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Title: Impact of the Asian gall wasp (*Dryocosmus kuriphilus*) on the radial growth of the European chestnut (*Castanea sativa*).

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Abstract

1. The invasion of the Asian chestnut gall wasp *Dryocosmus kuriphilus* (ACGW) in Europe has caused serious biological and economic impacts on chestnut stands that have been partially solved with the introduction of the biological control agent *Torymus sinensis*. However, information concerning tree-ring growth during the ACGW epidemic has been lacking so far.

2. Using dendrochronology techniques, we analysed the impact of the ACGW on tree-ring growth and the capacity of the chestnut tree to recover when biocontrol was achieved in seven sites covering the area of first detection and subsequent spread of the ACGW in Europe. In each site, a non-target control species (i.e., trees not attacked by the ACGW) has been included as a reference in the analysis.

3. Results show a reduction in the tree-ring increment by 60% on average during the ACGW epidemic. Such effects were higher in the magnitude and longer in the duration when compared to other stresses such as insect defoliation or extreme summer droughts.

Synthesis and applications. Marked reductions in radial growth were evident in the years of ACGW attack regardless of the age of the chestnut coppices. Since most of the trees only recovered to an almost normal growth rate after three/four years of biocontrol by *T. sinensis*, an immediate release of the antagonist at the first ACGW appearance is highly recommended. The consequences and perspectives of ACGW's attacks on the quality of the timber produced are also discussed.

Keywords: Asian chestnut gall wasp outbreak; chestnut coppices; classical biological control; insect pest; *Torymus sinensis*; tree damage; tree-ring growth.

Introduction

Invasive alien species may have significant direct and indirect impacts on biodiversity and ecosystem services and are thus among the most important threats to ecosystems (Bacher et al., 2018; T. P. Holmes, Aukema, Von Holle, Liebhold, & Sills, 2009; Kenis et al., 2009). In Europe, invasive alien gall makers have exposed both native and non-native forest trees to severe attacks, in particular when native natural enemies were not effective in regulating pest populations

(Branco, Battisti, & Mendel, 2016). In this respect, the accidental introduction of the Asian chestnut gall wasp *Dryocosmus kuriphilus* Yasumatsu (Hymenoptera: Cynipidae; hereafter ACGW) is a very illustrative example. Native to China, the ACGW is a parthenogenetic (thelytokous) and univoltine gall maker attacking all species and hybrids of the genus *Castanea* (Aebi, Schonenberger, & Bigler, 2011; Avtzis, Melika, Matošević, & Coyle, 2019; Stone, Schönrogge, Atkinson, Bellido, & Pujade-Villar, 2002). Since the first report of its presence in Northwest Italy at the beginning of the century (Brussino et al., 2002), the gall-maker proved to be a severe pest even for European chestnut (*Castanea sativa* Mill.) due to its life-cycle (well synchronized with the host-tree phenology) and its effectiveness in terms of both population growth and dispersal ability (Gilioli, Pasquali, Tramontini, & Riolo, 2013; Graziosi & Santi, 2008). In addition to this, human assisted transport of asymptomatic infested material facilitated the ACGW long distance dispersal. Therefore, the insect colonized almost the whole European chestnut growing area, from Great Britain to Russia, in about 15 years (Avtzis et al., 2019).

Based on the successful Japanese experience of reducing the ACGW population through a classical biological control approach, the biocontrol agent *Torymus sinensis* Kamijo (Hymenoptera: Torymidae) (Moriya, Shiga, & Adachi, 2002) was introduced in Italy in 2005 in the area of first ACGW detection, where it proved to be very effective in controlling the ACGW (Ferracini et al., 2018; Quacchia, Moriya, Askew, & Schönrogge, 2014). After its introduction at large scale in Italy, the biocontrol agent was released in most European chestnut-growing countries (Avtzis et al., 2019) or spread spontaneously by stratified dispersal (Colombari & Battisti, 2016b) into other ones such as Switzerland (Gehring, Bellosi, Quacchia, & Conedera, 2018) and the Balkan region (Matošević et al., 2017). As a result, the biocontrol agent generally caused a significant reduction of the ACGW population in a few years (Colombari & Battisti, 2016a; Ferracini et al., 2018).

Without any control, repeated and severe ACGW attacks prevented a normal vegetation of the chestnut trees, affecting stomata conductance as well as CO_2 assimilation capacity (Ugolini et al., 2014) and leading to a reduced capacity of developing buds (Gehring, Bellosi, et al., 2018). This resulted over the years in a malformation of the branch architecture and a general crown deterioration with a corresponding loss in green biomass (up to 70% on average, Gehring, Bellosi, et al., 2018; Gehring et al., 2020). Heavily infested trees displayed a reduced shoot vigour (Ugolini et al., 2014), an increased susceptibility to other biotic stresses, such as the specific chestnut pathogens *Cryphonectria parasitica* (Murril) Barr and *Gnomoniopsis castaneae* Tamietti

(Lione, Giordano, Ferracini, Alma, & Gonthier, 2016; Meyer, Gallien, & Prospero, 2015), as well as a significant reduction in non-woody chestnut products, such as nut production (reduction up to 80% of the harvest, Battisti et al. 2014) and in the chestnut component of honey (Gehring, Kast, et al., 2018). However, little information exists so far about the impact of ACGW in terms of tree-ring increments, which become a key issue whenever timber represents the main forest product, as in the 1.8 million ha of chestnut coppices and high forests in Europe (Conedera, Manetti, Giudici, & Amorini, 2004). Abrupt reductions in the tree-ring growing rates do not only cause significant losses in terms of timber biomass, but also increase the risk of ring shake failures, which are the main cause of value loss in chestnut wood (Fonti & Macchioni, 2003).

In this study, we applied dendrochronology techniques (Ryerson, Swetnam, & Lynch, 2003; Swetnam & Lynch, 1989) to analyse the variation in tree-ring increments of chestnut coppices attacked by the ACGW therefore exploiting the possibility of a retrospective analysis of tree growth (see Dendroecology in Speer, 2010). Specifically, we selected seven study sites covering the area of first detection of the ACGW in Europe. The selected sites displayed different time lags between the beginning of the ACGW outbreak and the effective biological control. Our specific objectives were:

1) To detect and quantify the ACGW impact on the tree-ring growth of affected chestnut coppice trees;

2) To investigate the possible role of stand age (i.e., young ≤ 25 years and over-aged ≥ 40 years shoots) on such ACGW impact;

3) To verify whether the tree-ring growth in chestnut trees returns to the pre-ACGW increment rates when the biocontrol by *T. sinensis* becomes effective.

Materials and methods

Study area and sampling design

The study was carried out in seven sites distributed from southern Switzerland to northern and central Italy (including the Chiusa Pesio site that is the area of first European detection of the ACGW). The selected stands display time lags ranging from 4 to 11 years since the beginning of the ACGW infestation to successful biological control, this latter defined as at least 75% parasitism of ACGW by *T. sinensis* (Quacchia et al., 2014). Elevation ranges from 450 to 950 m a.s.l., mean annual temperatures vary from 9 to 13 °C, and annual precipitation spans from 870 to 1545 mm (Fig. 1; Table 1).

-here Fig. 1-

In each site, two among the nearest almost pure chestnut coppices differing in age between young (≤ 25 years) and over-aged (≥ 40 years) stands were chosen (see Table 1 for details on young and old coppices).

Because of the absence of healthy reference chestnut trees (unaffected by ACGW attacks), in each site we additionally selected control trees (i.e., species not attacked by the ACGW) such as *Quercus petraea* (Matt.) Liebl. (sessile oak), *Robinia pseudoacacia* L. (black locust) and *Pinus nigra* Arnold (black pine) that did not display any damage by species-specific enemies during the ACGW epidemic. We used these trees as base-line reference for the non-ACGW local environmental effects (Fritts & Swetnam, 1989; Schweingruber, 1996).

-here Tab. 1-

Field measurements

In order to record the main characteristics of the investigated chestnut coppices, we first selected a homogenous circular plot of 10 m radius located in a representative part, where we recorded the stool density as well as the species and diameter (DBH) of all trees and shoots taller than 130 cm.

In a second step, at-stand level we selected the largest shoot of twelve dominant chestnut stools and eight dominant control species trees that we first measured (DBH and height) and then cored at breast height. As a rule, dominant trees growing upright and with round stems were cored only once. A second core has been taken only in rare, doubtful cases.

Data pre-processing

Tree-ring data

The tree-Ring Widths (RW) of the sampled cores were measured using a linear table LINTAB and the software TSAP-Win (Rinn, 2003). RW series of chestnut and control species were visually cross-dated and synchronized separately at site level using COFECHA (Holmes, 1983). To minimize the non-desired growth trends (age-trend and long-term forest dynamics), RW series were additionally treated with ARSTAN (Cook & Holmes, 1999) applying cubic smoothing splines with a 50% frequency cut-off at 32 years (Cook & Peters, 1981). For each site, a Tree-Ring Index (TRI) was computed using a bi-weight robust mean of the individual-tree RW series standardized to a mean of 1.0 as residuals from the estimated growth and variance stabilization (Cook, 1985).

The quality of stand chronologies (i.e., Young and Old coppices, control species) was then evaluated at site level in a common period calculating the mean R-bar (cross-correlation between single series) and the EPS (expressed population signal) at stand level (Wigley, Briffa, & Jones, 1984), while annual within-stand variability was rendered by the MS (mean sensitivity). R-bar is a measure of the common signal between single series, while EPS reveals how well a finite sample of tree-ring data represents an infinite population chronology (Buras, 2017; Fritts, 1976; Speer, 2010).

We finally converted the cross-dated RW series into basal area increments (BAI, $cm^2 \cdot yr^{-1}$). Age-related BAI trends usually take the form of a sigmoid-like positive growth (Duchesne, Ouimet, & Morneau, 2003; Fritts, 1976; Phipps & Whiton, 1988) suggesting that negative trends in BAI may be linked to tree growth decline (Pedersen, 1998). The choice of sampling exclusively dominant trees allowed us to exclude a-priori the effects of competition on tree-ring growth.

Eligibility of the selected control species

The eligibility of the control species was checked by analyzing the within-site similarity with respect to *C. sativa* in terms of climate-growth relationships (Ryerson et al., 2003; Swetnam, Thomson, & Sutherland, 1985). Due to heterogeneity and in some cases also unavailability of data from local weather stations, we used the 1901-2016 monthly total precipitation and the monthly average temperature derived from the Climatic Research Unit CRU TS4.02 dataset at 0.5° of spatial resolution (all the study sites showed a good correlation between the data from local weather stations and the CRU TS4.02 database). For each site, we excluded the years following the ACGW arrival. We used DendroClim2002 (Biondi & Waikul, 2004) to analyze the data through graphical plots, correlation coefficients and response function analyses (Paritsis, Veblen, & Kitzberger, 2009)

Drought as climatic anomaly

Drought episodes were identified on the base of the Standardized Precipitation Evapotranspiration Index (SPEI; Vicente-Serrano et al. 2010). We considered in particular the temporal series of monthly SPEI cumulating the effects of the previous three months. Given chestnut sensitivity to summer climatic extremes (Fonti & Garcia-Gonzalez, 2004; Knüsel, Conedera, Rigling, Fonti, & Wunder, 2015), a drought episode was defined as a monthly summer SPEI_jja (June, July and August months) value less or equal to -1 (Potop, Boroneanţ, Možný, Štěpánek, & Skalák, 2014).

Indicators of the ACGW outbreak

Unfortunately, we lacked detailed information on site-specific ACGW infestation rates (e.g. proportion of attacked buds; Kotobuki et al. 1985) and the percentage of parasitism by *T. sinensis* since its release. To overcome this limit, we selected proxies of the ACGW outbreak evolution that proved to be reliable epidemic indicators in different European chestnut areas (Borowiec et al., 2018; Ferracini, Ferrari, Pontini, Saladini, & Alma, 2019; Gehring et al., 2020), such as i) time since ACGW arrival (Dk_{yrs}); ii) time since *T. sinensis* release or arrival (Ts_{yrs}); iii) time since the achievement of the ACGW biocontrol by *T. sinensis* (BC_{yrs}) (Table 1). We finally drew a synthetic damage index calculated as follows:

Dk_damage (yrs) = Dk_{yrs} (until 4 maximum) - BC_{yrs}.

Dk_{yrs} has been set to a maximum of 4 years based on the assumption that the proportion of infested buds, dead crown parts and alteration of the branch architecture reaches its maximum after four years of repeated and uncontrolled ACGW attacks (Gehring, Bellosi, et al., 2018; Gehring et al., 2020). On the other hand, the achievement of the biocontrol (BC) by *T. sinensis* causes a significant decline in the ACGW population and in the proportion of infested buds, although the full recovery of the whole tree structures is further delayed in time (Gehring et al., 2020).

Data analysis

Growth differences between C. sativa and control species

Aiming at assessing possible differences between the growth of all *C. sativa* (Old and Young coppices) and control species trees (question 1), we applied the following equations proposed by (Nash, Fritts, & Stokes, 1975) and (Swetnam et al., 1985):

$$I_t = I_{Cst} - \left[\frac{SD_{Cs}}{SD_{ctrl}} \cdot \left(I_{ctrl} - \bar{I}_{ctrl}\right)\right]$$

$$\text{Corrected index (CI)} \quad CI_t = I_t - 1$$

where I_{Cst}, I_{ctrl} are the *C. sativa* and the Control species chronologies at year t, SD_{Cs}, SD_{ctrl} are the standard deviations of the *C. sativa* and control species chronologies, and $\bar{I}_{ctrl}$ is the mean of the control species chronology.

The corrected series were individually normalized by subtracting the mean and dividing by the standard deviation. Negative values in the CI indicated a reduced growth of *C. sativa* with respect to the control species, while positive values indicated higher growth.

Significant growth reductions (anomalies) were assigned to years exhibiting values lower than -1SD of the normalized corrected series in at least 30% of the trees. This threshold is lower than the values suggested by the literature (Ryerson et al., 2003; Welsh, Lewis, & Woods, 2009) because of the assumption that the ACGW does not completely compromise the photosynthetic performance of the canopy, at least in the first years of the outbreak (Gehring, Bellosi, et al., 2018).

Theoretical BAI growth model without disturbances

Various methodological steps have been undertaken in order to calculate the BAI variation due to events known for their extreme growth-depressing effect (e.g., summer drought, crown defoliation by the gypsy moth *Lymantria dispar*, and ACGW).

First, we excluded from the tree chronologies all BAI values associated with known extreme events, such as drought episodes (years with SPEI_jja value < -1) and *L. dispar* attacks (e.g., Asshoff et al. 1999), with the purpose to compute a theoretical (undisturbed) BAI growth model for single chestnut tree and related stands (young and old separately). In order to use a generalized linear mixed model, the relationship between the variables BAI and age has been linearized applying a square root transformation to the response variable, i.e., sqrt(BAI), and the natural logarithm to the explicative one, i.e., ln(age). Alternatively, orthogonal polynomials have also been applied to the explicative variable and tested in the model. The random effect (tree individual) configuration (random intercept or random intercept and slope) was determined following the procedure described by (Zuur, Ieno, Walker, Saveliev, & Smith, 2009), which consists in creating the so called “beyond optimal model” including all explanatory variables in the fixed component. Then, using the “beyond optimal model”, various random configurations are applied. These models were then compared by means of the Akaike information criterion (AIC), so that the random structure of the one with the lowest AIC was thereafter used for subsequent model analysis.

Models were selected according to the AIC and the adherence of the residuals to the assumptions of the generalized mixed effect model.

Quantification of the stress-induced BAI variations

The resulting models were then used to predict the theoretical BAI growth that every tree would follow during the entire study period without the influence of any known disturbance or extreme event ($BAI_{reference}$).

The BAI variation due to known extreme events was then calculated as follows:

$$deltaBAI\ (\%) = \frac{(BAI_{measured} - BAI_{reference})}{BAI_{reference}} \cdot 100$$

where $BAI_{measured}$ refers to the effective BAI measured every year.

The *delta*BAI has been subsequently used with descriptive statistics and univariate comparative analysis (using Pairwise Wilcoxon Rank Sum Tests with $p < 0.05$) to detect and quantify the effects of the known extreme events on tree growth.

Finally, generalized linear mixed models were used in Young and Old coppices and in Control species separately to model the relationship between $BAI_{measured}$ and extra events, such as droughts (SPEI_jja < -1) and ACGW infestation (Dk_{yrs}, Ts_{yrs}, BC_{yrs}, Dk_damage), so as to quantify the impact of those events considering the whole tree life. The random effect (tree individual nested in locality) configuration was determined following the procedure mentioned above.

All analyses were performed in R (version 3.5.1; R core Team 2018). Linear mixed effects models were fit using the lme4 package (Bates, Mächler, Bolker, & Walker, 2015) and their goodness of fit evaluated with the r.squaredGLMM function of the MuMIn package (Barton, 2015). Model prediction was implemented through the predict() R-function (Chambers & Hastie, 1992). Further details that support the results can be found in the Supporting Information.

Results

Age and growth rate of the stands

The mean age of Young coppices ranged between 19 and 25 years, while their average radial growth rate varied from 3.2 mm/y in Euganei to 4.8 mm/y in Torre Canavese (TRW_tot in Table

S1 in Supporting Information). Among Old coppices, the mean age of the samples varied between 40 and 65 years, with an average radial growth rate spanning from 2.2 mm/y in Bedano to 3.2 mm/y in Euganei (TRW_tot in Table S1). *C. sativa* stands in Combai exhibited the highest average growth rate over the last 20 years, irrespective of coppice age ($TRW_{1996-2016}$ in Table S1) (Tukey-HSD post-hoc test, $p < 0.05$). In the same period (1996-2016), Euganei and Chiusa Pesio showed the lowest values of radial growth among Young coppices, while Bedano and Iseo exhibited the lowest performances throughout Old coppices (Table S1).

Tree-ring chronologies and eligibility of control species

Generally, the RW series of *C. sativa* exhibited a good common within-site signal, as shown by the series correlations ranging from 0.41 to 0.60 (Table S2). Furthermore, the average correlation at site level in the common period (1975-2016) defined by R-bar statistic (with a range between 0.0 and 1.0, i.e. from no common variance to perfect common variance) displayed R-bar values ranging from 0.332 (Torre Canavese) to 0.512 (Chiusa Pesio).

The values of the expressed population signal were between 0.84 (Combai) and 0.92 (Euganei, Amiata), indicating that the theoretical population was well represented in each site (Wigley et al. 1984). Mean sensitivity values were between 0.24 (Amiata) and 0.28 (Euganei) (Table S2).

Within each site, the mean sensitivity for *C. sativa* series was quite similar to that of the control species (ranging from 0.21 to 0.28) indicating a comparable inter-annual variability of ring width (Table S2). Chronologies of control species were correlated with those of *C. sativa* with values between 0.39 and 0.58 (Table S2), while the graphical comparison indicated a good agreement in growth trends (Fig. S1).

Response function analyses and correlation coefficients exhibited a similar climate-growth relationship between *C. sativa* and control species chronologies: the temperature extremes and the scarcity of precipitation throughout the growing season (particularly from May to August) negatively affected both *C. sativa* and control species (Figs. S2a, 2b).

ACGW impact on tree-ring growth

The comparisons with control species allowed detecting a high percentage of chestnut trees (ranging from 40% to 100%) that showed a significant annual growth reduction during the documented ACGW outbreak (Fig. 2). In all sites (except for Chiusa), the peak in outbreak incidence (ca. 80%-100% of all sampled trees) was reached 2-3 years after the arrival of the

ACGW (Fig. 2).

-here Fig. 2-

Accordingly, the *delta*BAI (%) displayed a quite good correspondence with the tree-ring reductions (Fig. 3 and Fig. 4) in all the sites and stands analyzed throughout the documented outbreak (Table 1), whereas control species showed a completely independent pattern (Fig. 3 and 4).

-here Fig. 3 & Fig. 4-

Within the ACGW outbreak, the average reduction in *delta*BAI (%) was -60% (95%CI [-64, -57]) when considering all stands, with mean losses of the single stand spanning from -40% in Combai [-64, -16] to -79% [-86, -72] in Chiusa (*D.* kuriphilus epidemic Old and Young in Table 2). On the contrary, the growth of control species did not apparently change during the ACGW outbreak, exhibiting on average *delta*BAI (%) values of 15% [4, 26] (*D.* kuriphilus epidemic Control in Table 2).

The impact of the ACGW outbreak on the chestnut trees was twice as large as the one registered during the drought occurred in 2003 (Old -59% [-65, -53] vs. -32% [-39, -25] respectively, Young -61% [-65, -57] vs. -36% [-40, -32], Table 2 and Fig. S3), when even the control species showed a significant *delta*BAI reduction of -14% [-23, -5] (Drought 2003 in Table 2).

-here Table 2-

During the ACGW outbreak, Young coppices showed higher BAI loss in Bedano and Torre if compared to the Old stands (Fig. 5). Conversely, in Chiusa and Iseo the BAI reduction in Young coppices was lower than in the Old stands, while Amiata, Euganei and Combai did not display any significant difference (Fig. 5).

-here Fig. 5-

The best model considering Young and Old coppices separately always included ln(age), Dk_damage, and SPEI_jja (Table 3). Obviously, the variable ln(age) was positively correlated with the response variable ($BAI_{measured}$) and had by far the highest relative importance (85.6 and 94 % for Young and Old coppices respectively; Table 3). On the contrary, Dk_damage was always negatively correlated with $BAI_{measured}$ reflecting a significant and gradual annual decrease in *delta*BAI (%) since ACGW arrival (Fig. 3, Fig. S4). Furthermore, Dk_damage had higher relative importance for Young coppices (14.3%) rather than for Old coppices (5%; Table 3) and higher than SPEI_jja for both Young and Old coppices (Table 3). Finally, the best model for Control species retained as explanatory variables ln(age) and SPEI_jja only (Table 3).

-here Table 3-

Efficacy of the biological control

Figure 6 reports the evolution of the *delta*BAI (%) over the years before the ACGW arrival and without any known extreme growth-depressing events, the ACGW outbreak peak, and the first four years since the biological control. All the sites showed a similar trend: they all progressively recovered (although not always significantly) from the maximum negative *delta*BAI (%) values when the biocontrol became effective (Fig. 3, Fig. 4 and Fig. 6). However, a significant complete recovery did not take place before 3-4 years of biocontrol in Bedano (Old), Combai (Young), Iseo (Old and Young), partially in Torre (Old), Euganei (Old and Young) and Combai (Old).

-here Fig. 6 -

Discussion

Existing studies on the effects of repeated ACGW attacks highlighted various biological responses in chestnut trees, such as a reduction of the leaf area (Gehring, Bellosi, et al., 2018; Guyot et al., 2015; Kato & Hijii, 1997) as well as the shoot vigor and elongation (Maltoni, Mariotti, & Tani, 2012). These effects were inevitably coupled with a decrease in photosynthetic efficiency (Ugolini et al., 2014) and a reduction of tree reserves in terms of dormant buds (Gehring, Bellosi, et al., 2018). In our study, we demonstrated that repeated ACGW attacks eventually affect the secondary growth of chestnut coppice trees. During the outbreak peak, the annual Basal Area Increment (BAI) in chestnut coppices may undergo reductions from 40% to 79%, regardless of the stand age (Table 2 and Fig. 5).

Furthermore, ACGW-induced BAI reductions were higher than those caused by outbreaks of defoliating insects (Camarero, Álvarez-Taboada, Hevia, & Castedo-Dorado, 2018). For the gypsy moth outbreak (*Lymantria dispar* L.) in southern Switzerland, characterized by a total defoliation in the first outbreak year (1992) and a partial one in the following season, Asshoff et al. (1999) reported a single tree-ring reduction in 1992 by a magnitude of 44% in average. In the same area, also the negative effects due to single drought events such as the summer of 1976 and 2003 did not exceed 50% in tree-ring reduction (Asshoff et al., 1999; Knüsel et al., 2015).

Nonetheless, although chestnut trees seem to be able to adapt to xeric conditions (Gehring et al., 2016) or overcome drought stress (Ellenberg, 1996), it is reasonable to assume that prolonged dry periods may potentially produce reductions in tree-ring width similar to those caused by repeated ACGW attacks, especially when combined with the synergistic effect of the chestnut blight (*Cryphonectria parasitica*) (Waldboth & Oberhuber, 2009). In fact, like many ring porous species, chestnut is fairly resilient to canopy damages, as it rarely reduces the tree-ring growth below the 20-40% of average radial growth and almost never drops rings (George, Ault, & Torbenson, 2013). Our results seem to confirm chestnut resilience, whereby the magnitude of BAI reductions could be connected to the fact that ACGW mostly damages the tree crown when the chestnut tree has already completed 30-40% of its annual tree-ring growth (Čufar et al., 2011; Zweifel, Zimmermann, Zeugin, & Newbery, 2006).

Under normal conditions, resilience can mask isolated one-year events of defoliation in many ring porous species (e.g. deciduous oaks, chestnut), as their carbon reserves allow the equivalent of 4 canopies in terms of recovery (Hoch, Richter, & Körner, 2003). In our study sites, a clear and generalized reduction in growth was observed 2-4 years after ACGW arrival, which apparently confirms that cumulative canopy damages can seriously deplete the C storage leading to a 50-60% reduction in wood growth (Naidoo & Lechowicz, 2001; Wiley, Huepenbecker, Casper, & Helliker, 2013). This assumption is also indirectly confirmed by the systematic and progressive activation of dormant buds to produce substitutive green biomass in chestnut trees after the second year of repeated ACGW attacks (Gehring, Bellosi, et al., 2018). Accordingly, a higher number of suckers was also observed in chestnut trees that experienced three or more time-lag years between the ACGW arrival and the biological control (Gehring et al., 2020).

Compared to single drought events, the effect of the repeated ACGW attacks has been well depicted by a far-higher relative impact of Dk_damage respect to drought (i.e., SPEI_jja index).

The effectiveness of the biocontrol agent *T. sinensis* on the ACGW population (Ferracini et al., 2019; Matošević et al., 2017) is reflected in the (at least partial) recovery of the ring growth, which takes place after the second or third year of biological control. Similar results are reported in terms of nut production in chestnut orchards, where a yield recovery of at least 50 percent has been observed within 3 to 5 years after the establishment of *T. sinensis* (Colombari & Battisti, 2017; Kenis et al., 2019).

The two sites located in Southern Switzerland (Bedano and Iseo) exhibited tree growth reduction in more than a third of the sampled trees even in the years immediately preceding the documented arrival of the ACGW (Fig. 2). A similar behavior, however limited to a minor portion of the trees (<30%), occurred in the Amiata and Chiusa sites. These anticipated reductions suggest a possible earlier arrival and spread of the ACGW in these sites with respect to the year of first official report (Table 1). In fact, it is quite common in case of newly introduced alien species that the first official records of their presence do not correspond with the actual time of first arrival (Seebens et al., 2018).

From a methodological point of view, our approach proved its reliability in quantifying the effects of ACGW attacks when reference trees of the same species are missing. In addition to this, combining the radial growth analysis on both *C. sativa* and control species enables to disentangle the impact of climate from the one caused by a chestnut-specific biotic agent (Trotter, Cobb, & Whitham, 2002).

From a practical point of view, the lack of a clear differentiation in the growth reaction patterns between coppices of different ages, prevents the chance of developing specific sylvicultural strategies (e.g. thinnings, changes in the length of the rotation time) aimed at mitigating the impact of repeated ACGW attacks and of potentially connected secondary pathologies, such as the chestnut blight (*Cryphonectria parasitica*). Although we cannot exclude that other stand characteristics such as stem density or species mixture may influence the impact of a pest such as the ACGW (e.g., Fernandez-Conradi et al., 2018), we strongly recommend an immediate release of the antagonist since the first ACGW appearance. This will allow to avoid repeated ACGW attacks that pose a threat for chestnut coppices devoted to high-quality wood production because of the abrupt reductions in radial growth that usually increase the risk of ring-shake (Fonti & Macchioni, 2003; Fonti & Sell, 2003; Spina & Romagnoli, 2010).

In conclusion, ACGW-induced BAI reductions may reach peak values of 60% - 80% as early as two years since the start of the outbreak, irrespectively of the stand and tree age. Such effects are higher in the magnitude and longer in the duration when compared to other stresses such as insect defoliation or extreme summer droughts. Finally, tree radial growth shows the earliest signs of recovery only after the third year of biological control.

Authors' contributions

EM, MC and MP conceived the study and the field protocols. EM, MC, MP, MCM conducted the fieldwork. EG and EM analyzed the data. EG, EM, MC, and FC wrote the manuscript draft. EM submitted the paper. MP, MCM, and FP revised the manuscript. MP provided the research funding and led the project. All authors read and approved the final manuscript.

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Data Availability Statement

Data available via the ITRDB (International Tree-Ring Data Bank) managed by NCEI's Paleoclimatology Team (https://www.ncei.noaa.gov).

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Table 1 – Site and stand description, chronological reports of *Dryocosmus kuriphilus* (ACGW) presence and timing of biological control impact.

Location		Bedano (CH)		Iseo (CH)		Amiata (I)		Combai (I)		Euganei (I)		Chiusa Pesio (I)		Torre Canavese (I)	
Coordinates	Lat-Lon	46.04° N – 8.91° E		46.01° N – 8.89° E		42.98° N – 11.54° E		45.92° N – 12.05° E		45.33° N - 11.73° E		44.32° N – 7.67° E		45.39° N – 7.76° E	
Elevation	m a.s.l.	550		650		950		500		450		800		450	
Mean Temp	°C	11.6		11.6		12.0		12.0		13.0		9.0		12.0	
Annual Rainfall	mm	1545		1545		1200		1400		870		1350		1150	
Meteo station	Location	(1)Lugano		(1)Lugano		(6)Abbadia S. Salvatore		(2)Valdobbiadene		(3)Teolo		(4)Mondovì		(5)Vialfrè	
	m a.s.l.	273		273		855		225		465		560		459	
ACGW first detection	year	2010		2010		2009		2009		2008		2002		2010	
***Torymus* release**	year	2012-2013		2012-2013		2010		2011		2012		2006		2013	
Biocontrol beginning	year	2014		2014		2015		2014		2014		2013		2014	
Lags ACGW-bio control [a]	years	4		4		6		5		6		11		4	
Coppice age class		Young	Old	Young	Old	Young	Old	Young	Old	Young	Old	Young	Old	Young	Old
Stands-distance	km	0.1		0.1		2.7		0.35		5.1		4.8		0.5	
Stool	$n·ha^{-1}$	510	446	701	541	669	446	573	318	1115	764	828	287	510	287
Shoots	$n·ha^{-1}$	2611	924	2739	860	1306	605	1306	828	3217	987	1783	573	1274	573
$D_m$shoots [b]	cm	10.3±3.9	26.6±5.1	12±4.5	21±9.5	15.5±6.1	27.4±5.3	20.4±6.5	29.2±10.5	10.5±4.6	19.7±7.3	15.2±4.7	24.8±5.9	17.7±6.0	26.2±4.6
N shoots/stool [b]	-	5.1±3.8	2.0±1.4	3.7±2.8	2.0±1.2	1.9±1.1	1.3±0.4	2.7±2.1	2.3±1.4	2.9±1.6	1.2±1.4	2.2±1.3	2.0±1.1	3.1±2.1	2.0±1.3

Meteo dataset (monthly average of air Temperature, monthly sum of Precipitation in the range 1994-2018) provided by:

- Federal Office of Meteorology and Climatology MeteoSwiss (Lugano (1));
- Agenzia Regionale per la Prevenzione e Protezione Ambientale del Veneto (Valdobbiadene (2), Teolo (3)) e del Piemonte (Mondovì (4), Vialfrè (5));
- Regione Toscana – Settore idrologico Regionale (Abbadia San Salvatore (6)).

[a] Time interval from the ACGW first detection to the beginning of the biological control.

[b] Standard deviation reports the variability around the mean values of shoots diameter ($D_m$shoots) and ratio of shoots per stool (N shoots/stool).

Table 2 - Average of the minimum *delta*BAI % value per stand type and site during the ACGW epidemic and the 2003 drought.

Site	ACGW epidemic			Drought 2003		
	Control	Old	Young	Control	Old	Young
Amiata	42 [7, 77]	-55 [-69, -41]	-48 [-61, -35]	-23 [-38, -8]	-38 [-54, -22]	-25 [-36, -14]
Bedano	-4 [-30, 22]	-47 [-65, -29]	-72 [-83, -61]	-20 [-50, 10]	-24 [-35, -13]	-29 [-41, -17]
Chiusa	6 [-42, 54]	-79 [-86, -72]	-65 [-82, -48]	-42 [-75, -9]	-42 [-62, -22]	-39 [-54, -24]
Combai	6 [-43, 55]	-40 [-64, -16]	-54 [-63, -45]	-21 [-31, -11]	-44 [-69, -19]	-38 [-46, -30]
Euganei	23 [-18, 64]	-68 [-79, -57]	-62 [-71, -53]	-22 [-51, 7]	-13 [-33, 7]	-40 [-49, -31]
Iseo	-1 [-27, 25]	-69 [-75, -63]	-62 [-71, -53]	-3 [-12, 6]	-34 [-64, -4]	-36 [-49, -23]
Torre	31 [11, 51]	-41 [-60, -22]	-67 [-79, -55]	22 [-20, 64]	-35 [-45, -25]	-42 [-57, -27]
[a]All	15 [4, 26]	-59 [-65, -53]	-61 [-65, -57]	-14 [-23, -5]	-32 [-39, -25]	-36 [-40, -32]

Values in brackets represent the lower and upper 95% confidence intervals.

[a] Average value of every site and according to Control, Old, Young stands.

Table 3 Best mixed-effects regression models of whole BAI series considering control species, young and old coppices separately.

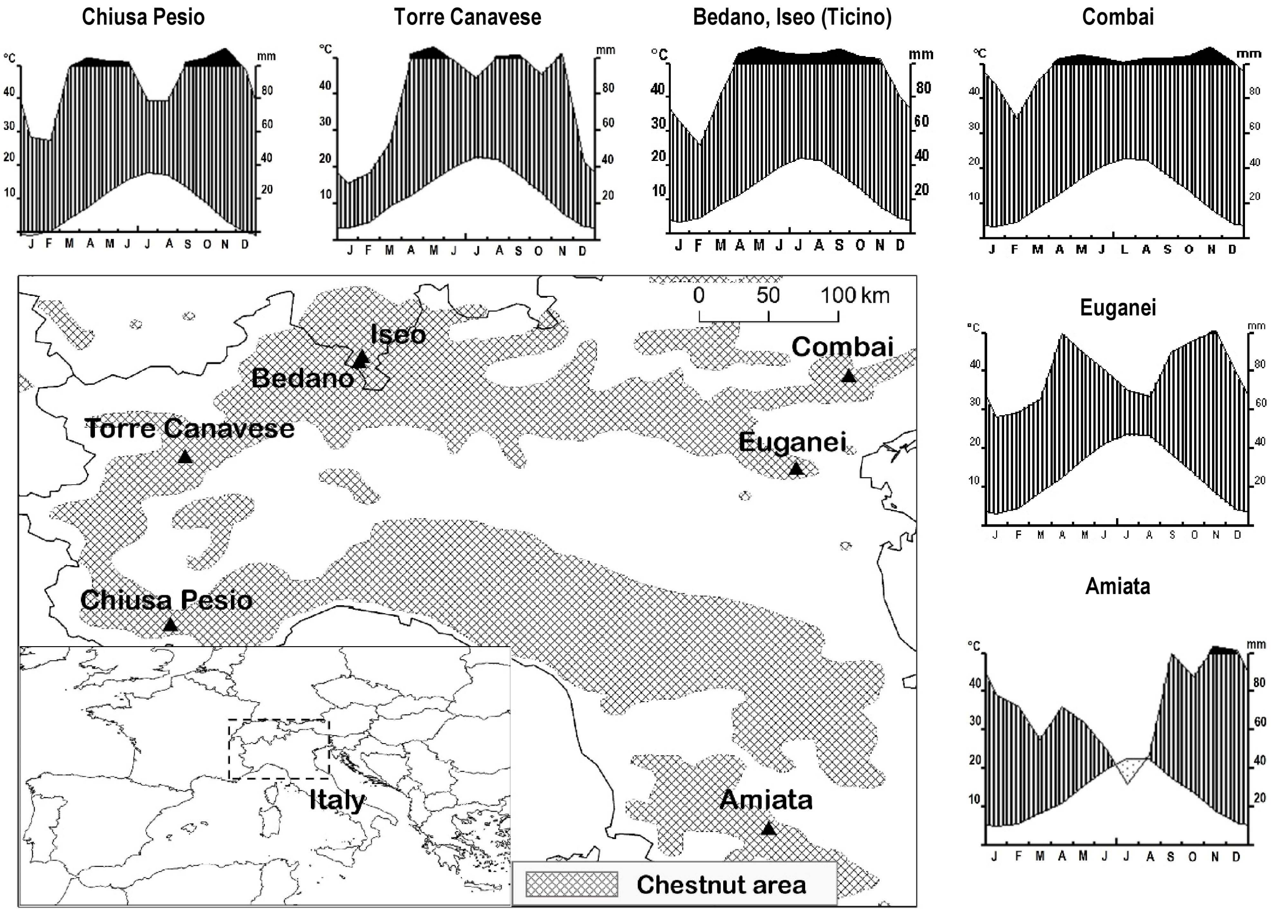
	Estimate *[95% Confidence Interval]*				Relative importance (%)[a]			R^2	
	Intercept	ln(age)	Dk damage	SPEI_jja[b]	ln(age)	Dk damage	SPEI_jja	Marg. [c]	Cond. [d]
Control	0.95 *[0.59, 1.31]*	0.78 *[0.73, 0.82]*	NA	0.11 *[0.05, 0.16]*	99.7	NA	0.3	0.23	0.64
Young	1.61 *[1.29, 1.92]*	0.96 *[0.91, 1.01]*	-0.28 *[-0.31, -0.25]*	0.06 *[0.02, 0.1]*	85.6	14.3	0.1	0.31	0.59
Old	1.25 *[1.04, 1.46]*	0.81 *[0.78, 0.84]*	-0.27 *[-0.29, -0.24]*	0.09 *[0.06, 0.13]*	94.0	5.0	1.0	0.34	0.56

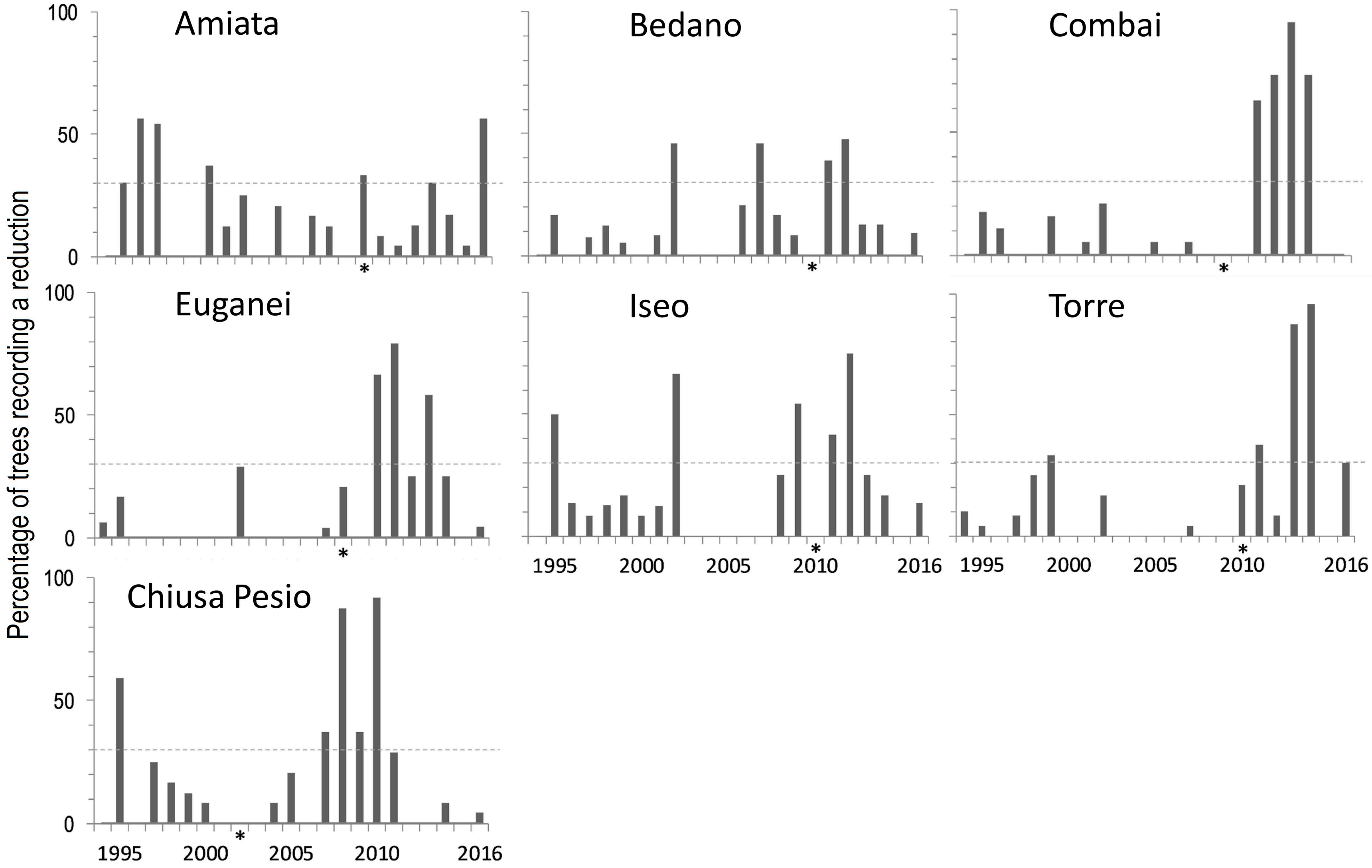
[a] Ri. *(%)* = relative importance calculated using the r-cran package relaimpo (Grömping 2006)

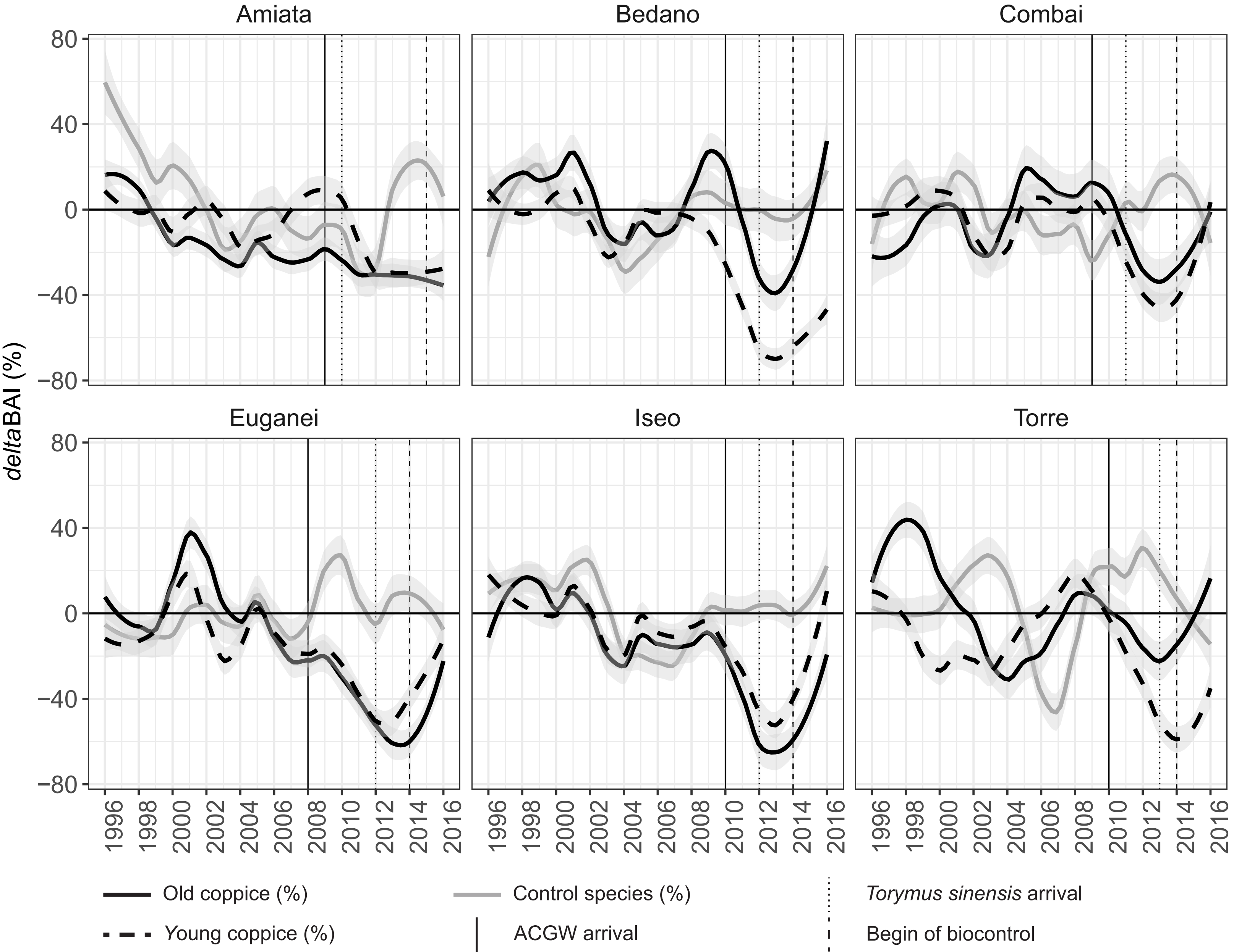
[b] SPEI_jja = Standardized Precipitation-Evapotranspiration Index calculated over 3 months' time-scale and averaged among the summertime months (June, July, August).

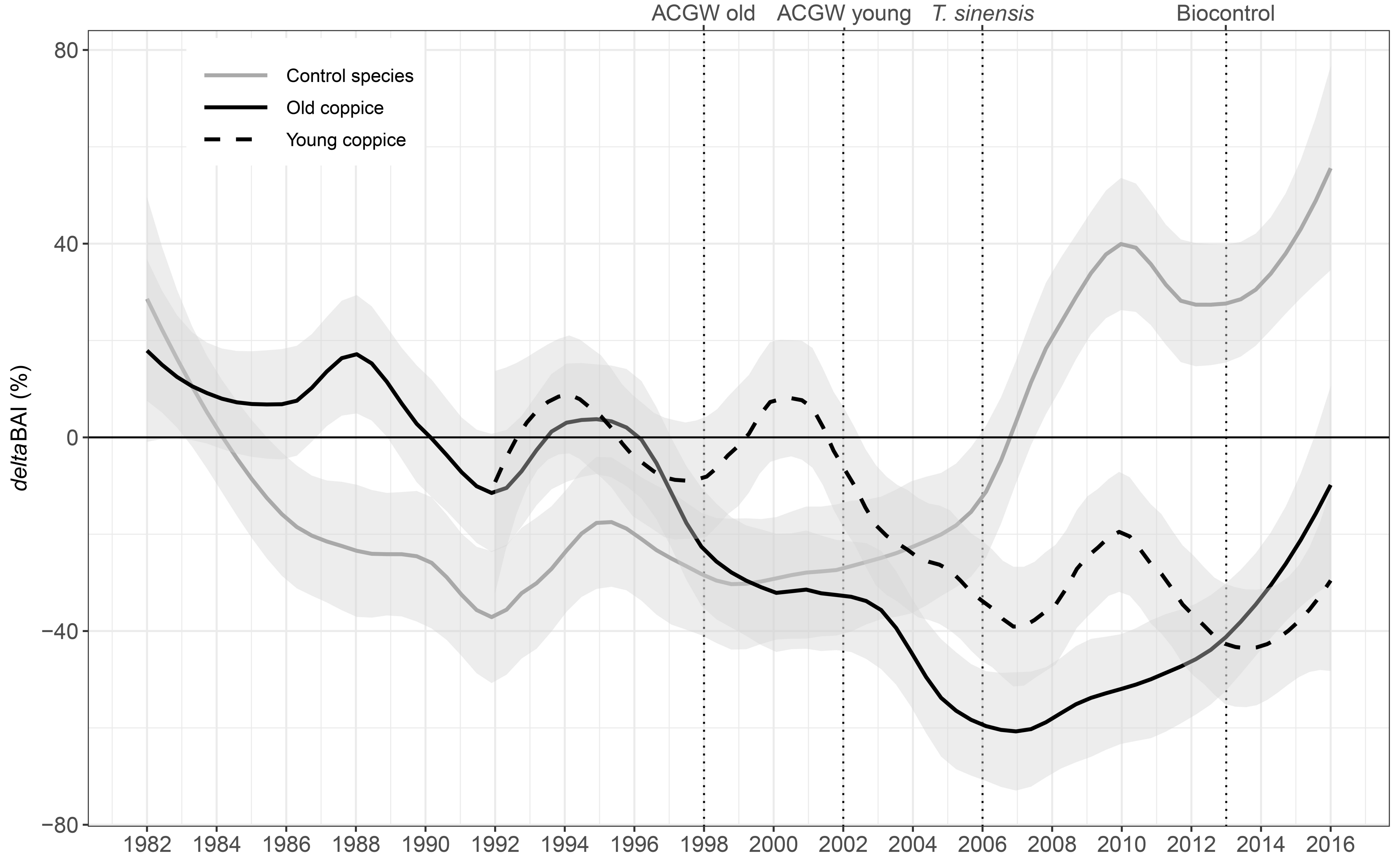
[c] Marg. = R^2 Marginal showing the proportion of variance explained by the fixed factors.

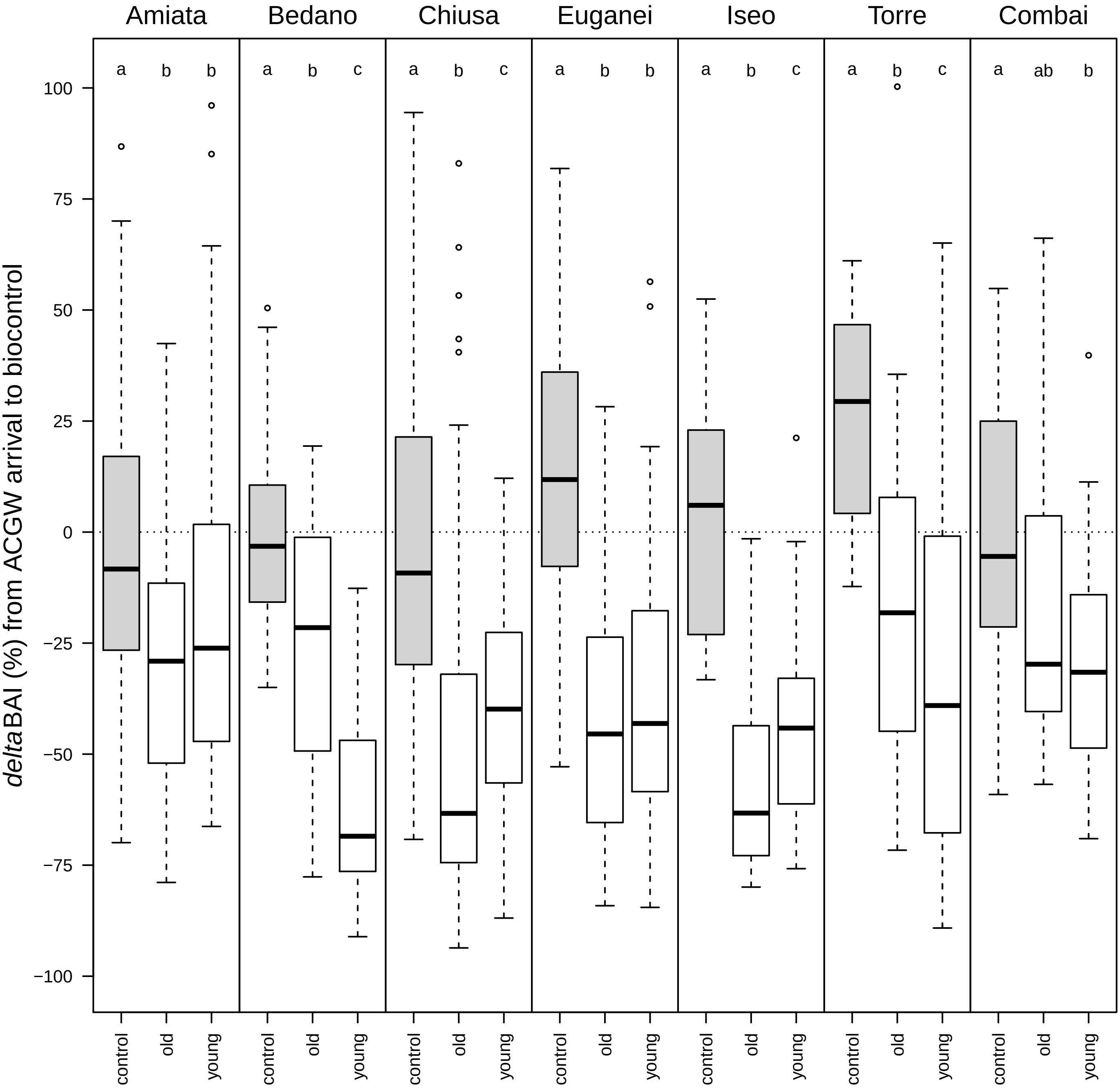
[d] Cond. = R^2 Conditional describing the proportion of variance explained by the entire model (fixed and random factors).

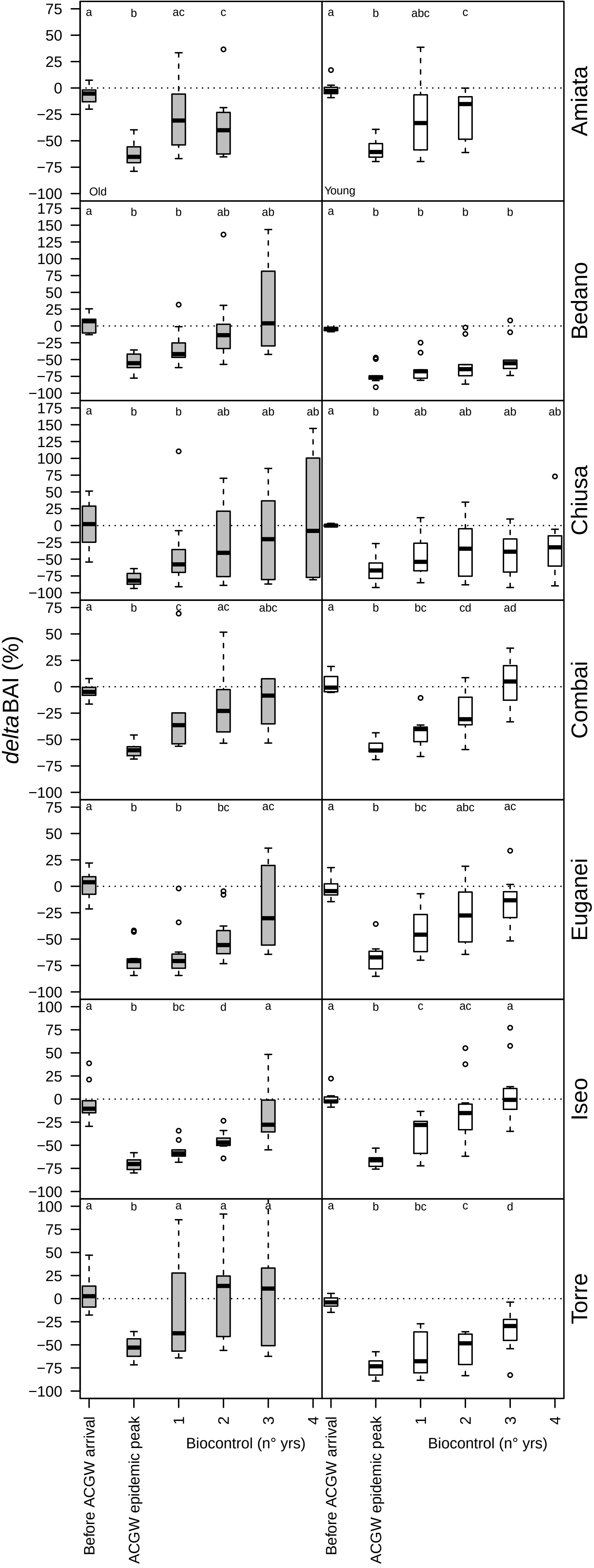

Chiusa Pesio
Torre Canavese
Bedano, Iseo (Ticino)
Combai
Euganei
Amiata
°C
mm
10
20
30
40
20
40
60
80
J F M A M J J A S O N D
J F M A M J L A S O N D
0 50 100 km
Iseo
Bedano
Combai
Torre Canavese
Euganei
Chiusa Pesio
Amiata
Italy
Chestnut area


Percentage of trees recording a reduction
Amiata
Bedano
Combai
Euganei
Iseo
Torre
Chiusa Pesio
100
50
0
*
1995
2000
2005
2010
2016


Amiata
Bedano
Combai
Euganei
Iseo
Torre
deltaBAI (%)
80
40
0
−40
−80
1996
1998
2000
2002
2004
2006
2008
2010
2012
2014
2016
Old coppice (%)
Young coppice (%)
Control species (%)
ACGW arrival
Torymus sinensis arrival
Begin of biocontrol


ACGW old
ACGW young
T. sinensis
Biocontrol
Control species
Old coppice
Young coppice
*delta*BAI (%)
80
40
0
−40
−80
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000
2002
2004
2006
2008
2010
2012
2014
2016


Amiata
Bedano
Chiusa
Euganei
Iseo
Torre
Combai
a b b
a b c
a b c
a b b
a b c
a b c
a ab b
deltaBAI (%) from ACGW arrival to biocontrol
100
75
50
25
0
−25
−50
−75
−100
control
old
young


deltaBAI (%)
Amiata
Bedano
Chiusa
Combai
Euganei
Iseo
Torre
Old
Young
a
b
ac
c
abc
ab
bc
cd
ad
d
Before ACGW arrival
ACGW epidemic peak
1
2
3
4
Biocontrol (n° yrs)
75
50
25
0
−25
−50
−75
−100
175
150
125
100