How future-proof is Sweet chestnut (*Castanea sativa*) in a global change context?

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ABSTRACT

In the debate about tree species suited to cope with the ongoing global changes, Sweet chestnut (*Castanea sativa* Mill.) is frequently discussed as a potentially future-proof tree species for Central Europe. This is mainly due to its current southern distribution range, which climatically corresponds to what is expected for Central Europe in the near future. Present chestnut forests are, however, the result of historic long-term intensive management, which has extended and partially obscured the species’ natural ecological range and autecology. Therefore, knowledge about the competitiveness and suitability of chestnut for future conditions is still poor. Here, we analysed data of the Swiss National Forest Inventory (NFI) for Southern Switzerland to compare the survival probability of chestnut to other co-occurring tree species and detect drivers of chestnut mortality under natural dynamics including the Asian Chestnut Gall Wasp (*Dryocosmus kuriphilus*) using survival models, such as the Kaplan-Meier estimator and the Cox-Proportional Hazards model.

Despite the potential longevity of cultivated chestnuts, under natural conditions the survival curves rank the chestnut among short-lived and light-demanding tree species, especially for individuals smaller than 50 cm diameter at breast height. Moreover, the survival models confirm the pioneer-like characteristics of the chestnut tree such as its low shade tolerance and poor competitiveness in comparison to late-successional species. The mortality probability of chestnut increases when growing under dry conditions and under grazing pressure from goats, while fire disturbances have a positive effect on survival. Severe damage due to repeated *D. kuriphilus* attacks represents an additional significant factor of increased chestnut mortality risk.

Our results suggest that chestnut is not per se a future-proof tree species. Rather, forest managers should be aware that chestnut might not be the best option to face expected rises in summer temperatures and dry periods on xeric site conditions, whereas the species can be considered on good site conditions when regular silvicultural management is provided.

1. Introduction

Sweet chestnut (*Castanea sativa* Mill.) is probably one of the tree species most associated with humans in Europe (Conedera et al., 2004a). It is cultivated for fruits as an orchard tree as well as for timber production in coppice systems, and it provides numerous secondary products (e.g., honey, litter) and ecosystem services (e.g., protection forests again natural hazards) (Conedera and Krebs 2008). Therefore, humans introduced and managed the chestnut tree as a multipurpose monoculture in several southern and partially also Central European countries (Conedera et al., 2004b), giving rise to what is usually referred to as the ‘chestnut civilization’ (Pitte 1986).

The central economic role of the chestnut cultivation began to decline because of the climatic changes during the Little Ice Age, with the agricultural and industrial revolutions that brought alternative staple food (i.e., maize and potatoes) and new employment possibilities for...
most European chestnut areas (Pitte, 1986; Conedera and Krebs, 2008). The process accelerated in the 20th century due to the introduction and spread of severe diseases such as the soil-borne ink disease (*Phytophthora* spp., Vettraino et al., 2005) and the chestnut blight (*Cryptonecctria parasticta*, Rigling and Prospero 2018) as well as the socio-economic development after World War II (Conedera and Krebs 2008). Finally, the accidental introduction of the Asian Chestnut Gall Wasp (*Dryocosmus kuriphilus*, hereafter referred to as ACGW) to Europe further discouraged the management of chestnut groves (Avtzis et al., 2019). At present, the species still covers more than 2.5 million ha of forest area in Europe, most of them in the Mediterranean and Sub-Mediterranean areas corresponding to a climatic envelope with mean annual temperatures

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Fig. 1. The study area covering the Swiss canton Ticino and the region of Moesa (canton Grisons) with Swiss National Forest Inventory plots with (dot and circle) and without (dot) chestnut trees.
ranging between 8 and 15 °C and minimum annual precipitation between 600 and 800 mm (Conedera et al., 2004b, 2016).

In view of current climate change, chestnut is receiving renewed attention as a potentially future-proof tree species for Central Europe (e.g., De Avila and Albrecht, 2017; Hän, 2018; Lüpke et al., 2018; Forker et al., 2020). This suggestion is typically derived from species distribution models (SDMs; Elith and Leathwick 2009) that use species occurrence data to infer the environmental envelope in which a species can potentially persist (Thurm et al., 2018). For chestnut, such static approaches of defining future ranges are particularly problematic since the ‘chestnut civilization’ has had a significant impact on both the present distribution and structure of the species’ forests. For instance, SDMs typically ignore biotic interactions and successional dynamics and thus cannot reflect that in the absence of forest management, chestnut may become outcompeted by other species (e.g., Zlatanov et al., 2015). Although recent studies have highlighted the low competitiveness of chestnut when subjected to post-cultural succession in abandoned chestnut stands (Conedera et al., 2001; Pezzi et al., 2011; Zlatanov et al., 2013) and its sensitivity to summer droughts (Lemaire, 2008; Conedera et al., 2009), more detailed knowledge regarding the species is needed to assess its suitability for future forests.

Here, we investigated chestnut mortality patterns and related drivers in abandoned chestnut forests of Southern Switzerland subject to post-cultural stand dynamics using the historical data series (1983–2017) of the Swiss National Forest Inventory (NFI). Specific aims of the study were to (i) compare the survival probabilities of chestnut with other main co-occurring tree species, (ii) quantify main mortality drivers with particular attention to the additional stress caused by ACGW, and (iii) detect possible variation of these drivers as a function of the development stage of the concerned chestnut trees. We finally discuss the results and the suitability of chestnut as a future-proof tree species in the light of expected climatic changes.

2. Material and methods

2.1. Study area

The study area is located on the southern slopes of the Swiss Alps represented by 3308 km² of the joined territories of the canton of Ticino and the Moesano region (part of the canton Grisons), which form the hotspot of Swiss chestnut forests (Brändli et al., 2020; Fig. 1). The chestnut tree is the dominant species at low elevations (up to 900–1100 m a.s.l.). At mid elevations (900–1400 m a.s.l.), forests mostly consist of almost pure beech stands (Fagus sylvatica L.), followed by coniferous forests (Picea abies (L.) H. Karst, Abies alba Mill., Larix decidua Mill., and Pinus cembra L.) at high elevations (Ceschi 2014). In the lowlands (i.e., < 1100 m a.s.l.), the climate is warm-temperate and rainy, with a mean annual precipitation of 1700 mm and a mean annual temperature of about 12 °C (MeteoSwiss Locarno-Monti, climate normals 1981–2010, MeteoSwiss 2020).

2.2. Historical development of chestnut forests in the study area

The mild climate, rich in summer precipitation, and the prevailing siliceous bedrock in the study area favoured the introduction and intense cultivation of chestnut to its ecological limits during the late Middle Ages (Krebs et al., 2012) to a point at which chestnut monocultures almost completely substituted the natural forest vegetation at middle elevations (Tinner et al., 1999; Conedera et al., 2004a; Krebs et al., 2014). This nearly continuous chestnut belt was only occasionally interrupted by the presence of other broadleaved species, such as Tilia cordata Mill., Quercus petraea (Matt.) Liebl., Q. pubescens Willd., Alnus glutinosa (L.) Gaertn., Prunus avium L., Acer spp., or Fraxinus spp. (Krebs et al., 2014). The subsequent abandonment and almost total suspension of forest management, combined with the arrival of chestnut-specific diseases (e.g., ink disease; Krebs et al., 2014), transformed the chestnut forests in ‘latent reserves’ sensu Portier et al. (2020), which tend to naturally evolve towards mixed forest stands (Conedera et al., 2001). Finally, the ACGW was first recorded in 2007 in the study area near the Italian border (Forster et al., 2009). Since then, it causes varying degrees of damage depending on the site conditions and the time lag until the arrival of the natural antagonist Torymus sinensis (Gehring et al., 2020). Despite this disadvantageous development, chestnut is still the dominant forest species on around 20’000 ha and acts as an accompanying species on 5’000 additional ha of forests (Brändli et al., 2020).

2.3. Chestnut forest data

Data on chestnut forests were extracted from the four Swiss National Forest Inventories NFI 1–4. The first NFI field campaign was done in 1983/85 (NFI 1) with two follow-ups in 1995 (NFI 2) and 2006 (NFI 3). For the last measurement (NFI 4), a new sampling method has been adopted and only 1/9 of the plots were assessed every year, distributing the field campaign over the period from 2009 to 2017. As a result, time intervals between NFI 1–3 covered a period of approx. 10 years, whereas the period from NFI 3 to NFI 4 ranged from 3 to 10 years.

The NFI-net spans a rectangular grid of 1.4 × 1.4 km mesh size over Switzerland. At each node, all trees larger than 12 cm and 36 cm in diameter at breast height (DBH) are recorded on small (200 m²) and large (500 m²) circular plots, respectively. For the analysis, we retained all chestnut trees from NFI 1 to NFI 4 plots that have been recorded (dead or alive) in at least two consecutive surveys on unmanaged or only anecdotally managed plots (e.g., single tree harvesting by private owners). Regularly managed plots (N = 6) were discarded from the analysis, irrespective of the presence of chestnut trees.

On NFI plots, up to 300 different site-, stand-, and tree characteristics are recorded. Among site characteristics, we extracted slope position (Relief: upper slope, middle slope, foothill), soil pH, potential natural forest community, and morphometric terrain variables such as aspect (transformed after Beers et al., 1966), slope, and elevation (Table 1). The latter three variables are considered as proxies for local climate conditions (e.g., Beers et al., 1966; Schönberger et al., 1995), while soil pH is included because the chestnut tree is known to prefer acidic to neutral soils and avoid limestone (De Avila and Albrecht, 2017).

As part of NFI 4, the potential natural vegetation (PNV) has been systematically defined (Ott et al., 1997; Frehner et al., 2009). The PNV is expected to develop when forest stands would grow totally in balance with the environmental conditions and without any anthropogenic impact. We grouped the resulting PNV into three main types: (i) acidophilous oak forests, (ii) mesophilous deciduous forests, and (iii) other forest types (Table 1) and used it as a proxy for the suitability of the site conditions for a tree species to grow.

Possible interspecific competitive pressure exerted on chestnut was evaluated by grouping the other tree species into three categories (pioneer, intermediate, and late-successional) according to their growth-rate (especially when young) and shade tolerance (Oberdorfer, 2001; see Appendix A Figure A.1). The possible interspecific competition was then expressed as the total basal area of each category (BApion, BAtint, BAlate).

The time elapsed since the last regular silvicultural treatment (Las'Tuse) was included as a proxy for the length of natural stand dynamics. To assess the possible role of external disturbances that can change species dominance and competition within the stands, we created the category disturbance (Disturb) including grazing by goats and other livestock (sheep, cattle, donkey, horse) based on the browsing behavior, and forest fires that we extracted by overlaying recorded fire perimeters (area burnt ≥ 0.5 ha) according to the Swiss forest fire database (Pezzatti et al., 2010) with the NFI-plot coordinates. The damage caused by the ACGW at plot level was expressed in six categories ranging from 0 to 5 (no to extreme gall wasp damage) according to Gehring et al. (2018, 2020)). We finally extracted the tree position with respect to the canopy.
layers (Layer: upper, middle, and lower stand layer) for each considered tree, which roughly corresponds to the social position and may thus be used as a proxy for competitiveness (Table 1).

<table>
<thead>
<tr>
<th>Variable name</th>
<th>Abbreviation</th>
<th>Units or categories</th>
<th>Mean [SE] or number of observations</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Site indicators</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aspect</td>
<td>Aspect</td>
<td>°</td>
<td>190.18 [±1.25]</td>
</tr>
<tr>
<td>Slope</td>
<td>Slope</td>
<td>°</td>
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</tr>
<tr>
<td>Slope position</td>
<td>Relief</td>
<td></td>
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</tr>
<tr>
<td><strong>Soil pH</strong></td>
<td></td>
<td></td>
<td>3.99 [±0.01]</td>
</tr>
<tr>
<td><strong>Stand characteristics</strong></td>
<td></td>
<td></td>
<td>1:acidophilous oak N 2988</td>
</tr>
<tr>
<td><strong>Climate variables</strong></td>
<td></td>
<td></td>
<td>0.05 [± 0.19]</td>
</tr>
<tr>
<td>Standardized meanSPEI</td>
<td></td>
<td></td>
<td>1.20 [± 0.15]</td>
</tr>
<tr>
<td><strong>Tree characteristic</strong></td>
<td></td>
<td></td>
<td>3.06 [± 0.09]</td>
</tr>
<tr>
<td>Stand Layer Position</td>
<td>Layer</td>
<td>1:upper N 4025</td>
<td>2:middle N 1105</td>
</tr>
</tbody>
</table>

1. Correlated with basal area of intermediate tree species and standardized precipitation evapotranspiration and therefore excluded from the Cox-PH model.
2. Only used in the ACGW-damage model for NFI data.
3. Not used in the Cox-PH model.

2.4. Data analysis

2.4.1. Survival analysis

We used survival models to analyse chestnut survival probabilities. Survival models are often used in analysing ecological experimental designs (see review in Fox 2000) and they became more popular in forest science in the last few years (e.g., Neuner et al., 2015; Neumann et al., 2017; Brandl et al., 2020). The central concept of survival analysis is the survival function $S(t)$ (or the mortality hazard $h(t)$), which defines the probability that an individual survives from the time of origin (e.g., the date of establishment or entry time under observation) to a time point ($t$) in the future (e.g., field assessment).

In contrast to logistic regression models, which are often used to analyse tree mortality, survival analyses do not unify the length of re-measured periods (Salas-Eljatib and Weiskittel, 2020). Further, they take censoring and left-truncation into account. Censoring arises when the true event time ($t_e$) is potentially unobserved (right-censored). The observation time is left-truncated in case the studied object has to cross a threshold to be included. Klein and Moeschberger (2003) call this a ‘delayed entry time’ as individuals are only observed from this time until they experience the event of interest or are censored. Ignoring left truncation may introduce substantial bias in the estimation of the survival time distribution (Klein and Moeschberger, 2003). NFI data are left-truncated since trees have to cross a DBH-threshold to be included.

We censored the data in case a tree has not experienced natural death at the end of the observation period, even if it moved outside the NFI-plot (e.g., by slanting). Since we are interested in natural mortality, we also classified removed trees due to salvage logging as censored, in line with previous studies (e.g., Staupendahl and Zucchini, 2010; Brandl et al., 2020). On the other hand, trees were classified as failure (i.e., having experienced death) in case of undifferentiated cutting (i.e., sanitary logging of single ailing trees) and natural mortality potentially caused by environmental stressors, self-thinning or senescence.

Transferring the idea of survival analyses to our study, we used the DBH of the target tree at the beginning and the end of the observation interval as the time variable (Canchola et al., 2003) together with the coded event (censored/failure) to estimate the survival function $S(DBH)$. This enabled us to model the survival probability as function of the DBH, which represents one of the most important parameter in relation of tree development, architecture, and ontogeny (Barthelmy and Caraglio, 2007), and it is frequently used for forest management decisions. We calculated and visualized the results using the trees’ development stage based on DBH-classes as defined by IUFRO (2000), see also Fig. 2.

2.4.2. Survival models

We used the non-parametric Kaplan-Meier estimator (KM-estimator; Kaplan and Meier, 1958) to compare the survival probabilities of different tree species and the semi-parametric Cox Proportional Hazard model (Cox PH-model, Cox, 1972) to test the influence of different predictors on chestnut’s failure probability.

The Kaplan-Meier estimator assumes no parametric form of the survival distribution and the survival function $\hat{S}(t)$ of $T$ (in our case DBH) is defined as:

$$\hat{S}(DBH) = \prod_{DBH_i \leq DBH} \left(1 - \frac{d_i}{n_i}\right)$$

where $\hat{S}(0) = 1$, $d_i$ are trees that fail at DBH$_i$, and $n_i$ represents the total number of trees at risk at DBH$_i$.

We calculated semi-parametric Cox-PH models avoiding the specification of a parametric survivor distribution that corresponds to a left-truncated distribution (Brostrom, 2012). We used then following hazard function:

$$h(DBH) = h_0(DBH) \exp(x_1 + x_2 + \cdots + x_n)$$

where, $h(DBH)$ is the hazard function with DBH denoting the “time” variable, $x_1, \ldots, x_n$ the set of predictors (Table 1) and $\beta$ the estimated coefficients measuring their impacts. The term $h_0(DBH)$ is the baseline hazard that corresponds to the hazard if all predictors are equal to their means. The quantities exp(\beta) are called the hazard ratios (HR) with values greater than one indicating a predictor that is positively associated with the event probability, and thus negatively associated with the
length of survival (in our case the DBH, which can be reached). A HR less than one means negative association of the predictor with the event probability and therefore longer survival.

To identify multiplicative drivers on chestnut mortality before and after the appearance of the ACGW we fitted two different Cox-PH models. The first one included the two periods between the first and third NFI before the ACGW arrived (NFI 1–3 model). In order to isolate the specific effect of the ACGW, we calculated a separate Cox-PH model (ACGW-model) using NFI 3–4 data, which represent the period after the arrival of the pest in the study area (Gehring et al., 2020).

The computations were performed in R (R Development Core Team, 2019) using the packages data.table (Dowle et al., 2018), survival (Therneau, 2018), and ggplot2 (Wickham 2016). Data exploration followed the guidelines of Zuur et al. (2010), who suggest the use of Pearson’s correlation coefficient and the variance inflation factor (VIF) to detect collinearity among variables. All variables were z-score transformed to facilitate the comparative interpretability of the estimated coefficients. Since trees belonging to the same inventory plot show a higher correlation in their behavior than trees between plots, we used inventory plot as a random intercept.

For model selection, we first fitted Cox-PH models with single predictors. Significant variables at the 0.2–0.25 level were then fitted in a multivariable model (Sveinbjörnsson et al., 2011). In a following step, the variables that resulted as non-significant in the first step were added back to the model to confirm or reject the lack of statistical significance. The contribution of a variable to the model was checked applying a likelihood ratio test. In the last step, we tested for interactions between variables.

Model assumptions were checked by testing the proportional hazard assumption (PHA), analysing the residual patterns and calculating the concordance. The PHA is fundamental in Cox-PH models that assumes that the hazard ratio of two units experiencing an event are proportional to one another and that this relationship is constant over time. We tested the PHA calculating the Grambsch and Therneau (1994) modified Schoenfeld residuals using the ‘cox-zph’ function in the survival package (Therneau, 2018). In our specific case, the selected ACGW model did not meet the PHA. Therefore, we organized the datasets into DBH intervals (strata see Table 2) using the split-function in the survival package (Therneau, 2018). The underlying assumption when splitting the data set into time intervals (in our case DBH intervals) are constant hazards within the intervals, but a possible hazard variation between them. Variables violating the PHA were considered as time-dependent and included with a DBH interaction ($\delta$DBH).

The analysis of residuals for survival models differs in comparison to regression models (Mills, 2011) because of the censored data structure. Therefore, we calculated the dfbeta residuals (Klein and Moschberger, 2003) to detect observations that have a large influence on the model, and the Martingale residuals to evaluate the functional form of the model. The models showed no pattern in residuals (see Appendix B). In case the model assumptions were violated, we tested square root, cube root, log and box-cox transformation.

Finally, we used the concordance statistic (Therneau and Atkinson, 2020) as a measure of goodness-of-fit of the survival models. The concordance calculates the probability that a predicted value goes in the
same direction as the actual data and is equivalent to the area under the ROC curve (AUC) used as a measure of goodness-of-fit in logistic regression analysis. Models with concordance values above 0.5 imply good prediction ability, while those equal or below 0.5 have no predictive ability.

3. Results

A total of 154 plots were available for the analyses of chestnut mortality, distributed over an altitudinal range from 283 m a.s.l. to 1090 m a.s.l. In total, data on 1757 chestnut trees were collected with 5292 individual observations (4404 censored observations and 888 failures). Chestnut was the dominant species in terms of basal area in 59% of the plots. Beside chestnut, 34 other tree species were found on the plots (Appendix A, Fig. A.1), mostly birch (Betula pendula) and beech (Fagus sylvatica).

3.1. Species-specific survival probabilities

The non-parametric KM-estimator shows on the one hand the capacity of the chestnut individuals to become larger (DBH > 160 cm) than other tree species, but also reveals its lower survival probability in the earlier development stages (12 cm ≤ DBH < 50 cm) when compared to the pioneer-, intermediate- and late-successional species (Fig. 2). Such differences are especially marked for the large pole stage (DBH 20 – 30 cm), when the survival probabilities for chestnut are around 15%, 31%, and 41% lower than for pioneer-, intermediate, and late-successional tree species, respectively. Only at DBH above 48 cm, the survival probability of pioneer species drops below that of chestnut, which has a stable survival probability for DBHs larger 110 cm.

The species-specific Kaplan-Meier curves (Appendix A, Fig. A.2) of chestnut show a similar pattern to pioneer trees in the lower end range, which is represented by willow trees (Salix spp.). At the small timber stage (30 cm ≤ DBH < 40 cm), chestnut has an even lower survival probability than pronounced pioneer species such as birch (Betula pendula). At the large timber stage (40 cm ≤ DBH < 50 cm), the late-successional-species Fagus sylvatica (S(DBH) = 0.95), Abies alba (S (DBH) = 0.87), Tilia (S(DBH) = 0.85), and Picea abies (S(DBH) = 0.85) show the highest survival probabilities, which are more than two times higher than for chestnut (S(DBH) = 0.37).

With regard to the amount of dead and living trees in the four NFI-intervals, the chestnut trees show the highest total numbers of dead individuals in comparison to pioneer-, intermediate and late-successional trees (Fig. 3). While only 5% of the chestnut trees were recorded as dead in NFI 1, the percentage doubled in NFI 2-4. Similarly, the number of dead pioneer trees slightly increase from NFI 1 (2%) to NFI 4 (9%), while those for intermediate and late-successional species were nearly constant.

3.2. Concurring drivers of chestnut mortality

The Cox-PH model for the pre-ACGW period (NFI 1–3 model) includes basal area of other pioneer (BApion), intermediate (BAint) and late-successional tree species (BAlate), mean standardized precipitation evapotranspiration index (meanSPEI), type of disturbances, site indicators (elevation, slope, aspect) and tree’s position within the stand (Layer) (Table 2). The ACGW-model includes similar predictors, except meanSPEI, disturbances, BAint and slope, plus the level of ACGW damage and highlights how the ACGW pressure generated interactions between environmental drivers (e.g., elevation or aspect) and development stage (DBH classes). Both, the NFI 1–3 and ACGW-models reveal a high concordance of 0.95 and 0.86, respectively. By holding all variables at their mean values, the probability for chestnut trees to survive until DBH 30, 40 and 50 cm decreases from 0.8 to 0.74, and 0.7, respectively (NFI 1–3 model, Fig. 4 baseline curve). For larger chestnut trees, the survival probability stabilizes at ca. 50% (Fig. 4).

MeanSPEI has a strong influence on chestnut mortality in the NFI 1–3 model, revealing that chestnut trees growing on sites with good water availability have a lower hazard to die (HR < 0.22). On sites with good water availability, chestnut’s survival probabilities are ca. 0.90, while they drop down to between 0.30 and 0.48 at dry site conditions (Fig. 4a). Competition, expressed as both chestnut tree competitiveness (position of the tree in the canopy layers) and presence of late-successional tree species, has a strong impact on chestnut’s survival probability (Table 2). Trees in the middle canopy layer have an 8 to 9- times higher risk to die (HR_{NFI 1-3} = 9.38, HR_{ACGW} = 7.95) than those in the upper

### Table 2

Estimated hazard ratio (exp(β)), z-values and p-values of variables from the final Cox-proportional hazards models for the NFI 1–3 (NFI 1–3 model) and NFI 3–4 (ACGW model) data.

<table>
<thead>
<tr>
<th>Variable</th>
<th>NFI 1–3 model</th>
<th>ACGW model</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>exp(β)</td>
<td>z-value</td>
</tr>
<tr>
<td>Layer (middle)</td>
<td>9.38</td>
<td>9.07</td>
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<tr>
<td>Layer (lower)</td>
<td>18.37</td>
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</tr>
<tr>
<td>BApion</td>
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<td>BAint</td>
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<tr>
<td>BApion</td>
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<td>-1.63</td>
</tr>
<tr>
<td>meanSPEI</td>
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</tr>
<tr>
<td>Disturb (goat)</td>
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</tr>
<tr>
<td>Disturb (other)</td>
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</tr>
<tr>
<td>Disturb (fire)</td>
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<tr>
<td>GallDamage (low-mild)</td>
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<td>-</td>
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<tr>
<td>GallDamage</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>(moderate)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>GallDamage (high)</td>
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<td>-</td>
</tr>
<tr>
<td>GallDamage (severe)</td>
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<td>damage</td>
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<td>GallDamage (high): BApion</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>BAint</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>GallDamage (severe)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>damage: BAlate</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>GallDamage (low-mild): BAlate</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>GallDamage (moderate): BAlate</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>BAlate</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>GallDamage (severe)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>damage:3BAlate</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Layer(middle): BAint</td>
<td>0.65</td>
<td>-2.2</td>
</tr>
<tr>
<td>Layer(lower): BAint</td>
<td>0.61</td>
<td>-2.2</td>
</tr>
<tr>
<td>Concordance</td>
<td>0.95</td>
<td>-</td>
</tr>
</tbody>
</table>

A hazard ratio (HR) < 1 reduces the hazard to die and vice versa. The mean and standard deviation of the original variables, as well as their acronyms, are presented in Table 1. Due to the violation of the proportional hazard assumption, strata refers to the DBH group 12 – 20 cm (strata 1), DBH 20.1 – 40 cm (strata 2), DBH 40.1 – 50 cm (strata 3) and DBH > 50 cm (strata 4). Significance codes: ‘***’, p < 0.001, ‘**’, p < 0.01, ‘*’, p < 0.05, ‘.’, p > 0.1; ‘n.s.’ not significant, ‘-’ not retained in the model.

* Square root transformed in the ACGW model and NFI 1-3 model, "Tukey’s Ladder of Powers transformation in the NFI 1-3 model."
layer, whereas for trees growing in the lower layer, the risk increases up to 14- to 18-times (HR$_{NFI 1-3}$ = 18.37, HR$_{ACGW}$ = 14.3, Fig. 4b).

Among competition parameters, the presence of pioneer, intermediate and late-successional tree species are included in the models, except BAint in the ACGW model. Both the presence of late-successional and intermediate tree species has a significant negative impact on chestnut’s survival probability, while the effect of intermediate tree species was less pronounced for chestnut trees growing in the lower and middle layer (HR$_{NFI 1-3}$ = 0.65, BAint:layer(middle), HR$_{NFI 1-3}$ = 0.61, BAint:layer(lower)). The hazards for chestnut to die increases in the presence of late-successional trees by around 50% in the NFI 1–3 (HR$_{NFI 1-3}$ = 1.54) and ACGW-models (HR$_{ACGW}$ = 1.46), respectively. At DBH < 50 cm, the 0.05- (corresponding to less than 1 m$^2$ ha$^{-1}$) and 0.95-percentiles (corresponding to 14.41 m$^2$ ha$^{-1}$) for BAlate range between 0.81 and 0.61, respectively (Fig. 4c). For both the NFI 1–3 and ACGW models, the basal area of pioneer tree species displays an opposite effect (HR$_{NFI 1-3}$ = 0.79, HR$_{ACGW}$ = 0.29) than for late-successional species, although non-significant (Fig. 4d).

Elevation is significantly related to chestnut survival probability in both models, but with opposite effects. Before the arrival of the ACGW (NFI 1–3 model), chestnut trees growing at higher elevation faced a higher risk to die than those at lower elevation (HR$_{NFI 1-3}$ = 1.88). At 390 m a.s.l., which corresponds to the 0.05-percentile, the survival probabilities for chestnut trees DBH < 50 cm are close to 0.90 (Fig. 4e) but decreases up to 0.64 for trees in the timber stage at 956 m a.s.l. (0.95-percentile). Contrastingly, the effect reverses and the hazard ratios varied with increasing DBH in the ACGW-model (OH$R_{ACGW}$ = 0.70, Table 2). In the ACGW-model, also the aspect is significantly related to chestnut’s survival probability, with a higher survival probability on northeastern than on southwestern exposition (HR$_{ACGW}$ = 0.73).

In the NFI 1–3 model, disturbances by goats and fire have a significant influence on the hazard for chestnut to die. Comparing undisturbed forests to those disturbed by fire, the hazard for chestnut to die decreases by 81% (HR$_{NFI 1-3}$ = 0.19). While the risk of death is approximately 3-times higher (HR$_{NFI 1-3}$ = 3.09) under grazing pressure by goats (Table 2, Fig. 4f).

Infestation by ACGW as a biotic disturbance shows a significant influence on the hazard for chestnut to die. By comparing the different damage levels due to the ACGW infestation, the model reveals a 3-times (HR$_{ACGW}$ = 3.15) higher risk to die for severely damaged chestnuts (level 5) compared to undamaged ones. This effect is even more pronounced when late-successional and pioneer trees are present (HR$_{ACGW}$...
Fig. 4. Influence of individual variables included in the Cox-PH model (NFI 1–3) on the survival probability of the chestnut tree, a = Mean SPEI, b = Stand layer position, c = Basal area late-successional species, d = Basal area pioneer species, e = Elevation, f = Disturbances. The white line and the shaded area represent the survival baseline curve (all variables at their mean values) and the confidence interval (95%), respectively.
Finally, chestnut’s survival probability decreases toward higher elevation, where the species has often been cultivated to its ecological limits (Muster et al., 2007).

Since the ACGW arrival in the study area, severe ACGW damage (level 5) became a high mortality factor for the chestnut tree, partially masking or altering the impact of other drivers. As a general rule, interactions between environmental drivers (e.g., elevation or aspect) and chestnut tree related features such as the development stage (DBH classes) increase in their explicative power because of the different impact of the gall wasp as a function of the chestnut tree development stage and growing site (Gehring et al., 2020). For instance, disturbances or the mean Standardized Precipitation Evapotranspiration Index (meanSPEI) has no impact in the ACGW model, whereas elevation is reversing its effect. Similarly, the effect of aspect increases and the detrimental competition effect by late-successional trees intensifies in case of simultaneous high level of ACGW damage. According to Gehring et al. (2018), repeated and severe attacks by the ACGW (damage level 5) may reduce the foliar area of the chestnut crown by up to 70%. This highly weakens the trees, which further increases their energy consumption by activating the dormant buds in the attempt of restoring the lost crown biomass (Gehring et al., 2018). Such green biomass loss and energy depletion additionally reduce the competitive fitness of chestnut against the shading effect of late-successional tree species, as revealed by the interacting effect the ACGW damage level 5 and the basal area of late-successional tree species in the ACGW model.

As reported by Gehring et al., (2020), the biological control by the natural ACGW antagonist Torymus sinensis may fail to fully functioning on southern-facing slopes where higher temperatures possibly cause an earlier emergence of the majority of the antagonist population and a desynchronization with ACGW appearance. The desynchronization of the phenology of the two insects and the related failure of the parasitic action of the antagonist on south-facing slopes may explain the effect of the aspect in the ACGW model.

Finally, the reduced time lag between the ACGW and the antagonist arrival at higher elevations (Gehring et al., 2020) may explain the contrasting effect of elevation on the chestnut tree survival in the ACGW model compared to the NFI 1–3 model. The rapid biological control of the epidemic in case of a reduced time lag between the arrival of the two insects lowers the chance of repeated attacks by the ACGW on the chestnut crowns. This increases the survival probably especially for the rapidly growing chestnut trees at strata 2 and 3 of development (DBH between 20 and 80 cm).

4.3. Suitability and limits of the approach

Using data of the first four Swiss National Forest Inventories allowed us to analyze a large set of systematic and representative observations of chestnut trees growing under post-cultural stand dynamics on the southern slopes of the Swiss Alps. This resulted in a broad range of site characteristics, and a general long time since last silvicultural treatment and a correspondent advanced post-cultural stand dynamic (i.e., ‘latent reserves’ sensu Portier et al., 2020).

Due to the time-series character of the data (e.g., follow-up intervals), we used survival models for the analysis. In medical studies, survival models are primarily developed for the analysis of survival times after a specific treatment (e.g., Campbell et al., 2010) of individuals which have almost the same initial conditions (e.g., breast cancer). Health conditions of the individuals may then change after the treatment, making the survival time precisely measurable from the start (treatment) to the end (last observation) of the study. In our approach, precisely defined boundary conditions are present for the ACGW-model only, since all chestnut trees experienced the ACGW arrival, although with short time lags and different degree of damage (which is in our case equivalent to treatment). A specific treatment is on contrary missing for the NFI 1–3 model, although the general suspension of the management inputs that took place in the late 1960ies due to the socio-economic
development of the area (Krebs et al., 2014) may be considered a general driving factor consisting of the increasing time under natural stand dynamic conditions. Despite such limitations, survival models consider censored data and are thus suitable for forest inventories even when such specific treatments are lacking (Neuner et al., 2015; Brandl et al., 2020).

The quite long inventory intervals (up to 10 years) did not allow a time-sharp record of the mortality event, which makes the precise definition of the mortality cause almost impossible. Therefore, possible predisposing mortality causes such as the chestnut blight (Prídya et al., 1996) or extreme drought events (Conedera et al., 2010a) could not be included in our analysis. For the same reason, also the slightly significant but hardly explainable interaction between the basal area of late-successional tree species and the ACGW damage level 2 only (but not levels 3 and 4) may be an artefact of the lack of yearly surveys in our approach.

The lack in the NFI of a systematic and reliable record of the tree origin (i.e., seed-trees vs shoots from stool) and of existing grafting marks in the orchard trees precluded us to consider these parameters in our analysis and in particular to distinguish former coppice stands for timber production from abandoned chestnut orchards for fruit production. The different growing dynamics and physiology between seed- and bud-organised chestnuts (Manetti et al., 2020) as well as between wild seed trees and grafted orchard trees (Conedera et al., 2001) may indeed have a significant impact on the survival probability of the trees.

Finally, most of the analysed chestnut stands consist of former pure chestnut groves, which are now subjected to a post-cultural natural stand dynamic after the suspension of cultural inputs. In mixed stands, chestnut trees growing since the early stages with other tree species with similar growth behaviour and ecological needs may result in a different interspecific competition fitness.

5. Conclusions

Fitting survival models with data from ‘latent chestnut forest reserves’ enabled us to gain more knowledge about the ecology of the chestnut tree, which goes beyond static assessments of SDMs. By using two different models that include data before and after the ACGW arrival in the study area, we could additionally demonstrate the effect of the ACGW arrival on chestnut mortality in areas where the late arrival of the specific antagonist caused severe damage to the chestnut trees. This highlights the importance of a timely control of newly introduced pests in forestry whenever possible.

We can conclude that the chestnut tree is not per se a future-proof tree. On poor sites and in case of drought, the species seems to be particularly prone to rising water-stress leading to a higher mortality risk. Forest managers should thus be aware that the chestnut tree might not be the best option on xeric site conditions to face expected rises in summer temperatures and dry conditions. Despite the constant risk represented by historical (chestnut blight, ink disease) and new (ACGW) biotic agents, the chestnut tree can however be a very good option for producing quality wood (Manetti et al., 2020). This may be the case on good sites and on forest patches where regular silvicultural treatments are warranted. The species may be on the contrary highly sensitive when consociated with shade-tolerant tree species or to the lack of silvicultural interventions as revealed by its low shade-tolerance and the poor competitiveness when subjected to post-cultural stand dynamics, especially at good growing conditions. Furthermore, due to abundant resprouting capacity of the species, chestnut stands usually turn to coppice systems from the second generation on, which then requires adapting the silvicultural system.

Declaration of Competing Interest

The authors declare that there is no conflict of interest.

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Authors’ contributions

MC, JW and LH conceived the idea of the manuscript. MC and JM designed the methodology, analyzed the data, and wrote the manuscript. MA, PK and EG have prepared the data. All authors contributed critically to the drafts and gave final approval for publication.

Data availability

The raw data from the Swiss NFI can be provided free of charge within the scope of a contractual agreement (http://www.lfi.ch/dienstleist/daten-en.php).

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119320.

References
