

## Manuscript Details

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<b>Title</b>	Abrupt and gradual temperature changes influence on the climatic suitability of Northwestern Alpine grapevine-growing regions for the invasive Grape leafhopper <i>Scaphoideus titanus</i> Ball (Hemiptera, Cicadellidae)
<b>Article type</b>	Full Length Article

### 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

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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.

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1) REVISED MANUSCRIPT WITH CHANGES MARKED

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

9

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21 ABSTRACT

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23 for colonization of *Scaphoideus titanus* populations in grapevine-growing areas of the Northwestern  
24 Alpine region. This study spans several decades of temperature recordings and is carried out in ten  
25 grapevine-growing areas. A time-varying distributed delay with attrition **model**, linked to a  
26 grapevine phenology model, is used to simulate the development of *S. titanus* populations and  
27 produce an annual Climatic Suitability Index (CSI). Area-specific CSI time series were obtained.  
28 The Breusch-Godfrey test revealed few significant partial autocorrelations in nine areas and the  
29 occurrence of six consecutive - first decreasing and then increasing - partial correlations in one case  
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32 time. However, gradual and abrupt temperature changes were not consistently reflected in gradual  
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39 results obtained here cannot be transferred to other areas without site-specific evaluations.

40

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42 forecast, colonization risk

43

## 44 **1. Introduction**

45

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

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

63 The second category of interest here comprises of physiologically-based demographic models  
64 (PBDMs), built on mechanistic representations of poikilothermic population development. PBDMs  
65 model the biology of the target species, and, when driven by weather, predict the phenology, age-  
66 structured dynamics, and distribution of the species across wide geographic areas independent of

67 the availability of distribution information (Ponti et al., 2015). Since weather is an important driver  
68 for PBDMs, they are particularly appropriate for dealing with climate change effects.

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

76 The Nearctic leafhopper *Scaphoideus titanus* Ball (Hemiptera, Cicadellidae), vector of the  
77 Grapevine Flavescence dorée (FD) phytoplasma, is a key pest of grapevine in Europe. *S. titanus*  
78 was accidentally introduced in France in the 1950s (Bonfils and Schvester 1960; Schvester et al.  
79 1961, 1962a, 1962b) and gradually extended its area of distribution. Actually, it is present  
80 throughout Western and Southeastern Europe from the Atlantic Ocean to the Black Sea, and the  
81 area of distribution is still expanding (Chuche and Thiéry, 2014; Tóthová et al., 2015).

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

94 Since the temperature regime in European grapevine-growing regions has and will undergo  
95 changes (IPCC, 1996), a previously-unsuitable region may become suitable through time. Mariani  
96 et al. (2012) viewed climate variability as the superimposition of gradual and abrupt changes.  
97 Gradual changes can be interpreted as the effect of progressive changes in forcings (IPCC, 2013),  
98 while abrupt changes are the result of sharp changes in the frequency and persistence of different  
99 circulation patterns (Sneyers et al., 1993). During the period 1977-1998, European temperatures

100 increased by about 1.3°C, while the main part of this increase was observed at the end of the 1980s,  
101 where an abrupt change is evident on thermal time series (Mariani et al., 2012).

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

108

## 109 **2. Materials and Methods**

110

### 111 *2.1. Study sites and temperature recordings*

112

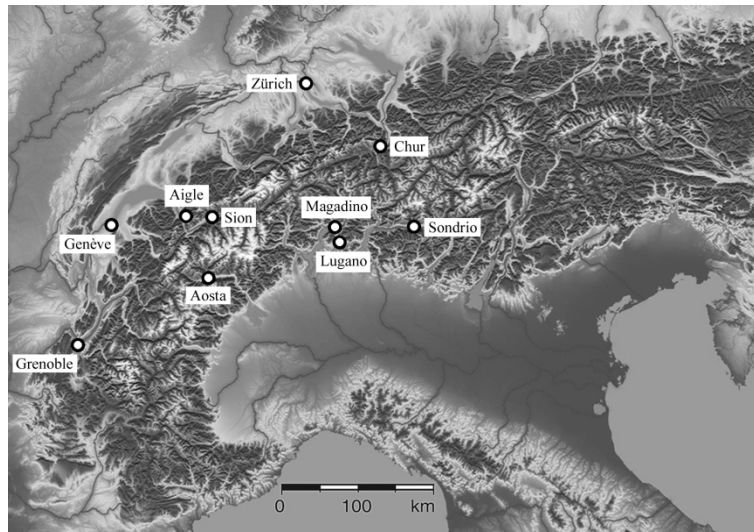
113 The suitability of grapevine-growing regions for *S. titanus* colonization is assessed in a region  
114 referred to as Northwestern Alps (Figure 1, Table 1). This region has been selected because of its  
115 location near the northern limits of *S. titanus* distribution and the high climatic variability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

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



134 the nearby Poschiavo station operated by MeteoSwiss, and linear regression of Aosta data were  
 135 regressed from data measured at the Torino-Caselle station.

136



137

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

140

141 Table 1. Information on the Northwestern Alpine region with the different areas in that the  
 142 development of Grape leafhopper *Scaphoideus titanus* populations was simulated. The  
 143 homogenized daily temperature maxima and minima for the Swiss meteorological stations were  
 144 kindly made available by MeteoSwiss (National Weather Service of Switzerland). Additional  
 145 temperature data were retrieved from the Texas A&M University, Beaumont, USA  
 146 (<https://beaumont.tamu.edu/ClimaticData/>), the National Climate Data Centre (NCDC), Climate  
 147 Services Branch (USA) and the Fojanini Foundation (FFS), Sondrio (I). Gaps in the data sets for  
 148 Aosta and Sondrio were filled by using information from Torino Caselle (I) and Poschiavo (CH),  
 149 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

150

151 2.2. *Model characteristics and computation of the Climatic Suitability Index*

152

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

162

$$163 \quad \frac{dr_{ji}(t)}{dt} = \frac{k_j}{DEL_j(t)} \left[ r_{ji-1}(t) - r_{ji}(t) \left( 1 + AR_j(t) \frac{DEL_j(t)}{k_j} + \frac{d DEL_j(t)}{k_j dt} \right) \right] \quad [1]$$

164

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

165

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

166

167 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  
 168 the number of delay substages in the  $j$ -th life stage,  $DEL_j(t)$  is the time-dependent developmental  
 169 time (days) in the absence of losses in the  $j$ -th life stage, and  $AR_j(t)$  is the time dependent  
 170 proportional change or attrition in the  $j$ -th life stage. The occurrence  $Q_j(t)$  of individuals in each life  
 171 stage can be obtained from

172

$$173 \quad Q_j(t) = \sum_{i=1}^{k_j} \frac{DEL_j(t)}{k_j} r_{ji}(t) \quad [2]$$

174

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

177

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

180 i) The stage-specific developmental rate  $d_j[T(t)]$ , *i.e.*, the inverse of developmental time  $DEL[T(t)]$ ,  
 181 is temperature-dependent between lower and upper thresholds, and 0.001 or 0.01, for diapausing

- 182 and non-diapausing stages respectively, outside this range. The time-dependent temperatures  
183  $T(t)$  are obtained by forcing a cosine function through daily temperature maxima and minima.
- 184 ii) The stage-specific survival rate  $s_j[T(t)]$  is composed of a) a temperature-dependent survival,  
185 modeled through attrition  $AR[T(t)]$ , operating between lower and upper thresholds, b) a  
186 temperature-dependent survival below the lower threshold, and c) mortalities of non-diapausing  
187 life stages between the grapevine plant phenological stages BBCH 93 (beginning of leaf fall) and  
188 BBCH 11 (first leaf unfolded and spread away from shoot) (Lorenz et al., 1994). Before and after  
189 these plant stages, nymphs and adults are suffering from an additional mortality of 0.5 % per  
190 day.
- 191 iii) The reproduction rate  $m[T(t)]$  of females becomes the input into the diapausing egg stage. It is  
192 the product of the reproductive profile, *i.e.* the relative age-specific fecundity rate and the  
193 temperature-dependent reproductive potential  $F(T)$ , *i.e.*, the total number of eggs laid by a  
194 female (*cf.* Curry and Feldman, 1987) ( $m[T(t)] > 0$  between the lower and an upper thresholds  
195 and  $m[T(t)] = 0$  outside this range).
- 196 iv) The model is initialized with a flow of hatching eggs into the nymphal stage (see below). The  
197 use of a single data set for model initialization at other locations may negatively affect the  
198 model performance in the first years. Therefore, the subsequent analysis disregards the first  
199 computations of the CSI. The simulations are carried out over the time periods specified below.

200

201 *Model parametrization.* The respective temperature-dependent rate functions (i, ii, iii) were  
202 developed and parametrized under constant temperatures but used under time-varying temperature  
203 regimes. Briefly, temperature-dependent values for the developmental time and mortality of  
204 nymphs older than the first stage were obtained from age-specific life tables established under  
205 various but constant temperatures (Rigamonti et al., 2011, 2014a). The developmental time of post-  
206 diapausing eggs, and the developmental time and mortality of first stage nymphs were obtained  
207 from field observations carried out in four vineyards located in Southern Switzerland over a period  
208 of three years, whereas data from literature were used to estimate adult female developmental time  
209 and associated variability. The respective field data, expert opinions and literature information were  
210 used to compute diapause periods. A linear model for first stage nymphs and the non-linear model  
211 of Brière et al. (1999) for the remaining stages were used to represent the temperature-dependency  
212 of developmental rates. The developmental rate of the widely-cultivated Chardonnay variety, and  
213 the phenological stages BBCH 11 and 93, were obtained from the model of Mariani et al. (2007,  
214 2013) and calibrated with information obtained in vineyards located in Southern Switzerland.

215 Reproduction is composed of the reproductive profile  $f_i$ , *i.e.*, the relative age-specific

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

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

224

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

232

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

242

### 243 2.3. *Autocorrelation analysis*

244

245 To correct for the influence of the abrupt temperature shift occurring in the late 1980s  
246 (Mariani et al., 2012), we deducted 1°C from the daily maximum and minimum temperatures, after  
247 1987, in all data sets. Autocorrelation is the similarity between observations as a function of the  
248 time lag between them. For visual examination, the partial CSI autocorrelations, as obtained by the  
249 SPSS software package (IBM Software Group, 2016) for each area, are depicted in Figure 2. To test

250 whether the autocorrelations of CSI values over differently lagged years are different from zero, the  
251 Lagrange multiplier based Breusch-Godfrey test (Breusch, 1978; Godfrey, 1978) is used since Rois  
252 et al. (2012) consider it as the most appropriate test for detecting autocorrelation in dynamic  
253 models. The number of lags reported is limited to 13 for Swiss locations and 10 for the other  
254 locations to limit the analysis to statistically-reliable data series. The statsmodels module of the  
255 PYTHON programming language (Seabold and Perktold, 2010) computes the Breusch-Godfrey test  
256 statistics for time lags, compares it with the  $\chi^2$  distribution and produces lag-specific  $p$ -values. If  
257 the  $p$ -value exceeds the standard significance level of 0.05, the null hypothesis of no autocorrelation  
258 is not rejected.

259

#### 260 2.4. Regression analysis

261

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

264

$$265 \quad \text{CSI}(t, D) = a_0 + b_1 t + b_2 D \quad [3]$$

266

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

277

### 278 3. Results and Discussion

279

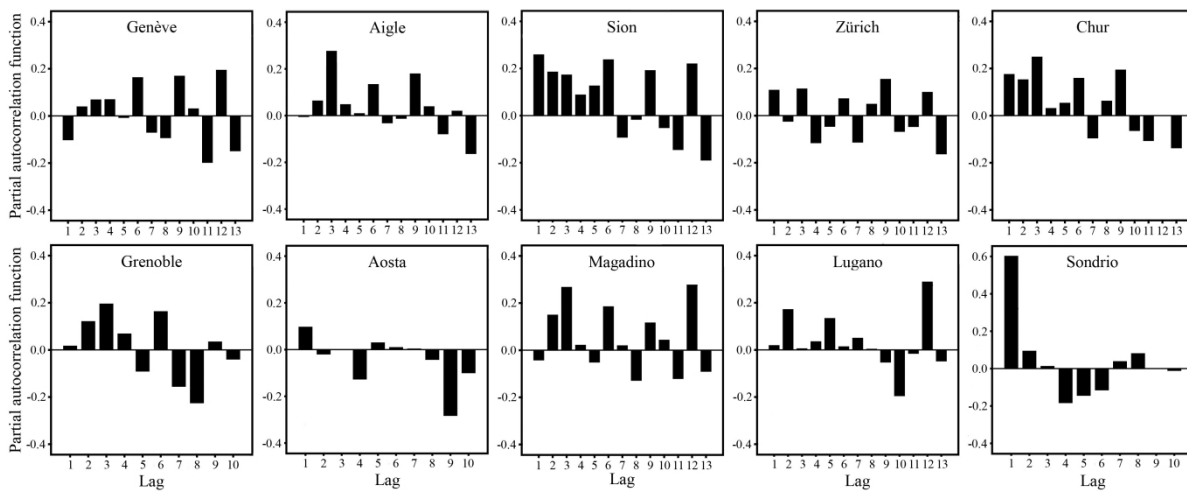
#### 280 3.1. Analyses of suitability index time series

281

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

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

298



299

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

302

303 Table 2. The  $p$ -values of the Breusch-Godfrey test for autocorrelation in area-specific Climatic  
 304 Suitability Indices (CSI) for *S. titanus* in Northwestern Alpine grapevine-growing areas. If the  $p$ -  
 305 value is smaller than the standard significance level of 0.05 (numbers in bold), the null hypothesis  
 306 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	<b>0.0302</b>	0.1517	0.3404	0.4930	<b>0.0002</b>
2	0.3538	0.3972	0.2145	0.8909	0.8900	0.0706	0.2780	0.5163	0.7121	<b>0.0010</b>
3	0.5084	0.4321	0.3784	0.9647	0.9341	0.1165	0.4494	0.7112	0.6624	<b>0.0031</b>
4	0.6768	0.5330	0.4400	0.8244	0.9782	0.2057	0.4665	0.7062	0.7948	<b>0.0058</b>

5	0.6681	0.5900	0.4468	0.7490	0.9547	0.2827	0.2997	0.6894	0.7560	<b>0.0102</b>
6	0.7461	0.3884	0.5404	0.7660	0.7344	0.2725	0.2995	0.7588	0.8292	<b>0.0172</b>
7	0.6530	0.4388	0.4159	0.4190	0.6790	0.3194	0.4748	0.8252	0.8700	<b>0.0305</b>
8	0.4396	0.5432	0.3478	0.5160	0.7569	0.2880	0.4674	0.6484	0.8787	<b>0.0483</b>
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	<b>0.0378</b>	n.c.	n.c.	0.6759	0.8506	n.c.

307

### 308 3.2. Climatic suitability patterns

309

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

321

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

329

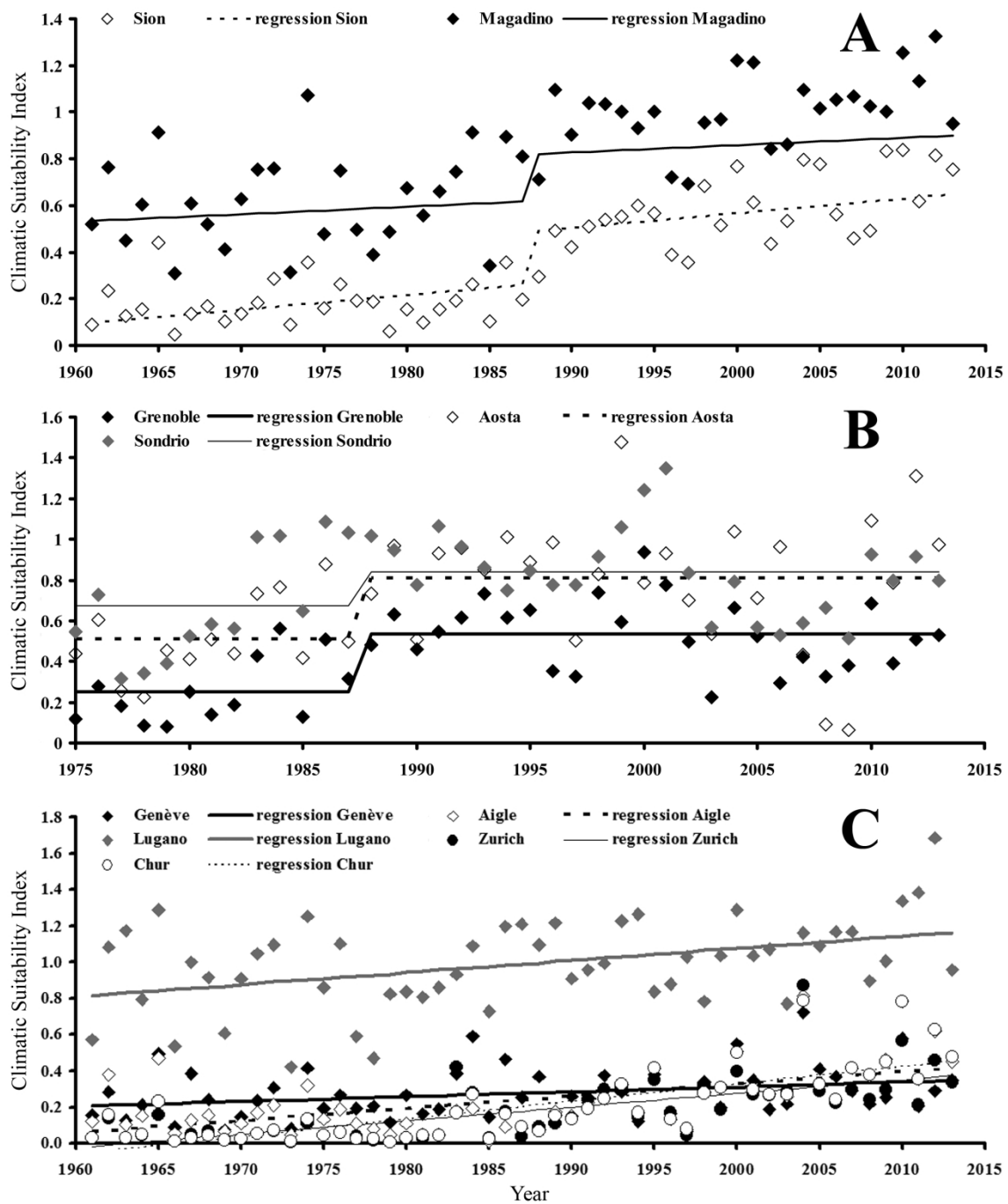
330 The appropriateness of the area-specific models has to be evaluated under two aspects. First,  
331 the temperature recordings have been made at weather stations often located at some distance from  
332 the actual vineyards (Genève, Zürich, Chur, Grenoble, Aosta). Since the vineyards have been 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

345 If we accept an area-specific response of the suitability index, the responses of CSI in Table 3  
346 and Fig. 3, depicting the CSI time series for each of the 10 areas, do not correspond to the responses



347 obtained when using yearly mean temperatures. Namely, Mariani et al. (2012) stated that the yearly  
348 temperatures predicted by an LTM are less accurate than the predictions by the equally well-  
349 performing SSM and FSM models. Nevertheless, the different performances of the SSM, the FSM  
350 and the LTM to describe the patterns of CSI and the analyses of yearly temperatures is not  
351 unexpected. This is because the temperature influences CSI through a series of uncorrelated  
352 curvilinear functions (Rigamonti et al., 2014a). The influence of these functions on CSI patterns  
353 becomes clear in a highly variable temperature environment. Hence, the results support the  
354 hypothesis that the selection of a region located at the northern limit of the geographic distribution  
355 with areas characterized by high temperature variability facilitates the study of abrupt and gradual  
356 climate change effects. It also confirms the utility of weather-driven PBDMs, operating at small-  
357 time resolutions, for investigating climate change effects on population dynamics and species  
358 distributions.

359



360

361 Figure 3. The simulated Climatic Suitability Index (CSI) for Sion and Magadino (A), Grenoble,  
 362 Aosta and Sondrio (B) and Genève, Aigle, Lugano, Zürich and Chur (C) by a sloped step model  
 363 (SSM), a flat step model (FSM), and linear trend model (LTM), respectively.  
 364

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

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

375

### 376 3.3. *Pest management considerations*

377

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

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

397

## 398 4. **Concluding Remarks**

399

400 **The Northwestern Alpine region, located near the northern limits of the actual geographical**  
401 **distribution of *S. titanus*, with grapevine-growing areas characterized by high temperature**  
402 **variability, was appropriate for studying the effects of gradual and abrupt temperature changes on**  
403 **the suitability of the areas to *S. titanus*. From a methodological standpoint, an annual Climatic**  
404 **Suitability Index (CSI) developed on the basis of a physiologically-based demographic model was**

405 useful for providing critical area-specific information on changing pest presence over time periods  
406 with changing climates. Furthermore, time series analyses of CSIs were instrumental to obtain the  
407 information required for the design and use of regression models aiming at quantifying the effect of  
408 temperature changes on CSIs. Thus, the methodology was useful to study the influence of abrupt  
409 and gradual temperature changes on the climate suitability of Northwestern Alpine grapevine-  
410 growing areas for *S. titanus*.

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

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

## 427 **Author contributions**

428  
429 IE Rigamonti, overall project coordinator with leading role in model parametrization.

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

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

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

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

437

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439

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448

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673

674 Table 1. Information on the Northwestern Alpine region with the different areas in that the  
 675 development of Grape leafhopper *Scaphoideus titanus* populations was simulated. The  
 676 homogenized daily temperature maxima and minima for the Swiss meteorological stations were  
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 678 temperature data were retrieved from the Texas A&M University, Beaumont, USA  
 679 (<https://beaumont.tamu.edu/ClimaticData/>), the National Climate Data Centre (NCDC), Climate  
 680 Services Branch (USA) and the Fojanini Foundation (FFS), Sondrio (I). Gaps in the data sets for  
 681 Aosta and Sondrio were filled by using information from Torino Caselle (I) and Poschiavo (CH),  
 682 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	
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	Sondrio (I)	1973	46.168	9.853	323	FFS

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688 Table 2. The  $p$ -values of the Breusch-Godfrey test for autocorrelation in area-specific Climatic  
 689 Suitability Indices (CSI) for *S. titanus* in Northwestern Alpine grapevine growing areas. If the  $p$ -  
 690 value is smaller than the standard significance level of 0.05 (numbers in bold), the null hypothesis  
 691 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	<b>0.0302</b>	0.1517	0.3404	0.4930	<b>0.0002</b>
2	0.3538	0.3972	0.2145	0.8909	0.8900	0.0706	0.2780	0.5163	0.7121	<b>0.0010</b>
3	0.5084	0.4321	0.3784	0.9647	0.9341	0.1165	0.4494	0.7112	0.6624	<b>0.0031</b>
4	0.6768	0.5330	0.4400	0.8244	0.9782	0.2057	0.4665	0.7062	0.7948	<b>0.0058</b>
5	0.6681	0.5900	0.4468	0.7490	0.9547	0.2827	0.2997	0.6894	0.7560	<b>0.0102</b>
6	0.7461	0.3884	0.5404	0.7660	0.7344	0.2725	0.2995	0.7588	0.8292	<b>0.0172</b>
7	0.6530	0.4388	0.4159	0.4190	0.6790	0.3194	0.4748	0.8252	0.8700	<b>0.0305</b>
8	0.4396	0.5432	0.3478	0.5160	0.7569	0.2880	0.4674	0.6484	0.8787	<b>0.0483</b>
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	<b>0.0378</b>	n.c.	n.c.	0.6759	0.8506	n.c.

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

705 FIGURE LEGENDS

706

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

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710

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

713

714

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

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2) REVISED MANUSCRIPT WITHOUT CHANGES MARKED

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724

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

728

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733 <sup>b</sup>Dipartimento di Scienze Agrarie e Ambientali – Produzione, Territorio, Agroenergia (DISAA),  
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740 ABSTRACT

741 The paper aims to elucidate the influence of abrupt and gradual climate changes on the suitability  
742 for colonization of *Scaphoideus titanus* populations in grapevine-growing areas of the Northwestern  
743 Alpine region. This study spans several decades of temperature recordings and is carried out in ten  
744 grapevine-growing areas. A time-varying distributed delay with attrition model, linked to a  
745 grapevine phenology model, is used to simulate the development of *S. titanus* populations and  
746 produce an annual Climatic Suitability Index (CSI). Area-specific CSI time series were obtained.  
747 The Breusch-Godfrey test revealed few significant partial autocorrelations in nine areas and the  
748 occurrence of six consecutive - first decreasing and then increasing - partial correlations in one case  
749 only. The occurrence of abrupt and gradual changes of the index were studied via multiple least  
750 square regression analyses. In general, the climatic suitability of all areas tended to improve through  
751 time. However, gradual and abrupt temperature changes were not consistently reflected in gradual  
752 and abrupt CSI patterns: abrupt and gradual CSI changes were observed in two areas, abrupt

753 changes were detected in three areas, and exclusively gradual changes in the remaining five. Pest  
754 control institution of the region under study may deal with different scenarios of pest status such as  
755 long-time presence and increasing risks, high colonization risks or limited colonization risks for the  
756 foreseeable future. Institutions charged with pest control elsewhere are advised to use a mechanistic  
757 demographic model to study area-specific infestation patterns and colonization risks because the  
758 results obtained here cannot be transferred to other areas without site-specific evaluations.

759

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

762

## 763 1. Introduction

764

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

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

782 The second category of interest here comprises of physiologically-based demographic models  
783 (PBDMs), built on mechanistic representations of poikilothermic population development. PBDMs  
784 model the biology of the target species, and, when driven by weather, predict the phenology, age-  
785 structured dynamics, and distribution of the species across wide geographic areas independent of



786 the availability of distribution information (Ponti et al., 2015). Since weather is an important driver  
787 for PBDMs, they are particularly appropriate for dealing with climate change effects.

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

795 The Nearctic leafhopper *Scaphoideus titanus* Ball (Hemiptera, Cicadellidae), vector of the  
796 Grapevine Flavescence dorée (FD) phytoplasma, is a key pest of grapevine in Europe. *S. titanus*  
797 was accidentally introduced in France in the 1950s (Bonfils and Schvester 1960; Schvester et al.  
798 1961, 1962a, 1962b) and gradually extended its area of distribution. Actually, it is present  
799 throughout Western and Southeastern Europe from the Atlantic Ocean to the Black Sea, and the  
800 area of distribution is still expanding (Chuche and Thiéry, 2014; Tóthová et al., 2015).

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

813 Since the temperature regime in European grapevine-growing regions has and will undergo  
814 changes (IPCC, 1996), a previously-unsuitable region may become suitable through time. Mariani  
815 et al. (2012) viewed climate variability as the superimposition of gradual and abrupt changes.  
816 Gradual changes can be interpreted as the effect of progressive changes in forcings (IPCC, 2013),  
817 while abrupt changes are the result of sharp changes in the frequency and persistence of different  
818 circulation patterns (Sneyers et al., 1993). During the period 1977-1998, European temperatures

819 increased by about 1.3°C, while the main part of this increase was observed at the end of the 1980s,  
820 where an abrupt change is evident on thermal time series (Mariani et al., 2012).

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

827

## 828 **2. Materials and Methods**

829

### 830 *2.1. Study sites and temperature recordings*

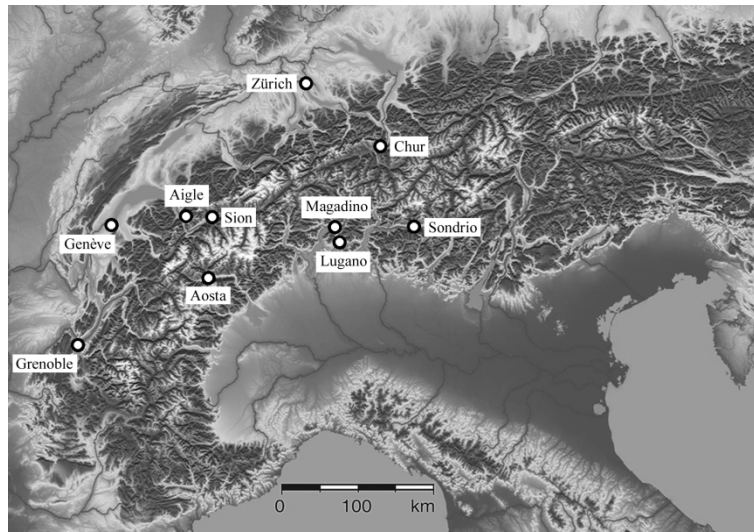
831

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

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

853 the nearby Poschiavo station operated by MeteoSwiss, and linear regression of Aosta data were  
 854 regressed from data measured at the Torino-Caselle station.

855



856

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

859

860 Table 1. Information on the Northwestern Alpine region with the different areas in that the  
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 865 (<https://beaumont.tamu.edu/ClimaticData/>), the National Climate Data Centre (NCDC), Climate  
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 867 Aosta and Sondrio were filled by using information from Torino Caselle (I) and Poschiavo (CH),  
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869

870 2.2. *Model characteristics and computation of the Climatic Suitability Index*

871

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

881

$$882 \quad \frac{dr_{ji}(t)}{dt} = \frac{k_j}{DEL_j(t)} \left[ r_{ji-1}(t) - r_{ji}(t) \left( 1 + AR_j(t) \frac{DEL_j(t)}{k_j} + \frac{d DEL_j(t)}{k_j dt} \right) \right] \quad [1]$$

883

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

884

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

885

886 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  
 887 the number of delay substages in the  $j$ -th life stage,  $DEL_j(t)$  is the time-dependent developmental  
 888 time (days) in the absence of losses in the  $j$ -th life stage, and  $AR_j(t)$  is the time dependent  
 889 proportional change or attrition in the  $j$ -th life stage. The occurrence  $Q_j(t)$  of individuals in each life  
 890 stage can be obtained from

891

$$892 \quad Q_j(t) = \sum_{i=1}^{k_j} \frac{DEL_j(t)}{k_j} r_{ji}(t) \quad [2]$$

893

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

896

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

899 i) The stage-specific developmental rate  $d_j[T(t)]$ , *i.e.*, the inverse of developmental time  $DEL[T(t)]$ ,  
 900 is temperature-dependent between lower and upper thresholds, and 0.001 or 0.01, for diapausing

- 901 and non-diapausing stages respectively, outside this range. The time-dependent temperatures  
902  $T(t)$  are obtained by forcing a cosine function through daily temperature maxima and minima.
- 903 ii) The stage-specific survival rate  $s_j[T(t)]$  is composed of a) a temperature-dependent survival,  
904 modeled through attrition  $AR[T(t)]$ , operating between lower and upper thresholds, b) a  
905 temperature-dependent survival below the lower threshold, and c) mortalities of non-diapausing  
906 life stages between the grapevine plant phenological stages BBCH 93 (beginning of leaf fall) and  
907 BBCH 11 (first leaf unfolded and spread away from shoot) (Lorenz et al., 1994). Before and after  
908 these plant stages, nymphs and adults are suffering from an additional mortality of 0.5 % per  
909 day.
- 910 iii) The reproduction rate  $m[T(t)]$  of females becomes the input into the diapausing egg stage. It is  
911 the product of the reproductive profile, *i.e.* the relative age-specific fecundity rate and the  
912 temperature-dependent reproductive potential  $F(T)$ , *i.e.*, the total number of eggs laid by a  
913 female (*cf.* Curry and Feldman, 1987) ( $m[T(t)] > 0$  between the lower and an upper thresholds  
914 and  $m[T(t)] = 0$  outside this range).
- 915 iv) The model is initialized with a flow of hatching eggs into the nymphal stage (see below). The  
916 use of a single data set for model initialization at other locations may negatively affect the  
917 model performance in the first years. Therefore, the subsequent analysis disregards the first  
918 computations of the CSI. The simulations are carried out over the time periods specified below.

919

920 *Model parametrization.* The respective temperature-dependent rate functions (i, ii, iii) were  
921 developed and parametrized under constant temperatures but used under time-varying temperature  
922 regimes. Briefly, temperature-dependent values for the developmental time and mortality of  
923 nymphs older than the first stage were obtained from age-specific life tables established under  
924 various but constant temperatures (Rigamonti et al., 2011, 2014a). The developmental time of post-  
925 diapausing eggs, and the developmental time and mortality of first stage nymphs were obtained  
926 from field observations carried out in four vineyards located in Southern Switzerland over a period  
927 of three years, whereas data from literature were used to estimate adult female developmental time  
928 and associated variability. The respective field data, expert opinions and literature information were  
929 used to compute diapause periods. A linear model for first stage nymphs and the non-linear model  
930 of Brière et al. (1999) for the remaining stages were used to represent the temperature-dependency  
931 of developmental rates. The developmental rate of the widely-cultivated Chardonnay variety, and  
932 the phenological stages BBCH 11 and 93, were obtained from the model of Mariani et al. (2007,  
933 2013) and calibrated with information obtained in vineyards located in Southern Switzerland.

934 Reproduction is composed of the reproductive profile  $f_i$ , *i.e.*, the relative age-specific

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

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

943

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

951

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

961

### 962 2.3. *Autocorrelation analysis*

963

964 To correct for the influence of the abrupt temperature shift occurring in the late 1980s  
965 (Mariani et al., 2012), we deducted 1°C from the daily maximum and minimum temperatures, after  
966 1987, in all data sets. Autocorrelation is the similarity between observations as a function of the  
967 time lag between them. For visual examination, the partial CSI autocorrelations, as obtained by the  
968 SPSS software package (IBM Software Group, 2016) for each area, are depicted in Figure 2. To test

969 whether the autocorrelations of CSI values over differently lagged years are different from zero, the  
970 Lagrange multiplier based Breusch-Godfrey test (Breusch, 1978; Godfrey, 1978) is used since Rois  
971 et al. (2012) consider it as the most appropriate test for detecting autocorrelation in dynamic  
972 models. The number of lags reported is limited to 13 for Swiss locations and 10 for the other  
973 locations to limit the analysis to statistically-reliable data series. The statsmodels module of the  
974 PYTHON programming language (Seabold and Perktold, 2010) computes the Breusch-Godfrey test  
975 statistics for time lags, compares it with the  $\chi^2$  distribution and produces lag-specific  $p$ -values. If  
976 the  $p$ -value exceeds the standard significance level of 0.05, the null hypothesis of no autocorrelation  
977 is not rejected.

978

#### 979 2.4. Regression analysis

980

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

983

$$984 \quad \text{CSI}(t, D) = a_0 + b_1 t + b_2 D \quad [3]$$

985

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

996

### 997 3. Results and Discussion

998

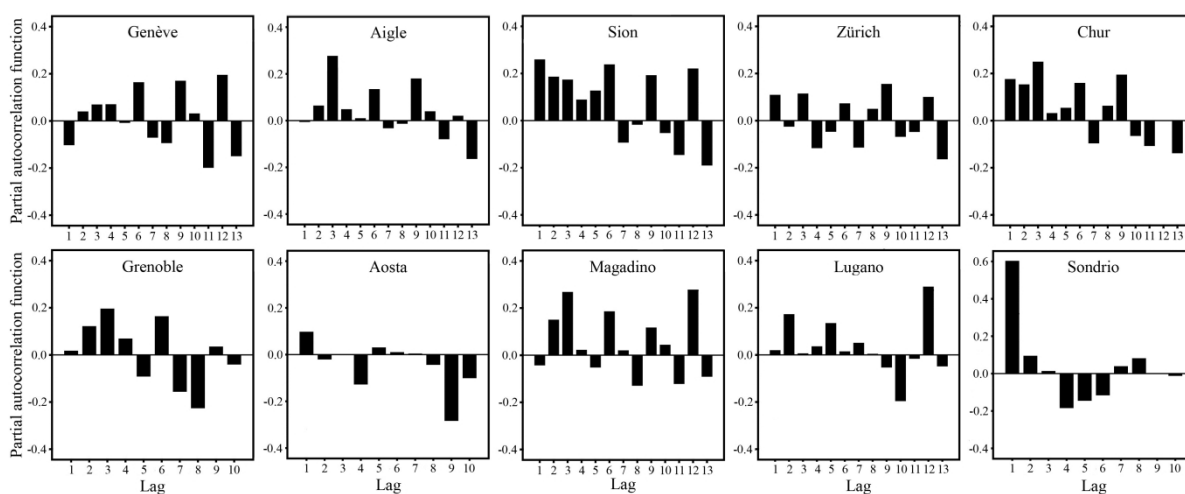
#### 999 3.1. Analyses of suitability index time series

1000

1001 Model design and multiannual temperature regimes produced few significant autocorrelations  
1002 (Table 2). After disregarding two rare cases (lag 13 for Chur, lag 1 for Grenoble), in all areas except

1003 Sondrio, the null hypothesis of no autocorrelation cannot be rejected at the standard significance  
 1004 level of  $p=0.05$ . In Sondrio, however, the null hypothesis of no autocorrelation has to be rejected for  
 1005 the first three decreasing partial autocorrelations and the next three increasing partial  
 1006 autocorrelations (Figure 2). The decreasing positive effect followed by the decreasing negative  
 1007 effect appearing in only 1 out of 10 cases (Table 2) is difficult to explain without detailed studies of  
 1008 demographic processes affecting the long-term dynamics of *S. titanus* populations. Undoubtedly,  
 1009 more cases than considered in this paper are required to ascertain the appearance of few significant  
 1010 autocorrelations in CSI time series and find explanations for distinct pattern as exemplified by the  
 1011 Sondrio case. The rare appearance of significant autocorrelations in most cases and a distinct  
 1012 pattern in one case only are presumably insufficient to sustain a dependency of observations that, in  
 1013 a statistical analysis, would violate the assumptions for statistical inference (Bence, 1995; Boyce et  
 1014 al., 2010; Monserud and Marshall, 2001). Nevertheless, we take into account the restrictions given  
 1015 by Bence (1995) who studied the effects of temporal dependencies on regression analyses and  
 1016 applied high probability requirements to regression analyses.

1017



1018

1019 Figure 2. Autocorrelation functions in differently-lagged Climatic Suitability Indices for *S. titanus*  
 1020 in Northwestern Alpine grapevine-growing areas.

1021

1022 Table 2. The  $p$ -values of the Breusch-Godfrey test for autocorrelation in area-specific Climatic  
 1023 Suitability Indices (CSI) for *S. titanus* in Northwestern Alpine grapevine-growing areas. If the  $p$ -  
 1024 value is smaller than the standard significance level of 0.05 (numbers in bold), the null hypothesis  
 1025 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	<b>0.0302</b>	0.1517	0.3404	0.4930	<b>0.0002</b>
2	0.3538	0.3972	0.2145	0.8909	0.8900	0.0706	0.2780	0.5163	0.7121	<b>0.0010</b>
3	0.5084	0.4321	0.3784	0.9647	0.9341	0.1165	0.4494	0.7112	0.6624	<b>0.0031</b>
4	0.6768	0.5330	0.4400	0.8244	0.9782	0.2057	0.4665	0.7062	0.7948	<b>0.0058</b>



5	0.6681	0.5900	0.4468	0.7490	0.9547	0.2827	0.2997	0.6894	0.7560	<b>0.0102</b>
6	0.7461	0.3884	0.5404	0.7660	0.7344	0.2725	0.2995	0.7588	0.8292	<b>0.0172</b>
7	0.6530	0.4388	0.4159	0.4190	0.6790	0.3194	0.4748	0.8252	0.8700	<b>0.0305</b>
8	0.4396	0.5432	0.3478	0.5160	0.7569	0.2880	0.4674	0.6484	0.8787	<b>0.0483</b>
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	<b>0.0378</b>	n.c.	n.c.	0.6759	0.8506	n.c.

1026

### 1027 3.2. Climatic suitability patterns

1028

1029 Table 3 shows a generally-improving climatic suitability through time across areas within the  
1030 region under study. Regarding the second observation on the reflection of gradual and abrupt  
1031 temperature changes in gradual and abrupt changes in CSI, however, no generalization across areas  
1032 is possible. Namely, Table 3 reports significant  $b_1$  and  $b_2$  values that indicate both gradual and  
1033 abrupt changes of CSI in the Sion and the Magadino areas only. In these areas, a sloped step model  
1034 (SSM), describing CSI by a linear trend model in the two sub-periods before and after 1988, is  
1035 adequate. Table 3 also reports significant  $b_2$  but insignificant  $b_1$  values, indicating abrupt changes in  
1036 the Grenoble, Aosta and Sondrio areas. These changes are adequately represented by an FSM. On  
1037 the other hand, an LTM is appropriate to describe the patterns of CSI in the remaining regions The  
1038 differences indicate that predictions of climate change on climatic suitability of grapevine-growing  
1039 areas should be done carefully.

1040

1041 Table 3. Regression statistics for selecting the adequate model to describe the response of the  
1042 Climatic Suitability Index in the different regions. The applicability of a sloped step model (SSM)  
1043 is tested in all regions; for Sion and Magadino, the SSM remained valid, while a flat step model  
1044 (FSM) is selected for Grenoble, Aosta and Sondrio, and a linear trend model (LTM) is appropriate  
1045 for Genève, Aigle, Lugano, Zürich and Chur. ( $n$  = simulation period in years,  $R^2$  = coefficient of  
1046 determination,  $F$  = F value,  $a$ ,  $b_1$ ,  $b_2$  = parameters of regression model [1],  $t$  = Student's  $t$ , if  $t$   
1047  $> t_{0.05(2), (n-2)}$  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

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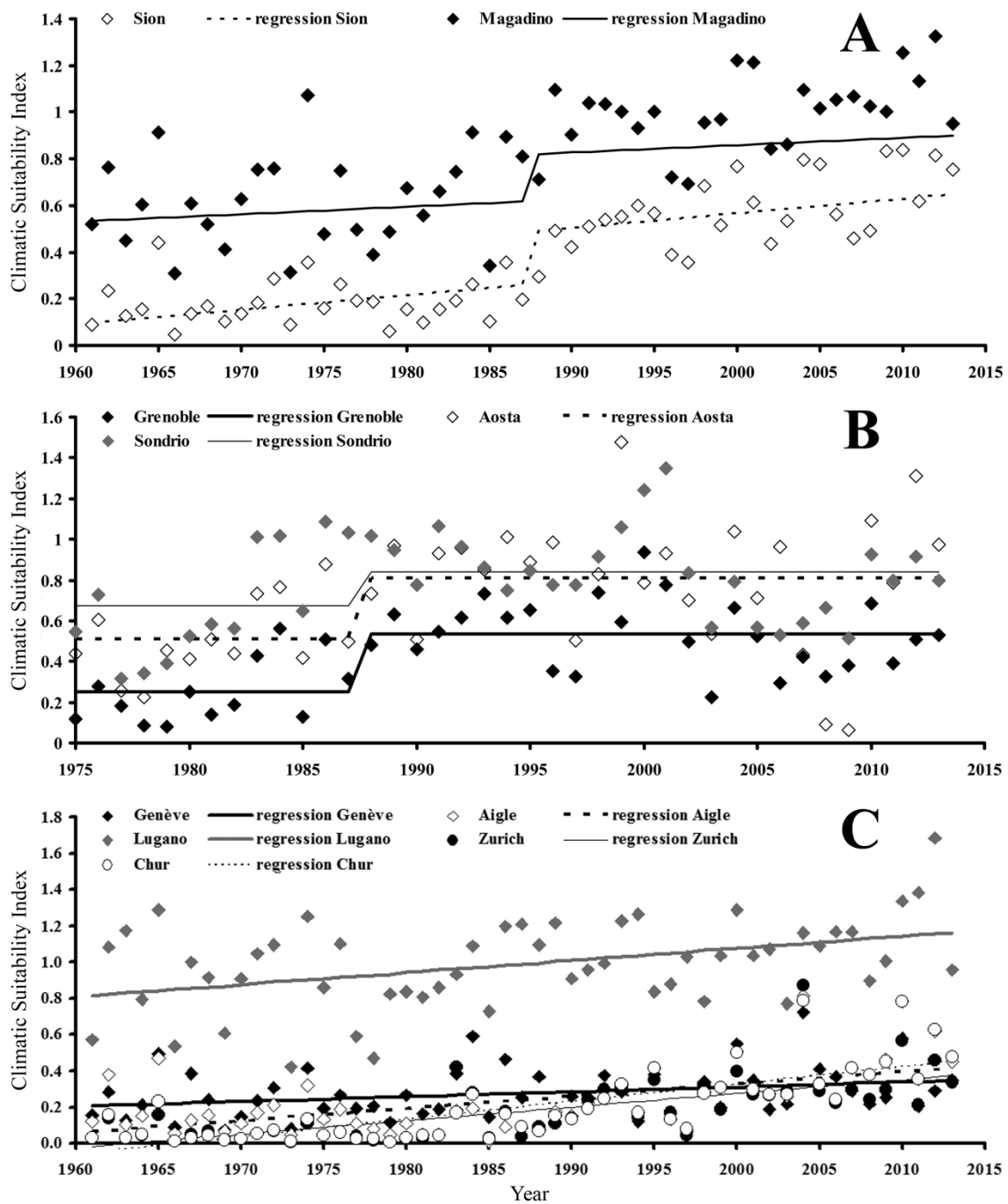
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The appropriateness of the area-specific models has to be evaluated under two aspects. First, the temperature recordings have been made at weather stations often located at some distance from the actual vineyards (Genève, Zürich, Chur, Grenoble, Aosta). 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

1066 obtained when using yearly mean temperatures. Namely, Mariani et al. (2012) stated that the yearly  
1067 temperatures predicted by an LTM are less accurate than the predictions by the equally well-  
1068 performing SSM and FSM models. Nevertheless, the different performances of the SSM, the FSM  
1069 and the LTM to describe the patterns of CSI and the analyses of yearly temperatures is not  
1070 unexpected. This is because the temperature influences CSI through a series of uncorrelated  
1071 curvilinear functions (Rigamonti et al., 2014a). The influence of these functions on CSI patterns  
1072 becomes clear in a highly variable temperature environment. Hence, the results support the  
1073 hypothesis that the selection of a region located at the northern limit of the geographic distribution  
1074 with areas characterized by high temperature variability facilitates the study of abrupt and gradual  
1075 climate change effects. It also confirms the utility of weather-driven PBDMs, operating at small-  
1076 time resolutions, for investigating climate change effects on population dynamics and species  
1077 distributions.

1078



1079

1080 Figure 3. The simulated Climatic Suitability Index (CSI) for Sion and Magadino (A), Grenoble,  
 1081 Aosta and Sondrio (B) and Genève, Aigle, Lugano, Zürich and Chur (C) by a sloped step model  
 1082 (SSM), a flat step model (FSM), and linear trend model (LTM), respectively.

1083

1084 The CSI patterns appear to depend on whether the area was suitable or not for *S. titanus* prior  
 1085 to this investigation. In unsuitable areas with initial values close to zero, the changes were  
 1086 negligible or too small to allow *S. titanus* to settle and reach an economically relevant pest status in  
 1087 the foreseeable future (Zürich, Chur), while in areas characterized by more favorable initial  
 1088 conditions the temperature changes led to continuously-increasing CSIs (Aosta, Sondrio) with  
 1089 favorable conditions appearing in the 1990s.

1090 In areas already suitable in the 1960s, the model predicts a small increase in CSIs (Lugano).  
1091 There are indications that, in warmer areas located at the southern limits of *S. titanus* distribution,  
1092 the temperature increase may lead to a decrease in CSIs that indicates negatively-affected  
1093 population development due by high temperatures.

1094

### 1095 3.3. *Pest management considerations*

1096

1097 In the different areas of the region under study, institutions charged with pest control may  
1098 take into account the following aspects. In the South, the Lugano and Magadino areas have been  
1099 colonized early and face increasingly favorable conditions for *S. titanus* development and possibly  
1100 FD transmission. They may represent areas that were colonized early without spreading to other  
1101 regions because of unfavorable conditions for colonization. The other areas in the South (Aosta and  
1102 Sondrio) became suitable after the climate shift in 1988 and may represent areas colonized in the  
1103 second wave of spread (Bertignono et al., 2006; Posenato et al., 2001). The spread will likely lead  
1104 to the colonization of the neighboring Aigle, Sion and Grenoble areas, if not yet colonized.  
1105 Institutions charged with pest control in the areas of Zürich and Chur should note that their areas are  
1106 unlikely to provide suitable climate conditions any time soon.

1107 In other regions, institutions charged with pest control may take note that CSI information  
1108 complements monitoring efforts by EPPO and local phytosanitary organizations to explain the past,  
1109 current and future colonization of grapevine-growing areas. However, pest control institutions  
1110 should take into account that the CSI is derived from a PBDM characterized by thresholds and  
1111 several non-linear temperature-dependencies, and the extension of the here obtained results to other  
1112 areas is questionable. Rather, they are advised to run the model with temperatures specific to the  
1113 areas of interest for representing infestation patterns and assessing the risk of colonization. In doing  
1114 so, they may acquire a quantitative tool that has been proven useful in supervised pest management  
1115 in already colonized areas (Jermini et al., 2013; Prevostini et al., 2013).

1116

## 1117 4. **Concluding Remarks**

1118

1119 The Northwestern Alpine region, located near the northern limits of the actual geographical  
1120 distribution of *S. titanus*, with grapevine-growing areas characterized by high temperature  
1121 variability, was appropriate for studying the effects of gradual and abrupt temperature changes on  
1122 the suitability of the areas to *S. titanus*. From a methodological standpoint, an annual Climatic  
1123 Suitability Index (CSI) developed on the basis of a physiologically-based demographic model was

1124 useful for providing critical area-specific information on changing pest presence over time periods  
1125 with changing climates. Furthermore, time series analyses of CSIs were instrumental to obtain the  
1126 information required for the design and use of regression models aiming at quantifying the effect of  
1127 temperature changes on CSIs. Thus, the methodology was useful to study the influence of abrupt  
1128 and gradual temperature changes on the climate suitability of Northwestern Alpine grapevine-  
1129 growing areas for *S. titanus*.

1130 In general, the climatic suitability of all areas tends to improve during the study period.  
1131 Across the areas, however, the gradual and abrupt temperature changes are not consistently  
1132 reflected in gradual and abrupt CSI changes. The different area-specific CSI patterns may be due to  
1133 the non-linear functions relating *S. titanus* life table parameters to temperature in the simulation  
1134 model. The respective relationships may be responsible for the CSI patterns arising under variable  
1135 area-specific temperature regimes. This indicates that the results of this study cannot be generally  
1136 applied to areas located within other regions and similar studies are required to elucidate respective  
1137 temperature change effects. Furthermore, it suggests the possibility that climate change may change  
1138 the area-specific climatic suitability to either the advantage or disadvantage of *S. titanus*.

1139 From a pest management standpoint, the study allows making recommendations to pest  
1140 management institutions located in the region. Specifically, the methodology allows the assessment  
1141 of colonization risk and the undertaking of adequate pest control measures. The application of the  
1142 methodology to areas outside the Northwestern Alpine region holds the promise to provide  
1143 decision-support to a wider range of institutions charged with *S. titanus* control then considered  
1144 here.

1145

#### 1146 **Author contributions**

1147

1148 IE Rigamonti, overall project coordinator with leading role in model parametrization.

1149 L Mariani, developed the plant phenology model, oversaw the linkage to the pest population model  
1150 and defined spatial scale resolution and extent.

1151 G Cola, participated in crop and pest model implementation, and in definition and use of the  
1152 Climatic Suitability Index (CSI).

1153 M Jermini, responsible for linking the project team with the viticultural practice, the agricultural  
1154 research institutions, the extension services and the Swiss Meteorological Service.

1155 J Baumgärtner, responsible for the design of plant and pest population system models.

1156

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1158

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1167

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1393 Table 1. Information on the Northwestern Alpine region with the different areas in that the  
1394 development of Grape leafhopper *Scaphoideus titanus* populations was simulated. The  
1395 homogenized daily temperature maxima and minima for the Swiss meteorological stations were  
1396 kindly made available by MeteoSwiss (National Weather Service of Switzerland). Additional  
1397 temperature data were retrieved from the Texas A&M University, Beaumont, USA  
1398 (<https://beaumont.tamu.edu/ClimaticData/>), the National Climate Data Centre (NCDC), Climate  
1399 Services Branch (USA) and the Fojanini Foundation (FFS), Sondrio (I). Gaps in the data sets for  
1400 Aosta and Sondrio were filled by using information from Torino Caselle (I) and Poschiavo (CH),  
1401 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

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1407 Table 2. The  $p$ -values of the Breusch-Godfrey test for autocorrelation in area-specific Climatic  
 1408 Suitability Indices (CSI) for *S. titanus* in Northwestern Alpine grapevine growing areas. If the  $p$ -  
 1409 value is smaller than the standard significance level of 0.05 (numbers in bold), the null hypothesis  
 1410 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	<b>0.0302</b>	0.1517	0.3404	0.4930	<b>0.0002</b>
2	0.3538	0.3972	0.2145	0.8909	0.8900	0.0706	0.2780	0.5163	0.7121	<b>0.0010</b>
3	0.5084	0.4321	0.3784	0.9647	0.9341	0.1165	0.4494	0.7112	0.6624	<b>0.0031</b>
4	0.6768	0.5330	0.4400	0.8244	0.9782	0.2057	0.4665	0.7062	0.7948	<b>0.0058</b>
5	0.6681	0.5900	0.4468	0.7490	0.9547	0.2827	0.2997	0.6894	0.7560	<b>0.0102</b>
6	0.7461	0.3884	0.5404	0.7660	0.7344	0.2725	0.2995	0.7588	0.8292	<b>0.0172</b>
7	0.6530	0.4388	0.4159	0.4190	0.6790	0.3194	0.4748	0.8252	0.8700	<b>0.0305</b>
8	0.4396	0.5432	0.3478	0.5160	0.7569	0.2880	0.4674	0.6484	0.8787	<b>0.0483</b>
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	<b>0.0378</b>	n.c.	n.c.	0.6759	0.8506	n.c.

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1415 Table 3. Regression statistics for selecting the adequate model to describe the response of the  
 1416 Climatic Suitability Index in the different regions. The applicability of a sloped step model (SSM)  
 1417 is tested in all regions; for Sion and Magadino, the SSM remained valid, while a flat step model  
 1418 (FSM) is selected for Grenoble, Aosta and Sondrio, and a linear trend model (LTM) is appropriate  
 1419 for Genève, Aigle, Lugano, Zürich and Chur. ( $n$  = simulation period in years,  $R^2$  = coefficient of  
 1420 determination,  $F$  = F value,  $a$ ,  $b_1$ ,  $b_2$  = parameters of regression model [1],  $t$  = Student's  $t$ , if  $t$   
 1421  $> t_{0.05(2), (n-2)}$  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

1422

1424 FIGURE LEGENDS

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1426 Figure 1. The Northwestern Alpine region with the different areas in that the development of Grape  
1427 leafhopper *Scaphoideus titanus* populations was simulated.

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1430 Figure 2. Autocorrelation functions in differently-lagged Climatic Suitability Indices for *S. titanus*  
1431 in Northwestern Alpine grapevine growing areas.

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1434 Figure 3. The simulated Climatic Suitability Index (CSI) for Sion and Magadino (A), Grenoble,  
1435 Aosta and Sondrio (B) and Genève, Aigle, Lugano, Zürich and Chur (C) by a sloped step model  
1436 (SSM), a flat step model (FSM), and linear trend model (LTM), respectively.

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