Forest Ecology and Management 260 (2010) 52–61

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Determining the vulnerability of Mexican pine forests to bark beetles of the genus *Dendroctonus* Erichson (Coleoptera: Curculionidae: Scolytinae)

Y. Salinas-Moreno[a,*], A. Ager[b], C.F. Vargas[a], J.L. Hayes[c], G. Zúñiga[a]

[a] Escuela Nacional de Ciencias Biológicas-IPN, Prol. de Carpio Esq. Plan de Ayala s/n, Casco de Sto. Tomás, México D.F., C.P. 11340, Mexico
[b] USDA Forest Service, Pacific Northwest Research Station, Western Wildlands Environmental Threat Assessment Center, 3160 NE 3rd Street, Prineville, OR 97754, United States
[c] USDA Forest Service, Pacific Northwest Research Station, Forestry and Range Sciences Laboratory, 1401 Gekeler Lane, LaGrande, OR 97850, United States

ARTICLE INFO

Article history:
Received 22 January 2010
Received in revised form 30 March 2010
Accepted 31 March 2010

Keywords:
Bark beetles
Pine
Vulnerability
México
Distribution
Richness

ABSTRACT

Bark beetles of the genus *Dendroctonus* are natural inhabitants of forests; under particular conditions some species of this genus can cause large-scale tree mortality. However, only in recent decades has priority been given to the comprehensive study of these insects in México. México possesses high ecological diversity in *Dendroctonus*–*Pinus* associations. The geographic coexistence of 12 *Dendroctonus* species suggests greater vulnerability or threat of tree mortality relative to other areas. We use a biogeographic strategy to identify and rank the areas most vulnerable to tree mortality caused by bark beetles in México. We aim to define the areas that might experience high impact by these insects and also to provide a geographic database useful to forest resource management and conservation policies in México. Using collection records of bark beetles and pines, we develop a quantitative estimate of the threat of beetle infestation of forest areas based on factors including pine and beetle species density, host preference and level of mortality caused by beetle species. A quantitative estimate of forest area vulnerability, the Bark Beetle Threat Index (BBTI) was calculated. Despite the vast area of geographic coincidence of *Pinus* and *Dendroctonus* in México, the regions of highest bark beetle pressure are restricted to small zones within some mountain systems. The region that has been most affected by this insect group during the past hundred years is the Transverse Volcanic Belt, followed by the Sierra Madre Occidental and Sierra Madre del Sur. Pine diversity is the major determining factor of BBTI at the regional level, while disturbances from extensive logging and ecosystem change are the key factors behind high BBTIs at the local level.

1. Introduction

Species of the genus *Dendroctonus* are natural inhabitants of coniferous forests in North America (Wood, 1982). Under certain forest conditions (Malmström and Raffa, 2000) and particular climatic events, such as extreme drought (Raffa et al., 2005), some species of this genus can cause large-scale mortality of trees in the *Pinus*, *Picea*, *Pseudotsuga* and *Larix* genera (Wood, 1982). The extensive mortality caused by bark beetle outbreaks has both economic and ecological impacts and affects forest resource management strategies (Malmström and Raffa, 2000; McFarlane and Witson, 2008).

In recent decades, priority has been given to the comprehensive study of bark beetles in México for forest conservation and restoration. Nevertheless, present-day management tends to be limited to local, small scale, direct control methods consisting primarily of sanitation treatments used thirty years ago (Malmström and Raffa, 2000). Only recently have forestry practices been directed to alternatives such as semichemical-based tactics commonly used in Canada and the US (Díaz-Núñez et al., 2006; Macías-Sámano et al., 2004).

Forest health assessments aided by bark beetle risk models or rating systems have been conducted in Canada, the US and Europe for several decades (Beukema et al., 1997; Lewis, 2002; Malmström and Raffa, 2000; Robertson et al., 2008). These risk models attempt to predict the susceptibility of forests to bark beetle attack and mortality at the landscape and regional scales. Prediction models developed in the US and Canada are based on abundant information about site conditions and vegetation characteristics at different scales, as well as on bark beetle biology and ecology (Beukema et al., 1997). In México these data are often scarce, lack necessary precision, and are maintained by different government agencies. This situation has prevented the development of predictive models for basic decision-making to prevent or mitigate adverse impacts of these insects.

Nevertheless, México has abundant fine-scale (presence/absence data) on both pines and *Dendroctonus* beetles (Salinas-Moreno et al., 2004; www.conabio.gob.mx) from the past hundred years, which can be aggregated at the mesoscale level to identify

* Corresponding author.
E-mail addresses: erfran_1960@hotmail.com, yosamo17@yahoo.com.mx (Y. Salinas-Moreno).

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doi:10.1016/j.foreco.2010.03.029

geographic areas where bark beetles pose the greatest risk to coniferous forests. Although this approach does not lead directly to risk analyses, it can identify geographic regions that should be monitored continuously (Malmström and Raffa, 2000).

1.1. Conditions in México

Temperate coniferous forests cover 13% of Mexico's land area (Challenger, 1998). The vast majority of these forests are composed of trees in the genus *Pinus*, with the remainder in *Pseudotsuga* and *Picea* (Rzedowski, 1981; Styles, 1998). México is a center of pine diversification and one of the top three areas worldwide for *Pinus* species diversity (42 species and 18 infraspecific taxa) (Farjon and Styles, 1997). High ecological diversity is characteristic of pine communities in México. Geographic relief is pronounced in the various mountain systems, affecting mesoclimate (Ferrusquía-Villafranca, 1998) and biotic species diversity. In addition, pine forest composition varies due to the substantial diversity of pine and associated vegetation (Richardson and Rundel, 1998; Styles, 1998). In México, pines are found primarily in three types of communities: pure pine forests and, depending on dominance, pine-oak and oak-pine forests, which occur at different elevations, climates and exposure conditions (Rzedowski, 1981).

Pine-dominated plant communities are present in the major mountain systems of México and regularly sustain disturbance from insect pests and diseases, fire, drought, logging, grazing and extensive land-use change (Challenger, 1998; Perry et al., 1998). Such stress factors, whether natural or anthropogenic, favor recurrent outbreaks of *Dendroctonus*; population levels can build-up in clusters of weakened host trees (Cibrián et al., 1995; SEMARNAT, 2006). There are 12 species of *Dendroctonus* bark beetles in México, six of which are considered primary tree-killing, and they have broad, often overlapping geographic distributions (Salinas-Moreno et al., 2004). In the US and Canada, *Dendroctonus* colonize four genera of Pinaceae, whereas in México, *Pinus* and *Pseudotsuga* species are colonized (Cibrián et al., 1995; Salinas-Moreno et al., 2004). Pine forests of México sustain constant pressure by these beetles.

Some *Dendroctonus* species in México are characterized by high polyphagy, colonizing over 20 species of pine, while others appear to be monophagous (Salinas-Moreno et al., 2004). The polyphagous species differ in relative occurrence on their hosts, suggesting that certain pine species are preferred by particular insect species and that such preference may vary by geographic area (Salinas-Moreno et al., 2004). High polyphagy and broad host distribution favors the geographic coexistence of *Dendroctonus* species. As elsewhere, secondary beetle bark species (those that do not initially colonize susceptible trees) commonly follow primary beetle species in México and it is also common for more than one primary species to occur in the same tree with secondary species (Zúñiga et al., 1995). In addition to within tree niche partitioning, polyphagy and the availability of alternate hosts may avert detrimental effects of direct competition in those areas of geographic coexistence (e.g., Macías-Sámano and Borden, 2000; Poland and Borden, 1998). Areas of *Dendroctonus* species sympatry have been documented mainly in the northwest (Sierra Madre Occidental) and central (Transverse Volcanic Belt) regions of México (Zúñiga et al., 1999).

The geographic coexistence of primary *Dendroctonus* species suggests an increased vulnerability to tree mortality in these areas. Similarly, areas of high pine diversity are likely at greater risk of experiencing mortality from at least one, if not more bark beetle species. In the absence of the detailed attribute data that are needed for local risk or hazard rating systems or more broad-based prediction models, information on occurrence and sympatry in this insect–host system can be used to identify forest regions that are potentially the most susceptible to bark beetle attack.

Table 1
Number and source of collection records for each *Dendroctonus* species considered in this study.

Species	No. of records	Collection[a]
Dendroctonus adjunctus	211	1,2,3,4,5,6,7,8,9,10
D. approximatus	106	1,3,4,5,7,8,9,10
D. brevicomis	18	4,7,8,10
D. frontalis	177	3,4,5,7,8,10,11
D. jeffreyi	6	1,4,10
D. mexicanus	566	1,2,3,4,5,6,7,8,9,10,11
D. parallelocollis	87	1,2,3,4,5,7,8,10
D. ponderosae	2	7,10
D. pseudotsugae	31	3,4,5,7,10
D. rhizophagus	104	1,3,4,5,7,8,10
D. valens	366	1,2,3,4,5,6,7,8,9,10
D. vitei	1	1
Total	1675	

[a] Collection: (1) Colegio de Posgraduados, México, MEX; (2) Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Morelos, Morelos, MEX; (3) Colección Nacional de Insectos, Ottawa, CAN; (4) División de Bosques. Universidad Autónoma de Chapingo, México, MEX; (5) Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional, D.F., MEX; (6) Instituto de Biología, Universidad Nacional Autónoma de México, D.F., MEX; (7) Instituto Nacional de Investigaciones Forestales Agrícolas y Pecuarias, Secretaría de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación, D.F., MEX; (8) Instituto de Silvicultura, Universidad Autónoma de Nuevo León, Nuevo León, MEX; (9) Museo Historia Natural, D.F., MEX; (10) Sanidad Forestal, Secretaría del Medio Ambiente y Recursos Naturales, D.F., MEX; (11) Sanidad Vegetal, Secretaria de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación, D.F., MEX.

In this study, we use a biogeographic strategy to identify and rank the areas most vulnerable to bark beetle outbreaks in México. Using collection records of bark beetles and pines, we develop a spatially explicit, quantitative estimate of the threat of beetle infestation based on factors such as pine and beetle species density, host preference and level of mortality caused by beetle species.

2. Materials and methods

2.1. Data on bark beetle locations

A database of point locations based on 1530 collection records, over one hundred years, was constructed for the six most widely distributed species of *Dendroctonus* in México: *D. adjunctus*, *D. approximatus*, *D. frontalis*, *D. mexicanus*, *D. rhizophagus* and *D. valens*. Species with highly restricted distributions or few records (≤100) were not included in the study (Salinas-Moreno et al., 2004) (Table 1). *D. pseudotsugae* was omitted because we focused on pine bark beetle species only. The database was initially built using location records previously published in Salinas-Moreno et al. (2004) and was subsequently expanded with data from 11 entomological collections (Table 1) and 42 locations identified during fieldwork from 1986 to 2007. Each location record included the bark beetle species, municipality, state, latitude, longitude, elevation, the host species, collecting date and the collection or bibliographical reference associated with the record. Unique records were those differing in any of the above features or in location data. Insects were collected during both endemic and outbreak population conditions. We recognize the limitation of relying on collection records, which may be incomplete and not represent the entire distribution of any given species; thus, our findings should be considered conservative.

2.2. Data on pine species distribution

A database of point locations based on 4561 collection records was created for the 25 pine species that are susceptible to bark beetles in México (Salinas-Moreno et al., 2004). This database followed the taxonomic classification system of Mexican pines proposed by Farjon and Styles (1997), which recognizes the species listed in

Table 2
Number and source of herbarium records for each species of *Pinus* considered in this study.

Species	No. of records	Herbaria[a]
Pinus arizonica	157	1,2,3,9,11,13,14,15,16,17,20
P. ayacahuite	166	7,8,9,10,12,13,16,18,19
P. cembroides	417	2,3,4,7,9,11,12,13,14,15,16,17,20,21
P. devoniana	125	7,9,12,13,14,17,19
P. douglasiana	99	7,9,12,13,17
P. durangensis	109	5,7,9,12,13,14,17
P. engelmannii	82	3,5,7,9,13,14,17,22
P. gregii	78	1,2,3,7,9,11,13,15,16,17,19,20
P. hartwegii	193	2,3,9,11,12,13,14,15,17,20
P. herrerae	92	7,9,12,13,17
P. jeffreyi	18	9,13,17
P. lawsonii	108	7,9,12,13,17
P. leiophylla	611	3,7,9,12,13,14,17,22
P. lumholtzii	108	3,9,12,13,14,17
P.maximinoi	96	3,7,9,12,13,14,17,19,22
P. montezumae	245	1,2,3,9,12,13,14,15,16,17,18,20
P.oocarpa	448	1,6,7,9,12,13,14,16,17,19,22
P. patula	230	2,7,9,11,12,13,16,17
P. pinceana	83	1,2,7,9,11,12,13,14,16,17,20
P. pringlei	90	9,12,17
P. pseudostrobus	411	1,2,3,7,8,9,10,11,12,13,14,15,16,17,19,20
P. quadrifolia	42	9,12,17
P. strobiformis	66	1,2,9,11,12,13,14,15,16,17,19
P. strobus	31	8,9,10,14,16,17,19
P. teocote	456	1,2,3,7,9,12,13,14,15,16,17,19,20
Total	4561	

[a] Herbaria: (1) Arnold Arboretum of the Harvard University, Cambridge Massachusetts, USA; (2) Herbaria of the Universidad Autónoma Agraria Antonio Narro, Coahuila, MEX; (3) Herbaria of the Arizona University, USA; (4) Herbaria of the Facultad de Ciencias de la Universidad Autónoma de Baja California, MEX; (5) Herbaria of the Universidad Autónoma Chapingo, Estado de México, MEX; (6) Herbaria of the Centro de investigación Científica de Yucatán, MEX; (7) Herbaria of the Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional, IPN, Durango, MEX; (8) Herbaria Paul C. Standley, HONDURAS; (9) Herbaria of the Escuela Nacional de Ciencias Biológicas, IPN, MEX; (10) Herbaria Forestal of the Oxford University, UK; (11) Herbaria of the Harvard University, USA; (12) Herbaria of the Instituto de Botánica, Universidad de Guadalajara, MEX; (13) Herbaria of the Instituto de Ecología-Bajío, A.C., MEX; (14) Herabria of the Instituto Nacional de Ecología A.C., Xalapa, Veracruz, MEX; (15) Herbaria of the Instituto Nacional de Investigacones Forestaes y Agropecuarias, MEX; (16) Herbaria of the Texas University, Austin, USA; (17) National Herbaria of the Instituto de Ecología, UNAM, MEX; (18) Herbaria of the Michigan University, Ann Arbor Michigan, USA; (19) w3 Trópicos, Missouri Botanical Garden, USA; (20) Herbaria of the Facultad de Ciencias Biológicas, Universidad Autónoma de Nuevo León, MEX; (21) Herbaria of the Nuevo Mexico University, USA; (22) Herbaria of the Universidad de Sonora, MEX.

Table 2. This database included the same information as in the bark beetle database and was constructed using information from 18 Mexican and foreign herbaria in the World Information Network on Biodiversity (REMIB, *Red Mundial de Información sobre Biodiversidad*, National Commission on the Knowledge and Use of Biodiversity, CONABIO, http://www.conabio.gob.mx). The database was supplemented with data from vouchers stored in four other Mexican herbaria (Table 2).

Latitude and longitude for each point location were determined in decimal degrees using topographic and vegetation maps (1:50,000 scale, INEGI, 2002). Records obtained through fieldwork were georeferenced using a Garmin V GPS (Garmin, Chicago IL). Information in both databases was screened by bark beetle and pine taxonomic authorities, and records deemed to have been from anomalous locations or with questionable taxonomic classifications were deleted.

2.3. Distribution areas and kernel densities

We used the point location data to draw continuous area distribution maps for each bark beetle or pine species (Bailey, 1994). We adopted this approach after discovering that published distribution maps were not consistent with our field location data from 1986 to 2007 (see Section 2.1). A kernel density estimator with a Least Square Cross Validation (Kenward et al., 2001) was used to calculate window radius. Because the density estimator is not sensitive to grid size, we used an *ad hoc* 2.5 km × 2.5 km grid cell (Kenward et al., 2001). Finally, the 95% probability function of the kernel was used to assign species' presence area (Beardah and Baxter, 1996). This procedure was carried out in ArcMap (ESRI, Redlands, CA) with the spatial analysis module of ArcGIS ver. 9.0.

With the kernel approach, multiple observations define a larger area, which is consistent with the assumption that a higher number of records from a location indicates a larger area within which the species would be present. We recognize the uncertainties of this approach; however, it was corroborated by our field observations.

To limit potential overestimation of pine species distribution, we excluded portions of the predicted species distribution that were not forested according to the México National Forest Cover Type Map (available at CONABIO website www.conabio.gob.mx). Specifically, we retained pixels that were classified as pine, pine–oak and oak–pine forest in the cover type map.

2.4. Percentage of beetle incidence on host species

Because there is little published information on host specificity of bark beetle species (Salinas-Moreno et al., 2004), we constructed a frequency table to describe the incidence of each beetle species on each pine host. This frequency table was then used to quantitatively weight the impact of each beetle species on each pine species. Data for the frequency table were obtained from the beetle inventories described above.

2.5. Bark Beetle Threat Index

A quantitative estimate of forest area vulnerability, the Bark Beetle Threat Index (BBTI), was calculated using an equation that includes the effect of pine species density (P_{xy}), the preference of a given beetle species for the host (HP_{xy}), and the density of the beetle species (D_{xy}), for each grid cell or pixel:

$$\mathrm{BBTI}_{xy} = \Sigma[(P_{xy}) \times (HP_{xy}) \times (D_{xy})]$$

Because of the elevated damage associated with the presence of four particular beetle species (*D. adjunctus*, *D. frontalis*, *D. mexicanus* and *D. rhizophagus*), we applied a weighting factor of 2.0 when $HP_{xy} > 0$ for any of these four species. The increased weight reflected our observations of increased host mortality associated with these species. Although the weighting was arbitrarily determined, the selected value reflected field and recorded observations of these species' impacts.

BBTI was calculated for each pixel and pine species using Modelbuilder 9.1 in ArcMap. In essence, BBTI sums the pressure exerted by each bark beetle species on each host, weighted by the average incidence of attack. These calculations resulted in a map of beetle threat for each pine species. The BBTI was then assigned one of three levels (low, medium and high) using the geometrical interval algorithm as implemented in ArcMap. A composite BBTI (CBBTI) was then calculated to estimate the BBTI summed over all pine host species and was used to construct national maps.

Finally, areas of moderate and high bark beetle threat were plotted on a map of the 151 Priority Land Regions proposed by CONABIO, to determine their ecological importance. Priority Land Regions are areas whose physical and biological characteristics make them particularly important for biodiversity conservation. These areas with stable ecosystems are particularly rich in species. They are known for having endemic species and pristine conditions, and are in some cases important biological corridors between regions (Arriaga et al., 2000).

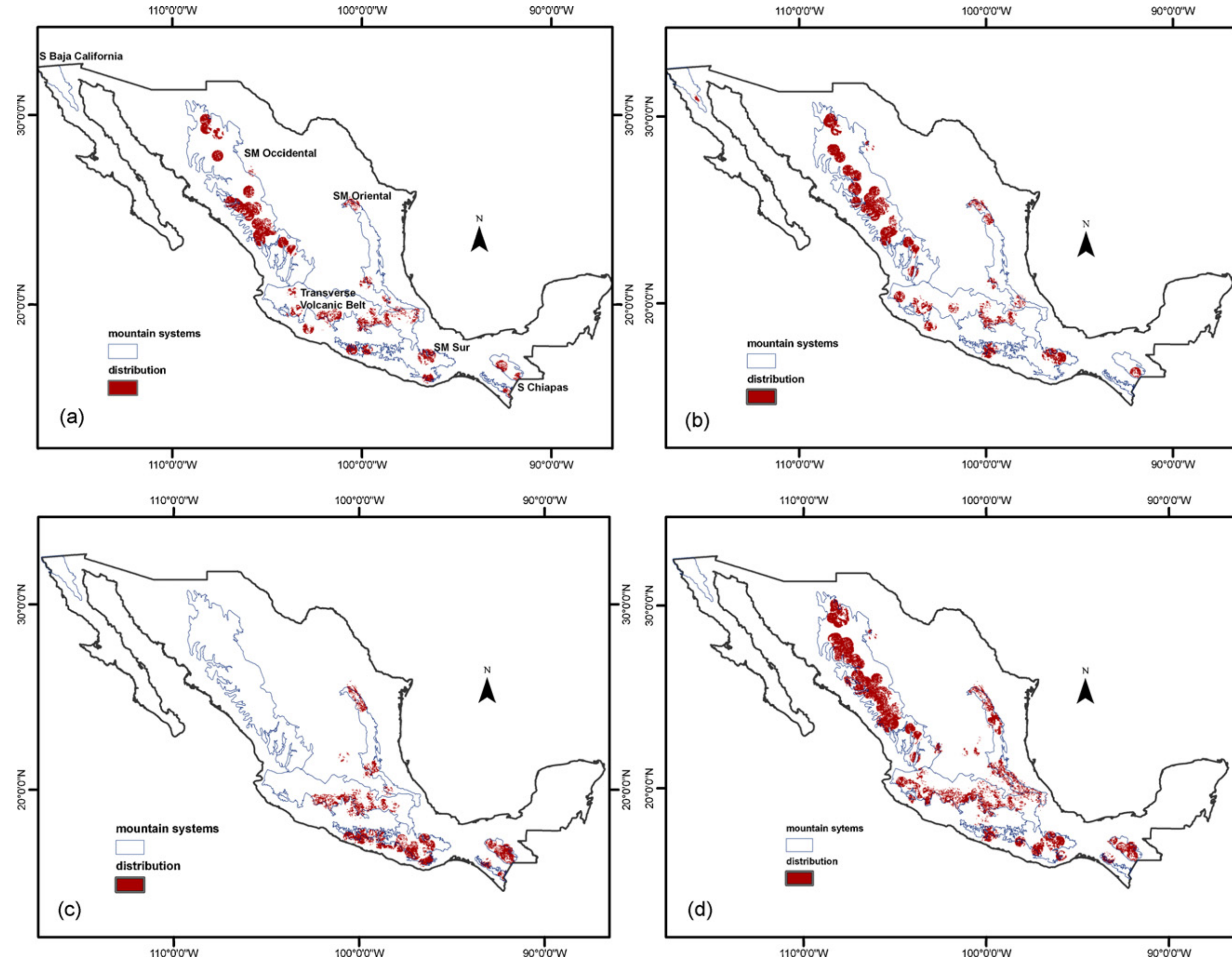

Fig. 1. Geographic distribution of (a) *Dendroctonus adjunctus*, (b) *D. approximatus*, (c) *D. frontalis* and (d) *D. mexicanus* in México, indicating the main mountain ranges in the country.

3. Results

3.1. Database

The number of records obtained for species of both genera (*Pinus* and *Dendroctonus*) varied greatly (Tables 1 and 2), but they appeared to reflect attributes of species biology and/or distribution rather than biased or deficient sampling. For instance, *D. rhizophagus*, which utilizes 11 hosts in the sapling stage, and *D. mexicanus*, which uses >20 host species, had the lowest (104) and highest (566) number of records, respectively. Of the pines, *P. jeffreyi*, a species limited to northern Baja California, had the fewest records (6), while *P. teocote* occurs over multiple states and had the most records (456). Of the six *Dendroctonus* species in this study, four are primary

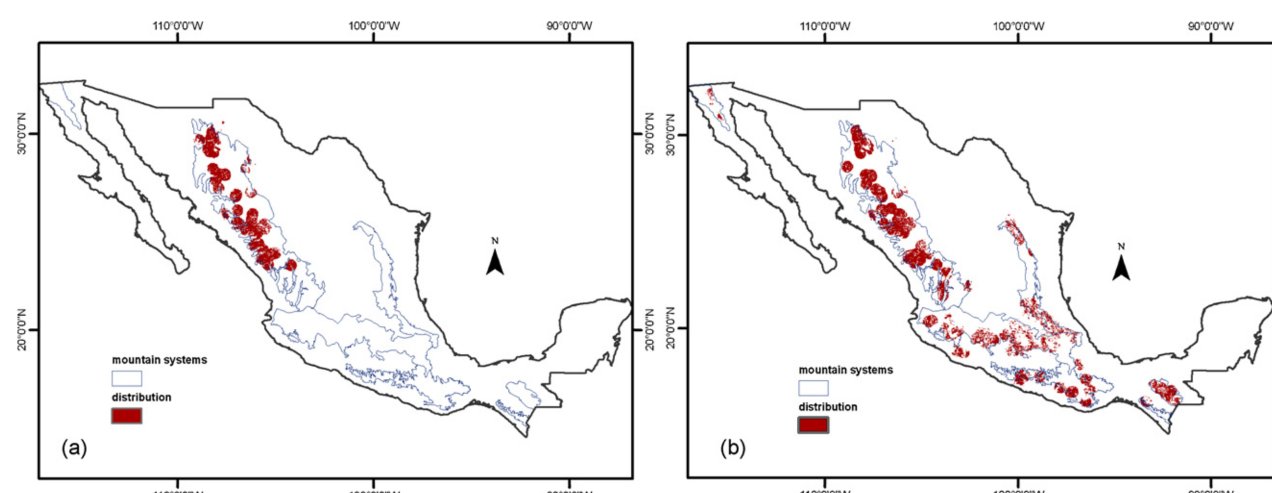

Fig. 2. Geographic distribution of (a) *Dendroctonus rhizophagus* and (b) *D. valens* in México, indicating the main mountain ranges in the country.

Table 3
Geographic distribution and maximum kernel densities for each *Dendroctonus* and *Pinus* species within the major mountain systems in México.

Dendroctonus/*Pinus* species	Mountain system					
	S Baja California	SM Occidental	SM Oriental	Transverse Volcanic Belt	SM Sur	S Chiapas
Dendroctonus adjunctus		x	x	*	x	x
D. approximatus	x	*	x	*	x	x
D. frontalis			x	x	*	x
D. mexicanus	x	x	x	*	x	x
D. rhizophagus		*				
D. valens	x	*	x	*	x	*
*Pinus greggii***			*			
*P. pinceana***			*			
*P. jeffreyi***	*					
*P. quadrifolia***	*					
*P. pringlei***				*	*	
P. patula			*	*	*	
P. montezumae			x	*	x	x
P. strobus			x	x	x	*
*P. engelmannii***		*				
*P. durangensis***		*		x		
*P. lumholtzii***		*		*		
P. lawsonnii		x		*	*	
P. leiophylla		*		*	x	
P. maximinoi		*		*	*	x
P. devoniana		*		*	x	*
*P. arizonica***		*	*			
P. cembroides		x	*	*		
P. strobiformis		*	*	*		
P. herrerae		x	x	*	*	
P. douglasiana		x	x	*	x	
P. hartwegii		x	*	*	x	
P. teocote		*	*	*	*	x
P. pseudostrobus		x	*	*	*	*
P. ayacahuite		*	x	*	*	*
P. oocarpa		*	x	*	*	*

x, geographic distribution.
*, maxim kernel density.
**, restricted distribution.

species (*D. adjunctus*, *D. frontalis*, *D. mexicanus*, *D. rhizophagus*) and two are secondary species (*D. approximatus*, *D. valens*).

3.2. Distribution ranges and kernel densities

Dendroctonus: The distributions of the six *Dendroctonus* species in this study are similar to those reported by Salinas-Moreno et al. (2004) (Figs. 1 and 2). Except for *D. rhizophagus*, a species endemic to the Sierra Madre Occidental (SM Occidental), and *D. frontalis*, which is not found in the SM Occidental, all species are widely distributed in the major mountain systems of México: the SM Occidental, Sierra Madre Oriental (SM Oriental), Transverse Volcanic Belt, Sierra Madre del Sur (SM Sur) and Sierra de Chiapas (S Chiapas). There are records of four of these species in the S Baja California and for five species in the SM Occidental, Transverse Volcanic Belt, SM Oriental, SM Sur and S Chiapas.

The maximum kernel densities for the primary species were located within a single mountain system, whereas they occurred in two mountain systems for the secondary species (Table 3). For instance, *D. adjunctus* and *D. mexicanus* showed maximum kernel densities in the Transverse Volcanic Belt surrounding the Valley of México. *D. frontalis* showed maximum kernel densities in several areas of the SM Sur, although it was widely distributed. *D. rhizophagus* had maximum kernel densities in several areas of its distribution in the SM Occidental. On the other hand, the secondary species *D. valens* and *D. approximatus* showed maximum kernel densities in various areas of the SM Occidental and the Transverse Volcanic Belt.

The Transverse Volcanic Belt mountain range contained the most areas with maximum kernel densities (4 *Dendroctonus* spp.), followed by the SM Occidental (3 spp.), the SM Sur and the S Chiapas (one species each) (Table 3).

Pinus: Pines showed higher differences in distribution and kernel densities. Nine of the 25 species in this study (27%) are restricted to one or two of the six major mountain systems. The most limited distributions occurred in species that are not endemic to México: *P. jeffreyi* and *P. quadrifolia* are found only in the S Baja California, *P. greggii* and *P. pinceana* in the SM Oriental, and *P. engelmannii* in the SM Occidental. Moderate and wide distributions in more than three mountain systems are the norm for other pine species. For example, *P. ayacahuite*, *P. pseudostrobus*, *P. oocarpa* and *P. teocote* occur in five mountain ranges and have the widest distributions (Table 3).

Regional species richness of *Pinus* was directly inferred from these distributions. The S Baja California (2 spp.) and S Chiapas (8 spp.) contained the fewest species, followed by the SM Oriental (15 spp.), SM Sur (15 spp.) and SM Occidental (17 spp.). The Transverse Volcanic Belt harbored the most species (19 spp.). Areas of maximum kernel density for most taxa were shared by two or more mountain systems, with the exception of *Pinus* species occurring in only one system. At the regional level, the Transverse Volcanic Belt contained the most areas of maximum kernel density (17 spp.), followed by the SM Occidental (11 spp.), SM Sur (10 spp.), SM Oriental (9 spp.), S Chiapas (8 spp.) and S Baja California (2 spp.).

3.3. Percent incidence on host species

The six species of *Dendroctonus* in this study were widely polyphagous. *D. rhizophagus* and *D. valens* were found on the lowest

Table 4
Incidence (%) of each bark beetle species on *Pinus* host species.

Pinus species	Incidence of *Dendroctonus* species (%)					
	D. adjunctus	*D. approximatus*	*D. frontalis*	*D. mexicanus*	*D. rhizophagus*	*D. valens*
P. arizonica	9.4	2.8	2.3	3.9	26.0	10.9
P. ayacahuite	0.7	2.8		0.3	2.6	1.7
P. cembroides				1.6		1.7
P. devoniana		8.3	3.1	7.4		5.5
P. douglasiana	1.4	1.4	2.3	0.5		0.4
P. durangensis	10.8	**19.4**	2.3	3.7	20.8	11.8
P. engelmannii	0.7	6.9	2.3	2.4	**32.5**	5.5
P. greggii			2.3	1.3		2.1
P. hartwegii	**57.6**	11.1	1.6	0.8		2.5
P. herrerae	1.4	2.8	1.6	1.6	1.3	0.4
P. jeffreyi		1.4		0.3		6.3
P. lawsonnii			1.6	0.5		
P. leiophylla	2.9	16.7	6.3	**37.6**	5.2	**15.5**
P. lumholtzii		1.4		0.5	7.8	0.4
P. maximinoi	0.7		3.1	1.1		0.4
P. montezumae	4.3	1.4	2.3	6.8		9.2
P. oocarpa	0.7	2.8	**36.7**	5.0		7.1
P. patula	2.9	6.9		3.7		2.5
P. pinceana	1.4					
P. pringlei	0.7		17.2	2.1		1.7
P. pseudostrobus	2.2	4.2	3.9	8.2	1.3	4.6
P. quadrifolia						0.4
P. strobiformis		1.4				
P. strobus						1.3
P. teocote	2.2	8.3	10.9	10.8	2.6	8.0
	100.0	100.0	100.0	100.0	100.0	100.0

Bold numbers indicate preferred host for a particular bark beetle species.

(10 spp.) and highest (22 spp.) numbers of host species, respectively (Table 4). The primary beetle species had eight host species in common, but each preferred different pine hosts.

The commonness of beetles on hosts varied widely. For instance, *D. adjunctus* was recorded on *P. hartwegii* 57.6% of the time, whereas *D. frontalis*, *D. mexicanus* and *D. rhizophagus* were found on a particular host species about 30% of the time (*P. oocarpa*, *P. leiophylla* and *P. engelmannii*, respectively). *D. approximatus* and *D. valens* occurred at the lowest incidences for a single host species (15.5% *P. durangensis* and 19.4% *P. leiophylla*, respectively). One-third of all recorded instances of host use for *D. adjunctus*, *D. mexicanus* and *D. valens* were occasional (<1%).

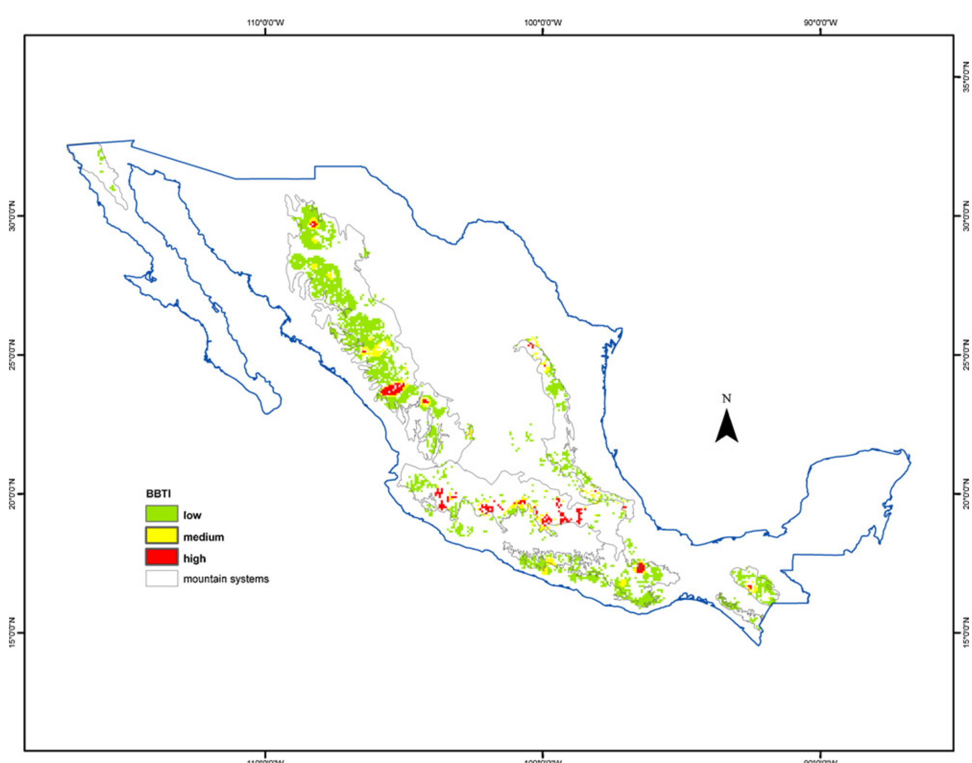

Fig. 3. Bark Beetle Threat Index of the genus *Dendroctonus* on pine forests in México.

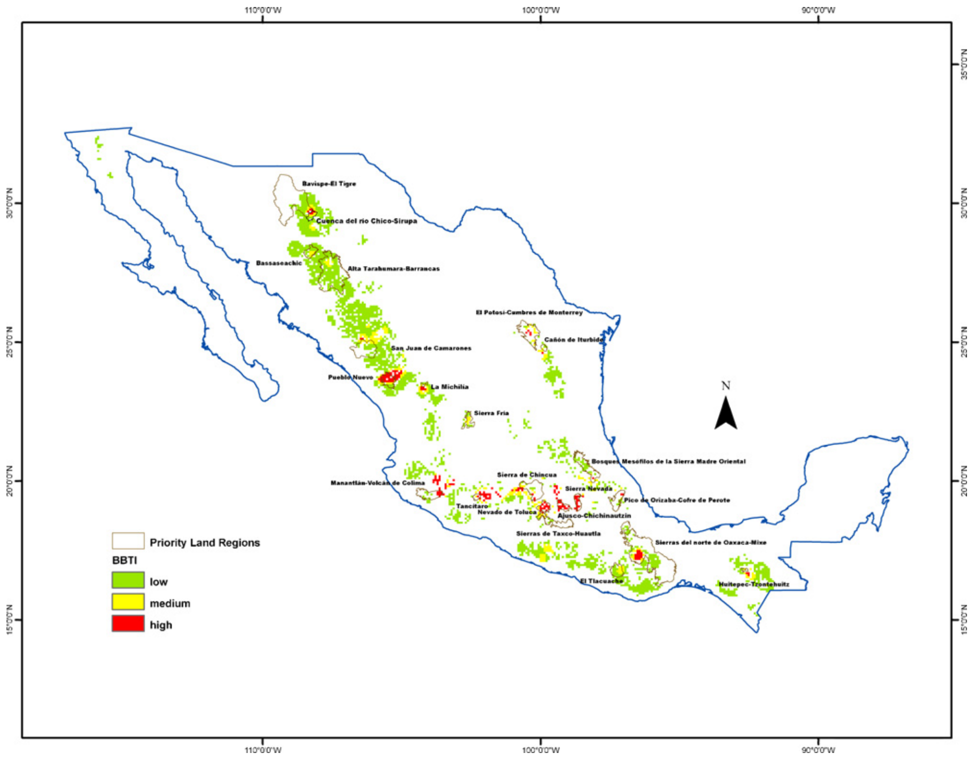

Fig. 4. Priority Land Regions that include areas with medium and high Bark Beetle Threat Index values.

Of the 25 *Pinus* species, almost one-third (7 spp.) were infested by all six *Dendroctonus* species and three-quarters (19 spp.) were infested by at least three of the beetle species.

3.4. Bark Beetle Threat Index

In BBTI maps of each pine species, most of the host species distributions show low-pressure values. This is the case for *P. leiophylla*, *P. durangensis*, *P. engelmannii*, *P. hartwegii* and *P. oocarpa*.

All three pressure intervals (low, moderate and high) occur in all mountain systems except the S Baja California (Fig. 3). Moderate and high-pressure zones cover small geographic areas compared with the total extent of the mountain systems. Furthermore, high-pressure zones are usually very close to each other within the same system.

Areas with high BBTIs are more common in the Transverse Volcanic Belt and SM Occidental; one such area is present in the SM Oriental, SM Sur and S Chiapas, and none are present in the S Baja California. High BBTIs can be used to identify some 16 vulnerable zones among the major mountain systems: SM Occidental (3), SM Oriental (1), Transverse Volcanic Belt (10), SM Sur (1) and S Chiapas (1). The largest vulnerable zones are in the SM Occidental, Transverse Volcanic Belt and SM Sur.

In the Transverse Volcanic Belt, 80% of the surface area from the western end to the eastern tip shows moderate and high BBTIs. In the SM Occidental, a large area in its southern portion has a high

Table 5
Priority Land Regions with highest BBTI values.

PLR name	State (mountain system)
(1) Sierra Fría	Aguascalientes, Zacatecas (SM Occidental)
(2) Alta Tarahumara-Barrancas	Chihuahua (SM Occidental)
(3) Bassaseachic	Chihuahua (SM Occidental)
(4) Cuenca del Río Chico-Suripa	Chihuahua (SM Occidental)
(5) Bavispe-El Tigre	Chihuahua, Sonora (SM Occidental)
(6) San Juan de Camarones	Durango y Sinaloa (SM Occidental)
(7) Pueblo Nuevo	Durango y Sinaloa (SM Occidental)
(8) La Michilía	Durango y Zacatecas (SM Occidental)
(9) El Potosí-Cumbres de Monterrey	Coahuila, Nuevo León (SM Oriental)
(10) Cañon de Iturbide	Nuevo León (SM Oriental)
(11) Manantlán-Volcán de Colima	Colima, Jalisco (Transverse Volcanic Belt)
(12) Ajusco-Chichinautzin	D. F., Estado de México y Morelos (Transverse Volcanic Belt)
(13) Nevado de Toluca	Estado de México (Transverse Volcanic Belt)
(14) Sierra de Chincua	Estado de México, Guanajuato, Michoacán (Transverse Volcanic Belt)
(15) Sierras de Taxco-Huautla	Estado de México, Guerrero, Morelos y Puebla (Transverse Volcanic Belt)
(16) Sierra Nevada	Estado de México, Morelos, Puebla y Tlaxcala (Transverse Volcanic Belt)
(17) Bosque mesófilos de la SM Oriental	Hidalgo, Puebla y Veracruz (Transverse Volcanic Belt)
(18) Tancítaro	Michoacán (Transverse Volcanic Belt)
(19) Pico de Orizaba-Cofre de Perote	Puebla, Veracruz (Transverse Volcanic Belt)
(20) El Tlacuache	Oaxaca (SM Sur)
(21) Sierras del Norte de Oaxaca-Mixe	Oaxaca, Puebla, Veracruz (SM Sur)
(22) Huitepec-Tzontehuitz	Chiapas (S Chiapas)

BBTI and two smaller areas show moderate values. In the rest of the country, only three other small areas stand out: one in the SM Oriental, a second in the SM Sur and a third in the S Chiapas.

The 16 areas of highest bark beetle pressure coincide at least partly with 22 of the Priority Land Regions, some of which have been designated Protected Natural Areas (Fig. 4, Table 5). The remainder of the high-BBTI areas fall outside of regions that are protected or proposed for conservation.

4. Discussion

The association between *Dendroctonus* species and their hosts is an ancient one (Labanderia et al., 2001; Sequeira et al., 2000). The common ancestor of the genus *Dendroctonus* is hypothesized to have occurred in North America in association with *Pinus* (Labanderia et al., 2001; Zúñiga et al., 2002). The present-day distribution of *Dendroctonus* appears to have followed the distribution of three groups of pines (*Ponderosae*, *Oocarpae* and *Leiophyllae*) in western North America, west México, and Central America (Farjon, 1996; Farjon and Styles, 1997; Wood, 1982; Zúñiga et al., 2002). The large extent of coniferous forest communities in western México is important in the history of this association because it is recognized as the setting for the diversification of pines in México (Eguiluz, 1985; Farjon and Styles, 1997) and also contains the highest diversity of *Dendroctonus* species in México (Salinas-Moreno et al., 2004). The availability and distribution of these groups of pines plays a major role in the biogeographic history and current ecology of these insects in México. The mountain systems create a mosaic of interactions between *Dendroctonus* and *Pinus* throughout México, directly influencing the vulnerability of pine forests to bark beetle outbreaks (Aukema et al., 2006; Raffa et al., 2008).

4.1. Geographic variation in species richness of Dendroctonus and Pinus

Despite the historic association of *Dendroctonus* with certain groups of pines, records obtained during the last hundred years for the genus *Dendroctonus* in México indicate differences in the geographic patterns of species richness of these insects and their hosts. The fact that species diversity of *Dendroctonus* is highest within the SM Occidental, which does not coincide geographically with the areas of highest host species diversity, can be explained by more recent ecological biogeography (Farjon and Styles, 1997; Millar, 1998; Zúñiga et al., 2002). The SM Occidental has the largest extent of continuous coniferous forest in México, a pronounced elevation gradient, a complex topography and consequently a climate gradient (Rzedowski, 1981; Sánchez et al., 2003). While the Transverse Volcanic Belt mountain system continues to support the highest diversity of pine in México, its forests are highly fragmented (Farjon and Styles, 1997). Discontinuity reduces the total available forest surface and the potential connectivity of insect populations (Challenger, 1998; Sánchez et al., 2003). Also, the east-west direction of the Transverse Volcanic Belt does not offer the variety of climates that the SM Occidental does, except for changes in isolated mountain peaks that derive from the elevation gradient.

4.2. Pressure on pine forests by Dendroctonus

Not surprisingly, given its high diversity of pines, the Transverse Volcanic Belt has experienced the greatest number of outbreaks of bark beetles than any other mountain range in México over the past hundred years (SEMARNAT, 2006). In the Transverse Volcanic Belt and elsewhere, high-BBTI areas seem to be the convergence of two factors: naturally greater host availability (Perry, 1991) and management and forest conditions (SEMARNAT, 2006).

The dominant tree species in the Transverse Volcanic Belt are *P. montezumae*, *P. teocote*, *P. leophylla* and *P. hartwegii* (Rzedowski, 1981). These are preferred hosts of *D. frontalis*, *D. mexicanus*, *D. valens* and *D. adjunctus*, respectively. Host presence, however, does not necessarily lead to recurrent beetle presence. Rather, the presence of other disturbance or stress factors seemingly has contributed to the vulnerability of these forests to beetle outbreaks. Extensive commercial logging, destruction of seedling sources necessary for natural forest regeneration, radical transformation of soil characteristics and land-use conversion to agricultural production, cattle-raising and human settlement have also resulted in the reduction and fragmentation of these forests (Challenger, 1998; Sánchez et al., 2003).

A fairly similar situation occurs in isolated areas of the SM Occidental with high BBTIs. Here, all the dominant pine species are hosts of *Dendroctonus* (Salinas-Moreno et al., 2004) and are of high commercial value (Rzedowski, 1981). During the past hundred years, forests in most of the tablelands have been extensively logged (Lammertink et al., 1996). This logging has altered the structure and composition of plant communities. The dominant pine species differ from the original species or have replaced other conifers (Challenger, 1998; SEMARNAT, 2006). As a result, most present-day forests are second-growth forests. Our results suggest that this process may have created unstable forest communities (i.e., more vulnerable insect-host relationships) and influenced the recurrent presence of *Dendroctonus* in particular areas.

At the same time, the integrity of many ecosystems and secondary forest communities within the SM Occidental remains high (Arriaga et al., 2000). A high integrity means that complete plant and animal communities exist in the area and that in that area natural processes of succession are occurring. In high-elevation areas, extreme temperatures (INEGI, 2004) probably keep the recurrent presence of these insects under control (Aukema et al., 2006; Beukema et al., 1997; Raffa et al., 2005) and may explain the low BBTIs.

In the SM Sur, pine community composition is very similar to that in the Transverse Volcanic Belt and *P. oocarpa* is the most widely distributed species. This diversity of pine species favors the presence of bark beetles of the genus *Dendroctonus*; however, as in the SM Occidental, high levels of ecological integrity have been reported for large areas of the SM Sur (Arriaga et al., 2000). This may explain the fact that most of the SM Sur has low BBTIs. The exceptions are areas that have been intensively logged, represented by the high-BBTI area in the mountain ranges of northern Oaxaca. In recent decades the logging industry has extracted mostly timber-yielding resources without sustainable forest management (Challenger, 1998). The high-BBTI area in northern Oaxaca coincides with extensive commercial logging in this region beginning in the 1950s (Challenger, 1998). Similarly, the area in the SM Occidental within the state of Durango has been subjected to intensive logging. Despite this, pine–oak forests in both mountain systems still maintain high biodiversity and important forest resources (Sánchez et al., 2003; Toledo and Ordoñez, 1998).

A number of moderate- and high-BBTI areas fall within Priority Land Regions (PLRs) or Protected Natural Areas (PNAs) (Arriaga et al., 2000). These areas have been proposed (PLRs) or designated (PNAs) for protection due to their unique ecological and biological values. In particular, high BBTIs in the Transverse Volcanic Belt represent areas included under both categories (PLRs and PNAs) such as the Sierra Nevada, Ajusco-Chichinautzin, Nevado de Toluca and Tancítaro. In these areas, deforestation, forest fires, forest fragmentation, and pressure on particular pine species have been ongoing for several decades or centuries (Sánchez et al., 2003). In terms of conservation, the Transverse Volcanic Belt is ranked along with the SM Occidental and SM Sur as one of the highest areas of pine species richness and in numbers of infraspecific pine taxa. Thus, they are of great importance in the evolutionary history of *Pinus* owing to the hybridization, adaptive radiation and speciation events which have taken place (Styles, 1998).

PLRs in the SM Occidental that are vulnerable to bark beetles (Pueblo Nuevo, Cuenca del Río Chico-Sirupa, Bavispe-El Tigre, Alta Tarahumara-Barrancas) are of biological importance. The SM Occidental is recognized as a center of natural diversity for *Pinus*, a biological corridor for *P. arizonica* and *P. durangensis* and a reservoir of *Ponderosae* species (Arriaga et al., 2000). PLRs with high BBTIs in the SM Sur (El Tlacuache, Sierras del Norte de Oaxaca-Mixe) are areas of high biological diversity in conifers and oaks, providing important ecosystem services (Challenger, 1998).

4.3. BBTI and use of preferred pine species

The preference for certain hosts (specifically *P. leiophylla*, *P. durangensis*, *P. engelmannii*, *P. oocarpa* and *P. hartwegii*) exhibited by *Dendroctonus* in México has been documented before (Salinas-Moreno et al., 2004). Our results indicate that preferred hosts in some areas have been more vulnerable to beetle attack. *P. leiophylla*, the preferred species of *D. mexicanus* and *D. valens*, is widely distributed in México from the SM Occidental to the Transverse Volcanic Belt and south to the SM Sur. Most of the *P. leiophylla* areas have low BBTIs, except the Transverse Volcanic Belt.

P. durangensis and *P. engelmannii* are preferred species of *D. approximatus* and *D. rhizophagus*, respectively, and are potential hosts of most *Dendroctonus* considered here. Because both pine species are widely distributed within the SM Occidental, they coexist throughout their distribution ranges and in the high-BBTI area in the state of Durango. A possible reason for the fact that both occur in areas with high BBTIs is that they have high commercial value and are the most frequently logged timber-yielding tree species in México. *P. durangensis* originally formed large, pure forests in Durango and Chihuahua, but now is found only in scattered, isolated, mixed-vegetation areas through most of its range (Perry, 1991). *P. durangensis* and *P. engelmannii* remain dominant species, even when occurring with other host species such as *P. leiophylla*, *P. arizonica*, *P. teocote* and *P. cooperi*, and may therefore sustain higher beetle incidence in these areas.

P. oocarpa is the preferred host species of *D. frontalis* and is, indeed, host to several species of *Dendroctonus* in western, central and southern México. The high-BBTI areas for this species are located in the Transverse Volcanic Belt and S Chiapas. That *P. oocarpa* occurs along with *P. leiophylla* in the Transverse Volcanic Belt probably contributes to the maximum BBTIs in that region. Both species are primary resin producers in México. As in the Transverse Volcanic Belt, high-BBTI areas in the central part of the country coincide with a resin-production area. The occurrence of *P. oocarpa* at lower elevations and further south in México probably contributes to the high-BBTI area in the S Chiapas.

Of the five preferred pine species mentioned here, *P. hartwegii* has the lowest percent incidence of bark beetle presence. It is, however, the preferred host of *D. adjunctus*, one of the most aggressive species in southwestern US, México and Central America. In México, *P. hartwegii* is typically found at elevations above 3000 m and is present primarily in the northeastern, central and southern portions of the country (Perry, 1991; Rzedowski, 1981). High-BBTI areas for *P. hartwegii* coincide with the high peaks that characterize the Transverse Volcanic Belt, in particular those surrounding the Valley of México, which have sustained greater impact (logging and fires) as a result of human activities (Challenger, 1998).

5. Conclusion

Despite the vast area of geographic coincidence of *Pinus* and *Dendroctonus* across all mountain ranges in México, the regions of highest bark beetle pressure are restricted to small zones within specific mountain systems (the Transverse Volcanic Belt, followed by the SM Occidental and the SM Sur), which have sustained the greatest impact from this insect group during the last hundred years. The forest communities in these regions are among the most important in species diversity and genetic resources of *Pinus* in México. Our results suggest this pine diversity is the primary factor determining vulnerability to beetle-caused mortality at the regional level, whereas disturbance from extensive logging and ecosystem change appear to be the key factors behind high vulnerability at the local level.

In practical terms, these results help define the areas that might sustain high impact by these insects. This study also provides a geographic database that can be used to determine forest resource management and conservation policies in México.

Acknowledgments

This paper presents part of the results of Project CONAFOR 2002-CO1-5829, funded by CONAFOR-CONACyT. Ager and Hayes were supported in part by PNW and WWETAC. We are grateful to Erika A. García N. and Gloriela Aldana V. for their help in preparing the databases, and to Bridgett Naylor for help with ArcMap. We thank to Guillermo Sánchez-Martínez for helpful comments on earlier drafts of the manuscript.

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