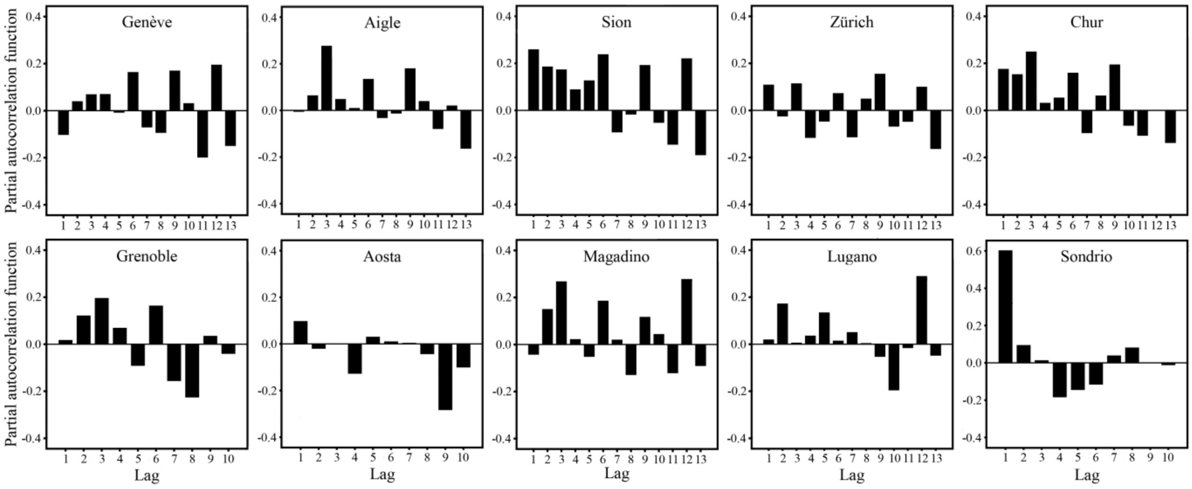

Figure 2. Autocorrelation functions in differently-lagged Climatic Suitability Indices for *S. titanus* in Northwestern Alpine grapevine-growing areas.

Table 2. The p-values of the Breusch-Godfrey test for autocorrelation in area-specific Climatic Suitability Indices (CSI) for *S. titanus* in Northwestern Alpine grapevine-growing areas. If the p-value is smaller than the standard significance level of 0.05 (numbers in bold), the null hypothesis of no autocorrelation is rejected (n.c. = not computed).

Lag	Genève	Aigle	Sion	Zürich	Chur	Grenoble	Aosta	Magadino	Lugano	Sondrio
1	0.1812	0.4103	0.0904	0.7810	0.8587	**0.0302**	0.1517	0.3404	0.4930	**0.0002**
2	0.3538	0.3972	0.2145	0.8909	0.8900	0.0706	0.2780	0.5163	0.7121	**0.0010**
3	0.5084	0.4321	0.3784	0.9647	0.9341	0.1165	0.4494	0.7112	0.6624	**0.0031**
4	0.6768	0.5330	0.4400	0.8244	0.9782	0.2057	0.4665	0.7062	0.7948	**0.0058**

5	0.6681	0.5900	0.4468	0.7490	0.9547	0.2827	0.2997	0.6894	0.7560	**0.0102**
6	0.7461	0.3884	0.5404	0.7660	0.7344	0.2725	0.2995	0.7588	0.8292	**0.0172**
7	0.6530	0.4388	0.4159	0.4190	0.6790	0.3194	0.4748	0.8252	0.8700	**0.0305**
8	0.4396	0.5432	0.3478	0.5160	0.7569	0.2880	0.4674	0.6484	0.8787	**0.0483**
9	0.5199	0.3368	0.2741	0.4324	0.3854	0.3357	0.1454	0.7372	0.6860	0.0752
10	0.6047	0.4244	0.3448	0.5195	0.4774	0.4184	0.1860	0.7533	0.6624	0.1108
11	0.3544	0.4979	0.4064	0.6090	0.5687	n.c.	n.c.	0.7896	0.7437	n.c.
12	0.3763	0.5788	0.4064	0.2786	0.5694	n.c.	n.c	0.8493	0.7998	n.c.
13	0.2095	0.1355	0.1660	0.0660	**0.0378**	n.c.	n.c.	0.6759	0.8506	n.c.

3.2. Climatic suitability patterns

Table 3 shows a generally-improving climatic suitability through time across areas within the region under study. Regarding the second observation on the reflection of gradual and abrupt temperature changes in gradual and abrupt changes in CSI, however, no generalization across areas is possible. Namely, Table 3 reports significant b_1 and b_2 values that indicate both gradual and abrupt changes of CSI in the Sion and the Magadino areas only. In these areas, a sloped step model (SSM), describing CSI by a linear trend model in the two sub-periods before and after 1988, is adequate. Table 3 also reports significant b_2 but insignificant b_1 values, indicating abrupt changes in the Grenoble, Aosta and Sondrio areas. These changes are adequately represented by an FSM. On the other hand, an LTM is appropriate to describe the patterns of CSI in the remaining regions The differences indicate that predictions of climate change on climatic suitability of grapevine-growing areas should be done carefully.

Table 3. Regression statistics for selecting the adequate model to describe the response of the Climatic Suitability Index in the different regions. The applicability of a sloped step model (SSM) is tested in all regions; for Sion and Magadino, the SSM remained valid, while a flat step model (FSM) is selected for Grenoble, Aosta and Sondrio, and a linear trend model (LTM) is appropriate for Genève, Aigle, Lugano, Zürich and Chur. (n = simulation period in years, R^2 = coefficient of determination, F = F value, a, b_1, b_2 = parameters of regression model [1], t = Student's t, if $t > t_{0.05(2),(n-2)}$ then $H_0{:}b_i=0$ is rejected for b_1, and b_2 (marked with *), *cf.* Zar (1974)).

Site	*n*	Model type	R^2, F	*A*	b_1	b_2
Genève	53	SSM	0.93E-01 F=2.56	0.19	0.40E-02 t=1.628	-0.47E-01 t=0.627
		LTM	0.86E-01 F=4.77	0.21	0.27E-02* t=2.184	
Zürich	53	SSM	0.47 F=22.30	-0.59E-02	0.61E-02* t=2.719	0.48E-01 t=0.695
		LTM	0.47 F=44.57	-0.18E-01	0.75E-02* t=6.676	
Aigle	53	SSM	0.34	0.77E-01	0.49E-02	0.67E-01

			F=13.08		t=1.819	t=0.815
		LTM	0.33 F=25.66	0.61E-01	0.68E-02* t=5.066	
Sion	53	SSM	0.76 F=80.50	0.97E-01	0.62E-02* t=3.101	0.23* t=3.466
Chur	53	SSM	0.59 F=36.55	-0.45E-01	0.88E-02* t=3.885	0.31E-01 t=0.444
		LTM	0.59 F=74.07	-0.53E-01	0.97E-02* t=8.606	
Grenoble	39	SSM	0.41 F=12.51	0.27	-0.24E-02 t=-0.586	0.99E-01* t=3.344
		FSM	0.40 F=25.12	0.25		0.28* t=5.012
Aosta	39	SSM	0.21 F=4.730	0.52	-0.12E-02 t=-0.170	0.32 t=1.911
		FSM	0.21 F=9.69	0.51		0.30* t=3.113
Magadino	53	SSM	0.57 F=33.78	0.53	0.31E-02* t=2.164	0.20* t=2.091
Lugano	53	SSM	0.18 F=5.43	0.83	0.52E-02 t=1.267	0.53E-01 t=0.424
		LTM	0.18 F=10.86	0.82	0.67E-02* t=3.295	
Sondrio	39	SSM	0.11 F=2.28	0.69	-0.30E-02 t=-0.534	0.22 t=1.622
		FSM	0.11 F=4.37	0.68		0.16* t=2.089

The appropriateness of the area-specific models has to be evaluated under two aspects. First, the temperature recordings have been made at weather stations often located at some distance from the actual vineyards (Genève, Zürich, Chur, Grenoble, Aosta). Since the vineyards have been established in favorable sites inside the areas, the temperatures experienced by *S. titanus* could have been underestimated. However, we do not expect a time effect on the reliability of the temperature measurements and hence, considered the responses to temperature changes as valid. Second, the regions with CSI undergoing only abrupt changes are separated from the other regions by three qualities. i) there was no information on possible changes in the measuring technique available for both Grenoble and Aosta and hence, we used raw data. As previously mentioned, no changes in the measuring procedure occurred at Sondrio. ii) gaps in the data sets for Aosta and Sondrio were filled by modified data from nearby weather stations as explained above. iii) the simulation period at Grenoble, Aosta and Sondrio were restricted to 39 years as opposed to 53 years of other regions. The influence of the reliability of temperature measurements and the influence of the duration (see below) on the patterns of CSI is unknown. Unlikely, however, these influences are responsible for the pattern and hence, the applicability of the FSM.

If we accept an area-specific response of the suitability index, the responses of CSI in Table 3 and Fig. 3, depicting the CSI time series for each of the 10 areas, do not correspond to the responses obtained when using yearly mean temperatures. Namely, Mariani et al. (2012) stated that the yearly temperatures predicted by an LTM are less accurate than the predictions by the equally well-performing SSM and FSM models. Nevertheless, the different performances of the SSM, the FSM and the LTM to describe the patterns of CSI and the analyses of yearly temperatures is not unexpected. This is because the temperature influences CSI through a series of uncorrelated curvilinear functions (Rigamonti et al., 2014a). The influence of these functions on CSI patterns becomes clear in a highly variable temperature environment. Hence, the results support the hypothesis that the selection of a region located at the northern limit of the geographic distribution with areas characterized by high temperature variability facilitates the study of abrupt and gradual climate change effects. It also confirms the utility of weather-driven PBDMs, operating at small-time resolutions, for investigating climate change effects on population dynamics and species distributions.

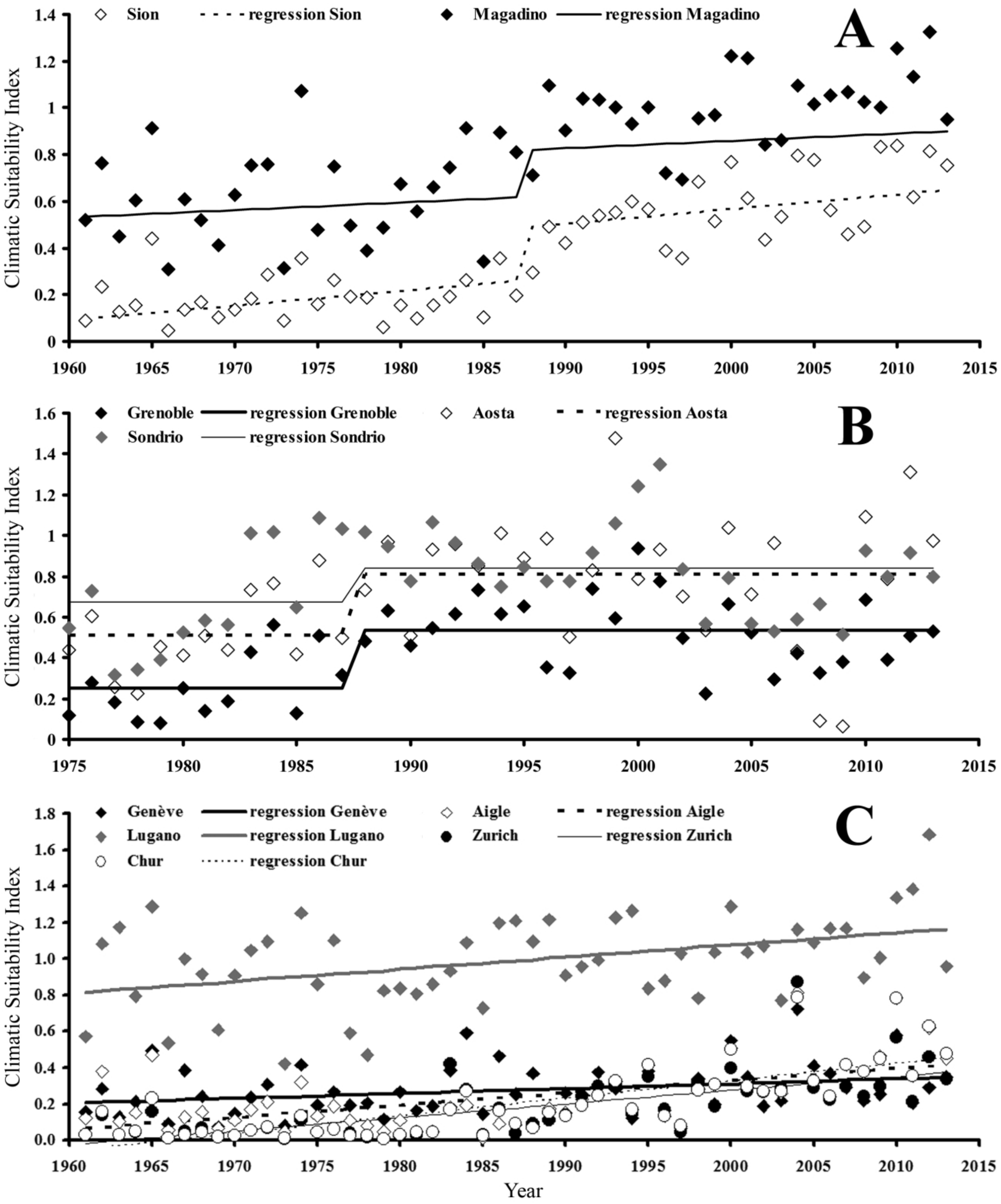

Figure 3. The simulated Climatic Suitability Index (CSI) for Sion and Magadino (A), Grenoble, Aosta and Sondrio (B) and Genève, Aigle, Lugano, Zürich and Chur (C) by a sloped step model (SSM), a flat step model (FSM), and linear trend model (LTM), respectively.

The CSI patterns appear to depend on whether the area was suitable or not for *S. titanus* prior to this investigation. In unsuitable areas with initial values close to zero, the changes were negligible or too small to allow *S. titanus* to settle and reach an economically relevant pest status in the foreseeable future (Zürich, Chur), while in areas characterized by more favorable initial conditions the temperature changes led to continuously-increasing CSIs (Aosta, Sondrio) with favorable conditions appearing in the 1990s.

In areas already suitable in the 1960s, the model predicts a small increase in CSIs (Lugano). There are indications that, in warmer areas located at the southern limits of *S. titanus* distribution, the temperature increase may lead to a decrease in CSIs that indicates negatively-affected population development due by high temperatures.

3.3. Pest management considerations

In the different areas of the region under study, institutions charged with pest control may take into account the following aspects. In the South, the Lugano and Magadino areas have been colonized early and face increasingly favorable conditions for *S. titanus* development and possibly FD transmission. They may represent areas that were colonized early without spreading to other regions because of unfavorable conditions for colonization. The other areas in the South (Aosta and Sondrio) became suitable after the climate shift in 1988 and may represent areas colonized in the second wave of spread (Bertignono et al., 2006; Posenato et al., 2001). The spread will likely lead to the colonization of the neighboring Aigle, Sion and Grenoble areas, if not yet colonized. Institutions charged with pest control in the areas of Zürich and Chur should note that their areas are unlikely to provide suitable climate conditions any time soon.

In other regions, institutions charged with pest control may take note that CSI information complements monitoring efforts by EPPO and local phytosanitary organizations to explain the past, current and future colonization of grapevine-growing areas. However, pest control institutions should take into account that the CSI is derived from a PBDM characterized by thresholds and several non-linear temperature-dependencies, and the extension of the here obtained results to other areas is questionable. Rather, they are advised to run the model with temperatures specific to the areas of interest for representing infestation patterns and assessing the risk of colonization. In doing so, they may acquire a quantitative tool that has been proven useful in supervised pest management in already colonized areas (Jermini et al., 2013; Prevostini et al., 2013).

4. Concluding Remarks

The Northwestern Alpine region, located near the northern limits of the actual geographical distribution of *S. titanus*, with grapevine-growing areas characterized by high temperature variability, was appropriate for studying the effects of gradual and abrupt temperature changes on the suitability of the areas to *S. titanus*. From a methodological standpoint, an annual Climatic Suitability Index (CSI) developed on the basis of a physiologically-based demographic model was useful for providing critical area-specific information on changing pest presence over time periods with changing climates. Furthermore, time series analyses of CSIs were instrumental to obtain the information required for the design and use of regression models aiming at quantifying the effect of temperature changes on CSIs. Thus, the methodology was useful to study the influence of abrupt and gradual temperature changes on the climate suitability of Northwestern Alpine grapevine-growing areas for *S. titanus*.

In general, the climatic suitability of all areas tends to improve during the study period. Across the areas, however, the gradual and abrupt temperature changes are not consistently reflected in gradual and abrupt CSI changes. The different area-specific CSI patterns may be due to the non-linear functions relating *S. titanus* life table parameters to temperature in the simulation model. The respective relationships may be responsible for the CSI patterns arising under variable area-specific temperature regimes. This indicates that the results of this study cannot be generally applied to areas located within other regions and similar studies are required to elucidate respective temperature change effects. Furthermore, it suggests the possibility that climate change may change the area-specific climatic suitability to either the advantage or disadvantage of *S. titanus*.

From a pest management standpoint, the study allows making recommendations to pest management institutions located in the region. Specifically, the methodology allows the assessment of colonization risk and the undertaking of adequate pest control measures. The application of the methodology to areas outside the Northwestern Alpine region holds the promise to provide decision-support to a wider range of institutions charged with *S. titanus* control then considered here.

Author contributions

IE Rigamonti, overall project coordinator with leading role in model parametrization.

L Mariani, developed the plant phenology model, oversaw the linkage to the pest population model and defined spatial scale resolution and extent.

G Cola, participated in crop and pest model implementation, and in definition and use of the Climatic Suitability Index (CSI).

M Jermini, responsible for linking the project team with the viticultural practice, the agricultural research institutions, the extension services and the Swiss Meteorological Service.

J Baumgärtner, responsible for the design of plant and pest population system models.

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Table 1. Information on the Northwestern Alpine region with the different areas in that the development of Grape leafhopper *Scaphoideus titanus* populations was simulated. The homogenized daily temperature maxima and minima for the Swiss meteorological stations were kindly made available by MeteoSwiss (National Weather Service of Switzerland). Additional temperature data were retrieved from the Texas A&M University, Beaumont, USA (https://beaumont.tamu.edu/ClimaticData/), the National Climate Data Centre (NCDC), Climate Services Branch (USA) and the Fojanini Foundation (FFS), Sondrio (I). Gaps in the data sets for Aosta and Sondrio were filled by using information from Torino Caselle (I) and Poschiavo (CH), respectively.

Site specification	Area and meteorological station	Beginning of simulations	Latitude N (degrees)	Longitude E (degrees)	Altitude (meters above sea level)	Source for temperatures data
Western and Northern areas	Genève (CH)	1959	46.250	6.133	416	MeteoSwiss
	Aigle (CH)		46.333	6.917	383	
	Sion (CH)		46.217	7.317	428	
	Zürich (CH)		47.383	8.567	569	
	Chur (CH)		46.867	9.533	533	
Western and Southern areas	Grenoble (F)	1973	45.367	5.333	386	NCDC
	Aosta (I)		45.740	7.376	547	Texas A&M
	Magadino (CH)	1959	46.167	8.883	198	MeteoSwiss
	Lugano (CH)		46.000	8.967	276	
	Sondrio (I)	1973	46.168	9.853	323	FFS

Table 2. The *p*-values of the Breusch-Godfrey test for autocorrelation in area-specific Climatic Suitability Indices (CSI) for *S. titanus* in Northwestern Alpine grapevine growing areas. If the *p*-value is smaller than the standard significance level of 0.05 (numbers in bold), the null hypothesis of no autocorrelation is rejected (n.c. = not computed).

Lag	Genève	Aigle	Sion	Zürich	Chur	Grenoble	Aosta	Magadino	Lugano	Sondrio
1	0.1812	0.4103	0.0904	0.7810	0.8587	**0.0302**	0.1517	0.3404	0.4930	**0.0002**
2	0.3538	0.3972	0.2145	0.8909	0.8900	0.0706	0.2780	0.5163	0.7121	**0.0010**
3	0.5084	0.4321	0.3784	0.9647	0.9341	0.1165	0.4494	0.7112	0.6624	**0.0031**
4	0.6768	0.5330	0.4400	0.8244	0.9782	0.2057	0.4665	0.7062	0.7948	**0.0058**
5	0.6681	0.5900	0.4468	0.7490	0.9547	0.2827	0.2997	0.6894	0.7560	**0.0102**
6	0.7461	0.3884	0.5404	0.7660	0.7344	0.2725	0.2995	0.7588	0.8292	**0.0172**
7	0.6530	0.4388	0.4159	0.4190	0.6790	0.3194	0.4748	0.8252	0.8700	**0.0305**
8	0.4396	0.5432	0.3478	0.5160	0.7569	0.2880	0.4674	0.6484	0.8787	**0.0483**
9	0.5199	0.3368	0.2741	0.4324	0.3854	0.3357	0.1454	0.7372	0.6860	0.0752
10	0.6047	0.4244	0.3448	0.5195	0.4774	0.4184	0.1860	0.7533	0.6624	0.1108
11	0.3544	0.4979	0.4064	0.6090	0.5687	n.c.	n.c.	0.7896	0.7437	n.c.
12	0.3763	0.5788	0.4064	0.2786	0.5694	n.c.	n.c	0.8493	0.7998	n.c.
13	0.2095	0.1355	0.1660	0.0660	**0.0378**	n.c.	n.c.	0.6759	0.8506	n.c.

Table 3. Regression statistics for selecting the adequate model to describe the response of the Climatic Suitability Index in the different regions. The applicability of a sloped step model (SSM) is tested in all regions; for Sion and Magadino, the SSM remained valid, while a flat step model (FSM) is selected for Grenoble, Aosta and Sondrio, and a linear trend model (LTM) is appropriate for Genève, Aigle, Lugano, Zürich and Chur. (n = simulation period in years, R^2 = coefficient of determination, F = F value, a, b_1, b_2 = parameters of regression model [1], t = Student's t, if t $>t_{0.05(2),\,(n-2)}$ then $H_0{:}b_i=0$ is rejected for b_1, and b_2 (marked with *), *cf.* Zar (1974)).

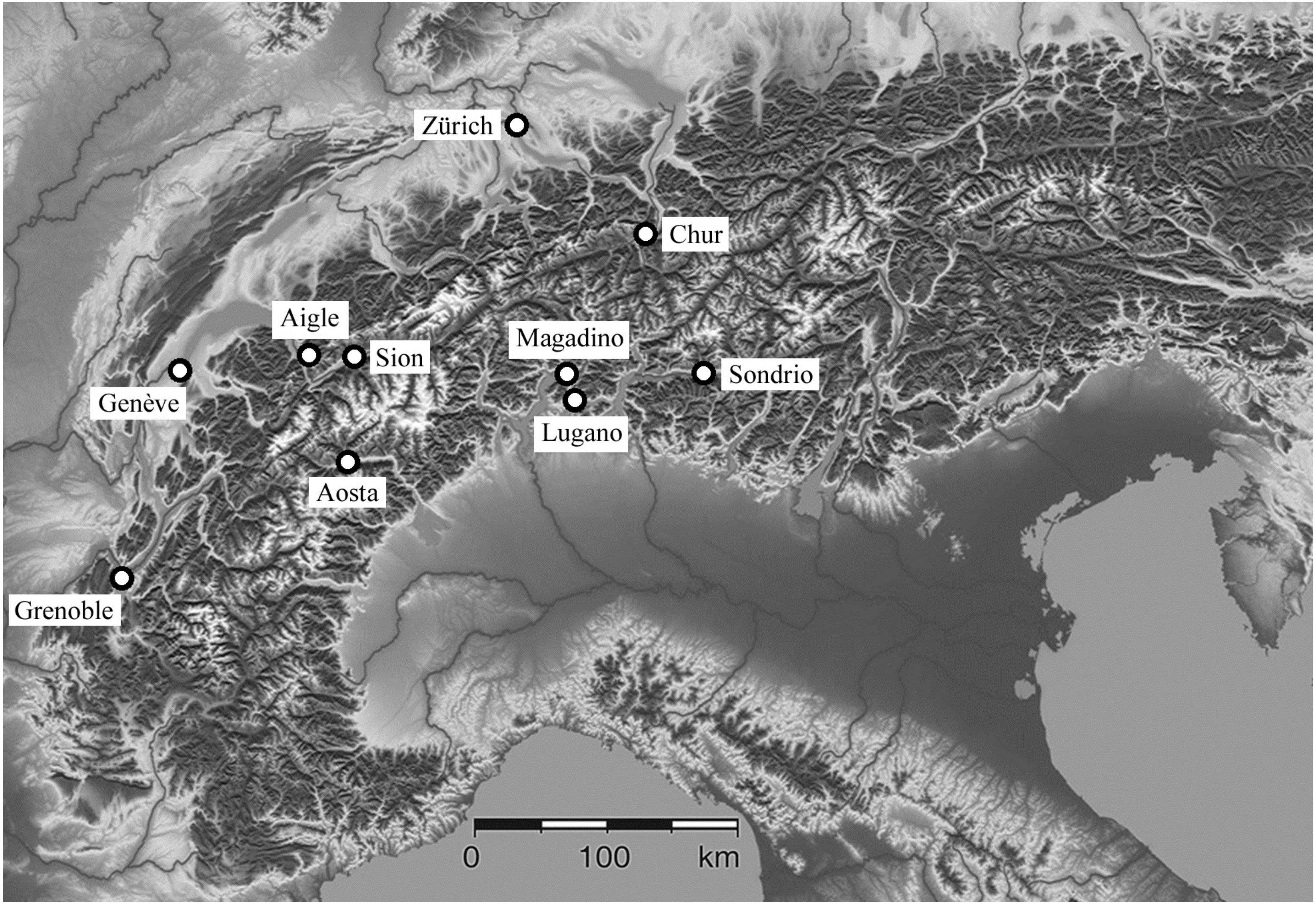
Site	n	Model type	R^2, F	a	b_1	b_2
Genève	53	SSM	0.93E-01 F=2.56	0.19	0.40E-02 t=1.628	-0.47E-01 t=0.627
		LTM	0.86E-01 F=4.77	0.21	0.27E-02* t=2.184	
Zürich	53	SSM	0.47 F=22.30	-0.59E-02	0.61E-02* t=2.719	0.48E-01 t=0.695
		LTM	0.47 F=44.57	-0.18E-01	0.75E-02* t=6.676	
Aigle	53	SSM	0.34 F=13.08	0.77E-01	0.49E-02 t=1.819	0.67E-01 t=0.815
		LTM	0.33 F=25.66	0.61E-01	0.68E-02* t=5.066	
Sion	53	SSM	0.76 F=80.50	0.97E-01	0.62E-02* t=3.101	0.23* t=3.466
Chur	53	SSM	0.59 F=36.55	-0.45E-01	0.88E-02* t=3.885	0.31E-01 t=0.444
		LTM	0.59 F=74.07	-0.53E-01	0.97E-02* t=8.606	
Grenoble	39	SSM	0.41 F=12.51	0.27	-0.24E-02 t=-0.586	0.99E-01* t=3.344
		FSM	0.40 F=25.12	0.25		0.28* t=5.012
Aosta	39	SSM	0.21 F=4.730	0.52	-0.12E-02 t=-0.170	0.32 t=1.911
		FSM	0.21 F=9.69	0.51		0.30* t=3.113
Magadino	53	SSM	0.57 F=33.78	0.53	0.31E-02* t=2.164	0.20* t=2.091
Lugano	53	SSM	0.18 F=5.43	0.83	0.52E-02 t=1.267	0.53E-01 t=0.424
		LTM	0.18 F=10.86	0.82	0.67E-02* t=3.295	
Sondrio	39	SSM	0.11 F=2.28	0.69	-0.30E-02 t=-0.534	0.22 t=1.622
		FSM	0.11 F=4.37	0.68		0.16* t=2.089

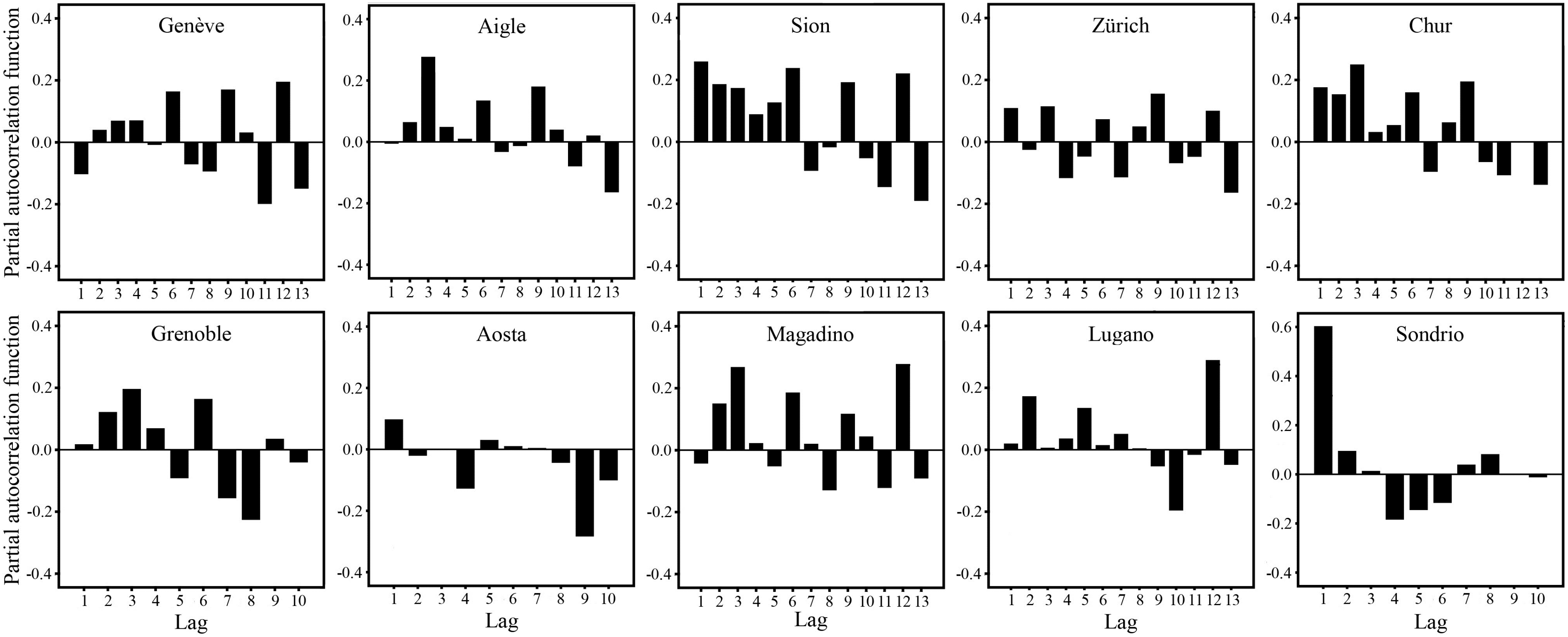
FIGURE LEGENDS

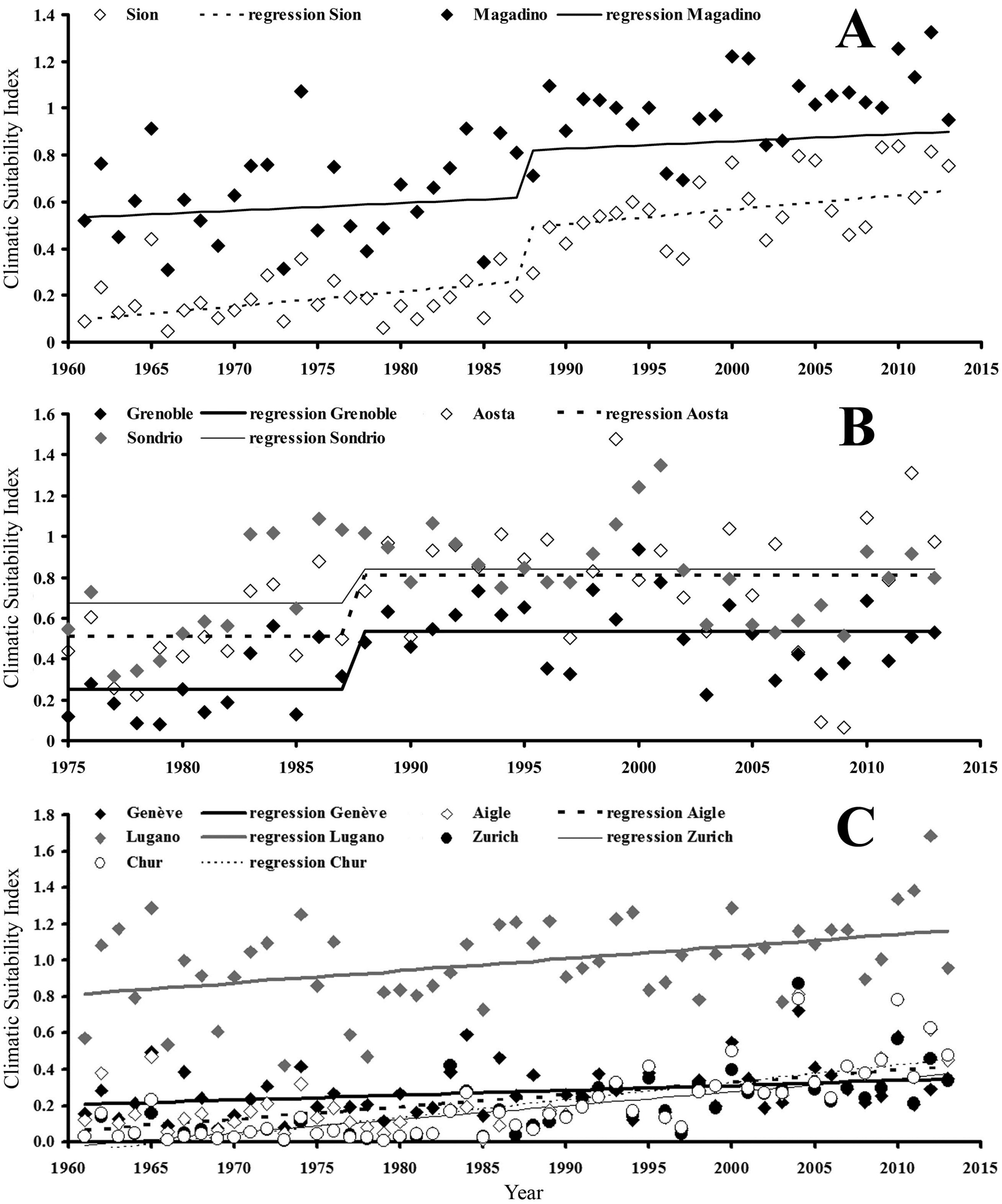
Figure 1. The Northwestern Alpine region with the different areas in that the development of Grape leafhopper *Scaphoideus titanus* populations was simulated.

Figure 2. Autocorrelation functions in differently-lagged Climatic Suitability Indices for *S. titanus* in Northwestern Alpine grapevine growing areas.

Figure 3. The simulated Climatic Suitability Index (CSI) for Sion and Magadino (A), Grenoble, Aosta and Sondrio (B) and Genève, Aigle, Lugano, Zürich and Chur (C) by a sloped step model (SSM), a flat step model (FSM), and linear trend model (LTM), respectively.


Zürich
Chur
Aigle
Sion
Magadino
Sondrio
Genève
Lugano
Aosta
Grenoble
0
100
km


Partial autocorrelation function
Genève
Aigle
Sion
Zürich
Chur
Grenoble
Aosta
Magadino
Lugano
Sondrio
0.6
0.4
0.2
0.0
-0.2
-0.4
1 2 3 4 5 6 7 8 9 10 11 12 13
1 2 3 4 5 6 7 8 9 10
Lag


A
Sion
regression Sion
Magadino
regression Magadino
Climatic Suitability Index
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1960
1965
1970
1975
1980
1985
1990
1995
2000
2005
2010
2015
B
Grenoble
regression Grenoble
Aosta
regression Aosta
Sondrio
regression Sondrio
Climatic Suitability Index
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1975
1980
1985
1990
1995
2000
2005
2010
2015
C
Genève
regression Genève
Aigle
regression Aigle
Lugano
regression Lugano
Zurich
regression Zurich
Chur
regression Chur
Climatic Suitability Index
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
1960
1965
1970
1975
1980
1985
1990
1995
2000
2005
2010
2015
Year