



Large-scale geostatistical mapping and occupancy-abundance patterns of *Cerambyx* species threatening SW Spain oak forests

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Received: 28 May 2022 / Revised: 30 June 2022 / Accepted: 20 July 2022 / Published online: 16 August 2022
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Abstract

Wood-boring insects are considered potential contributing/inciting factors to oak decline. *Cerambyx cerdo* (Cc) and *C. welensii* (Cw) are two sympatric oak-living large sapro-xylophagous longhorn beetles with different pest/legal status, whose larvae bore into living wood of healthy/decayed trees, and whose impact has increased alarmingly in recent years. We conducted a regional-scale multi-year (2017–2020) field study to model Cc and Cw distribution and to explore species-specific occupancy-abundance patterns. Records were obtained with 1650 feeding traps placed throughout the region of Extremadura (SW Spain) (41,634 km²) in holm, cork and pyrenean oak woodlands. Catch number (a proxy of abundance) was analysed through GLMMs, LMs and geostatistical interpolation (IK algorithm) to generate catch probability maps. Catch number was extremely variable between trees (traps), stands and years (Cc: 0–252, Cw: 0–219 adults/trap) with no repulsive interspecific association at the tree scale. Explanatory factors in the models (species, sex, year and host oak) and several interactions among them significantly affected catch number. As a whole, Cw was more abundant than Cc, but catch number greatly depended on host tree (Cw: cork > holm > pyrenean oak, Cc: holm > cork > pyrenean oak). Occupancy-abundance patterns were positive with significant occupancy x species interaction. Niche breadth was more than double in Cw (Levins' $B_A = 0.42$) than in Cc ($B_A = 0.19$) and niche overlap almost complete (Pianka's $O = 0.98$). Our large-scale pioneer study shows that Cc and Cw are widespread in SW Spain, but with huge host-mediated intra- and interspecific geographic variation in abundance, which has critical implications in population management/control strategies.

Keywords *Cerambyx cerdo* · *Cerambyx welensii* · Distribution probability maps · Feeding traps · Oak decline · Sympatry

Communicated by Claus Bässler.

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Introduction

Sclerophyllous oak forests are widespread across the Mediterranean Basin. In SW Iberia, they mostly appear as oak open woodlands, similar to the savannah landscape, the so-called *dehesas* in Spain and *montados* in Portugal. Oak open woodlands sustain a traditional agro-silvo-pastoral use shaping landscape multiplicity (Blondel 2006; Bugalho et al. 2011; Torres-Vila et al. 2017a, 2019), possess outstanding ecological and socioeconomic values (Montero et al. 1998; Moreno and Pulido 2009) and host the highest levels of biological diversity in Europe (Cowling et al. 1996; Ramírez-Hernández et al. 2014), so they are considered key biodiversity hotspots (Medail and Quezel 1999; Myers et al. 2000). As a result of its environmental importance, the *dehesa/montado* ecosystem is protected under the EU Habitats Directive (CEC 1992).

European oaks have undergone repeated decline and mortality episodes during the past three centuries (Thomas

et al. 2002), but the decay impact seems to have worsened in recent decades. Oak decline, rather than a single disease, is currently viewed as a complex syndrome resulting from an array of interacting abiotic and biotic causes that can act as either predisposing, contributing or inciting factors for oak decay (Manion 2003; Torres-Vila et al. 2019). Among the contributing/inciting factors, mostly pathogens and pests that ultimately can compromise the life of the trees, bark- and wood-boring insects are especially important (Thomas et al. 2002; Evans et al. 2004; Sallé et al. 2014). Within this functional group of xylophagous, beetles in the family Cerambycidae are especially relevant. Cerambycids, commonly called longhorns due to their long and slender antennae, is one of the largest insect taxa with more than 38,000 species. The subfamily Cerambycinae, one of the most hyperdiverse and evolved, constitutes a monophyletic group of 11–12,000 species in more than 1800 genera, extremely variable in morphology and behaviour (Napp 1994; Hanks 1999; Tavakilian and Chevillotte 2022; Rossa and Goczal 2021). The type genus *Cerambyx* Linnaeus, 1758, includes 13 medium-large sized species with a western Palaearctic distribution (Danilevsky 2022), of which seven are present in Europe (Bense 1995; Danilevsky 2022; Fauna Europaea 2022) and four in Iberia (Vives 2000; González-Peña et al. 2007), the same four being also recorded in the region of Extremadura (SW Spain), namely *C. cerdo* L., *C. welensii* (Küster), *C. miles* Bonelli and *C. (Microcerambyx) scopoli* Fuessly (Torres-Vila et al. 2022). Among them, *C. cerdo* (Cc) and *C. welensii* (Cw) stand out due to their wide distribution and close association with oaks. The two species are distributed throughout the western Palaearctic realm, but there are certain chorological peculiarities: Cw is more thermophilic and occurs especially in southern Europe and the Near East; Cc occurs in the circum-Mediterranean area, including North Africa, and is more present than Cw in Central and North Europe (Danilevsky 2022; Fauna Europaea 2022). In Iberia, the distribution pattern roughly reflects that described for Europe being both species quite less frequent in the continental climate regions (NW) than in the Mediterranean area (SW-NE) (Torres-Vila et al. 2022).

Both Cc and Cw are primary sapro-xylophagous beetles, whose larvae bore into the living wood of healthy or decayed host trees (Bense 1995; Buse et al. 2007; Torres-Vila et al. 2017a). The two species have usually been reported as polyphagous (Picard 1929; Villiers 1978; Bense 1995; Vives 2000), but host trees other than oaks are currently considered exceptional (Miroshnikov 2009), a fact consistent with the narrow host range characterising primary saproxylics (Speight 1989; Grove 2002). In Extremadura, host range is limited in practice to oak species (*Quercus* spp.), either evergreen—holm oak (*Q. ilex* L.) and cork oak (*Q. suber* L.)—, or deciduous/marcescent—pyrenean oak (*Q. pyrenaica* Willd.) and gall oak (*Q. faginea* Lam.)—(Torres-Vila

et al. 2017a, 2022). These oak species, chiefly holm and cork oaks, make up the main dehesa tree stratum, where Cc and Cw share a similar ecological niche, often coexist sympatrically, and even mate interspecifically and hybridise (Torres-Vila et al. 2012, 2013, 2017b; Torres-Vila and Bonal 2019).

Both Cc and Cw are univoltine in May–August, adult diel activity being mainly crepuscular and nocturnal. Adults feed on plant exudates and saps from their hosts and other trees. After mating, females lay eggs singly or in small groups into bark cracks, pruning cuts and other tree wounds. Females lay almost 150 eggs during its lifetime, which hatch in about two weeks, and then neonate larvae burrow through the bark and initiate feeding in the outer sapwood. As the larvae grow, they enter into the heartwood, making increasingly wide and long galleries that extend through the trunk, main branches and main roots of the host trees. Larvae develop for 2–3(4) years, and upon reaching maturity, they pupate in late summer or early autumn in a pupal cell closed by a calcareous plug. After about a month, the adult emerges but overwinter in a pre-reproductive stage inside the pupal cell until it leaves the tree in the spring of the following year through an exit hole and reinitiate lifecycle. Adult longevity in the wild is estimated at 2–3 weeks (maximum 2 months) although longer lifespans (4–5 months) have been recorded in the laboratory (Torres-Vila et al. 2012, 2013, 2016, 2017a; Torres-Vila 2017). Adults usually exhibit a more or less sedentary behaviour in oak open woodlands, even if they can potentially disperse several kilometres (Buse et al. 2007; Torres-Vila et al. 2017a; Drag and Cížek 2018).

Like many other longhorn beetles, Cc and Cw are included in the highly diverse assemblage of saproxylic insects, a functional group essential in the degradation of dead wood and in the formation of holes and cavities in the trees, which are often exploited as refuge or shelter for many animal species, including other arthropods, reptiles, birds and mammals. Hence, they have been defined as ecosystem engineers (Jones et al. 1997; Buse et al. 2008) who enhance forest biodiversity and are indicators of high-quality mature habitats (Speight 1989; Grove 2002; Saint-Germain et al. 2007; Buse et al. 2008; Davies et al. 2008; Regnery et al. 2013; Micó et al. 2015; Torres-Vila et al. 2017a, 2017b). Nevertheless, when Cc/Cw population levels become excessive, larval damage caused to oaks can become severe and even intolerable. Larval subcortical galleries in the sapwood, cambium and xylem can alter sap flow, triggering wilting, defoliation, vigour loss and decline of oaks. As larvae grow, larger galleries in the sapwood and heartwood cause significant physiological, mechanical, and structural damage. Main branches and trunk of the affected trees, with the mechanical resistance greatly compromised due to wood fibre breakage, end up collapsing sooner or later due to their own weight, especially in adverse wind and snow conditions (Torres-Vila

2017; Mannu et al. 2021). Adult exit holes and open larval galleries can also act as gateways for fungal and bacterial pathogens (Martín et al. 2005) further compromising the survival of affected oaks.

The impact of these xylophagous on oak open woodlands, many old, fragmented and without regeneration, has increased alarmingly in recent years in SW Spain, so that it is currently considered a critical variable in oak decline (Domínguez et al. 2022; Torres-Vila et al. 2022). Damage to oaks has usually been attributed to Cw, but recent researches show that this status quo is not realistic and that Cc is also a major actor in oak decline (Torres-Vila et al. 2022). The same authors also show a large variability in Cc and Cw population levels, and that these longhorns exhibit host preference. Interestingly, the two species differ in their pest and legal status: Cw is considered an emerging pest involved in oak decline in some areas including SW Spain, while Cc is an EU protected species (Torres-Vila 2017), even if it has been reported as a pest in several countries such as Morocco, Italy and Spain, in the last country mainly Extremadura and the island of Mallorca (El Antry 1999; González et al. 2010; Torres-Vila 2017; Mannu et al. 2021).

In order to face such a complex scenario and achieve effective pest management/control strategies, we need more basic and applied research on the behaviour and demography of Cc and Cw, especially in those habitats harbouring mixed longhorn populations. An adequate knowledge of the spatial distribution of Cc and Cw is relevant to issues such as sampling procedures, biological control, adult dispersal, gene flow, forest fragmentation or metapopulation dynamics (Thomas 2000; Ranius 2006; Buse et al. 2007; Holland 2009; Clobert et al. 2012), and critical to execute either conservation, management or control actions depending on the forest context. A precise appraisal of the species-specific abundance (population density) and occupancy (range size within a zone or region) would also allow designing risk analysis models to infer the short-medium-term impact of Cc and Cw on the oak dehesa ecosystem. This issue acquires greater relevance in the current climate change scenario, which could exacerbate oak decline, not only directly by global warming, but also indirectly by escalating the impact of xylophagous under warmer conditions (Allen et al. 2010; Sallé et al. 2014), in particular that of *Cerambyx* species (Duque-Lazo and Navarro-Cerrillo 2017).

In the described framework, the main objective of this work was threefold: (1) to model the distribution of Cc and Cw at regional scale in Extremadura using geostatistical techniques, (2) to evaluate the effect of some variables (year, host oak, species and sex) on geographical distribution, and (3) to identify interspecific differences between longhorn species in the occupancy-abundance patterns.

Materials and methods

Study area

The study area was the entire region of Extremadura (SW Spain), which extends over 41,634 km² and contains more than 1 million ha of oak forests, most of them open woodlands populated (in order of importance) by holm, cork and pyrenean oaks. Climate is typically Mediterranean with dry and warm summers (up to 40 °C). Altitude ranges from about 150 m (Guadiana and Tajo river valleys) to more than 2000 m (mountains of the Central System in the northern region), although the oak species rarely populate areas above 1100–1200 m (holm and cork oak) or 1500–1600 m (pyrenean oak) (Torres-Vila et al. 2022).

Adult catches

Adult catches of Cc and Cw were obtained during four consecutive years (2017–2020) from the Regional Sampling Network maintained by the Plant Health Service (SSV) of the Junta de Extremadura (Torres-Vila et al. 2022). The network uses pitfall traps (“tree traps”) with a feeding bait (simulating fermenting plant exudates) consisting of a mixture of red wine, vinegar, sugar, salt (2 l, 100 ml, 500 g, 500 g) and water until completing 5 l of solution. Traps are manufactured with 5 l cylindrical PET plastic containers (commercial water bottles), cutting the upper part at the neck and placing it in an inverted position forming a funnel. Traps are fixed to the tree trunk at 1.4–1.5 m above ground level, preferably facing north aspect to avoid direct sunlight and excessive bait evaporation (Torres-Vila et al. 2012, 2017b). In total, 1657 traps were installed, but seven were loss for various reasons (livestock activity, fires, or unknown causes), obtaining data finally from 1650 traps. Traps were arranged in groups (stands) of 2 or 3, more rarely isolated or in larger groups ($n = 809$ stands), depending on the topography and other features of the target forest to be sampled (Table S1). Within each stand, traps were placed about 50 m apart, so that trap density roughly ranged 1–4 traps/ha. Traps were located, throughout the region of Extremadura, in oak open woodlands and oak forests of the three major host species (holm, cork and pyrenean oak), covering the entire altitude range populated by oaks (180–1550 m). Additional criteria for stand choice were to cover the maximum number of UTM grids (Torres-Vila et al. 2022) and to have an acceptable access. Traps were geolocated using a GPS or the mobile app Google maps (WGS84, decimal latitude and longitude). Traps were active from mid-May to late-August every year and were checked a

variable number of times depending on the year and use of catch data for other researches, from one check per week to none (only trap setting and retrieval). A volume of bait between 0.5 and 2.5 l was added to each trap, depending on the checking scheduled. Captured adults were introduced in labelled plastic bags or containers and taken to the laboratory for identification. Trapping data were compiled and managed using Google Maps, Google MyMaps, SigPac 4.6 and Kosmo 3.0. The main diagnostic characters to determine specific membership were body shape, body colour, elytral sculpture, apex shape, sutural spine, and metatarsal hair pattern. For more information on trap location, sampling protocol and sample processing see Torres-Vila et al. (2022).

Statistical analyses

Generalised linear models (GLMMs) and additional tests

Catch number per trap per year was the explained variable, used as a proxy of population density (abundance) of the target species. Generalised Linear Mixed Models (GLMMs) were computed to explore the effects on catch number of the species (Cc, Cw), year (2017–2020), sex (male, female) and host tree (holm, cork and pyrenean oak). All GLMMs were performed with glmmTMB library (Brooks et al. 2019). The explained variable was log (ln) transformed to deal with zero-inflated data. Poisson family errors were applied and tested for over- and under-dispersion. Residuals plots were checked in order to verify assumptions of the fitted models, and final model selection was made following the Akaike information criterion (AIC). We computed a first model (GLMM1) studying the effects on catch number per trap per sex of the species and year, considering both factors with fixed effect, while the trap nested to the stand were included as random factors. Looking at the GLMM1 results, we computed a second model (GLMM2) studying the effects on catch number of the species, sex and host oak (as fixed factors), including the stand nested to the year as random factors. To circumvent the confounding effect of some interactions between factors in GLMM2 (see results), we computed two-way-GLMMs (host and sex as fixed factors) for each species (Cc or Cw) with the stand nested to the year as random factors. Analysis of Deviance (Type II Wald chi-square test) was used to assess the effect on catch number of the studied factors and their interactions in all GLMMs. Post hoc Tukey contrasts (z values, $p < 0.05$) were used when necessary for multiple comparisons of means in order to establish homogeneous groups.

We explore occupancy-abundance relationships for each species (years pooled). Data points were generated at the regional level, one for each of the 26 natural/historical zones (*comarcas*) into which the region of Extremadura is

divided (see results for the number of traps per zone). In each zone and for each longhorn species, occupancy was estimated as the percentage of traps in which at least one capture was recorded, and abundance as the mean number of catches per trap in the subset of traps with at least one capture (Gaston et al. 2000). Abundance and occupancy values were \log_{10} -transformed to improve data normality, and then, we computed linear regressions to assess intraspecific occupancy-abundance relationships and Linear Models (LM) to test whether these relationships differed between longhorn species. Standardised Levins' Measure of niche breadth (B_A) for Cc and Cw as a function of host oak, and niche overlap between both species—Pianka's measure (O) and Morisita index (C_H)—were also estimated (Lawlor 1980; Krebs 1999).

Spearman rank correlation coefficient (r_s) was used to test for correlations: (1) between the number of catches of Cc and Cw per trap ($n = 1650$ traps, years pooled), and (2) in the number of catches between traps within stands ($n = 809$ stands). To do this, the stands with a single trap were not considered, and in those stands with three or more traps, only a pair of traps were chosen at random (final sample size, $n = 692$ stands). All statistical analyses were computed with R 4.1.2. (R Core Team 2021). The G test was also used to compare sex ratios (Sokal and Rohlf 1995).

Geostatistics: probability maps

A geostatistical approach with ArcGIS software (version 10.3, ESRI Inc., Redlands, CA, USA) was used to model the spatial distribution of Cc and Cw at the regional scale in order to detect those endemic areas with higher populations and potential damage risk. Catch number per trap per year was the primary explanatory variable used as usual. Interpolation analyses were conducted with the nonparametric IK (Indicator Kriging) algorithm using the Geostatistical Analyst extension in ArcGIS. The IK approach makes no assumption of normality and is an effective way of limiting the effect of extreme values, which was appropriate for our dataset, as there was an excess of zeros from traps without captures (Torres-Vila et al. 2019). We computed IK in the same fashion as ordinary kriging to determine model values from the correlation between datapoints. The essence of the IK approach is the binomial coding of data into either 1 or 0, depending upon its relationship to a cut-off value (Journel 1983). IK involves modelling of an indicator variogram at a range of the cut-off which has to cover the range of the input data. IK builds a cumulative distribution function at each estimate location based on the behaviour and correlation structure of the transformed datapoints in the chosen neighbourhood. Probability maps may be produced since predictions from IK are interpreted as probabilities of the variable being in the class indicated by 1 (Torres-Vila et al.

2019). Prediction error statistics were computed and used as a diagnostic tool that indicates whether kriged surfaces were reasonable (Webster and Oliver 2007). We generated two sets of probability maps, depicting Cc and Cw distributions in Extremadura. First, eight maps (one map per species per year) showing the probability of capturing at least 1 adult per trap per year. Second, six maps showing for each species the probability of capturing at least 1, 10 or 20 adults/trap/year. Catch number was normalised within years (by subtracting the mean and dividing by the standard deviation in each year) and all datapoints ($n = 1650$) were pooled prior to IK analysis. All probability maps were generated with the ArcGIS/ArcMap module, using the ETRS89 geographic coordinate system projected in the UTM zone 30 N.

Results

Results showed that catch number (a proxy of abundance) of both Cc and Cw was extremely variable between trees (traps), stands and years. Overall, values ranged 0–252 and 0–219 adults/trap/year in Cc and Cw, respectively, traps with zero catches being rather frequent, about 45% in Cc and 37% in Cw. There was a positive correlation between the captures of the two traps in each stand, both in Cc ($r_s = 0.70$, $p < 0.001$) and in Cw ($r_s = 0.65$, $p < 0.001$), although correlations were lower than expected. There was a positive correlation between the number of captures of Cc and Cw per trap ($r_s = 0.51$, $p < 0.001$), suggesting no repulsive interspecific association at the tree scale; similar results were obtained when traps that captured neither Cc nor Cw adults (“double-zero traps”) were excluded from the regression analysis.

GLMM1 results showed that catch number per trap per sex depended on species ($\text{Chi}^2 = 99.03$, $df = 1$, $p < 0.001$) and year ($\text{Chi}^2 = 94.96$, $df = 3$, $p < 0.001$), but also on species \times year ($\text{Chi}^2 = 55.37$, $df = 3$, $p < 0.001$). A parallel GLMM pooling both sexes yielded similar results. Interaction indicates that relative differences in catch number between species were dependent on year (Fig. 1). Post hoc contrasts ($p < 0.05$) showed that: (1) catches in 2018 were exceptionally high in both species compared to other years, (2) catches were significantly higher in Cw than in Cc in three out of four years, and (3) abundance difference between species was quite variable among years, from high in 2017 to non-significant in 2020 (Fig. 1).

GLMM2 results showed that catch number depended on species ($\text{Chi}^2 = 89.65$, $df = 1$, $p < 0.001$), sex ($\text{Chi}^2 = 77.19$, $df = 1$, $p < 0.001$) and host oak ($\text{Chi}^2 = 120.55$, $df = 2$, $p < 0.001$), being significant the interactions species \times sex ($\text{Chi}^2 = 55.76$, $df = 1$, $p < 0.001$) and species \times host ($\text{Chi}^2 = 123.71$, $df = 2$, $p < 0.001$), and having no effect the interaction sex \times host ($\text{Chi}^2 = 2.51$, $df = 2$, $p = 0.29$) as well as the triple interaction species \times sex \times host ($\text{Chi}^2 = 2.75$,

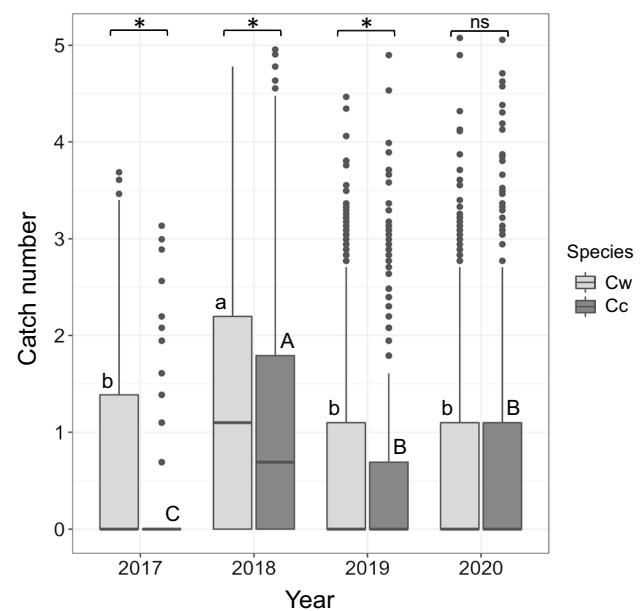


Fig. 1 Box-plots showing the effects of the longhorn species (Cw: *Cerambyx welensii* and Cc: *Cerambyx cerdo*), year (2017–2020) and their interaction on catch number per trap per sex ($\ln [x + 1]$ transformed) obtained with feeding traps as a proxy of population density (abundance). The species \times year interaction was significant (see GLMM1 statistics in text). Asterisks show significant differences between species within years (*: $p < 0.05$; ns: not significant) and lowercase/uppercase letters show significant differences between years within species ($p < 0.05$)

$df = 2$, $p = 0.25$). Subsequent two-way GLMMs computed separately for each species yielded the following results (Fig. 2). In the case of Cw, catch number depended on host ($\text{Chi}^2 = 79.01$, $df = 2$, $p < 0.001$) but not on sex ($\text{Chi}^2 = 3.59$, $df = 1$, $p = 0.06$) or host \times sex interaction ($\text{Chi}^2 = 4.97$, $df = 2$, $p = 0.08$), although both effects were close to the significance level. In the case of Cc, catch number depended on host ($\text{Chi}^2 = 126.37$, $df = 2$, $p < 0.001$) and sex ($\text{Chi}^2 = 129.30$, $df = 1$, $p < 0.001$) with no effect of the host \times sex interaction ($\text{Chi}^2 = 0.29$, $df = 2$, $p = 0.86$). These results showed two important differences between Cc and Cw. First, females of both species were less frequently captured than males, but in Cc, they were proportionally much less so (Fig. 2), so that the sex ratio (% males) was significantly higher in Cc (0.74) than in Cw (0.55) (G-test, $G = 1013.5$, $df = 1$, $p < 0.001$, hosts pooled). Second, Cc and Cw catch number greatly depended on host oak species: Cw was significantly more abundant in cork oak than in holm oak and, in turn, more abundant in holm oak than in pyrenean oak, while Cc was significantly more abundant in holm than in cork oak and, in turn, more abundant in cork than in pyrenean oak. As a result, Cw was almost fivefold more abundant than Cc in cork oak (Fig. 2).

Occupancy-abundance regressions (\log_{10} -transformed data) were positive and highly significant both in Cc

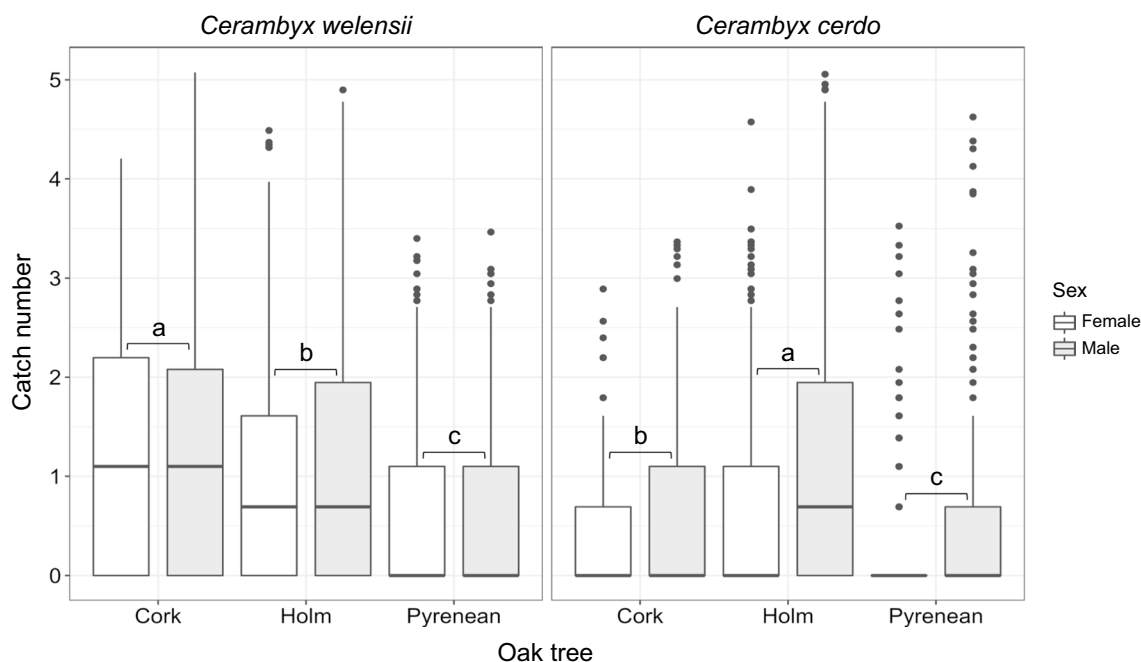


Fig. 2 Box-plots showing the effects of the longhorn species (Cw: *Cerambyx welensii* and Cc: *Cerambyx cerdo*), sex, host oak tree (cork, holm and pyrenean oak) and their interactions on catch number per trap per year ($\ln [x + 1]$ transformed) obtained with feeding traps

as a proxy of population density (abundance). All three effects and some interactions were significant (see GLMM2 statistics in text). Letters show significant differences between host oak trees within species ($p < 0.05$, sexes pooled)

($F_{1,24} = 65.12$, $p < 0.001$, $R^2 = 0.73$) and Cw ($F_{1,24} = 27.25$, $p < 0.001$, $R^2 = 0.53$) (Fig. 3). A subsequent LM confirmed that abundance depended on occupancy ($t = 7.89$, $p < 0.001$) and species ($t = 2.37$, $p < 0.05$), but also showed that the interaction occupancy \times species was significant ($t = -2.27$, $p < 0.05$). Thus, the occupancy-abundance relationship was species-specific, regression slope being higher in Cc than in Cw (Fig. 3). Niche breadth depending on host oak species was more than double in Cw ($B_A = 0.42$) than in Cc ($B_A = 0.19$), and niche overlap between both longhorns was very wide ($O = 0.98$, $C_H = 0.97$).

Geostatistical analyses showed that Cc and Cw are widespread in Extremadura and that catch probability could be regionalised in both species using the IK algorithm (Figs. 4, 5). Prediction error statistics for these 14 probability maps show that root mean square error, mean standard error and mean standardised error were close to zero. Moreover, root mean square error and mean standard error were very similar, so that generated probability maps were appropriate. Furthermore, standard deviations of the measured values in the test samples were higher than root mean square errors in all cases, which denote an effective prediction throughout the studied region (Torres-Vila et al. 2019). Probability maps showed appreciable differences between years and species (Fig. 4), IK results being highly consistent with GLMM1 results (Fig. 1).

Probability maps generated by pooling the four study years (Fig. 5) depict those areas in which there is a lower or higher probability of capturing a given number of adults of each species (at least 1, 10 or 20 adults/trap). These maps show evident spatial differences on a regional scale in the distribution of the two longhorn species. Regarding species-specific abundance (see Fig. 3 for situation of zones), Cc prevails along the N-S central regional strip, with main “hot spots” at Monfragüe, Sierra de Montánchez-Tamuja and Sierra Grande-Tierra de Barros (Fig. 5b, c), while Cw prevails in the NW sector, with major “hot spots” at Valle del Alagón, Tajo-Salor-Almonte and Sierra de San Pedro (Fig. 5e, f). In these zones, abundance was very high, almost disproportionate in some cases, since the probability of capturing at least 10 or 20 adults/trap exceeded 60% and even 80% in both Cc (Fig. 5b, c) and Cw (Fig. 5e, f). Last but not least, even if catch number was as a whole higher in Cw than in Cc (GLMM1 and GLMM2 results above), the regional surface with a high probability ($p > 80\%$) of capturing at least one adult was perceptibly higher in Cc (Fig. 5a) than in Cw (Fig. 5d) as revealed by the red colour pattern. Interestingly, this fact suggests a higher occupancy of Cc than of Cw when abundance is very low, which was in turn consistent with the species-specific occupancy-abundance regressions (Fig. 3). Such interspecific differences in the probability of capturing at least 1 adult/trap tended to

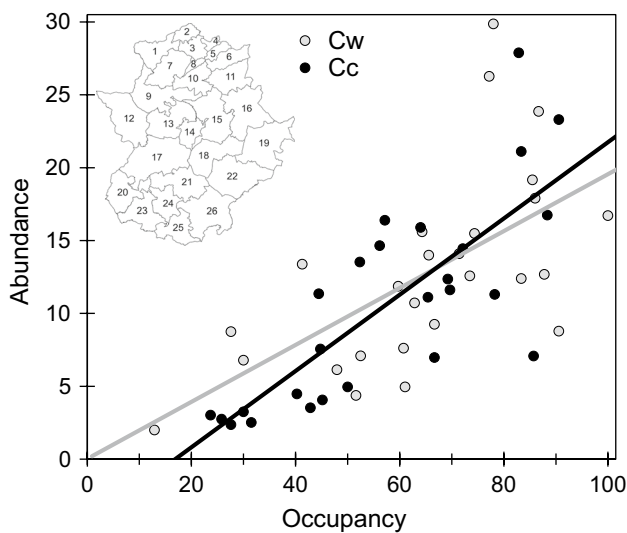


Fig. 3 Relationships between abundance (mean catch number per trap per year in traps with at least one catch) and occupancy (proportion of traps with at least one catch) in *Cerambyx cerdo* (Cc) and *Cerambyx welensii* (Cw). The feeding traps used in this study ($n=1650$, years 2017–2020) were arranged for occupancy estimates according to the 26 zones that make up the region of Extremadura (SW Spain) (see map). Occupancy-abundance regressions (log₁₀-transformed data) were significant in both longhorn species. The effects of species, occupancy and species \times occupancy were all significant (see LM statistics in text). Codes for the 26 zones are (trap number per zone between brackets), 1: Sierra de Gata ($n=73$), 2: Las Hurdes ($n=31$), 3: Trasierra-Tierras de Granadilla ($n=35$), 4: Valle del Ambroz ($n=31$), 5: Valle del Jerte ($n=29$), 6: La Vera ($n=40$), 7: Valle del Alagón ($n=57$), 8: Plasencia ($n=14$), 9: Tajo-Salor-Almonte ($n=50$), 10: Monfragüe ($n=49$), 11: Campo Arañuelo ($n=67$), 12: Sierra de San Pedro-Los Baldíos ($n=90$), 13: Llanos de Cáceres ($n=69$), 14: Sierra de Montánchez-Tamuja ($n=53$), 15: Llanos de Trujillo-Miajadas ($n=107$), 16: Villuercas-Ibores-Jara ($n=190$), 17: Tierra de Badajoz-Mérida-Vegas Bajas ($n=117$), 18: Vegas Altas ($n=56$), 19: La Siberia ($n=81$), 20: Llanos de Olivenza ($n=60$), 21: Sierra Grande-Tierra de Barros ($n=70$), 22: La Serena ($n=61$), 23: Sierra Suroeste ($n=50$), 24: Zafra-Río Bodión ($n=30$), 25: Tentudía ($n=77$), 26: Campiña Sur ($n=63$)

vanish in the probability maps of capturing at least 10 or 20 adults/trap (Fig. 5).

Discussion

Results show that Cc and Cw occupy in practice the entire region of Extremadura, Cw being generally more abundant than Cc, a fact consistent with the wider niche breadth of the former species. The two longhorns populated a wide altitude range (about 180–1400 m), reaching the upper colonisation limit of oaks in the region (Torres-Vila et al. 2022). A major strength of our study was that distribution data were obtained in the same spatio-temporal framework in which both longhorn species faced the same environmental conditions, so that occupancy-abundance data were synchronously

acquired and hence directly comparable. Feeding traps proved to be very effective for the capture of Cc and Cw as previously reported (Torres-Vila et al. 2012, 2013, 2017b) and our simple (albeit laborious) working protocol allowed us to estimate Cc and Cw populations separately. Previous researches have used exit holes (and associated larval frass) in the host trees as an indicator of beetle presence (Buse et al. 2007; Albert et al. 2012; Duque-Lazo and Navarro-Cerrillo 2017), but such methodology does not allow to establish species membership when Cc and Cw live sympatrically, as hole morphology has no taxonomic value (Torres-Vila et al. 2017a).

Considerable differences among years in adult longhorn abundance denote that fluctuating environmental factors strongly affect demographic parameters, among which reproductive output and survival stand up (Southwood 1978; Seber 1982; Millar et al. 2003; Haack et al. 2017). There also was huge intra- and interspecific variation in occupancy-abundance patterns, both at the regional scale and at the stand scale. The correlation of catch numbers from traps within stands was significant, but Spearman's coefficients were lower than expected in both species, suggesting that longhorn populations are rather heterogeneous at the stand scale. Cürten (1936) early reported that large swarms of adults often take place in the same trees, mostly straight trees in forest clearings, which curiously were not inhabited by larvae at all. It follows that some trees are more preferred than others, in which adults may meet up through male-produced aggregation-sex pheromones (Hanks and Millar 2016). Factors involved in non-random attraction among trees may include foliar volatiles used by adults as cues to select suitable trees (Millar and Hanks 2017; Sánchez-Osorio et al. 2019), presence of exudates/sapflows exploited by adults to feed on (Buse et al. 2007; López-Pantoja et al. 2008; Sánchez-Osorio et al. 2016) or even tree-mediated visual cues used by host-seeking adults (Torres-Vila et al. 2017b). Moreover, the coincidence of feeding, mating and oviposition sites in some trees (Hanks 1999) may account for the sedentary nature and reluctance of resident adults to leave their tree, which result in a patchy distribution (Sánchez-Osorio et al. 2016; Torres-Vila et al. 2017b).

Some endemic zones harboured much higher longhorn populations than others, with noteworthy intra- and interspecific differences at the regional scale. Note that the concepts of abundance and occupancy are underlying in the graphical output of the probability maps. A high probability of capturing at least one adult/trap was a robust proxy of occupancy, while a high probability of capturing many adults (10 or 20 adults/trap) was a good indicator of abundance. At least two main factors contributed to shape the occupancy-abundance patterns at the regional scale. First, the scarcity or local absence of host oaks in highly fragmented/deforested habitats within agricultural areas (e.g. wide areas of Tierra de

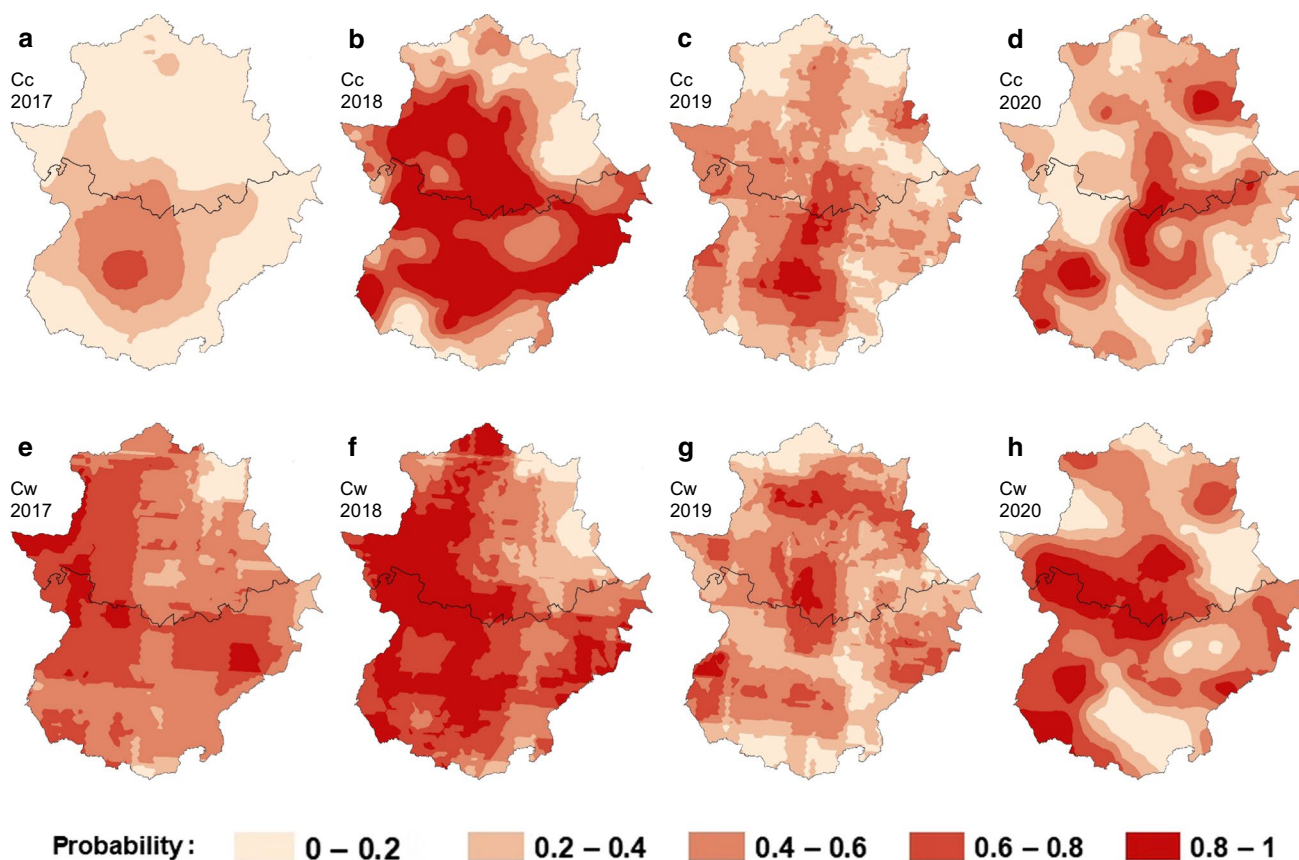


Fig. 4 Probability maps in Extremadura (SW Spain) generated with the Kriging Indicator algorithm for either *Cerambyx cerdo* (Cc, **a–d**) or *Cerambyx welensii* (Cw, **e–h**) with capture data from four consecu-

tive years: 2017 (**a, e**), 2018 (**b, f**), 2019 (**c, g**) and 2020 (**d, h**). All maps depict for each longhorn species the probability of capturing at least 1 adult per trap per year

Barros, La Serena and Campiña Sur) makes longhorns less frequent. Specifically, there is evidence that Cw abundance may be conditioned by the degree of isolation of the forest stand (Domínguez et al. 2022). Second, species-specific host preference shape Cc and Cw occupancy-abundance patterns because forests of different oak species are distributed heterogeneously across the landscape according to their own ecological requirements (Torres-Vila et al. 2022). This explain, for example, a high prevalence of Cw in cork oak forests at Sierra de San Pedro (W), or the scarcity of Cc and Cw in pyrenean oak forests at Villuercas-Ibores-Jara (E). Factors regulating host oak preference in Cc and Cw are poorly understood but they likely include wood hardness, bark depth or the perennial/deciduous nature of oaks (Buse et al. 2007; Torres-Vila et al. 2017a, 2022). Additionally, several mortality factors, acting on all longhorn stages throughout its long biological cycle, contribute to occupancy-abundance variations between years and zones. Among the biotic factors, overall still poorly known (Kenis and Hilszczanski 2004), the entomopathogenic fungus *Beauveria bassiana* (Balsamo) Vuillemin (Morales-Rodríguez et al. 2015), the tachinid fly larval parasitoid *Billaea adelpha*

(Loew) (Torres-Vila and Tschorsnig 2019) and especially the encyrtid egg parasitoid *Oobius rudnevi* (Nowicki) (Torres-Vila and Fusu 2020; Torres-Vila et al. 2021) have been reported to date in Extremadura. The predation by birds (Strojny 1977; Ceia and Ramos 2016; Redlarski et al. 2021) and meso-mammals (Torres-Vila et al. 2017c) may be also important.

Regarding longhorn abundance, those zones with a high probability of capturing at least 10 adults/trap/year involve a high potential damage to oak forests. A capture threshold of 10 adults/trap should be considered dangerous since it implies population densities of 40–50 adults/ha, considering an average trap attraction radius of 25 m (Torres-Vila et al. 2012, 2013). In several zones, the probability of reaching twice this threshold (20 adults/trap) was yet quite high for both longhorn species. Maximum catch number reached sometimes exaggerated values (252 and 219 adults/trap in Cc and Cw, respectively), with some traps capturing even more than 300 adults per season (Cc and Cw pooled), which means population densities of more than 1200 adults/ha, and thereby an absolutely unacceptable damage risk to oaks. Moreover, actual adult abundance in the wild could be even

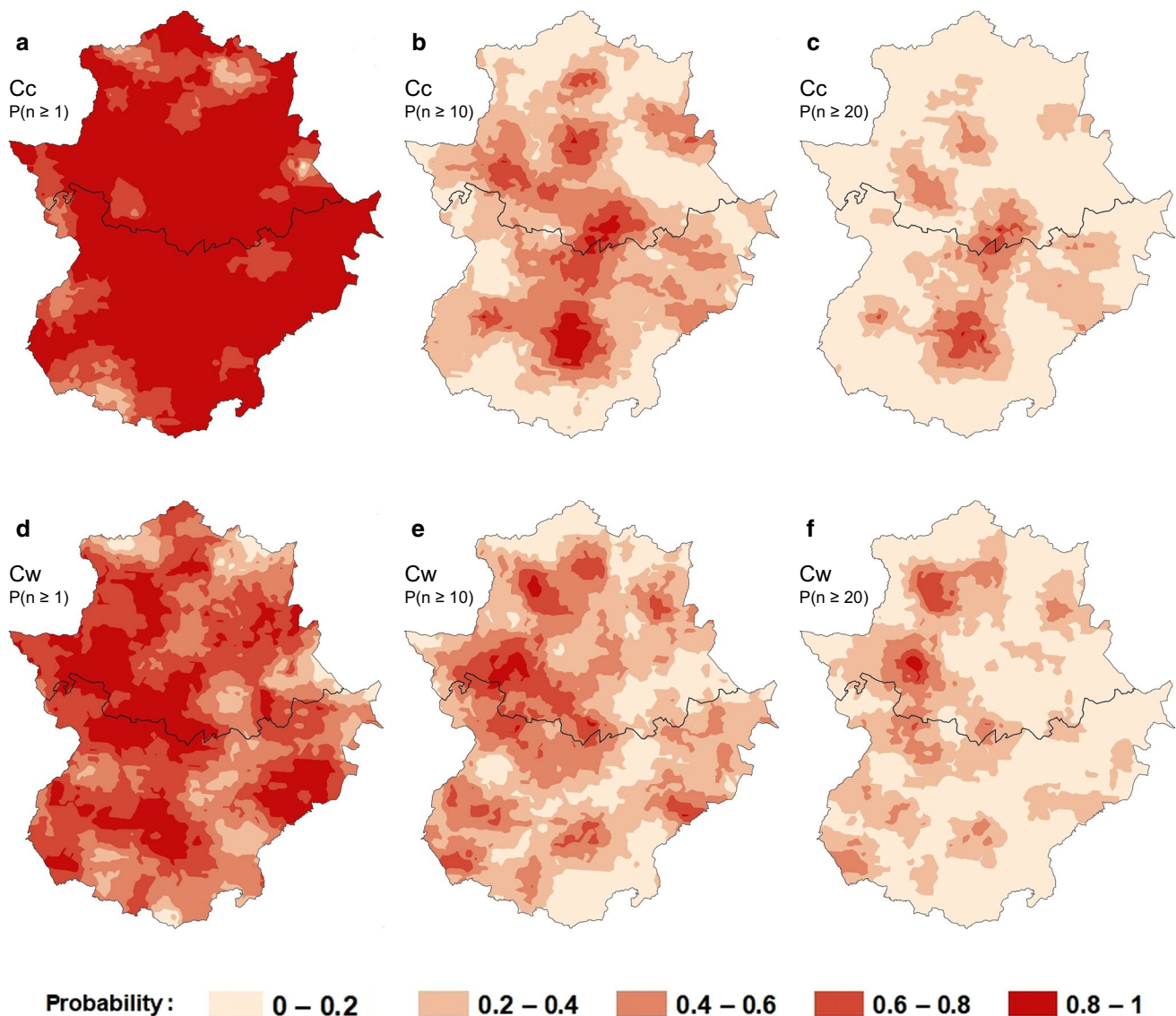


Fig. 5 Probability maps in Extremadura (SW Spain) generated with the Kriging Indicator algorithm for either *Cerambyx cerdo* (Cc, **a–c**) or *Cerambyx welensii* (Cw, **d–f**), by pooling the four studied years

(2017–2020) after normalise capture data within years. Maps depict for each longhorn species the probability of capturing at least 1 adult (**a, d**), 10 adults (**b, e**) or 20 adults (**c, f**) per trap per year

higher if we consider factors such as sex ratio and trapping efficiency. The sex ratio at emergence is usually quite balanced, about 50% males (Torres-Vila et al. 2018) but the sex ratio from trap catches is often strongly male-biased (e.g. this study), which could be explained if females have a more cryptic behaviour than males (López-Pantoja et al. 2008; Torres-Vila et al. 2012) or if the ethanol in the bait attracts males more than females (Sánchez-Osorio et al. 2016). It follows that a male-biased sex ratio from catches implies that females are taken less, so that abundance is likely underestimated, especially in the case of Cc in which sex ratio is strongly male-biased. Likewise, capture-mark-recapture trials with feeding traps as those used in this study have shown that trapping efficiency is only 48–61% when traps

are disposed at low density (≤ 4 traps/ha) (Torres-Vila et al. 2013), which also involves abundance underestimation.

In any case, population densities of Cc and Cw as high as those noticed in Extremadura—which poses a serious short-term threat to oak trees—have never been reported in other circum-Mediterranean regions or countries, even in those Spanish areas in which damage by either Cc (Mallorca island, Núñez et al. 2016) or Cw (Huelva province, Domínguez et al. 2022) is well known for years. It is worth noting that the intrinsic silvicultural and management features of the dehesa/montado ecosystem (in short, oak open woodlands of regularly pruned trees with sun-exposed trunks and limited/absent undergrowth due to grazing) are underlying factors prone to the development of *Cerambyx*

species (Buse et al. 2007; Duque-Lazo and Navarro-Cerrillo 2017; Torres-Vila et al. 2022). Our results confirm that damage inflicted by large woodborers in the Extremaduran dehesas (especially in holm oaks) not only have to Cw as the causal agent, but also to Cc. This finding questions if the current EU environmental standards for Cc protection (Bern Convention, Habitats Directive) are really necessary in most oak open woodlands of SW Spain. Therefore, our results can contribute to resolve or mitigate in Extremadura the current conflict of interest between the protection of either Cc or the dehesa ecosystem (Torres-Vila et al. 2022).

The occupancy-abundance relationships were significant and positive in the two longhorn beetles as usually found in other species (Gaston et al. 2000). However, regression slope was higher in Cc than in Cw, meaning that Cc exhibits a greater abundance increase per occupancy unit. Hence, Cw was more abundant than Cc with low occupancy levels, while the opposite was found when occupancy was high. A lower abundance of Cc than Cw when occupancy is low could be tentatively explained if Cc is more sensitive than Cw to deforestation and habitat fragmentation, or if the impact on Cc by *O. rudnevi* is exacerbated when occupancy is low, as parasitism rate does not increase with egg density (Torres-Vila et al. 2021). Remarkably, occupancy was higher in Cc than in Cw with low abundance values (a circumstance detected in both probability maps and occupancy-abundance regressions) for which we do not have clear explanation, although the fact that Cc is more prone to disperse than Cw by performing longer crosswind flights on windy days (Torres-Vila et al. 2017b) could be involved in some way (Holland 2009).

A central issue of community ecology is to elucidate the mechanisms allowing the coexistence of potentially competing sympatric species (Schoener 1974; Chesson 2000; Agrawal et al. 2007; Mayfield and Levine 2010; Satoh et al. 2016). Cc and Cw live in sympatry in nearly all forest contexts in the study area, but results did not show a repulsive association between both species. This suggests that interspecific competition for resources must be low or absent, even if host oak niche overlap between both longhorns is almost complete. A different host preference between both longhorns may result in niche segregation at the stand scale, or even at the tree scale in mixed holm oak-cork oak stands. Moreover, there is evidence based on vertical larval stratification in the host tree that Cw selects the fork and main branches to develop, while Cc prefers the trunk base and main roots (Torres-Vila et al. 2017a). This niche segregation at the tree scale is a crucial one because suggests that direct interspecific competition for larval feeding resources is not intense, which explain in turn the widespread sympatric coexistence of Cc and Cw in SW Iberia and other Mediterranean areas. The preference of Cc for the lower part of trunk and main roots was already reported time ago

(Rendu 1876; Richter 1942; Rudnev 1957; Săvulescu 1969). More recently, this behaviour has been confirmed in habitats in which Cw does not occur, showing also that Cc prefers the trunk base for reasons other than the higher resources available for larvae (Albert et al. 2012). These observations support that the preferred niche of Cc at the tree scale is not an adaptation resulting from its coexistence/competence with Cw. However, the opposite case might not be true as we have not robust data to reject that a niche preference by Cw is influenced by its competence with Cc.

Conclusion

We provide the first comprehensive overview on the distribution (occupancy-abundance) of Cc and Cw at a regional scale in SW Spain using geostatistic and GLMMs. A precise knowledge of the species-specific occupancy-abundance relationships is especially important when tools to manage or control bark and woodborer insects associated with oaks are almost nonexistent. Specifically, insecticide control is not appropriate at all to mitigate longhorn impact due to its low cost-effectiveness in forest landscapes, the cryptic nature of larvae living protected within the wood, and above all the extreme sensitivity of the oak ecosystem to chemical-mediated external disturbances. The information provided in this paper may be useful in a sustainable pest management/control framework to delimit risk areas, to evaluate the expected spatial spread of the target species in the current global warming scenario, or to delve into the sympatric relationship between Cc and Cw when they behave as pests in the wild. The complex black box of ecological, silvicultural, climatic and geographic factors that ultimately shape the distribution and occupancy-abundance patterns of Cc and Cw remains to be further investigated.

Acknowledgements The authors are grateful to all companions and colleagues who provided assistance in either field or laboratory; to the owners, tenants and managers of the dehesas and oak forests for their good disposition to conduct this study; to the companies Aguas del Suroeste (Los Riscos) and Gespesa (Ecoparque de Talarrubias) for the supply of PET containers; to Emiliano Zamora (Estación Enológica de Almendralejo) for the continued supply of red wine (just to be used in traps!); and to two anonymous reviewers for improving the manuscript. This research was supported by the Plant Health Service (SSV), Junta de Extremadura.

Author contributions LMT-V: contributed to conceptualisation, formal analysis, investigation, methodology, supervision, validation, writing—original draft, and writing—review and editing. FJM-D: contributed to conceptualisation, formal analysis, investigation, methodology, validation, and writing—review and editing. FJM-G: contributed to formal analysis, visualisation, and writing—review and editing. TC: contributed to formal analysis, visualisation, and writing—review and editing.

Funding TC benefited from a Margarita Salas postdoctoral fellowship (Next Generation EU). The remaining authors declare that no funds, grants, or other support were received.

Data availability Table S1—The raw dataset generated in this study is available at <https://www.researchgate.net/publication/362469352>.

Declarations

Conflict of interest The authors have no financial or non-financial interests to disclose.

Consent to participate Informed consent was obtained from all individual participants included in the study.

Consent for publication Not applicable.

Ethical approval Not applicable.

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