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Tree canopy patterns in a temperate forest in Oaxaca, Mexico after bark beetle outbreaks: Implications for ecological resistance and resilience

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A B S T R A C T

Bark beetles (BB) are an insect that can become a forest pest and that principally affects temperate regions globally, massively killing tree hosts, mainly coniferous species. When tree hosts are the dominant species in the canopy, BB outbreaks may impose important changes in the structure, composition and diversity of forests, from the stand to the regional scale. In Mexico, during the current century, BB pests have become the main biotic threat in forests where *Pinus* species are dominant. Questions addressed in this study are: What is the structure, composition and diversity of the forest canopy after BB disturbances? and "What are the implications for ecological resistance and resilience of the forest"? The study site was located in the Sierra Norte region in Oaxaca, Mexico, where more a decade ago BB outbreaks affected the forest. In ninety plots of 500 m^2 (4.5 ha) all live trees with $\geq$ 5 cm diameter at breast height (DBH) were located, their DBH was measured, and the species was identified. As well, all stumps resulting from previous sanitation logging and timber extraction (TE) were located and for each condition, basal diameter was estimated and the genera identified. For the post-disturbance canopy, density basal area, species composition and diversity (alpha and beta) were estimated. This data plus the analysis of the stumps was used to estimate the tree canopy structure before the BB outbreaks. Statistical comparisons among BB, TE disturbances and condition without disturbance were conducted. Based on interviews with local experts, a rank of risk to BB among *Pinus* species was established. A total of 4,053 live trees and 547 stumps were found. The live trees corresponded to 24 species from 8 genera. *Pinus* genus and, particularly *P. patula* predominated. Seventy-five percent of the individuals had $<$ 20 cm DBH and a J-inverted diametric distribution resulted. Individuals with DBH $\geq$ 100 cm were found only in the condition without disturbance. Three of the nine *Pinus* species, were BB main-host species, and the least preferred host was *P. ayacahuite*. The three BB main-host species dominated the post-disturbance canopy (including regeneration). In contrast, *P. ayacahuite* and other non-host tree species dominated in the conditions without disturbance, and the three main-host species showed low density. As well, high species richness occurred in areas affected by BB. Since climate change will likely continue to exacerbate BB outbreaks, it is proposed that to increase ecological resistance and resilience forest management practices should focus on reducing density, promoting a mix of host and non-host species, increasing tree diversity and avoiding stands with monodominance of main-host species.

1. Introduction

Forests are dynamic, even if some changes in structure and species composition can be almost imperceptible (Jõgiste et al., 2017). However, when biotic and abiotic disturbances cause massive and extensive tree mortality, tree canopy characteristics can be modified, sometimes in a very short time period (Meigs et al., 2017; Raffa et al., 2008). As an example, bark beetles pests (BB; Coleoptera: Curculionidae) are disturbances that can transform large stands in temperate landscapes (Bentz et al., 2010; Hlásny et al., 2019). These disturbances, depending on their intensity, may affect structural and functional features of forests (Audley et al., 2020; Fettig et al., 2019; Meigs et al., 2017). Because BB coevolved in host-plant interactions with conifers since the Cretaceous period (Labandeira et al., 2001; Wood, 1982), they are natural components of temperate forests and are a factor in continuous forest renewal (Biedermann et al., 2019; Cervantes-Martínez et al., 2019). However,

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there are a group of BB known as “primary pests” that in epidemic conditions may massively kill healthy trees (Gómez-Pineda et al., 2022). As a result, when BB kill their host trees, it opens gaps in the canopy, creating regeneration patches and offering opportunities for the establishment of different species (Collins et al., 2011; Kayes and Tinker, 2012).

In recent decades, forests in Asia, Central America, Europe and North America, where coniferous trees are dominant, have registered explosive BB population growth (Axelson et al., 2018; Janda et al., 2017; Kamińska et al., 2021; Nagel et al., 2017). The main reason proposed for this increase are climate change disruptions, including high temperatures and drought, as well as warmer winters (Weed et al., 2013; Fettig et al., 2022a). These factors are affecting the physiology of the host trees (hydric stress) and are modifying BB development cycles (Bentz et al., 2010; Gómez-Pineda et al., 2022; Hlásny et al., 2019). However, a more integral perspective has suggested that in addition to the biotic and abiotic drivers that govern the BB system, there are some forest management practices that can contribute to outbreaks (Biedermann et al., 2019; Windmuller-Campione, 2018). Until recently, climate change scenarios have not been taken into account in management and normally forest management for timber extraction has focused on few species (including BB hosts species). These factors can modify the structure, species composition and diversity in the tree canopy in ways that can exacerbate BB impact under certain species dominance or density conditions, among other tree canopy characteristics (de Groot et al., 2019; Hood et al., 2016; Hlásny et al. 2019; Monarrez-Gonzalez et al., 2020).

The effect of BB outbreaks on the tree canopy depends on the capacity of the forest to absorb a certain amount of disturbance or its ecological resistance –the aptitude to repel disturbances and to remain essentially unchanged- (DeRose and Long, 2014) and its ecological resilience –the capacity of the forest to recover following a disturbance- (Holling, 1973). After BB disturbances, resilient forests may be able to display rapid recovery of forest cover and ecological functionality through natural regeneration and the survival of both host and non-host species (Schmidt, 2021). The biological legacies of BB outbreaks may include a renewed and vigorous post-disturbance tree canopy with different ages and changes in the prior tree density and species dominance (Diskin et al., 2011; Jõgiste et al., 2017). However, when ecological resistance and resilience are insufficient, BB outbreaks may scale-up and cause severe disruptions and may contribute to other disturbances such as fires (Billings et al., 2004; Fettig et al., 2022b; Seidl et al., 2016). As well, BB pests may have social and economic impacts since its main-host coniferous species are commonly economically important for the timber industry (Biedermann et al., 2019; Morris et al., 2017). BB outbreaks may also affect the provision of ecosystem goods and services and climate change mitigation (Dhar et al., 2016; Leverkus et al., 2021). It can also have negative effects for the ecotourism and outdoor recreation industries (Hlásny et al., 2019; Qin and Flint, 2017). For these reasons, efforts to prevent and control BB outbreaks are urgent. When the disturbance happens, one widely recommended strategy is sanitation logging (Hlásny et al., 2019; Pacheco-Aquino and Duran, 2021); which is a physical–mechanical management practice to remove BB infected trees and avoid the spread to other tree hosts. It consists of the felling of the infested tree (when there are stages of egg, larva and pupa) and debarking of the trunk, with this material then being buried, burned or sprayed with insecticides (Ringle, 1940; DOF, 2008; Durán and Poloni, 2014). This practice could also diminish risk of catastrophic fires, by reducing the fuel load, and the risk of falling trees during windstorms (DOF, 2008). In some cases, the wood obtained from sanitation logging may help to recover economic losses from BB pests (Hlásny et al., 2019). However, it has also been suggested that this practice could be an additional forest disturbance (Leverkus et al., 2021).

The study of forest structure (density and basal area), species composition (particularly presence and dominance of BB host trees) and tree species diversity in the post-disturbance canopy can help to understand the impact of past events (Gadow et al., 2012; Monarrez-Gonzalez et al., 2020). It can also provide a basis for a forest management focus on canopy attributes, which may improve ecological resistance and resilience against BB, at the stand level. Thus, forest management practices could reinforce structural features that reduce competition and improve individual tree vigor (Fettig et al., 2007). They may also influence species composition by reducing the number of main-host species and placing barriers composed of non-host tree species (Pacheco-Aquino and Duran, 2021). These strategies may reduce BB movements in the forest landscape (Hood et al., 2016; Morris et al., 2022; Windmuller-Campione, 2018). It has also been suggested that tree canopy species diversity may inhibit the develop of BB outbreaks (Guo et al., 2019), apparently as a result of a semiochemical effect that reduces the success of insect spread (Jactel et al., 2011; Schiebe et al., 2019).

In Mexico, BB outbreaks (mainly of the *Dendroctonus* genus) have become the principal biotic threat in temperate forests (Soto-Correa et al., 2019), and usually occur in patches of hundreds of hectares or less (Pacheco-Aquino and Duran, 2021; Endara-Agramont et al., 2023), unlike the massive outbreaks in the US West. Official reports say that during the 1996–2018 period, a total 2,040,616 ha of forests were infested by BB outbreaks (SEMARNAT, 2018). The large total number over this long time period is partially explained by the fact that Mexican temperate forests harbor a huge diversity of potential BB tree hosts among the 49 species of the *Pinus* genus (Gernandt and Pérez-de la Rosa, 2014; Soto-Correa et al., 2019). Of the total of 13 species from the *Dendroctonus* genus, three of them (*D. adjuntus, D. frontalis* and *D. mexicanum*) are considered primary pests in Mexico (Armendáriz-Toledano et al., 2015; Salinas-Moreno et al., 2010). For many decades, silvicultural practices have intentionally encouraged pine regeneration to improve the economics of timber extraction (Plancarte, 2014; Torres-Rojo et al., 2016). This is the case for the study zone in Oaxaca, where *P. patula* (important for commercial timber extraction) is abundant, despite the fact that it is the most impacted species by the most present BB species*, D. adjuntus*.

Although BB outbreaks are not a new phenomenon in Mexico, they are occurring at higher rates in both managed and unmanaged forests (Gómez-Pineda et al., 2022; Vázquez-Ochoa et al., 2022). Particularly, in unmanaged forests BB outbreaks are likely occurring due to the lack of thinning and other silvicultural interventions and exposure to natural disturbances like fire, wind, and drought. To stay ahead of the problem, Mexican forest health policies promote sanitation logging, removing the affected BB host trees (Pacheco-Aquino and Duran, 2021). Some 60% of Mexican forests are community common properties, a form of corporate ownership by legal community members (Art. 9 in the Mexican Agrarian Law) (Bray, 2020). Mexican Forest Law (Art. 114) makes it mandatory that forest owners must respond to forest threats, so as a result community sanitation logging is widespread in the country. This situation makes it pertinent to analyze BB outbreaks with a social-ecological system approach (SES; Fischer, 2018), where the forest pest is part of the ecological subsystem, with strong interactions with the social subsystem, community forest management.

Analyses of changes in structure and composition in areas affected by extensive BB outbreaks have mostly been carried out in temperate forests in Canada, the United States and Europe (Audley et al., 2020; Crotteau et al., 2020; Diskin et al., 2011; Jonášová and Prach, 2004; Runyon et al. 2020; Shore et al., 2006; Zeppenfeld et al., 2015). However, much less information is available from countries like Mexico, where BB outbreaks cover smaller areas of temperate forests that are usually highly diverse in tree species, and communities have primary responsibility for carrying out BB forest sanitation. Thus, the objective of this paper is to analyze canopy structure, species composition and diversity after BB disturbance in a temperate forest in the particular social and ecological conditions of community forests in Oaxaca, Mexico. We then suggest policies and practices that may strengthen ecological resistance and resilience in the face of BB outbreaks.

2. Methods

2.1. Study site

The study site is the common property community of Pueblos Mancomunados, which includes seven separate human settlements, located in the Sierra Norte region of Oaxaca, Mexico (Fig. 1). The elevation gradient is 1,893–3,300 masl and the climate is temperate sub-humid with summer rains (García, 1988), with a mean annual temperature of 18 °C and mean annual precipitation of 1,000 mm. The prevailing vegetation is temperate forests with dominance of *Pinus*, *Quercus* and *Abies* species (Valencia, 2004). For much of the last century, commercial timber exploitation (unsustainable management focused on maintaining timber volumes), was practiced, first by a private enterprise and later a timber parastatal, both using selective silvicultural practices. Since 1986, commercial timber extraction has been under the control of highly participatory community forest enterprises (Pazos-Almada and Bray, 2018), with forest management plans approved by the government and increasing use of silvicultural practices that favor regeneration of pine (Bray, 2020). The study community has 27,219 ha (Bray, 2016) with 5,217 ha zoned for timber production, 15,537 ha dedicated to conservation and community-based ecotourism, and the remainder in agriculture areas and human settlements. Due to community conflicts over tensions between logging and forest conservation, Pueblos Mancomunados stopped harvesting timber for commercial purposes in 2002. Since then, only sanitation logging has been carried out, as discussed further below, within Pueblos Mancomunados. The study was conducted in the territory managed by one of the seven human settlements, the community of Yavesia (Fig. 1). It was due to protests over logging and sentiment in Yavesia in favor of forest conservation that Yavesia forced the entire community of Pueblos Mancomunados to stop commercial logging, with community agreements focused on conservation and ecotourism (Bray, 2016). However, from 2004 to 2011, the Yavesia community territory was heavily impacted by *Dendroctonus adjuntus* outbreaks, affecting 3,307 ha in dozens of patches, creating an estimated 631,900 m^3 of dead pine wood (Castellanos-Bolaños et al., 2013; Fig. 2). It forced Yavesia for begin in 2007 community sanitation logging to prevent the pest from spreading to surrounding areas (Castellanos-Bolaños et al., 2013). The sanitation logging was carried out with authorization by the National Forestry Commission (CONAFOR) and it was according with the technical guidelines of NOM-019/SEMARNAT, which provides regulations on how sanitation logging should be carried out.

2.2. Establishing sampling plots in disturbance conditions

According to the “natural experiments” approach (Sagarin and Pauchard, 2010) –which are real life phenomena that can be use as “treatments” to illustrate possible effects of forces that alter an ecosystem-, a total of 90 circular sampling plots of 500 m^2 (4.5 ha) were established in forest stands with two different disturbance conditions in recent years (see Fig. 1) and a control group (CG). The sample was stratified regular by three study conditions: 1) with bark beetle outbreaks (BB; 40 plots) and 2) with timber extraction (TE; 40 plots). Additionally, in order to compare results between these two disturbance conditions and forest stands not affected by BB outbreaks, a control group (CG; a condition without disturbance) was established. The CG included only ten plots, because there were a limited number of areas in this condition. The disturbed areas were precisely dated and located because they are registered in official documents from CONAFOR. The documents are: 1) for commercial logging extraction, the Annual Authorization of the Management Plan (*Autorización Anual del Programa de Manejo Forestal)* and 2) for sanitation logging, the Technical Phytosanitary Report” (*Informe Técnico Fitosanitario*). The stands were located

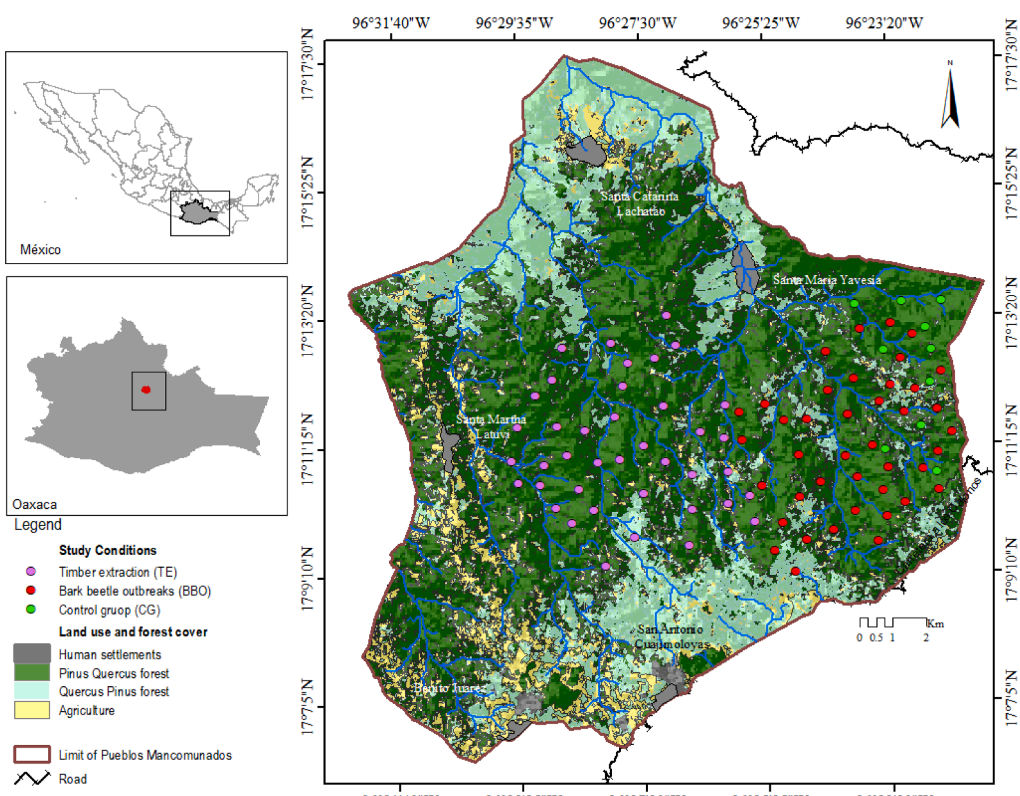

Fig. 1. Map of the study site, showing the distribution of plots by evaluated conditions: Bark beetle (BB) outbreaks, Timber extraction (TE) disturbance and Control group (CG).

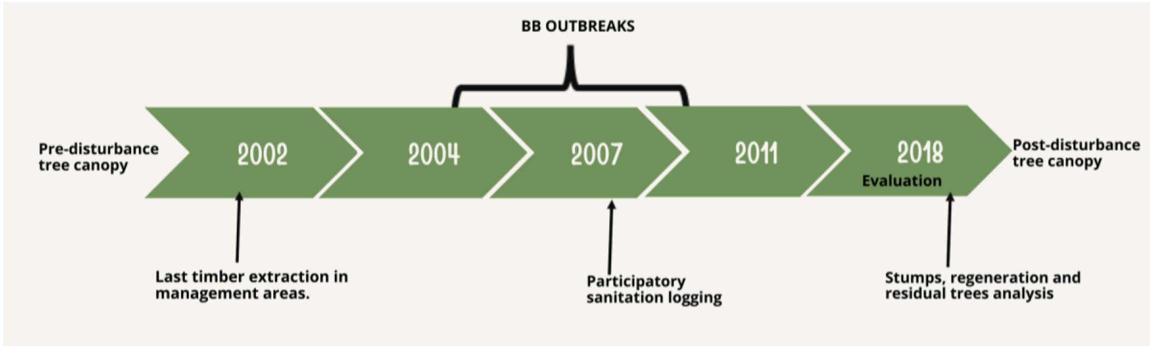

Fig. 2. Timeline for the occurrence of each disturbance, and the date when forest structure and composition were evaluated.

in the field with assistance from a professional forester employed for two decades in the Pueblos Mancomunados community forest enterprise and an experienced local forest expert, a farmer with decades of experience in community logging. The distance among plots was a minimum of 500 m and maximum of 900 m, which is within the BB flight range reported by Jones et al. (2019). It was adopted for this study because there is no information for *D. adjuntus* in the Oaxaca region and other places in Mexico. This reduced spatial autocorrelation, commonly present in BB infestations (de Groot et al., 2019; Kamińska, 2022).

2.3. Structure, composition and diversity

In 2018, for each study condition, the structure, species composition and diversity of the live tree component were evaluated (Fig. 2). All live trees with DBH $\geq$ 5 cm were documented and their local and scientific names were registered in situ. When necessary botanical samples were taken for identification to the Mexican National Herbarium (*Herbario Nacional de México-Instituto de Biologia de la UNAM*- MEXU). Structure included three parameters: DBH distribution, tree density and basal area. In each plot, all live trees with DBH $\geq$ 5 cm were counted, their DBH was measured, and its taxonomic identity established. The basal area was calculated (BA=(πDBHˆ2)/4) for each disturbance condition and the CG. This parameter was calculated individually, and then the BA of all the trees were added to estimate the total BA. The importance value index (IVI) is a structural descriptor for the ecological weight of each species in a mixed tree species stand (Cottam and Curtis, 1956; Khan et al., 2020), and this was estimated as a percentage with the equation IVI = RA + RF + RD, where RA is the relative abundance (number of trees of each species divided among the total number of individuals of all species), RF is the relative frequency (number of plots with trees of one species divided by per the total number of plots), and RD is the relative basal area (basal area of a species divided by area of all species) (Ellenberg and Mueller-Dombois, 1974). The IVI in the discussion was denoted as species dominance (Avolio et al., 2019).

For diversity analysis, the true diversity index ^{q}D (where the exponent q determines the sensitivity of the index to the relative abundances of the species) was used (Jost, 2010; Moreno et al., 2011). Thus, the diversity $q^0 = 0$, where ^{0}D is equal to species richness (the number of species recorded), $q^1 = 1$; where the value represented is an exponential value of the Shannon index ^{1}D = eH', in which each species is weighted according to its proportional abundance (pi) in the community, without favoring rare or common species; $q^2 = 2$ where ^{2}D is the reciprocal of the Simpson index, such that $2D = 1/\lambda$, where the weighted arithmetic mean is used to quantify average proportional abundance, taking into account the common species.

Beta diversity was estimated with the Morisita-Horn coefficient (Magurran, 1988) as follows: $I_{M-H} = 2\sum(an_i \text{x}\, bn_i)/(da+db)aN\text{x}bN$, where$an_i$ = total of individuals of *i*-species in site A, bn_i= total of individuals of i-species in site B, $da = \sum an_i^2/aN^2$, $db = \sum bn_j^2/bN^2$, for each disturbance condition and the control group. This index is influenced by species richness, but is sensitive to the presence of the more abundant species (Magurran, 1988). The similarity among the three conditions was graphically analyzed with a dendrogram, conducted with Past 4.03 (Hammer, 2020).

For the removed trees, the stumps were measured. Since they maintained basic characteristics and were not damaged, and with the help of our local experts, they were clearly measured and identifiable at the genus level (*Pinus* or *Quercus*). Initially, the basal diameter of 30 cm for individual stumps (called basimetric area) was measured, and this data was used for the BA estimations per genera, based on two equations derived from studies for the Sierra Norte region in Oaxaca. For *Pinus*, the model from Quiñónez et al. (2012) was adopted and the individual stump basimetric area was estimated, and then summed. For *Quercus* the equation proposed by Martínez-López and Ramos (2014) was used, the individual stump basimetric area estimated, and then summed for the total basal area.

2.4. Local knowledge of risk for BB tree host species

Because this study was conducted with a Zapotec indigenous community with pre-Hispanic roots, we adopted the "new ways of learning" focus in forest research (Lawrence, 2000) and the perspective of "decolonizing methods" (Wilson, 2001) both of which consider traditional ecological knowledge as a valid source of information (Meffe et al., 2002). Thus, this research relied on traditional ecological knowledge of forests to rank levels of risk to BB for all native Pine host species. For this purpose, the categorization used by Berthelot et al. (2021) was adapted, for the identification of preferred species by BB: : 1) main-host, 2) moderate-host and 3) less host. A total of 20 key regional experts (15 professional foresters and 5 local experts - farmers with decades of experience working in the community forest enterprise) were interviewed, selected using the snowball technique (Schreuder et al., 2004). For these informal interviews, a guide with three sections was used: 1) individual experience in forestry and their knowledge of the community forest 2) degree of individual involvement during the BB outbreak and the subsequent sanitation logging, and 3) individual knowledge about BB and the risk level of the local pine hosts. The data on local knowledge of the susceptibility of BB hosts species was crossed with the CONAFOR Technical Phytosanitary Report.

2.5. Statistical analyses

The paired comparisons of structural variables (density and basal area) between the disturbance conditions (BB and TE) and the control group (CG) were made using one-way ANOVA. If normality and homogeneity of variance were not satisfied, a Kruskal-Wallis test was used. When significant differences were presented, these were analyzed with the multiple comparisons Tukey, at an α level of 0.05. To find out if there were significant differences in the structural variables (density and basal area) between disturbance conditions (BB and TE), Student's *t*-test or

Mann-Whitney tests were performed according to the assumptions of normality and homogeneity of variance. Statistical analyses were conducted with 4.0.0 (R Development Core Team, 2020).

3. Results

3.1. Structure, composition and diversity

A total of 4,053 live trees with DBH ≥ 5 cm were found in the study sites. Trees corresponded to a total of 24 species, 8 genera and 7 families (Table 1). At the family level, Pinaceae included 9 species and represented 52% of total live trees. *Pinus patula, Pinus hartwegii* and *Pinus teocote* were recognized as the main-host species to BB. *Pinus ayacahuite* was observed to be BB less-host preferred species. Fagaceae had 9 species and represented 37% of total trees, while Betulaceae, Ericaceae, Rosaceae, Lauraceae and Rosaceae presented one species each (11% of trees).

The live tree canopy had *Pinus* and *Quercus* as the main structural component in both disturbances analyzed. The average total tree density in conditions affected by BB outbreaks was comparable with the other two analyzed conditions, but significant contrasts for *Pinus* were recognized between disturbance conditions (Table 2). *Quercus* tree density only contrasted between TE and the CG, and significant contrasts were found for "Other genera" among the paired comparisons for the three study conditions.

In contrast, the total basal area was statistically different among disturbance conditions and the CG, and the same pattern resulted for *Pinus* and other genera comparisons. The diameter frequency of the tree canopy in the post-disturbance tree canopy presented a J-inverted distribution (Fig. 3a–c). In general, 78% of trees were in the first two categories (DBH ≤ 20 cm) and very few trees presented DBH ≥ 40 cm where BB outbreaks occurred (Fig. 3a). In TE condition there were no trees ≥ 50 cm (Fig. 3b). In contrast, in the GC conditions the trees with DBH ≥ 50 cm were nearly 20% of individuals and 50% of BA (Fig. 3c) and the non-host trees frequency prevailed in most of the diameter categories. Tree density of removed individuals during BB sanitation logging and timber extraction was comparable between disturbance conditions (Table 3), but the removed basal area was significantly different among the study conditions. *Quercus* presented less BA in the forest canopy affected by BB outbreaks.

A total of 547 stumps were found, 254 resulted from sanitation logging and the rest came from commercial logging. Ninety-four percent of total stumps in the BB outbreak condition were pine trees and they accounted for 13% of the total trees and 16.1% of the total basal area. The results showed that BB killed trees of different sizes: 21.4% of affected trees had DBH of ≤ 20 cm, 44% had DBH of ≥ 20–40 cm and 34.5% were trees with DBH of > 40 cm (Supplementary material), but the dead trees maintained a size comparable to the diameter structure of the pre-disturbance forest stands. In contrast, in TE conditions pine stumps corresponded to 5.6% of total trees, and 15.2% had DBH ≤ 20 cm, 41.5% had DBH of ≥ 20–40 cm and 43.3% were trees with DBH of 40 cm. The pre-disturbance hypothetical tree canopy structure suggested that sites affected by BB outbreaks were denser than those in TE and the CG, principally with pines (Table 4), but almost comparable in their basal area with other study conditions. Although the CG presented significantly less *Quercus* density than the disturbance conditions, it had more density and basal area for other genera.

Table 1
Relative abundance of tree canopy species by evaluated conditions (*values ≤ 0.001): Bark beetle (BB) outbreaks, Timber extraction (TE) disturbance, and Control group (CG). The *Pinus* species at risk to be affected by BB were: main-host, moderate-host and less-host preferred. In parenthesis n = number of plots.

Family	Species	Disturbance conditions		CG (n = 10)	At Risk to Bark Beetle
		BB (n = 40)	TE (n = 40)		
	Pinus patula	0.15	0.12	0.05	Main
	Pinus hartwegii	0.14	–	0.07	Main
	Pinus teocote	0.00*	–	–	Main
	Pinus douglasiana	0.01	0.01	–	Moderate
Pinaceae	*Pinus leiophylla*	0.00*	–	–	Moderate
	Pinus moctezumae	–	0.00*	–	Moderate
	Pinus oaxacana	0.01	0.03	–	Moderate
	Pinus pseudostrobus	0.10	0.12	–	Moderate
	Pinus ayacahuite	0.13	–	0.33	Less
	Abies hickelii	0.02	–	0.27	No
	Quercus aff. rugosa	0.01	0.02	0.02	No
	Quercus acatenangensis	–	–	0.00*	No
	Quercus aff. *acatenangensis*	0.01	–	–	No
	Quercus crassifolia	0.16	0.24	0.02	No
Fagaceae	*Quercus glabrescens*	0.01	–	0.03	No
	Quercus laurina	0.04	0.06	0.02	No
	Quercus obtusata	–	0.03	–	No
	Quercus rugosa	0.11	0.17	0.04	No
	Quercus trinitatis	–	–	0.01	No
Betulaceae	*Alnus acuminata*	0.01	0.06	–	No
Ericaceae	*Arbutus xalapensis*	0.05	0.08	0.04	No
Rosaceae	*Cercocarpus macrophyllus*	–	0.01	0.00	No
Lauraceae	*Litsea glaucescens*	0.01	–	0.08	No
Rosaceae	*Prunus serotina*	0.01	0.06	–	No
TOTAL		1.00	1.00	1.00	

*Valores < a 0.001.

3.2. Species dominance and diversity

In general, in the post-disturbance tree canopy five species were dominant (>71%). The most relevant was the *Quercus* IVI, which was highest in the BB outbreaks (30.9%) compared with TE and the CG (Table 5), and there it was almost comparable with *Pinus* (32%). The *Pinus* IVI was 48.7% in TE, and the dominance is given for the three main-host species. However, this pattern contrasted with the IVI in the CG, where *Pinus* accounted for 44.7%, but the less-preferred BB host *Pinus ayacahuite* contributed with 27.4% of the total dominance. Two non-host species *Abies hickelii* and *Quercus rugose* accounted for 26.9% of total dominance.

Additionally, diversity in the BB post-disturbance tree canopy was higher than in TE and CG conditions (Fig. 4). Diversity order 0 (species richness) in BB was significantly different from other evaluated conditions, diversity order 1 (influenced by the most abundant species in the community) was significantly different between BB and TE, and also between BB and CG; while diversity order 2 (effective number of species, quantified by their average proportional abundance) was significantly different among the three paired comparisons.

4. Discussion

In general, there are still a limited number of studies that analyze the relationship of BB outbreaks to changes in the structure, species composition and diversity of the tree canopy. This paper, so far as we know, is the first attempt to describe the changes in forests affected by BB outbreaks in Mexico. Methods combined traditional tree forest sampling in plots, with social methods of interviews with local forestry experts. Considering the increase of BB outbreaks in the temperate forests (https://sivicoff.cnf.gob.mx/), the results allow us to suggest some strategies that may increase the ecological resistance and resilience of forests.

Table 2
Average and standard deviation of density (stems ha^{-1}) and total basal area (m^2 ha^{-1}) of live trees in the evaluated conditions: Bark beetle (BB) outbreaks, Timber extraction (TE) disturbance, and Control group (CG). In parenthesis n = number of plots.

		Disturbance Conditions					
	Variables	1.BB (n = 40)	2.TE (n = 40)	3.CG (n = 10)	Test value	Paired comparisons	Significance
Density	Total	969 ± 337	744 ± 413	737 ± 250	2.2**	ns	0.091
	Pinus	576 ± 357	220 ± 91	355 ± 210	3.3**	1–2	0.025
	Quercus	332 ± 226	424 ± 308	138 ± 167	3.0**	2–3	0.034
	Other genera	112 ± 112	120 ± 102	286 ± 248	6.6*	1–3,2–3	<0.001
Basal area	Total	35.4 ± 22.2	25.8 ± 9.4	55.8 ± 16.5	12.1**	1–3, 2–3	<0.001
	Pinus	21.4 ± 12.6	16.8 ± 8	35.5 ± 18.5	6.7**	1–3,2–3	<0.001
	Quercus	11.3 ± 9.2	5.8 ± 5.5	9.8 ± 8.1	7.6*	ns	0.056
	Other genera	3.3 ± 2.8	1.5 ± 1.0	10.5 ± 9	12.7*	1–3,2–3	0.005

*Kruskal-Wallis (Ji^2); ** ANOVA (F); ns = not significant.

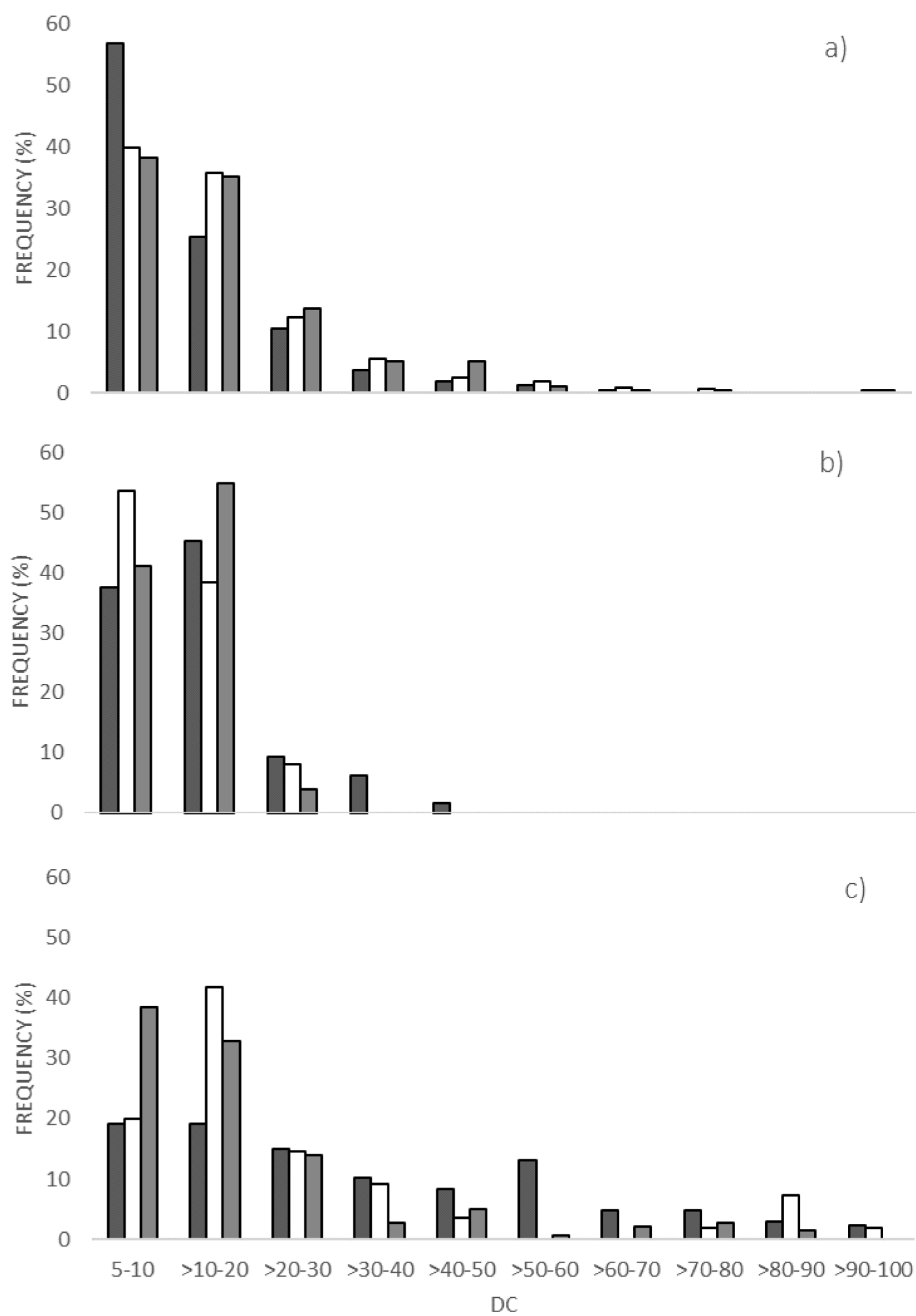

Fig. 3. Relative frequency of trees by diametric category in different evaluated conditions: a) BB = with Bark beetle outbreaks b) TE = with Timber extraction disturbance and, c) Control group. Black = *Pinus*; gray = *Quercus*; white = Other genera. Bars of the same color sum 100% of the total trees for each condition.

Table 3
Average and standard deviation of density (stems ha^{-1}) and total basal area (m^2 ha^{-1}) of trees removed by sanitation logging and timber extraction, and the paired comparisons for evaluated conditions: Bark beetle (BB) outbreaks and Timber extraction (TE) disturbance. In parenthesis n = number of plots.

		Disturbance Conditions			
	Variables	BB (n = 40)	TE (n = 40)	Test value	Significance
Density	Total	135 ± 96	122 ± 37	1.4*	0.476
	Pinus	129 ± 98	104 ± 44	1.6*	0.417
	Quercus	28 ± 15	45 ± 19	2.3*	0.310
Basal area	Total	7.2 ± 4.8	13.2 ± 6.2	7.0**	0.002
	Pinus	7.1 ± 4.8	11.3 ± 5.5	4.3**	0.016
	Quercus	0.8 ± 0.6	4.6 ± 5	4.1**	0.032

*Mann–Whitney U, ** t de student.

4.1. Structure, species composition and diversity

Temperate forests in the Sierra Norte region of Oaxaca have been recognized as a hotspot of Pinaceae diversity (Gernandt and Pérez-de la Rosa, 2014). According to this study, the Sierra Norte tree canopy presented more taxonomic diversity than any other temperate forest region in Mexico where pines were dominant (Monarrez-Gonzalez et al., 2020; Vázquez-Ochoa et al., 2022). Our findings of tree mortality by BB (13% of total live trees and 16% of total basal area; Table 3), suggest the studied canopy could be resistant to BB pests, because the low to moderate impact compared with regions in the western USA (Audley et al., 2020; Bentz et al., 2010; Kayes and Tinker, 2012; Pelz et al., 2018). For example, in some areas in the Rocky Mountains USA over twenty-three years' tree mortality exceeded>70% (Rodman et al., 2021). In Central and Eastern European, it was reported that sanitation logging frequently constituted 50% of the total annual timber extraction (Hlásny et al., 2019). The results on BB mortality in trees with different DBH was comparable with the tendency reported for the Western Carpathians and in the Southern Rocky Mountains (Buonanduci et al., 2020; Sproull et al., 2015). However, these pattern contrasted with evidence from Finland, where BB affected small trees (Blomqvist et al., 2018;) and with reports for some regions from Europe and USA, where BB killed many mature pine trees (DBH > 70–80 cm) (Bretfeld et al., 2021; Chisholm et al., 2021; Sproull et al., 2015; Vorster et al., 2017; Zolubas et al., 2009). In addition to tree size, consensus recognized that tree vigor is fundamental for the success for BB attacks and that large trees have reduced physiological defenses (Kirkendall et al., 2015; Kolb et al., 1998; Mulock and Christiansen, 1986).

The stump analysis showed that after sanitation logging there were very low effects in the non-host trees compared with the TE disturbance on *Quercus* trees (Table 3). The last result can be explained by the fact that in Mexico there is a technical recommendation for removing a proportion of the *Quercus* trees in order to reduce its abundance in commercial forest stands (Bray and Durán, 2022). As well, the inverted J shape diameter distribution in the current live tree canopy suggests that it is a young, uneven-aged forest (Oliver and Larson, 1996), with many pine trees of less than 20 cm DBH, likely new recruits. This is likely since, in contrast to forest fires, disturbances caused by BB pests and TE have reduced effects on the seed bank (Červenka et al., 2020). In addition, the growing capacity of *Pinus* may reach that diameter in two decades (Castellanos-Bolaños et al., 2008) and since a notable pine seedling carpet was observed. Some individuals may also be remnants from the previous tree canopy or released suppressed trees (Bretfeld et al., 2021; Kayes and Tinker, 2012; Meigs et al., 2017; Thorn et al., 2016). Thus, the studied stands are part of a landscape in regeneration and support the idea that BB can be a force for forest renewal (Chisholm et al., 2021; Diskin et al., 2011; Müller et al., 2008; Zhao et al., 2015).

Compositional changes may continue in the long term (Meigs et al., 2017) and *Pinus* principally, the main-hots species; Table 1) will likely recover their structural dominance (Rodman et al., 2021), as is likely in this study (Table 5; Fig. 6). This this is a pattern reported for *Picea* and *Abies* in Central Europe and for *Pinus ponderosa* in the southern Rocky Mountains (Collins et al., 2011; Rodman et al., 2021; Zeppenfeld et al., 2015). However, it has also been suggested that BB outbreaks may provide advantages to Fagaceas, a group that has resistance characteristics because it responds better to temperature increases such as those associated with climate change (Alfaro et al., 2022). Thus, the analysis of biological legacies (Jõgiste et al., 2017) in areas affected by BB outbreaks may allow the identification of species that can continue to fulfill

Table 5
Five species with the highest importance value index (IVI) in the current canopy for evaluated conditions: Bark beetle (BB) outbreaks, Timber extraction (TE) disturbance and Control group (CG). Bold letters indicate the BB main-host species. In parenthesis n = number of plots.

Disturbance conditions					
BB (n = 40)	%	TE (n = 40)	%	CG (n = 10)	%
Quercus crassifolia	17.7	***Pinus patula***	**23.4**	*Pinus ayacahuite*	27.4
Pinus pseudostrobus	**17.1**	*Quercus crassifolia*	16.0	*Abies hickelii*	20.6
Pinus patula	**14.9**	***Pinus hartwegii***	**14.0**	***Pinus patula***	**9.9**
Quercus rugosa	13.2	***Pinus pseudostrobus***	**11.3**	***Pinus hartwegii***	**7.4**
Arbutus xalapensis	8.8	*Quercus rugosa*	6.6	*Quercus rugosa*	6.3
Sum of *Pinus** (%)	32.0		48.7		17.3
Total (%)	71.7		71.3		71.6

*Only main-host *Pinus*.

Table 4
Average and standard deviation of density (stems ha^{-1}) and total basal area (m^2 ha^{-1}) of the pre-disturbance tree canopy, reconstructed with data from both the dead tree component (stumps) and the post-disturbance tree canopy. For evaluated conditions: Bark beetle (BB) outbreaks, Timber extraction (TE) disturbance and Control group (CG). In parenthesis n = number of plots.

		Disturbance conditions					
	Variables	1.BB (n = 4)	2.TE (n = 40)	3.CG (n = 10)	Test value	Paired comparisons	Significance
Density	Total	1104 ± 335	866 ± 425	737 ± 250	14.7*	1–3	0.002
	Pinus	705 ± 382	324 ± 138	355 ± 210	22.8*	1–2,1–3	0.001
	Quercus	360 ± 237	469 ± 328	138 ± 167	9.1*	1–3, 2–3	0.028
	Other genera	112 ± 112	120 ± 102	286 ± 248	6.6*	1–3,2–3	<0.001
Basal area							
	Total	42.6 ± 20.2	39.0 ± 13.0	55.8 ± 16.5	16.2*	2–3	0.001
	Pinus	28.5 ± 14.8	28.1 ± 10.7	35.5 ± 18.5	2.9	ns	0.409
	Quercus	11.3 ± 9.2	10.4 ± 8.9	9.8 ± 8.1	14.5*	1–3	0.002
	Other genera	3.3 ± 2.8	1.5 ± 1.0	10.5 ± 9	12.7*	1–3,2–3	0.005

*Kruskal -Wallis (Ji^2); ** ANOVA (F); ns = not significant.

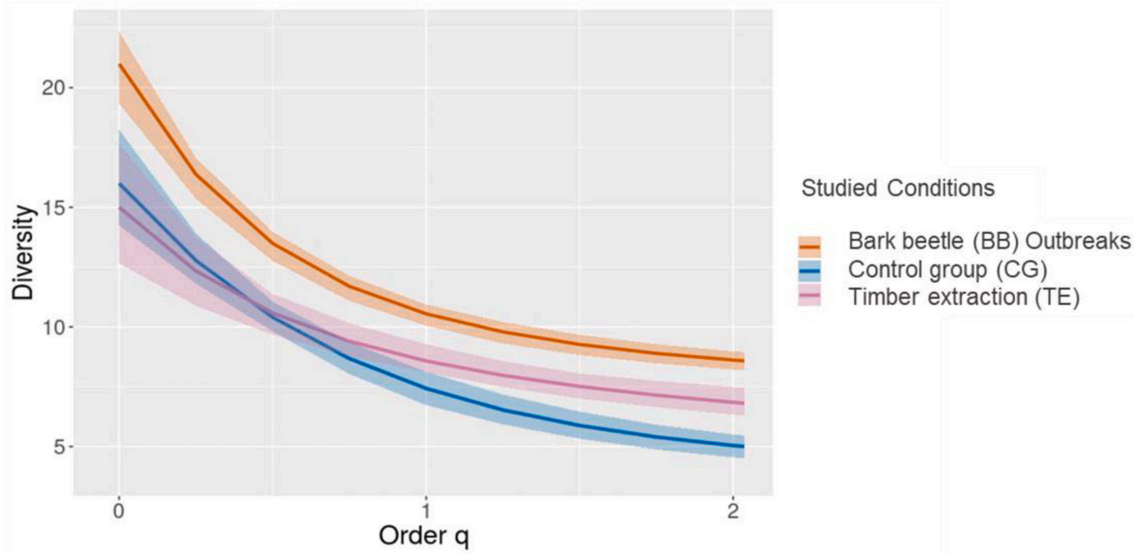

Fig. 4. A graphical image of the triad of true diversity estimators by study conditions. Diversity order zero (corresponds to species richness); order one and order two show the degree of species dominance in the tree community.

ecological functions.

It is important to emphasize that forests from Sierra Norte and other temperate regions in Mexico are dominated by *Pinus patula* (Alfonso-Corrado et al., 2014; Vázquez-Ochoa et al., 2022), one of the principal BB host species (Pacheco-Aquino and Duran, 2021), but which do not figure among BB main-host species nationally (Salinas-Moreno et al., 2010). This indicates the geographic variability of BB host species and highlights the importance of regional studies. The species composition of the current canopy (Table 1), together with dominance (Table 5) and the ranking of risk for BB among *Pinus* species (Fig. 6), provides information useful for visualizing future risk for forest pests (Collins et al., 2011; Fettig et al., 2007; Rodman et al., 2021; Windmuller-Campione, 2018).

The data from the non-BB affected sites (CG), where BB less-host preferred (*P. ayacahuite*) and the other non-host trees were dominant (Table 1 and Table 5), suggests that there are canopy conditions where there could be BB inhibition and dilution due to semiochemical diversity (Jactel et al., 2011). However, in general, the results of this study site suggest that there was no single canopy tree attribute but rather a simultaneous set of structural, compositional and diversity attributes. Which included: a low density, a mix of host and non-host species, maximization of species richness and reduction of stands with mono-dominance of main-host species as the basis that confers resistance and resilience in forests threated by BB. This is in agreement with Hlásny et al. (2019), who proposes that forest health is multifactorial, but that the dominance of tree host species is relevant, such as some *Pinus* and *Picea* species (Berthelot et al., 2021; Hýsek et al., 2021). As well, the absence of BB attacks on the CG could be related with the canopy characteristics –dominance of one less-host preferred species, and some non-hosts, like *Abies hickeli* (Table 1 y Table 5), which is according with Jactel and Brockerhoff (2007). Additionally, resistance and resilience to BB disturbances may be conferred by the beta-diversity observed in the forest landscape (Table 1, Fig. 5).

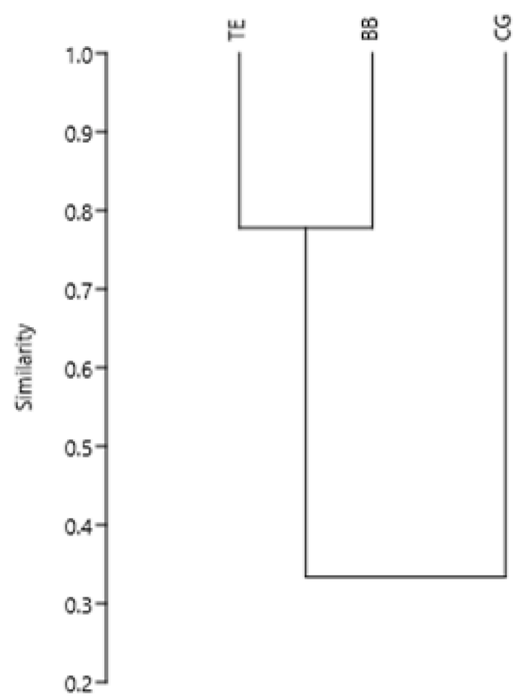

Fig. 5. Dendrogram of similarities in species composition, based on the Morisita-Horn index, for the evaluated conditions: Bark beetle (BB) outbreaks, Timber extraction (TE) disturbance and the Control group (CG).

4.2. Strengthening ecological resistance and resilience

Temperate forests almost everywhere are being affected by BB and future scenarios of climate change will increase the occurrence of forest pests (Trumbore et al., 2015). Thus, we need to learn to coexist with BB, and to improve ecological resistance and resilience in forest ecosystems (Hlásny et al., 2019; Pacheco-Aquino and Duran, 2021). Local forest managers have no influence over climate disruptions, but they can implement a set of feasible interventions to reduce or avoid some disturbances (Leverkus et al., 2021). Based on our results, and the literature, six forest management strategies to improve local resistance and resilience to BB pests are proposed:

1. *Structural attributes*. Management needs to include permanent thinning to reduce tree density. As Table 4 shows, BB outbreaks happened where the highest tree density occurred. Reducing basal area, and promoting an uneven diameter distribution has also been suggested (Fettig et al., 2007; Windmuller-Campione, 2018).

2. *Species composition and dominance*. Management should promote a mix of host and non-host tree species and reduce the dominance of BB main-host species, as well as increase the presence of less preferred hosts

and non-host species. This pattern was found in the CG, where there was more presence of *Quercus* and other genera species (Table 1), and the abundance and dominance was different from BB affected sites. Also, while only one *Pinus* species represented 27.4% of the dominance, it was a less preferred host (Table 5). Although our results do not offer a clear conclusion on the effects of tree species diversity, according to BB inhibition hypothesis (Guo et al., 2019), we observed unaffected forest patches close to stands strongly affected by BB outbreaks.

3. *Identify and propagate BB resistant individuals*. The survival of some *P. patula* with DBH > 40 cm observed in stands affected by BB outbreaks (Fig. 6) suggested that there is potential resistance among the main BB host species. This phenomenon could have a genetic basis, since *P. patula* species has high genetic diversity (He = 0,802; measure of heterozygosity) in the Sierra Norte region, which has not been impoverished despite many decades of forest management (Alfonso-Corrado et al., 2014). The presence of natural genetic resistance to BB is important since the propagation of individuals of this commercially important species could be a strategy for climate change adaptation (Six et al., 2018).

4. *Establish goals to improve forest resistance in the timber production zones*. Forest managers and the timber industry should reduce the size of patches for timber production and surround them with belts of a mix of species, including the locally less preferred and non-host species (Jactel and Brockerhoff, 2007). Thus, if BB pest massively affects *Pinus* trees, “the forest has been reset—not destroyed” (USFS, 2011), and the residual non-host species like *Quercus* can still preserve forest cover and ecological functionality, including the capacity for water filtration, carbon capture, and soil retention, among other ecosystem services (Nelson et al., 2014).

5. *Forest monitoring and early sanitation logging*. Forest monitoring, supported by local knowledge and expertise, is fundamental for early detection of BB outbreaks in forest landscapes and sanitation logging should be implemented as quickly as possible (Pacheco-Aquino and Duran, 2021). However, the Mexican legal framework for forest health needs modifications in order to reduce bureaucratic requirements to speed up authorization of sanitation logging. Bureaucratic delays are currently an obstruction for effective BB control (Fernández-Vázquez and Mendoza-Fuente, 2015).

6. *Encourage forest recovery after BB infestations*. A key indicator of forest resilience to BB pests and other disturbances is the capacity for quick recovery by natural regeneration (Collins et al., 2011; DeRose and Long, 2014). In the study case, the prevalence of ≤ 20 cm DBH trees suggested that natural regeneration after BB outbreaks occurred (Fig. 3a). However, the new tree canopy was still dominated by *P. patula* and other main host pine species, which could be a risk for BB in the future.

5. Conclusion

After BB outbreaks, which directly affected several pine species, the Yavesia forest presented structural changes. For example, there was a notable reduction in density and basal area of *Pinus* trees, but significantly less was observed in non-host trees. A similar pattern occurred with basal area, but it was greater in the TE condition. The diameter distribution, after the occurrence of BB outbreaks was an inverted-j, which is consistent with the idea that BB is a forest regenerator. The canopy tree species composition in the studied forest included 24 species: 9 *Pinus* species and 9 *Quercus* species, plus another 6 species. Trees of the genus *Pinus*, particularly of species considered main-host (*P. patula*, *P. pseudostrobus*), were dominant in the conditions of disturbance by BB and TE, but although two main-host species were present in the CG, their importance value was minor. In the CG condition, *P. ayacahuite* (a less preferred host species) presented the highest importance value recorded. The sites affected by BB presented the highest diversity, compared to the other two conditions studied, which support the idea that BB pests can increase tree diversity. The mixed methodologies adopted, with traditional forest sample plots and data from local forest knowledge allowed for a better understanding on the effects of BB outbreaks. We propose that forest management should focus on a set of different structural, compositional and diversity attributes as the basis for improving resilience in forests threatened by BB. Specifically, in the context of common property forests, it is important to understand how the canopy changes after BB outbreaks. This is highly useful information for owners that will allow them to design management strategies to increase resistance and resilience.

Authors contribution

Guadalupe Pacheco-Aquino contributions included: to conceive the idea and methods, to obtain field data, the data analysis and to write the manuscript.

Elvira Duran contributions included: to conceive the idea and methods, to participated in the data analysis and to write the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

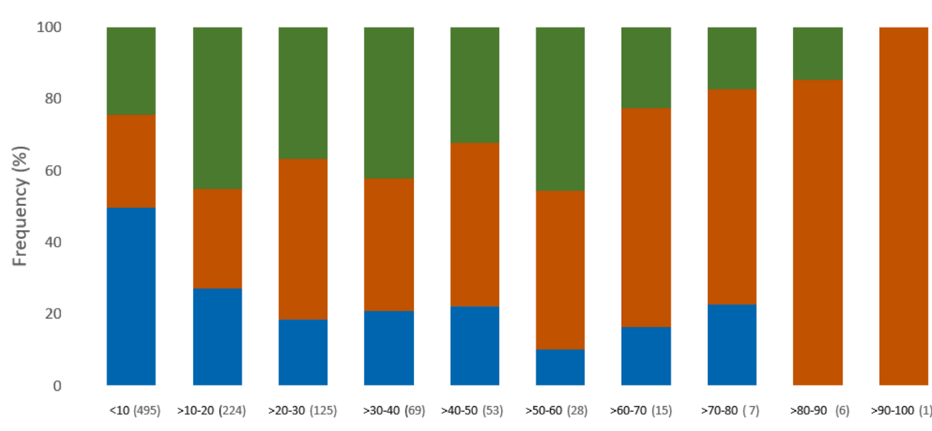

Fig. 6. Relative frequency of BB *Pinus* hosts by diameter category in the post-disturbance tree canopy, from affected sites by BB outbreaks. The three different BB risk levels were: Blue = main-host; orange = moderate-host; green = less-host preferred. It was based on the local forest knowledge. In parenthesis, n = number of trees. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.121099.

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