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ARTICLE

RESEARCH ARTICLE

Predisposing factors and spatio-temporal dynamics in two co-occurring cone pests in *Pinus pinea* (*Leptoglossus occidentalis* and *Dioryctria mendacella*)

Factores de predisposición y dinámica espacio-temporal de dos plagas de las piñas de *Pinus pinea (Leptoglossus occidentalis y Dioryctria mendacella)*

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Abstract: *Aim of study*: To assess the impact of the exotic western conifer seed bug *Leptoglossus occidentalis* (WCSB), and the native pine cone moth, *Dioryctria mendacella* (PCM), two pests simultaneously feeding on cones and nuts of *Pinus pinea;* to identify the potential exogenous and endogenous factors controlling the impact of each pest, and to evaluate the occurrence of synergies and trade-offs between the pests. *Area of study*: Spanish Northern Plateau. *Material and methods*: Annual data on cone, nut and severity from each pest, collected in an extensive net of 52 plots (250 trees) installed in pure-even aged forests of *Pinus pinea*, covering nine years (2013-2021). Given the structure of the data and the proposed conceptual modelling, structural equation modelling (SEM) and path analysis were used. *Main results*: We observed an increasing pattern on the severity due to WCSB in the recent years, which may affect over 60% of pine nuts, while PCM tended to show a constant pattern, affecting on average 20% of the cones. Rate of severity of each pest was directly affected by the average size of a single cone, which was controlled by annual rainfall and stand age. Moreover, rising temperatures and age also exerted a direct and positive effect over the rate of severity of both pests, while the total amount of available cones in the year exerted a direct and negative effect. Complex temporal interactions between pest severities were identified. *Research highlights:* Severity of both pests is influenced by exogenous and endogenous factors, which may be aggravated under scenarios of climate change. These results support adaptive silviculture aimed at maintaining high cone availability to dilute pest impact.

Keywords: exotic pest; native pest; pine cone moth; pine nuts; structural equation models; western conifer seed bug.

Resumen: *Objetivo del estudio:* Cuantificar el impacto real de la chinche exótica succionadora de yemas de coníferas *Leptoglossus occidentalis* (WCSB), y la polilla nativa *Dioryctria mendacella* (PCM), dos plagas que se alimentan de forma simultánea sobre piñas y piñones de *Pinus pinea;* identificar los potenciales factores exógenos y endógenos controlando la dinámica de cada plaga, y evaluar la ocurrencia de sinergias y compromisos entre ambas plagas. *Área de estudio:* Meseta Norte (España). *Material y métodos:* Datos anuales de producción de piña, piñón y severidad de ambas plagas, medidos en una red de 52 parcelas (250 árboles) localizada en masas puras regulares de *Pinus pinea,* cubriendo nueve años (2013-2021). Dada la estructura de los datos y el modelo conceptual propuesto se utilizan modelos de ecuaciones estructurales (SEM) y análisis de camino. *Resultados principales*: En los últimos años se ha observado un patrón creciente en la severidad debida al chinche WCSB, que ha llegado a afectar al 60% de los piñones, mientras que la polilla PCM mostró un nivel de severidad constante, afectando en promedio al 20% de las piñas. La tasa de severidad de cada plaga estaba directamente influida por el tamaño medio de la piña, variable que a su vez era controlada por la precipitación anual y la edad del rodal. Temperaturas más elevadas y edades avanzadas de la masa ejercieron un efecto directo y positivo sobre la tasa de severidad de ambas plagas, mientras que la cantidad de piña disponible influyó de manera directa y negativa. Se han identificado interacciones temporales complejas entre la tasa de severidad de ambas plagas. *Aspectos destacados de la investigación:* La severidad de ambas plagas está influida por factores exógenos y endógenos que pueden verse agravados bajo escenarios de cambio climático. La aplicación de una selvicultura adaptativa orientada aumentar la producción individual de piña puede mitigar el efecto de ambas plagas.

Palabras clave: chinche succionadora de semillas de coníferas; modelo de ecuación estructural; piñón; plaga exótica; plaga nativa; polilla de las piñas.

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Supplementary information ↓

1. INTRODUCTION

Herbivores, including wood-borers, sap-feeders, foliage-feeders and seed eaters, are among the most damaging forest pests (Brockerhoff & Liebhold, 2017). Native pests can erupt in large outbreaks, especially under changing environmental conditions, and can be influenced by landscape and climate leading to increased host mortality and altered forest structure (Kausrud et al., 2012). Similarly, invasions by non-native (or alien) pests have profound ecological consequences, often disrupting established plant–pest dynamics and overwhelming the natural defences of native tree species. Indeed, the ecological and economic impacts of non-native pest species are estimated to be second only to those caused by habitat destruction and fragmentation (Wilcove et al., 1998), with substantial areas of forest worldwide suffering severe degradation or loss each year as a result of such invasions (Roy et al., 2014).

The establishment and spread of both native and non-native pests are shaped by a complex interplay of environmental, biological, and human-driven factors. Key determinants include climate suitability,

host availability, propagule pressure, human activity (often unintended consequence of international trade), and species-specific traits (Skendžić et al., 2021). For example, warmer temperatures and increased CO_2 levels generally enhance the performance and spread of invasive species more than natives, reducing barriers to establishment and dispersal (Liu et al., 2017; Skendžić et al., 2021). Furthermore, the interaction between pest requirements and local environmental conditions (e.g., temperature, precipitation) is critical for pest success (Liu et al., 2017; Tobin & Robinet, 2022). Similarly, the abundance and distribution of host species are also critical factors. Studies show that the summed abundance of host trees, rather than individual host density, often has a greater influence on pest distributions, suggesting that areas with high host availability are more susceptible to multiple pest invasions (Gougherty et al., 2024).

Several pest species, both native and non-native, can affect the same host tree within the same geographic area, leading to complex interactions and cumulative impacts on forest ecosystems (Morin & Liebhold, 2015). Although trees and their natural pests have coevolved over long timescales, the introduction of non-native pests—many of which lack natural enemies or encounter hosts with limited defences due to minimal evolutionary exposure—now poses a significant and growing threat to native forest ecosystems, with some pests causing drastic ecological changes (Brockerhoff & Liebhold, 2017). The simultaneous presence of multiple pests on the same host in a given area complicates management efforts. For example, in recent years, integrated pest management programs in the United States have targeted both native and non-native pests, primarily using suppression and prevention strategies (Coleman et al., 2023).

Herbivory problems have traditionally been addressed through either dynamic or static approaches. The former, such as the popular Lotka-Volterra model and its generalisations (e.g. Kolmogorov population model), aim at describing population dynamics of prey and predator through systems of differential equations (Din 2013). On the other hand, static approaches - typically based on advanced regression modelling (Manso et al., 2014) - seek to explain the observed number of prey individuals (e.g. seed or seedlings) as a function of predator abundance and possibly other environmental factors. A main limitation of both approaches is that they cannot easily deal with systems that include interactions of more than two predators or preys (e.g. Adamu, 2018) and both predators' and prey's population may further be affected by common climatic and environmental conditions.

One static approach specifically designed to disentangle complex interactions between many agents as those described above, is structural equation modelling (SEM, Lei & Wu, 2007). In SEM, a conceptual framework is set where the interactions between different random (measurable and/or latent) variables are established according to previous knowledge. Through different statistical techniques, the strength of these interactions is then calculated. The main advantage of SEM over fitting individual models for each of these interactions is that the fit is simultaneous, thus leading to a more accurate and coherent parameter estimation of the whole system. SEM has already been used to study the interaction between forest pests, multiple tree hosts and the environment (Guo et al., 2019) and it is the approach we are using here as well.

Pinus pinea L. is a Mediterranean pine species especially relevant for its nutlike edible seed production, their seeds being one of the most important non-wood forest products in the Mediterranean area (Mutke et al., 2012). Thus, cone and nut production are currently the main objectives of *P. pinea* forest management, providing forest owners with a higher income than that obtained from timber (Ovando et al., 2010). In Spain, with 490,000 ha of *P. pinea* forests, annual cone production has been traditionally between 30,000 and 35,000 t cones per year (which corresponds to ca. 6,000 t of nuts in shell per year), even reaching 60,000 t in good yield years (Calama et al. 2020a). Such high interannual variability in cone production is a consequence of the climate-mediated masting habit of the species (Calama et al., 2011) and a three-year cone

development (greatly affected by drought and extreme winter frosts; Mutke et al., 2012), but also due to a high spatial variability related to water availability and soil characteristics (Calama et al., 2020a), as well as to the effect of cone pests.

The most important pest attacking *P. pinea* cones are the larvae of the native pine cone moth (from now on PCM) *Dioryctria mendacella* Staudinger and the exotic western conifer seed bug (from now on WCSB) *Leptoglossus occidentalis* Heidemann, recorded in Spain since 2003 (Ribes & Escolà, 2005). Both pests attack cones on different developmental stages, producing abortion of immature cones and severe damage to pine nuts. Both insect pests are responsible of important reductions in cone and pine nut production, 20-25% related to PCM (Calama et al., 2017) and as high as 60% due to WCSB (Farinha et al., 2018; Calama et al., 2020b).

Despite the relevant impact of both pests on cone production, little is known about the potential environmental, stand-level and tree-level factors influencing their ecology. Focusing on PCM, Calama et al. (2017) identified that damage due to the species increases at higher locations (commonly showing lower site quality) and denser stands. Both effects may be related to lower cone productivity at tree and stand level, and thus, lower availability of the feeding resource. The authors identified that rising maximum summer temperatures reduce the rate of damage, may be due to increased mortality at all developmental stages in extreme heatwave (temperatures > 35 ºC) days. On the other hand, rising winter and summer temperatures tend to increase the rate of damage, which was explained by the greater likelihood of a second adult generation in the year. Finally, the authors identified a negative correlation between the rate of damage and the total productivity of cones in the current year, and a positive correlation with the rate of damage experienced in the previous year.

In the case of WCSB, its population dynamics remain poorly understood, although they are likely strongly influenced by resource availability (Barta, 2015). Temperature also plays a crucial role; the lower temperature thresholds for development are around 13–14 °C, and 533 degree-days are required to complete development, with the potential to produce up to four generations per year depending on local conditions (Barta, 2015). A recent study by Ponce-Herrero et al. (2024) demonstrated that the severity of damage caused by the insect feeding varies with the season and is influenced by the stage of cone and kernel development. Additionally, Farinha et al. (2021) reported a strong positive correlation between seed loss per cone and the average insect density during both the current and previous year.

The main objective of the study is to improve the current knowledge on the dynamics and degree of affection (severity) of the native *Dioryctria mendacella* and the exotic *Leptoglossus occidentalis*, two pests simultaneously affecting cone production in the *P. pinea* forests in the Northern Plateau of Spain. To this aim we have defined the following specific objectives:

- Provide an accurate assessment of the severity of both pests in terms of reduction of cone and pine nut production.
- Identify spatial and temporal patterns of occurrence of both pests.
- Identify environmental and stand-level factors affecting the severity of each pest, and highlight those factors that may be simultaneously affecting both pests.
- Check for the existence of a significant correlation between the occurrence of both pests.

Our main hypotheses to contrast are:

- There is a relationship between the rates of damage due to both insects and the current and past availability of the feeding resource (total amount of cones cropped, individual weight of the cones…).
- Stand-level and climate attributes influence the availability of the resource, thus indirectly may be affecting the rates of damage (or severity).
- Stand-level and climate attributes may directly influence the rates of damage, by means of climate control over the size of populations and flight curves, or due to the preference of the insects on different forest structures.
- A lagged positive effect of the severity in the previous year is expected in the current year, evidencing complex dynamic interactions between cone crop size and probability of damage.

2. MATERIAL AND METHODS

2.1. Permanent plots network and cone collection

In 1996 a net of 141 permanent plots was installed in pure and even-aged forests of *P. pinea* within the Northern Plateau, in order to study growth and both timber and pine nut production. This region corresponds to one of the four main provenance regions of *P. pinea* in Spain (Prada et al., 1997), and is considered as one of the regions with a larger tradition for cone and pine nut collection and industrial processing (Calama et al., 2020a). The net was enlarged in 2017, adding twenty-three new plots.

The plots are circular, with variable radius, and include 20 trees. At the moment of plot installation tree coordinates, diameter at breast height, total height and crown diameter of all the trees were recorded, and increment cores were extracted in a subsample of trees to determine past growth and stand age. Since plot installation up to 2010, in the five trees nearest to the centre, the complete crop of cones has been collected every year. In 2013, and just after the identification of damages that could be attributed to the western conifer seed bug *Leptoglossus occidentalis* (WCSB), cone collection was reinitiated in a subsample of 34 plots. In 2017 the activity was extended to the new plots, thus by 2022 crops are collected every year in a sample of 52 plots (250 trees approx.). In the current work we use data from the nine campaigns elapsing between 2013 and 2021, including four years (2013-2016) where only data from original plots are available (116 plot x year records) and five years (2017-2021) with data from both original and new plots (248 plot x year records). More information about the study area can be found at Supplementary material Annex I.

2.2. Cone and nut processing

Cones from each tree were classified as "*healthy",* if no external signs of damage are observed, or as "*damaged"* if signs or damage by pine cone moth (PCM, *Dioryctria mendacella*) are shown. Sign of attack by PCM are quite evident, with the cones commonly maintaining their size, but they bear resin exudates, browning of the damaged bracts, partial abortion of the cones, severe damage to pine nuts and irregular holes used by the adult moths to abandon the cone after completing their maturation (Figure 1a). Cones of each category were counted and weighed separately.

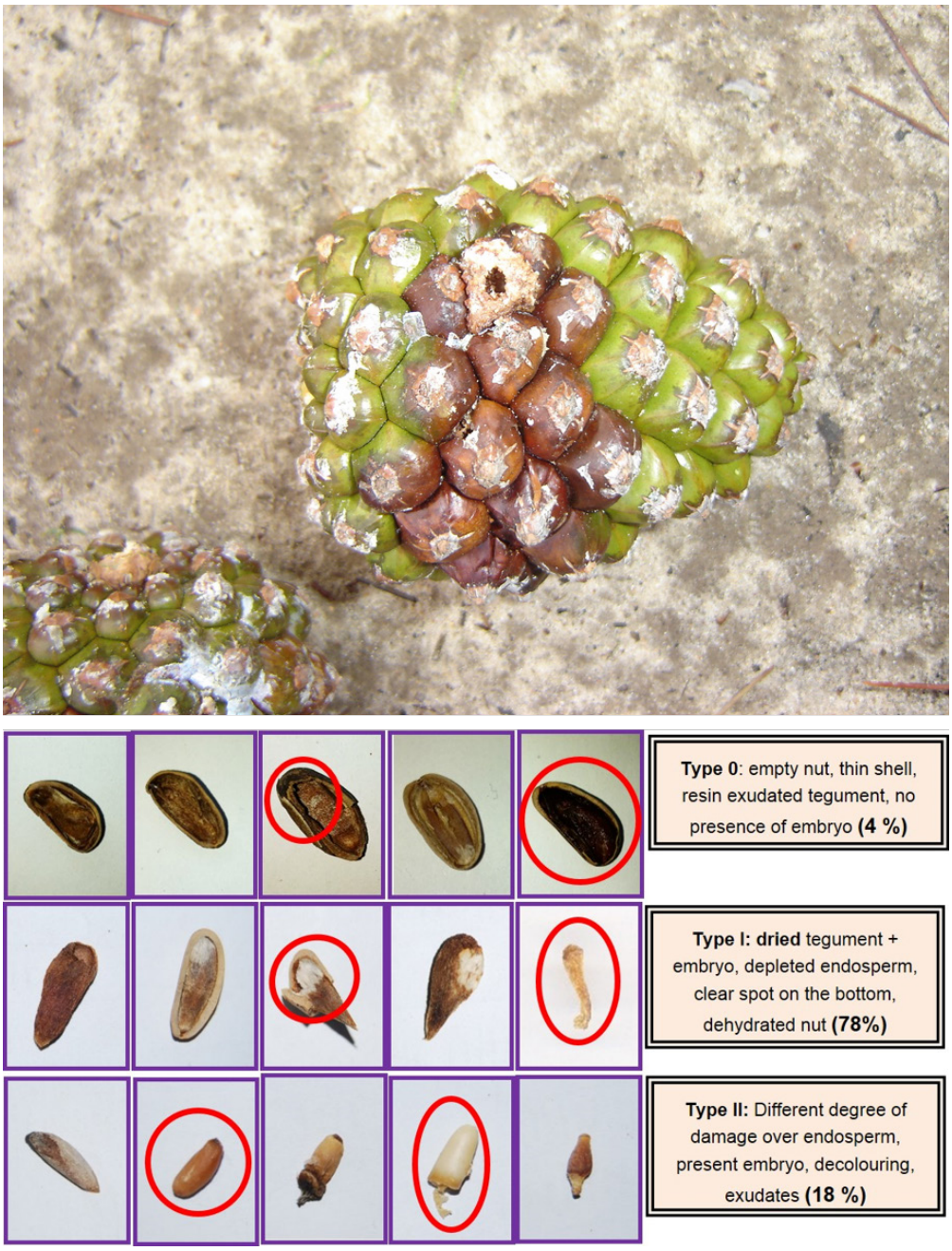

Figure 1. Typical damage in cones due to pine cone moth (*Dioryctria mendacella*, above), and different type of damage on pine nuts provoked by western conifer seed bug (*Leptoglossus occidentalis*, below).

Contrary to the damage caused by PCM, mature cones attacked by western conifer seed bug (WCSB, *Leptoglossus occidentalis*) do not show external signs of damage. WCSB feeds on the immature pine nuts by entering its stylet among the scales of the cone, provoking the abortion or severe damage to the nut, and then reducing the final yield of the crop, so the only way to assess damage consists of analysing pine nuts. To this aim, since 2013 a subsample of fifteen cones per plot, randomly selected among those classified as healthy, were sent to laboratory, in order to identify damage by WCSB. In the case there were not fifteen healthy cones in the five trees close to the centre, cones were then collected in nearby trees, to complete the sample.

Once in the laboratory, the cones from a given plot and year were randomly separated into three sets, including five cones each. Each set of cones was labelled, and its fresh weight was recorded using a scale with a precision of 1 g. Each set of cones was oven dried at 45 °C for a minimum period of a week until the cones opened. After completing the opening of the cones, the sample was

weighed again. The pine nuts, still in the shell, were manually extracted from each set. Pine nuts shorter than 4 mm were considered as aborts and removed. The rest of the pine nuts were counted using an automatic seed counter, and weighed with a precision of 0.1 g. A subsample of 50 pine nuts from each set was randomly selected for the analysis of kernel yield and weighed with a precision of 0.1 g. Pine nuts were cracked using a manual nut cracker and classified and counted as "*sound kernels*" or as "*damaged nuts*". Similitude of damage with those observed in WCSB experimental cages and feeding assays allowed us to use the severity damage classification established for the species (Figure 1b; Farinha et al., 2018; Calama et al., 2020b). In this sense, we are not considering other agents that may cause partially overlapping symptoms on pine nuts, thus damage due to WCSB should be interpreted as a proxy for cone/nut damage compatible with WCSB feeding rather than a direct measure of exclusive damage.

2.3. Response variables

Annual damage at plot level due to each of the two pests (WCSB and PCM) affecting cone production was assessed in a different manner. The severity of damage by PCM in plot *i* in the year *j* (defined as Dam_PCMij) was computed as the ratio between the number of cones attacked by pine cone moth collected in the plot *i* in the year *j* (Ndamaged) divided by the total number of cones (Ncones = *Ndamaged + Nhealthy)* collected in the plot:

In the case of WCSB, we used the rate of affected pine nuts (Dam_WCSBij) as a proxy for evaluating the severity of the pest. This rate was defined as the ratio between the number of damaged pine nuts in the subsample (N_damaged_nuts*)*, and the total number of pine nuts (commonly 50) in the subsample, averaged over the three lots analysed in each plot:

Both the rate of damage by PCM (Dam_PCM) and the rate of damage by WCSB (Dam_WCSB) are indicators of the relative severity of the pests at plot level.

Given the type of damage provoked by PCM in a given cone, it is not possible to identify whether there was a previous attack by WCSB or not. On the other hand, we can affirm that cones considered as attacked by WCSB were free of attack by PCM. In this sense, we are assuming no interaction between the pests at the cone level (i.e. if a cone is attacked by one of the pests, we assume that it is not attacked by the other). This assumption represents a necessary simplification, but it could introduce bias in the results, since (1) it may lead to underestimating the total damage due to WCSB at plot-level, especially in years with severe PCM attack, and (2) it could lead to misinterpretation of the interactions between both pests within a given year.

2.4. Predictors

We have grouped the factors potentially affecting the severity of both pests into four different categories:

- *Plot level attributes*: defining the horizontal and vertical structure of the plot.
  - Stand density *N* (stems/ha)
  - Basal area *BA* (m2/ha)
  - Mean squared diameter *dg* (cm)
  - Reineke´s Stand Density Index *SDI.*
  - Stand age *T* (years)
  - Mean height *H* (m)

- *Cone crop production*: computed for the current and past years, representing the total amount of resource available for the pests.
  - Total number of cones *Ntotal* per hectare in the i^{th} plot, computed for the current j^{th} and the previous j-1^{th} years.

    Where Area represents the surface (m2) of the plot.

  - Average weight of a single cone *Wc* for the ith plot, computed for the current *j*th and the previous *j-1*th years, defined as the ratio between the total weight of the cones collected in the plot (Wconesij)and the number of cones collected in the plot.
  - Number of pine nuts per cone (NPPC) and per kg of fresh cones (NP_KGC), computed for the current year.

- *Climatic variables.*
  - Annual value of cumulative rainfall (pp_annual) and seasonal cumulative rainfall occurring in winter (from January to March, pp_winter), spring (April to June, pp_spring), summer (July to September, pp_summer) and fall season (October to December, pp_fall) in plot *i* and year *j*.
  - Annual and seasonal mean values of minimum (t_min), mean (tm) and maximum (t_max) temperatures.
  - Annual value of Martonne's aridity index, computed as the ratio between cumulative annual rainfall and mean annual temperature + 10

Monthly climatic variables were obtained for each plot for the whole analysed period 2013-2021 using the European 1 km x 1 km grid climate model E-OBS (Moreno and Hasenauer, 2016) extracted using the R package 'easyclimate' (Cruz-Alonso et al., 2023). Given the spatial and temporal extent of the experiment (52 plots distributed in more than 10.000 km2 over nine years), it was not possible to collect *in situ* climate data. This limitation may obscure the impact of microclimate conditions on pest dynamics.

- *Current and past incidence of the pests.*

Given the large interannual variability in cone production, we also defined two proxies for the real raw severity of the pests at the hectare, given by the total weight of cones per hectare damaged by pine come moths (W_PCM) and the total weight of pine nuts per hectare damaged by WCSB (W_WCSB):

Where $Ncones_{ij}$ represents de total number of cones collected in the plot i the year j, Wc_{ij} the average weight of a single cone collected in in the plot i the year j, $Area_i$ and Dam_PCM_{ij} as previously defined.

Where NPC_{ij} represents the average number of pine nuts per cone collected in the plot i the year j, $WPNut_{ij}$ is the mean weight of a single pine nut (with shell) in the plot *i* the year *j*. The rest of symbols as previously defined.

In order to identify temporal patterns of correlation in the levels of severity we evaluated the effect of *Dam_PCM*, *Dam_WCSB*, *W_PCM* and *W_WCSB* computed in the previous year *j-1* on the degree of severity due to the same and the other pest in the year *j*th. In addition, in order to identify patterns of competition/facilitation among the pests, we evaluated the effect that the rate of damage and the total weight of damaged pine cones (or pine nuts) due to one of the pests observed in a given *j*th year may have on the responses variables representing damage due to the other pest in that year.

2.5. Exploratory analysis

Spatio-temporal pattern of pest affection was evaluated by means of graphical analysis and maps of severity. Person's correlation analysis was carried out to unravel on a preliminary step the relationship between the mean rate of severity of each pest and the potential predictors, divided in the four different groups previously defined: plot-level, cone production, climatic and current and past incidence of pests. Since the two response variables (Dam_PCM and Dam_WCSB) are expressed as rates, and censored between 0-1, we used the asrcsin-square root transformation.

2.6. Conceptual structural equation model (SEM)

Our initial hypothesis is that the rates of damage due to both pests may be affected by different factors on different ways. The factor (from now on defined as an exogenous factor) may exert a direct impact over the response variable, or may exert an indirect effect, through and intermediate factor (from now

on defined as endogenous factors). In our study we can hypothesize that rainfall may exert a direct impact over the rate of damage by one of the pests (e.g. by promoting the population of the pest in dry years). We can also hypothesize that rainfall may exert an indirect effect, as it may be related with the weight of the cones, a factor that may also influence the severity (since is a proxy for the total availability of the feeding resource). So in this case, rainfall would act as an *exogenous factor* and weight of cones would act as an endogenous one. In addition, we can assume the existence of patterns of interdependence between the two analysed rates of damage. In order to analyse this type of data including causal complex relations and different degrees of dependency among the predictors and the response variables *Structural Equation Models* (Lei & Wu, 2007) are commonly used.

The conceptual structural equation model (Figure 2) for analysing the potential relations between the rate of damage due to the PCM (Dam_PCM) and the WCSB (Dam_WCSB) relies on the following hypothesis:

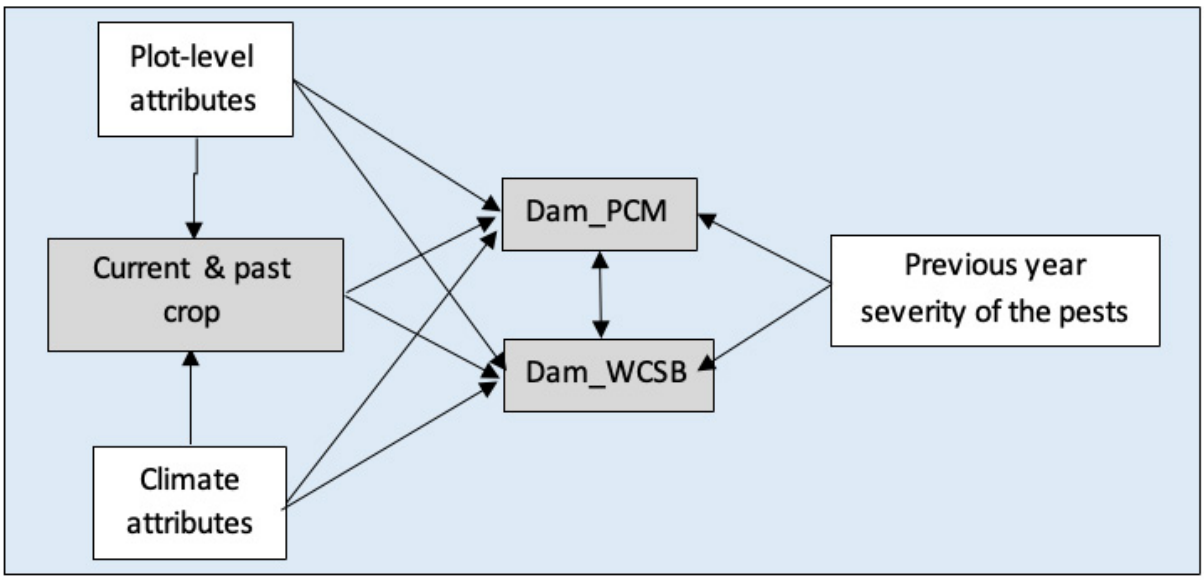

Figure 2. Conceptual Structural Equation Model for the analysis of rate of damage due to pine cone moth (*Dioryctria mendacella*) and western conifer seed bug (*Leptoglossus occidentalis*). Shaded cells indicate endogenous variables, white cells exogenous ones.

- Assumption 1: current year climatic conditions may exert a direct influence on the rate of damages due to the pests, but also and indirect influence by affecting current crop attributes, as the weight of a single cone or pine nut content.
- Assumption 2: plot-level attributes may exert a direct influence on the rate of damages due to the pests, but also and indirect influence by affecting current crop attributes, as the weight of a single cone or the total number of cones produced in a given year.
- Assumption 3: attributes related with current and past crop (total number of cones per ha, weight of a single cone, pine nut content) may have a direct effect over the rate of damage.
- Assumption 4: the severity of both pests in the previous year (either as a rate or as an absolute value) may exert a direct effect over the current year rate of affection.
- Assumption 5: no additional indirect effects are assumed (i.e. we assume independence between plot characteristics, climate and previous year incidence)

The structural model is then formulated as a pure path analysis model, where some current crop attributes, as well as *Dam_PCM* and *Dam_WCSB* are considered as endogenous variables, while the rest of predictors are considered exogenous variables.

2.7. Structural equation model construction

Based on the preliminary analysis of correlation, we identified those potential exogenous plot-level and climate-attributes that may be directly and indirectly (through current crop attributes) influencing the rate of damage for both pests. In a subsequent step we identified those current and past crop attributes not explained by plot-level and climate attributes significantly related with the rate of damages. In a third step we evaluated the impact of previous year severity of the same pest. In the subsequent step we evaluated the entrance into the model of additional plot-level or climate attributes directly acting over the rates of damage. At each step of the sequential procedure the first evaluated covariates were those showing larger correlation in the previous analysis, and the covariate showing large significant correlation with the response variable was selected. Comparison between the different covariates to enter the model at each step were carried out using the level of significance of the correlation between the covariate and the response variable, and changes in Expected Cross Validation Index (EVCI) and R^2.

Once the individual SEM is constructed independently for each response variable, we constructed a complete model to analyse the existence of potential dependencies among both pests. To this aim we have considered the same covariates identified in the individual fit, but also included the variables indicating the current and past incidence of each pest (W_PCM and W_WCSB) as potential predictors of the other pest. Finally, we evaluated the existence of significant correlation between *Dam_PCM* and *Dam_WCSB*. Goodness of fit of the complete model was evaluated using statistics as R^2 for each of the response variables, EVCI, the Goodness of Fit Index (GFI, percentage of the total variability explained by the model), Root Mean Square Error of Approximation (RMSEA), the Standardized Root Mean Square Residual (SRMR) and the Normed-Fit Index (NFI). For GFI and NFI values over 0.95 are preferred, while for RMSEA and SRMR values below 0.10 are indicators of fair fit (Hooper et al., 2008).

Exploratory analysis and model construction were carried out using proc CORR and proc CALIS in SAS® Studio. In order to prevent bias in the computation of standard errors associated with a high rates of zeroes in *Dam_PCM* (> 20%) the parameters of complete SEM were estimated using Robust Maximum Likelihood methods.

3. RESULTS

3.1. Exploratory analysis: Severity of *Dam_PCM* and *Dam_WCSB* in the study area

Rate of damage due to pine cone moth (Dam_PCM) and due to western conifer seed bug (Dam_WCSB) showed different spatial and temporal patterns through both the territory and the period of analysis. Average value of *Dam_PCM* reached 0.1873 (std error = 0.0142), with more than 40% of records corresponding to plots were rate of damage due to pine cone moth is below 0.1, few records associated with higher rates of damage, and even some plots where in a given year all the cones were infected by PCM (Figure 3). Contrarily, *Dam_WCSB* reached much higher values, with a mean value for the whole study of 0.6285 (standard error = 0.0123), and a histogram of frequencies pointing to a prevalence of infection values over 0.3 in the vast majority of the observations, with only less than 1% of the analysed lots of cone with *Dam_WCSB* below 0.1. This indicates a much larger severity of WCSB in the studied region, since while PCM may be responsible for the loss of approximately 20% of the cones, WCSB is attacking on average more than 60% of the pine nuts in the cones.

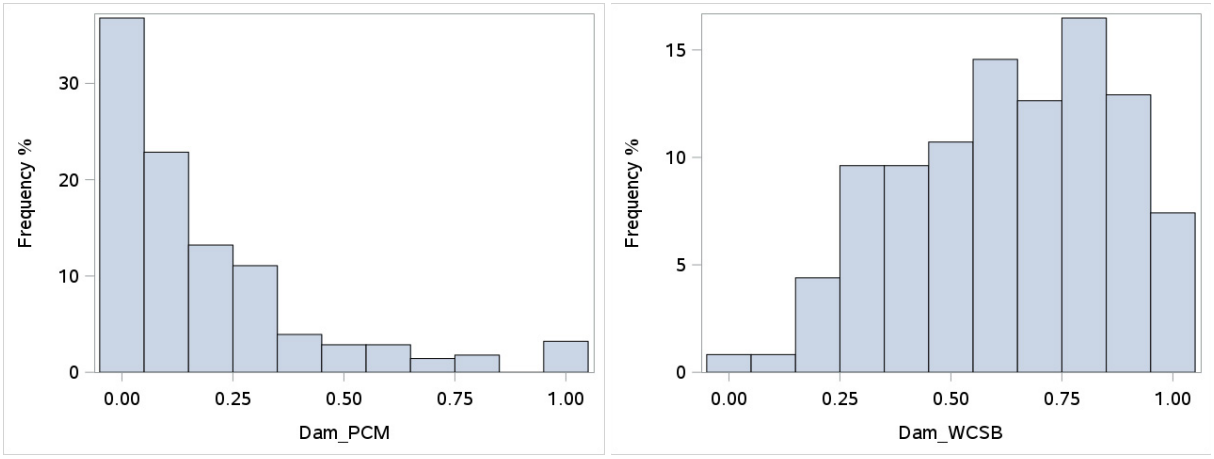

Figure 3. Histogram for the observed frequencies of Dam_PCM (rate of damage due to pine cone moth, left) and Dam_WCSB (rate of damage due to western conifer seed bug, right).

A spatial analysis at a regional scale (Figure 4) permitted to show patterns of spatial dependence, showing that nearby plots tend to have a similar value of rate of damage. As an example, it can be seen that larger rates of *Dam_WCSB* are observed in the southernmost part of the study region, while lower rates are observed in the eastern part. In the case of PCM the distribution of the pest over the territory seems to be much more uniform, showing less differences, and being difficult to identify hotspots for the pest. It does not exist any evident pattern of spatial correlation among both pests, with areas showing large rates of infection due to one of the pests but no due to the other.

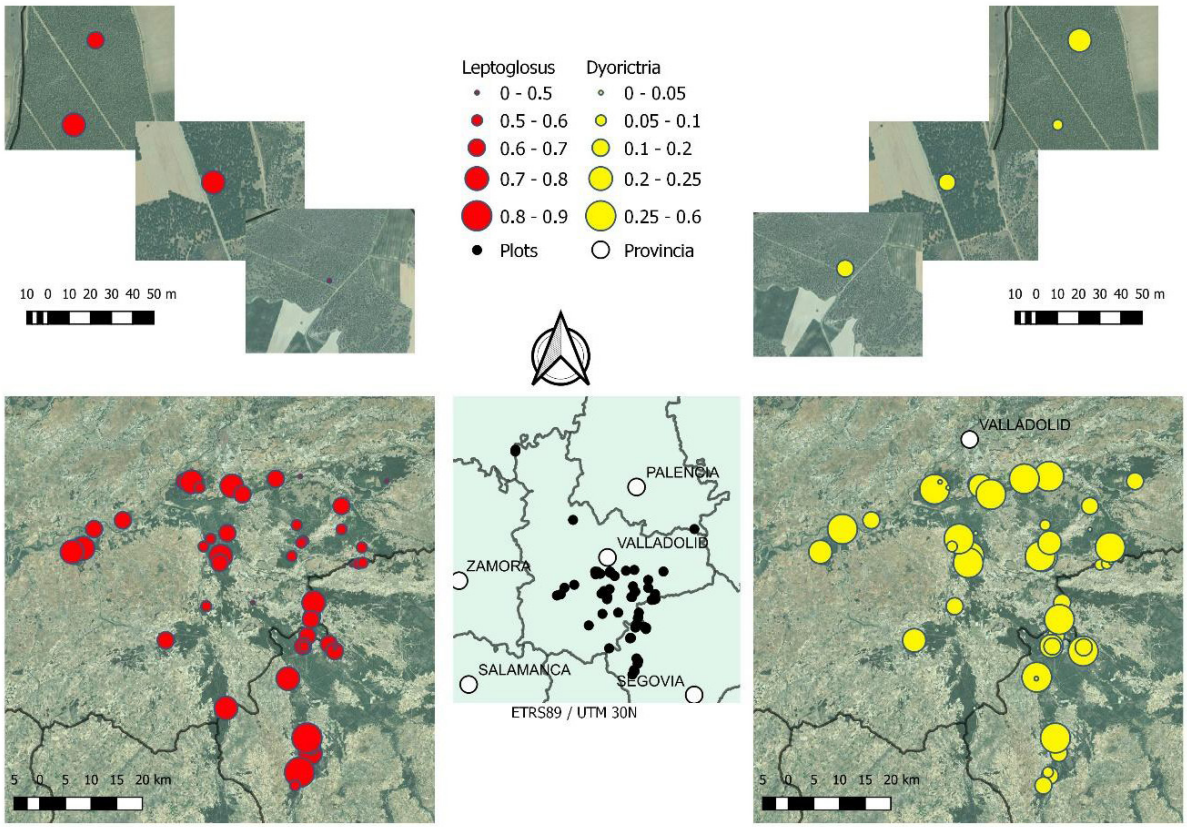

Figure 4. Rates of severity at regional scale due to *Leptoglossus occidentalis* (left) and *Dioryctria mendacella* (right). Size of the circles indicates severity of the damage (note that different scales are used for both pests). Squares in the upper part of the figure represent isolated plots in the map.

From a temporal point of view, we observed (Figure 5) than within the nine-year period 2013 – 2021 *Dam_WCSB* has reached all the years mean values over 40%, with maximum values over 80% in 2017 and 2019, with a clear increasing trend between 2012 and 2019, and reduced values in the last two years of the series. On the contrary, *Dam_PCM* showed a clear decreasing trend through the analysed period, starting with a rate of damage over 40% pf the cones, and ending below 10%. Not clear pattern of relation was observed neither between both rates of damage nor between rates of damage and the total number of cones in the hectare (Figure 5).

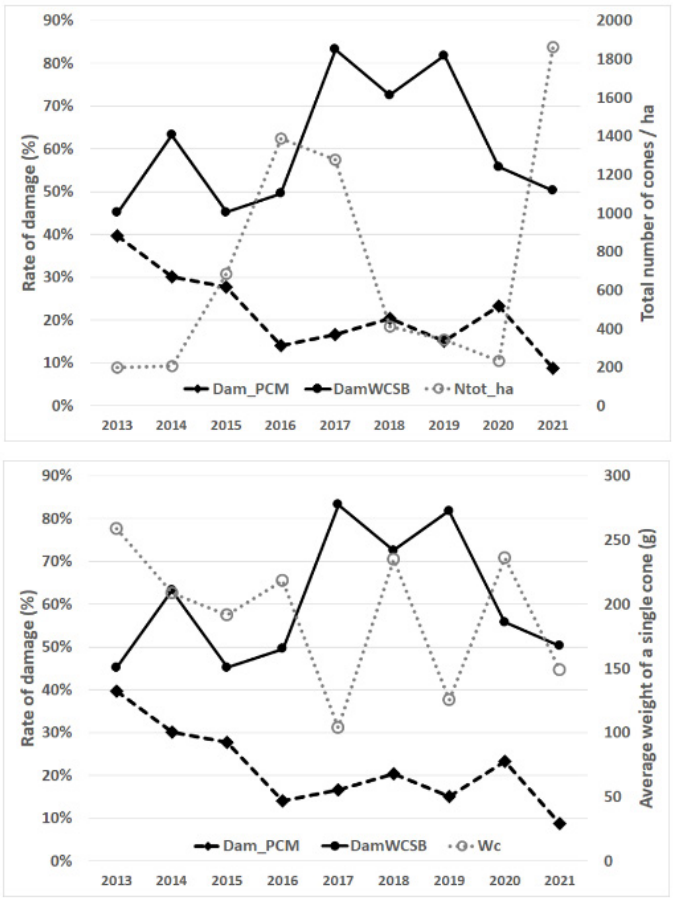

Figure 5. Annual pattern of rate of damage due to pine cone moth (dashed line) and western conifer seed bug (solid line), plotted against total number of cones per ha (above, dotted line) and average weight of a single cone (below, dotted line). Abbreviations in figures as stated in table 1.

However, a significant positive relationship existed between *Dam_PCM* and the average weight of a single cone, while negative relationship existed between *Dam_WCSB* and the average weight of the cones. In this sense, the maximum rates of damage due to WCSB were found in those years (2017 and 2019) where average cone weight was over 140 g.

3.2. Correlation analysis

The correlation analysis between the arcsin root transformed *Dam_PCM* and *Dam_WCSB* and the different predictors (Table 1) evidenced the existence of several significant correlations. Focusing on plot level attributes, both *Dam_PCM* and *Dam_WCSB* showed the largest correlation (r: 0.10 – 0.12, p-value approx. 0.05) with stand age. Both rates of damage showed significant (p-value < 0.01) correlation with the average weight of a single cone (Wc), as well as with the number of pines per cone and per kilograms of fresh cones. Surprisingly the sign of the relationship is opposite, with *Dam_PCM* showing a positive significant correlation with the three indicators of cone yield, while *Dam_WCSB* showed a highly significant (p-value <0.0001) negative correlation with the same indicators. Total number of cones cropped in the hectare showed a negative correlation with both *Dam_PCM* and *Dam_WCSB*, but was only slightly significant (p-value = 0.0587) for the later one, while the number of cones collected in the previous year showed a positive significant correlation also with *Dam_WCSB*. With respect to the current and past severity of the pests, we observed that the current rate of damage due

to PCM positively correlated with the total weight of cones affected by the pest in the current and the previous year. On the other hand, the current rate of damage due to WCSB was positively correlated with the rate and the total weight of pine nuts affected by the pest in the previous year. Focusing on significant interactions between the two pests, we observed that both rates are slightly (p-value = 0.0652) negatively correlated (r = -0.1126). Moreover *Dam_WCSB* is negatively correlated (p-value = 0.0156) with the *W_PCM*, the weight of cones per ha affected by pine cone moth in the year, while slightly positively correlated (p-value = 0.0833) with the same trait but occurring in the previous year.

Concerning the effect of climate variables on the rate of damage (Suppl. Table S1) we identified a highly significant negative correlations between *Dam_WCSB* and winter, spring and annual cumulative amount of rainfall, as well as with Martonne index, indicating that the larger the amount of rainfall, the lower the rate of damage. On the other hand, increasing rates of *Dam_WCSB* are highly significantly correlated (p-value < 0.0001) with rising maximum and mean temperatures during winter, spring and fall seasons (as well as with mean annual temperature), but no with summer temperatures. This indicates that the rising temperatures in winter and spring may increase rate of damage by WCSB. With respect to rate of damage by pine cone moth, no relations with climate traits are identified.

Table 1. Correlation coefficients (and associated p-value in italics) between the rates of damages due to pine cone moth (Dam_PCM) and western conifer seed bug (Dam_WCSB) and different predictors representing plot attributes, crop characteristics and severity of pests. Shaded cells indicate significant (p-value < 0.05, grey) or slightly significant (p-value < 0.1, cream) correlations

Type	Predictor	Dam_PCM	Dam_WCSB	Type	Predictor	Dam_PCM	Dam_WCSB
Plot_level	N	-0.0459	-0.0233	Severity	Dam_PCM		-0.1126
		0.4657	*0.6703*				0.0652
Plot_level	T	0.1249	0.1028	Severity	Dam_WCSB	-0.1126	
		0.0463	*0.0595*			*0.0652*	
Plot_level	BA	0.0121	0.0151	Severity	W_PCM	0.2199	-0.1543
		0.8478	*0.7818*			*0.0004*	*0.0156*
Plot_level	dg	0.1203	0.0625	Severity	W_WCSB	-0.0900	-0.1344
		0.0551	*0.2524*			*0.1600*	*0.0355*
Plot_level	SDI	0.0115	0.0760	Severity	Dam_ PCM_t-1	0.0326	0.0453
		0.8555	*0.1641*			*0.6168*	*0.4282*
Plot_level	H	0.1106	0.0576	Severity	Dam_ WCSB_t-1	0.0507	0.2359
		0.0780	*0.2915*			*0.4422*	*<0.0001*
Crop	Wc	0.2089	-0.3580	Severity	W_PCM_t-1	0.1268	0.0988
		0.0005	*<0.0001*			*0.0507*	*0.0833*
Crop	Ntotal	-0.0831	-0.0992	Severity	W_ WSCB_t-1	0.0079	0.1973
		0.1658	*0.0587*			*0.9051*	*0.0006*
Crop	NPPC	0.1525	-0.3995				
		0.0123	*<0.0001*				
Crop	NP_KGC	0.1959	-0.2422				
		0.0015	*<0.0001*				
Crop	Ntotal_t-1	0.0835	0.1373				
		0.1993	*0.0159*				
Crop	Wc_t-1	-0.1015	0.0463				
		0.1635	*0.4978*				

Note: BA (Basal area), Dam_PCM (rate of severity due to pine cone moth), Dam_WCSB (rate of severity due to western conifer seed bug), dg (mean squared diameter), H (mean height), N (stand density), NPPC (Number of pine nuts per cone), NP_KGC (Number of pine nuts per kg of fresh cones), Ntotal (total number of cones per hectare), SDI (Reineke`s stand density index), T (stand age), Wc (average weight of a single cone), W_PCM (weight of cones per ha affected by PCM), W_WCSB (weight of pine nuts per ha affected by WCSB, t-1 refers to the same variable measured in the previous year.

3.3. Sequential process for individual model construction

Based on the previous findings on correlation (Table 1 and Suppl. Table S1), we started the sequential procedure for both rates of damage by, in a first step, entering the weight of a single cone (Wc) as a potential predictor. We prioritised this covariate since it is the crop related predictor showing largest correlation with both severities. Since previous knowledge about this variable pointed to a high correlation with annual rainfall (Calama et al., 2011), we decided to include both predictors in the first step, with annual rainfall acting as an exogenous factor, and weight of a single cone as an endogenous one.

The sequential process of model construction (see Table 2) for each of the two response variables resulted in a set of common predictors. Stand age enters the models in a second step, directly affecting the rates of damage, but also indirectly affecting through the weight of cones. The total number of cones collected in the hectare in the current year entered in the next step, directly affecting with a negative sign both rates of damage. In the subsequent step the proxy of the total weight of cone or pine nut affected by the own pest in the previous year entered the models with a positive sign. In the final step a thermal covariate entered as a predictor in the models with a positive sign, being in the case of *Dam_PCM* the maximum temperature in spring, while in the case of *Dam_WCSB* is the mean temperature of fall season.

Table 2. Sequential procedure for the individual structural equation modelling (SEM) construction for each of the response variables. Abbreviations for the variables as shown in Table 1

Response variable	Step	Exogenous					Endogenous	ECVI	R^2
Dam_PCM	1	pp_annual					Wc	0.0451	0.0442
	2	pp_annual	T				Wc	0.0833	0.0848
	3	pp_annual	T	Ntotal			Wc	0.1541	0.1342
	4	pp_annual	T	Ntotal	W_PCM_t-1		Wc	0.2590	0.1357
	5	pp_annual	T	Ntotal	W_PCM_t-1	t_max_spring	Wc	0.3392	0.1670
Dam_WCSB	1	pp_annual					Wc	0.0469	0.1308
	2	pp_annual	T				Wc	0.0866	0.1453
	3	pp_annual	T	Ntotal			Wc	0.1585	0.1868
	4	pp_annual	T	Ntotal	W_CSB_t-1		Wc	0.2449	0.2039
	5	pp_annual	T	Ntotal	W_CSB_t-1	tm_fall	Wc	0.3492	0.2839

The final structure of each individual model (see Suppl. Figure S1) showed that stand age exerted a direct, positive and significant effect over the severity of both pests (p-value 0.0056 and 0.0253 for Dam_PCM and Dam_WCSB respectively), irrespectively of the indirect effect through the weight of cones. On the contrary, in the case of annual rainfall, we observed that the direct effect over *Dam_PCM* was only slightly significant (p-value 0.0568), while for *Dam_WCSB* was not significant (p-value 0.3861). This finding indicated that the effect of annual rainfall on the rates of damage was mainly mediated through the impact of rainfall on the average weight of a single cone.

3.4. Complete model construction: testing for dependence among the two pests

The final joint path analysis model included the same endogenous and exogenous variables as the independent path analysis models, together with *W_PCM_t-1* and *W_WCSB_t-1* acting as predictors of *Dam_WCSB* and *Dam_PCM* respectively, and the correlation between *Dam_PCM* and *Dam_WCSB*.

Our final model (Figure 6) evidences that the average weight of a single cone (Wc) exerts a significant effect on *Dam_PCM* (p-value = 0.0003, positive) but not a significant effect on *Dam_WCSB* (p-value = 0.1451). Both annual rainfall (positive) and stand age (negative) significantly influences (p-values < 0.0001) the weight of a single cone *Wc*. However while stand age significantly and positively influences *Dam_PCM* (p-value = 0.0105) and *Dam_WCSB* (p-value = 0.0276), irrespectively of the mediation of *Wc*, annual rainfall *per se*, and independently of its impact on the average weight of a single cone, has no significant effect on the rate of damage by neither *PCM* (p-value = 0.1977) nor *WCSB* (p-value = 0.3883). The total number of cones per ha (Ntotal) has a negative and significant effects over both rates of damage (p-value < 0.0001 for Dam_PCM and 0.0047 for Dam_WCSB). Meanwhile, the selected thermal predictors have a positive and significant effect over the rates of damage (t_max_spring for Dam_PCM, p-value 0.0025 and tm_fall for Dam_WCSB, p-value < 0.0001).

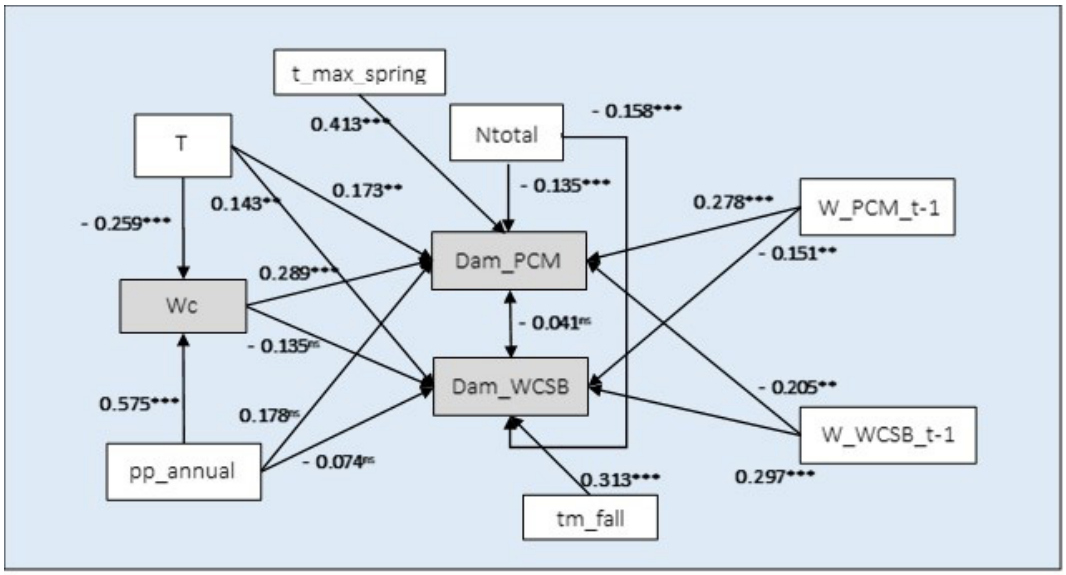

Figure 6. Final structure for the selected Structural Equation Model for both Rate of Damage due to pine cone moth (Dam_PCM) and due to western conifer seed bug (Dam_WCSB). Arrows show the direction of the relation between variables, and the number the standardized parameter for the relation. Shaded cells represent endogenous variables and empty cell exogenous ones. *** p-value < 0.01, ** p-value < 0.05, * p-value < 0.10, ^{ns} non-significant. Abbreviation are: Dam_PCM (rate of severity due to pine cone moth), Dam_WCSB (rate of severity due to western conifer seed bug), Ntotal (total number of cones per hectare), pp_annual (annual mean precipitation), T (stand age), tm_fall (mean temperature in fall season), t_max_spring (mean value of maximum temperatures in spring), Wc (average weight of a single cone), W_PCM_t-1 (weight of cones per ha affected by PCM in the previous year), W_WCSB_t-1 (weight of pine nuts per ha affected by WCSB in the previous year).

The past severity of both pests (approached by means of the total weight of cones affected by PCM or the total weight of nuts affected by WCSB) was significantly and positively correlated with the current rate of damage of the own pest (p-value = 0.0013 for both PCM and WCSB). Surprisingly, there exists a negative and significant correlation (p-value = 0.0363) between the past incidence due to WCSB (W_WCSB_t-1) over the current rate of damage due to PCM, as well between the past incidence due to PCM (W_PCM_t-1) and the current rate of damage due to WCSB (p-value = 0.0387). Finally, no significant direct relation was observed between both rates of damage (r = -0.041, p-value = 0.4610). Goodness of fit statistics of the complete model are presented in Table 3. R^2 for both rates of damage, as well as ECVI showed larger values than those obtained in the independent fit of the individual models (see Table 3). With respect to the rest of indices, both GFI and NFI showed values > 0.95, which is considered as a threshold for well-fitting models, as in the case of SRMR, which showed a value < 0.05. In the case of RMSEA we obtained a value of 0.1119, slightly over the threshold value of 0.10, fixed for fait fit of the model (Hooper et al., 2008).

Table 3. Values for the goodness of fit statistics of the final complete model

Statistic	Value
R^2 Dam_PC	0.1810
R^2 Dam_WCSB	0.2868
ECVI	0.9605
GFI	0.9793
RMSEA	0.1119
SRMR	0.0375
NFI	0.9712

4. DISCUSSION

4.1. Spatial and temporal patterns of severity

Our study evidences that both pests have a significant influence over the total amount of cones and pine nuts yielded every year in the Northern Plateau. The pine cone moth is responsible for the loss of approximately the 20% of the cones, while the WCSB may be attacking 60% of pine nuts in the healthy (non-attacked by the PCM) cones. However, it is important to note that, because damage caused by WCSB cannot be reliably distinguished from that induced by other agents producing partially overlapping symptoms in pine nuts, this estimate may be inflated. Focusing on the distribution of the damage, PCM showed a left-assymetric distribution, indicating that the main part of the stands showed lower rates of damage. On the contrary, WCSB showed high rates of severity (Dam_WCSB > 0.30) through the studied territory, with very few locations with no affection. Focusing on a temporal perspective (figure 5), rate of damage due to WCSB has experienced a generalized increase through the studied period, while rate of damage due to PCM has experienced the opposite trend. This differential spatial and temporal patterns on the severity of the attack due to both pests may indicate that WCSB, as a recent exotic invader, is still experiencing an expansive phase, with no control or regulation from native biotic agents. On the other hand, PCM, as a native pest of the cones, is expected to show more stability in the rate of damage, with punctual events of population increase (Aukema et al., 2008).

4.2. Insects select cones based on the cone size

In our study, a significant positive relationship was observed between the damage produced by PCM and the average weight of a single cone, while a non-significant relationship was found between damage by WCSB and the average weight of the cones. Larger *P. pinea* cones are generally more susceptible to damage by PCM, with increased cone size attracting more pests and leading to greater seed loss. However, the extent of damage is also shaped by other factors, such as chemical cues, and environmental factors, making the relationship complex (Blatt et al., 1999; Richardson et al., 2017). Previous studies agreed that the probability and extent of PCM damage are strongly linked to the overall cone crop size in a given year, with larger crops supporting higher pest populations and more widespread damage (Calama et al., 2017).

In our study, we observed a negative but non-significant relationship between cone weight and the damage caused by WCSB, with smaller cones experiencing greater damage. This finding differs from previous research, especially with Richardson et al. (2017), who reported that WCSB was more frequently found on clones with larger and heavier cones, suggesting a stable preference for larger cones across years. The insect typically prefers trees with moderate cone loads and larger cones, avoiding both small trees with few cones and very tall trees with high cone density (Blatt et al., 1999). Other studies have also related larger cones with increased susceptibility to partial kernel damage (Loewe-Muñoz et al., 2021).

Our findings challenge the pattern previously observed in the literature. One possible explanation is that smaller cones may offer less physical protection or have thinner scales, making the kernels more accessible to the insect's feeding apparatus. Alternatively, smaller cones might mature earlier or exhibit chemical profiles that are more attractive or less deterrent to WCSB under the specific environmental conditions of our study area. These results suggest that host selection behaviour may be more flexible than previously assumed and influenced by chemical traits, ecological or genetic factors. Host selection by WCSB has shown to depend on chemical cues such as monoterpene composition, particularly levels of α-pinene, δ-3-carene, and limonene (Richardson et al., 2017). Volatile compounds were not analysed in our study, conforming a proposal with high potential for future studies.

4.3. Annual rainfall indirectly affects but temperature directly affects the rate of severity for both pests

Precipitation does not directly influence the damage caused by either PCM or WCSB on *P. pinea* cones. Its role is primarily indirect, through its effect on cone size and production, which can influence pest damage levels in a given year (Calama et al., 2017; El Khoury et al., 2021; Farinha et al., 2021). Pest dynamics and damage are more closely associated with cone availability, temperature, and previous pest abundance than with precipitation itself (Farinha et al., 2018). At a broader scale, precipitation can affect insect outbreaks by modifying forest composition. For instance, higher rainfall may promote the growth of non-host species, reducing defoliator outbreaks through associational resistance (Haynes et al., 2022).

Precipitation also interacts with other climatic variables, particularly temperature, influencing population dynamics and outbreak potential (Gely et al., 2019; Frank, 2020). These effects vary depending on insect feeding guilds, host species, and forest types (e.g., mesic vs. xeric) (Jactel et al., 2012; Gely et al., 2019). Experimental studies confirm that reduced precipitation (simulated drought) leads to higher insect attacks and mortality in drought-sensitive tree species, such as pinyon pines, but not always in more drought-tolerant species, such as junipers (Gaylord et al., 2013). Although temperature often shows a stronger correlation with long-term insect damage trends, precipitation remains a relevant factor, especially in shaping host tree communities (Haynes et al., 2022).

On the other hand, we observed that temperature played a significant role in the damage caused by both pests on the cones. Higher temperatures are related to increased pest damage and reduced cone production, since the insects have more time to be active and therefore to feed on the cones. Previous studies suggested that PCM presents a first annual generation completed in early summer, with a subsequent second, or even third generation completed in early autumn and/or with overlapping generations also possible (Naves et al., 2023). Furthermore, it has a flight period extending for more than eight months that can be prolonged if the temperature rises. In this sense, the positive relationship between damage by PCM and the maximum temperatures of spring may indicate earlier completion of the first generation and more likely second and third generations of the insect.

Wester conifer seed bug damage has previously shown seasonal patterns in damage affecting cone development (Ponce-Herrero et al., 2024). In agreement with our results, higher temperatures, especially during key periods of cone development, are linked to increased WCSB damage. The combined stress of pest invasion and warming climate appears to drive these negative trends. After 2012, when both the invasion by WCSB and higher temperatures were observed, cone production dropped by 50%, and the percentage of damaged seeds rose from 3% to 60%. The data suggest that higher temperatures may exacerbate the impact of the insect, leading to more severe damage to pine cones (El Khoury et al., 2021). Finally, male pine strobili are warmer and more reflective than cones and needles, potentially attracting WCSB, which receive more heat when sucking from male cones (Kitajima et al., 2022).

The expected future scenarios of joint occurrence of drier and warmer climate conditions in the region, with forecasted increase in 3 ºC in mean temperatures and more frequent droughts out of summer period (Bravo et al., 2022) may lead to a significant reduction in the total amount of available cone and pine nuts due to the incidence of the pests. According to the constructed Structural Equation Model, increasing spring and fall temperatures may positively influence the rate of damage for both pests. This effect is aggravated under the reduced annual cone crops expected under these climate scenarios (Calama et al., 2011). In addition, under warmer and drier conditions the cones tend to be of smaller size, which may result in smaller rates of damage due to PCM but larger rates due to WCSB.

4.4. Stand age matters: older pinewoods are more vulnerable to cone damage

In our study, stand age had a direct effect independent of cone size, with older pine stands experiencing higher levels of damage from both pests. To our knowledge, there is no direct evidence linking stand age to increased susceptibility to cone damage in pines. However, older stands are known to be more vulnerable to other stressors such as bark beetle infestations, drought-induced mortality, and growth decline (Socha et al., 2023; Li et al., 2024).

Furthermore, forest structure—encompassing factors like tree diversity, age, vertical layering, and canopy openness—has a significant and multifaceted influence on insect communities. Considering forest structure, previous research showed that WCSB caused less seed damage in mixed-species plots than in pure pine stands. While pine density and relative proportion in mixtures had no significant effect, seed damage was higher in aggregated pines than in dispersed ones, suggesting that the insect may inflict less damage when host trees are harder to locate (Farinha et al., 2024).

4.5. Impact of resource availability and previous damage

In our study, we observed that the total number of cones per ha had a significant and negative effect on the severity of damage of both pests. This indicates that the higher the resource availability (larger cone crops) the lower the severity of the damage by WCSB and PCM. This can be explained by the existence of a pest preference for certain host traits, which are more likely to occur in years with larger crops, as well as by resource dilution effects, which occurs when an increase in cone abundance outpaces the increase in the capacity of insects to attack cones (Turgeon et al., 1994).

Our results are also in clear agreement with the predator-satiation hypothesis (Bogdziewicz et al., 2020). This hypothesis postulates that masting behaviour– defined as the synchronous pattern of interannual variability in fruit and seed production – is a mechanism aiming to starve predators in low crop years, in order to maintain low levels of population. This will ensure that a relevant number of fruits/seeds may escape for predation (and thus permits regeneration of the plant species) in bumper crop years. The coevolution between *P. pinea* and the native PCM*,* together with the inherent cycles of cone crop size – rate of severity – population dynamics already described in Calama et al. (2017) and Bogdziewicz et al. (2020) support this hypothesis. In the case of the recent feeder WCSB, we hypothesize that insect population cycles may not be still well adapted to the masting habit of the pine.

In addition, we have found a positive correlation between the severity of each of the pest in the previous year *t-1* (defined by the weight of cones or pine nuts affected by hectare, W_PCM_t-1 and W_WCSB_t-1) and the rate of damage in the current year *t*, indicating that the larger the previous year pest incidence, the higher the current year rate of damage. These results have been also previously observed for PCM (Calama et al., 2017) and WCSB (Farinha et al., 2021). One possible explanation is given by the slow maturation process of the cones, which means that the same cone may be exposed to the insects for two to three years, resulting in an accumulation of damage which is difficult to track (Farinha et al., 2018). Another possible explanation is that the weight of damaged cones in the previous year due to a given pest can be seen as a proxy of the insect population in that year, which is the starting point for the next generation of insects that will affect the current year cone crop (Aukema et al., 2008; Zhu et al., 2008). However, this potential explanation has not been tested given the lack of

reliable monitoring systems (pheromone or traps) for both pests up to recent years (Hall et al., 2017; Millar et al., 2022).

4.6. Interaction between pests

Our study found that the severity of a pest outbreak in one year can reduce the impact of another pest on the same host tree the following year. However, we did not observe a significant relationship between the damage caused by both pests within the same year. This pattern aligns with research showing that herbivores often interact indirectly through mechanisms such as resource depletion, induced plant defenses, or altered ecosystem conditions (Castagneyrol et al., 2021). Early herbivory can deplete plant biomass (exploitative competition) or trigger hormonal responses that lead to the production of anti-herbivore defences and resource reallocation within the plant (Hilker & Fatouros, 2015). These changes typically reduce plant quality and, consequently, the performance of later-arriving herbivores (Abdala-Roberts et al., 2019). Such interactions have been documented in both inter- and intraspecific contexts (Moreira et al., 2018). Although less common, facilitative effects have also been reported, where early herbivory increases susceptibility to later pests (Sarmento et al., 2011). These findings underline the importance of considering multi-pest interactions and temporal feedbacks in forest pest management, as early infestations can have cascading effects on future herbivore dynamics and forest health. Nevertheless, it is important to reiterate a key limitation of our approach: simultaneous damage by PCM and WCSB within the same cone cannot be detected, which may introduce some bias in estimating the interaction between the two pests in a given year.

4.7. SEM approach in testing complex insect-host dynamics: utility and limitations

The application of SEM to this case study made it straightforward to quantify the correlation between the different variables considered. These results provided meaningful and interpretable insights on the complex interactions involved. The main criticism is, however, that by relying on expert knowledge to establish the network of interactions, one may unknowingly be altering the results according to one's biases (Tarka, 2018). We believe that this risk is minimized since the assumed relations are based in existing scientific literature. In addition, all our variables are observed, i.e., none of them is latent. Latent variables are common in social science studies, where abstract concepts cannot be measured (Hair et al., 2021) and are instead linked to observed variables thought to either cause them or be their result. The fact that we did not need this extra layer of complexity adds, under our point of view, robustness to our results.

Other static approach to address the problem presented here could have been the so-called seemingly unrelated regression (SUR) (Gallant, 1987). SUR is a form of advanced regression where several responses are modelled simultaneously. Each response is explained by a specific set of parameters and predictors, with the responses possibly being each other predictors. Such a system is extremely useful when stochastic predictions of the processes at hand are necessary, and it is not a surprise that SUR is so common in the forestry biometrics literature (Vonderach et al., 2018; Manso et al. 2020a). However, the main drawback of SUR if compared with SEM approach is the need to interpret the relationships and interactions between variables in the light of the covariance matrices of the residuals and the parameter estimates, which is not always clear (Manso et al., 2020b). In systems as complex as the one studied here, where we mostly aimed at an exploratory analysis of the data, SEM is clearly a more suitable technique.

5. CONCLUSIONS

Both the exotic *Leptoglossus occidentalis* and the native *Dioryctria mendacella* have a significant and negative effect over the total amount of available pine cone and nut, which may be aggravated under future climate scenarios. The rate of severity of each pest depends on different exogenous – climate, stand age – and endogenous – cone crop size and single cone weight – controlling factors. Complex temporal interactions between the rate of severity between the pests and within the same pest were also identified. This may have severe ecological and economic implications, potentially affecting the

natural regeneration of the stands, but also the economic expected revenue to forest owners, cone collectors and pine nut processing industries. In addition, our findings permit to propose an adaptive silviculture aiming to maintain a balanced age structure and promote high individual cone production by applying early and intense thinning. Enhanced individual-level and stand-level productions may mitigate pest impact through resource-dilution effect.

The use of SEM permitted us to give insight into the complex dynamics of both pests, but we must acknowledge once again the limitations of our approach. The first one is that given the lack of reliable methods for monitoring the population of both species, we have used the rate of severity as a proxy for population size. The second is the assumed no-occurrence of both pests in the same cone, which may lead to some biases in the interpretation of the results. Future research should focus on solving these limitations by deepening into the knowledge of the ecology of both insects, developing methods for accurate monitoring and control of both exotic WCSB and native PCM, and testing the impact of other silvicultural options (e.g. increasing diversity of pinewoods by promoting mixtures) on buffering the pressure of both pests.

Supplementary information ↑

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Supplementary material

Annex I, Table S1, and Figure S1 accompanies the paper on *Forest System´*s website.

Data availability

Data used in this work are available at Zenodo public repository https://doi.org/10.5281/zenodo.15862935

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Authorship contribution statement

Rafael Calama: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Resources, Methodology, Project administration, Writing – original draft.

Carmen Romeralo: Conceptualization, Formal analysis, Investigation, Resources, Visualization, Writing – review & editing.

Rubén Manso: Conceptualization, Formal analysis, Methodology, Resources, Writing – review & editing.

Guillermo Madrigal: Data curation, Methodology, Resources, Visualization, Software, Writing – review & editing,

Javier Gordo: Conceptualization, Funding acquisition, Investigation, Resources, Writing – review & editing.

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Competing interests

The authors have declared that no competing interests exist.

Statement on the use of Artificial Intelligence

Not applicable.

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