



Impact of the first recorded outbreak of the Douglas-fir tussock moth, *Orgyia pseudotsugata*, in southern California and the extent of its distribution in the Pacific Southwest region



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ABSTRACT

The Douglas-fir tussock moth (DFTM), *Orgyia pseudotsugata* McDunnough (Lepidoptera:Erebidae: Lymantrinae), is a native western North American defoliator of true fir, *Abies* spp. Mill., and Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco. We investigated the population genetics and impact associated with the first recorded outbreak of DFTM in southern California (USA), and report the first collection of DFTM in Baja California Norte, Mexico. This latter population is similar genetically to populations from Washington, USA and British Columbia, Canada. We assessed forest stand characteristics, levels of defoliation, and mortality of white fir, *Abies concolor* Lindl., associated with the DFTM outbreak in the Transverse Mountain Ranges of southern California. We compared these data to those from southern California non-outbreak stands of *A. concolor*, and from virgin stands with an *A. concolor* component in the Sierra San Pedro Martir National Park (Mexico). Total stand density (ha^{-1}) was significantly higher (22%) in non-outbreak stands than in outbreak stands. However, outbreak stands had significantly higher mortality of *A. concolor* than non-outbreak stands [whether expressed as density (70%) or basal area ($\text{m}^2 \text{ha}^{-1}$) (32%)]. Total stand and *A. concolor* density and basal area for living and dead trees were significantly lower in the Sierra San Pedro Martir National Park than in southern California. Dead *A. concolor* comprised >95% of all tree mortality in both outbreak and non-outbreak areas in southern California, which corresponded to a mean 20% basal area loss of *A. concolor* associated with DFTM feeding injury within the outbreak area. The mean level of defoliation of *A. concolor* by DFTM was 39%, and 62% of all dead *A. concolor* were associated with DFTM defoliation. In stands with high levels of defoliation, larval feeding and tree mortality were also noted in Jeffrey pine, *Pinus jeffreyi* Grev. & Balf. The amount of dead *A. concolor* basal area associated with the fir engraver, *Scolytus ventralis* LeConte (Coleoptera: Scolytidae), in non-outbreak stands was 96% greater than in outbreak stands. Using the U.S.D.A. National Insect and Disease Risk Map software, a total of 13,534 ha were predicted to be at risk to basal area loss from future DFTM outbreaks on national forest lands in southern California. Changes in forest management practices and fire suppression policies likely led to an increase in the density and continuity of DFTM's preferred host in southern California and to a southward shift in the historic range of DFTM outbreaks.

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1. Introduction

Changes in forest land management objectives and practices have subsequently increased the economic and ecological

significance of native forest insect species in Asia, Europe, and North America (Nilsson, 1976; McFadden et al., 1981; Dahlsten and Rowney, 1983). Timber management practices leading to greater forest stand densities, off-site plantings, and even-aged monocultures have resulted in higher levels of activity and impact of native bark beetles, defoliators, and regeneration pests (Graham, 1956; Sartwell and Stevens, 1975; Smith, 1976; Knight and Heikkinen, 1980; Wermelinger, 2004; Chen and Tang, 2007; Grodzki, 2008;

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Schaupp et al., 2008). Furthermore, successful wildfire suppression policies in North America have altered the composition and structure of forests and led to new forest pest impacts (Baker, 1992; McCullough et al., 1998; Taylor, 2001; Parker et al., 2006).

Similar shifts in forest stand composition occurred throughout California (USA) following timber harvesting, fire suppression, and grazing in the late 1800s and early 1900s (Leiberg, 1899; McKelvey and Johnston, 1992; Taylor, 2004). Following these anthropogenic disturbances, shade-tolerant species, like true firs, *Abies* spp. Mill., increased in density, and there was a reduction in the number and distribution of age and size classes of these species (North et al., 2007). As a result, white fir, *Abies concolor* Lindl., now represents a greater component of forest stands in California (Parsons and DeBenedetti, 1979; Minnich et al., 1995).

The Douglas-fir tussock moth (DFTM), *Orgyia pseudotsugata* McDunnough (Lepidoptera: Erebidiae: Lymantriinae), is a native defoliator found throughout coniferous forests of western North America (Furniss and Carolin, 1977; Brookes et al., 1978). Larvae of the DFTM feed preferentially on Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, and grand fir, *Abies grandis* Lindl. in old-growth pine-fir forests (Brookes et al., 1978). Outbreaks of this insect have also occurred in subalpine fir, *A. lasiocarpa* [Hook] Nutt., along the northern edge of its range (Hansen, 1995). At the southern extent of the range of the moth (Arizona, California, Nevada, and New Mexico), *A. concolor* is the primary host (Brookes et al., 1978; Wickman et al., 1981). Since the early 20th Century, DFTM outbreaks were recorded every decade in the western USA (Wickman et al., 1973; Berryman, 1978; Shepherd et al., 1988; USDA FHTET, 2013). High levels of defoliation by DFTM during outbreaks can cause reductions in growth, top-kill, and tree mortality across all size classes of host conifers (Wickman et al., 1981; Alfaro et al., 1987). When population densities are elevated at high-use recreation sites, urticating hairs from larvae can cause human discomfort and health concerns, commonly known as “tussockosis” (Perlman et al., 1976). Tree mortality associated with DFTM feeding has occurred frequently following complete defoliation (>90% needle loss) of a tree (Wickman, 1978). However, top-kill can occur when 50–90% of the crown is injured by caterpillars (Wickman, 1978). Low level defoliation by DFTM rarely kills host trees, but injury can predispose trees to attack by either the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, or the fir engraver, *Scolytus ventralis* LeConte (both Coleoptera: Scolytidae, *sensu* Bright, 2014) (Wickman et al., 1981; Wright et al., 1984).

The DFTM is univoltine and male moths fly typically from July to November, when mating occurs (Wickman, 1963). Flightless females can lay up to 150–200 eggs in a single egg mass, which is deposited on the cocoon from which the female emerged. Populations overwinter in the egg stage, and egg hatch is synchronized the following year with bud burst and shoot elongation of host trees, which occurs from May to early June (Brookes et al., 1978). Larvae complete four to six instars during the summer months. First-instar larvae migrate to the tops of trees where they feed preferentially on new foliage or balloon to other host trees within the stand to feed (Brookes et al., 1978). Late-instar larvae typically consume older foliage and will feed throughout the crown when population densities reach outbreak levels. Pupation occurs from late July to August on foliage with eclosion occurring 10–18 d later (Wickman et al., 1981).

Outbreaks of DFTM can persist for three to four years in forest stands, and population densities can increase and decrease dramatically during the outbreak cycle (Wickman et al., 1973; Hansen, 1995). Increases in densities of insect natural enemies, the naturally occurring nuclear polyhedrosis virus (NPV), and the loss of suitable host material can contribute to population collapse (Wickman et al., 1973; Mason et al., 1983; Otvos et al., 1987). Fire suppression activities have transformed pine-fir forests to true

fir- and Douglas-fir-dominated stands across the native range of DFTM, which has increased the likelihood of outbreaks (Wickman et al., 1981).

Historically (1916–1984), DFTM outbreaks in California were limited to the Sierra Nevada Mountain Range (Shepherd et al., 1988; Fig. 1). However, in 1996 an outbreak on *A. concolor* was recorded in the southern Sierra Nevada, and, in 2009, high-levels of defoliation of *A. concolor* by the DFTM were first detected in the Transverse Mountain Ranges of southern California on the San Bernardino National Forest (San Bernardino Co.). The DFTM had been collected in the 1950s, 1960s, and 1970s on the Angeles and San Bernardino National Forests, but no outbreak was ever reported (Natural History Museum, Los Angeles Co., USDA Forest Service Hopkins U.S. System Index, 1929–1955; Wickman et al., 1973, 1981; Shepherd et al., 1988). These collections also represented the southernmost recorded collection of the species in the Pacific Southwest region of North America.

This first recorded DFTM outbreak in southern California provided an opportunity to compare the forest stand characteristics and impact associated with this event to previous outbreaks in the western USA. It also allowed us to compare these characteristics and impacts with those in similar, nearby lightly infested or uninfested forest stands in California and in Baja California Norte, Mexico. At the latter location, no previous timber management and limited fire suppression activities had occurred (Maloney and Rizzo, 2002; Stephens and Gill, 2005). We also compared mitochondrial DNA sequence similarity of DFTM from populations in southern California and Mexico to populations along the northern edge of its distribution (Washington, USA and British Columbia, Canada) to verify DFTM species status in these isolated populations in the Transverse Mountains and Sierra San Pedro Martir (Fig. 1). We predicted basal area loss from future DFTM outbreaks in southern California by assessing forest stand measurements collected in this study with the U.S.D.A. National Insect and Disease Risk Map software (Krist et al., 2013). The risk model is a multi-criteria geographic information system (GIS) application built on ArcGIS technology that can account for regional variations and can be applied at varying landscape scales (ESRI Inc., Redlands, CA, USA). As an outcome of the risk analysis, spatial predictions were made for future DFTM population increases so that stand thinning prescriptions could be developed to reduce short- and long-term negative impacts from future outbreaks.

2. Methods

2.1. Genetic analyses

Larvae from the Pacific Southwest region were collected on foliage and bark surfaces of *A. concolor* and stored in 99% ethanol at -80°C (San Bernardino National Forest) or -2°C (Baja). These larvae and those from a northern site (10 specimens: San Bernardino National Forest, N 34.22425°, W 116.87723°; 7 specimens: collected on *P. menziesii* from the Okanagan National Forest, WA, USA N 48.575°, W 120.258333°; and 2 specimens: Sierra San Pedro Martir National Park, Baja California Norte, Mexico, N 30.99863°, W 115.55489°) were subjected to population genetic analysis. Whole genomic DNA was extracted from individual specimens by using a Nucleospin® Tissue XS Kit (Macherey-Nagel, Düren, Germany). Genetic variation was examined by amplifying a 658 bp fragment of the mitochondrial gene (mtDNA) for cytochrome oxidase c subunit 1 (COI) with the polymerase chain reaction (PCR). Reactions were performed in 25 μl volumes containing 2 μl of DNA template (concentration around 30 ng/ μl), 1x PCR Buffer without MgCl_2 (Sigma, St. Louis, MO, USA), 2.5 mM MgCl_2 , 400 μM of each dNTP, 1 U REDTaq Genomic DNA polymerase (Sigma), and 1 μM each of



Fig. 1. Location of Douglas-fir tussock moth (DFTM), *Orgyia pseudotsugata*, outbreaks prior to 1984 in western North America (Modified from Shepherd et al., 1988). Outbreaks (solid perimeters) are grouped into zones (dashed perimeters) and black regions indicate where outbreaks occurred in more than 50% of potential outbreak periods from 1916 to 1984. Recent DFTM outbreaks in California south of previously known outbreaks are also indicated on the map (●: 1996–1999 Sequoia National Forest and ■: 2009–2012 San Bernardino National Forest). The site of collection of DFTM from the Sierra San Pedro Martir National Park, Baja California Norte, Mexico is also indicated (*). The geographic region of the current study (Pacific Southwest) is delimited by the rectangle on the map.

the primers LCO1490 (5'-GGTCAACAAATCATAAAGATATTGG-3') and HCO2198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3') (Folmer et al., 1994). PCR was carried out by using a 2720 Thermal Cycler (Applied Biosystems, Foster City, CA, USA) with the following settings: 5 min at 94 °C; followed by five cycles of 30 s at 94 °C, 40 s at 47 °C, and 1 min at 72 °C; followed by an additional 40 cycles of 30 s at 94 °C, 40 s at 52 °C, and 1 min at 72 °C; and a final extension of 5 min at 72 °C. Successful amplification was confirmed by agarose gel electrophoresis and PCR products were subsequently cleaned by using a Nucleospin® Gel and PCR Clean-up Kit (Macherey-Nagel).

PCR fragments were sequenced in both directions by using the ABI Prism® BigDye® Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems). Sequencing reactions were purified by ethanol precipitation, loaded on a 3500 Genetic Analyzer (Applied Biosystems)

and analyzed with Sequencing Analysis v5.4 software. Sequences were aligned by ClustalW Multiple alignment in BioEdit 7.0.9.0 (Hall, 1999), and primer sequences were removed from the analysis. COI sequences were translated by using the EMBOSS-Transeq website (<http://www.ebi.ac.uk/Tools/emboss/transeq/index.html>) to confirm the absence of nuclear pseudogenes (Song et al., 2008). The sequences were aligned with the sequences of three *O. pseudotsugata* accessions retrieved from BOLD SYSTEMS databases (<http://www.barcodinglife.com/>) (GenBank Accessions: HM868458, HM868376, and HM869385 from N 50.643°, W 120.485°; N 49.291°, W 119.591°; and N 49.318°, W 119.507°, respectively, from unrecorded hosts in the vicinity of Kamloops and Okanagan Falls, British Columbia, Canada). All sequences were cut to obtain a similar size of 647 bp. A haplotype (H) network was constructed by using TCS version 1.21 with default run settings

(Clement et al., 2000). The genetic distances were computed by using MEGA 4.0 software according to the K2P model (Tamura et al., 2007). The phylogenetic tree was built by using the NJ method and three congeneric outgroup taxa from the GenBank Database: *Orgyia antiqua* Linnaeus (GU707344.1), *Orgyia definita* Packard (GU090644.1), and *Orgyia vetusta* Hampson (DQ116166.1). The sequences analyzed in this study were deposited in GenBank [accession numbers KF419176 to KF419185 (California); KF419186 and KF419187 (Mexico); and KF419169 to KF419175 (Washington)].

2.2. Forest stand assessments

Preliminary ground surveys were conducted to delimit the distribution of the DFTM outbreak prior to sample site establishment (Coleman, unpublished data). To determine the presence and level of DFTM injury (defoliation, top-kill, and tree mortality), we surveyed the twigs, branches, and main stem of *A. concolor* for partially eaten needles, old and new egg masses, and pupal cocoons (Wickman et al., 1981). Survey sites were established in the San Bernardino National Forest from June to September in 2011 and 2012 within areas affected by the DFTM outbreak (outbreak stands) and in stands with no DFTM defoliation (non-outbreak stands). Non-outbreak sites were chosen to provide a comparison to allow us to differentiate previous *A. concolor* top-kill and mortality from other biotic and abiotic factors not associated with DFTM injury (Blais, 1981; Alfaro et al., 1987). Non-outbreak sites were established in forest stands with similar management histories and similar species composition to the outbreak sites, either dominated or co-dominated by *A. concolor*, to highlight the impact of the DFTM outbreak by reducing the variation in forest stand age, composition, and disturbance history. Subsequent surveys were conducted in January 2013, after the outbreak, to record any additional tree mortality.

Following the preliminary ground surveys, sites were located arbitrarily within the outbreak to assess the impact from DFTM, and included areas exposed to a single year or multiple years of defoliation. Twenty-four sites were established in outbreak stands, whereas 15 sites were established arbitrarily in non-outbreak stands. Sites were separated by >100 m within the outbreak area and often separated by forest roads, ski runs, and steep slopes. Non-outbreak sites were located at Jenks Lake, Heart Bar, Barton Flats, Bear Mountain Resort, Snow Summit Resort, and adjacent to the San Gorgonio Wilderness on the San Bernardino National Forest, Mountaintop Ranger District. In 2011 and 2012, twelve sites were established randomly in the Sierra San Pedro Martir National Park (Baja California Norte, Mexico) to survey *A. concolor* in areas with limited forest management activities (i.e., tree thinning and fire suppression). At least 1 km separated these sites, which were all classified as non-outbreak. All sites were located >30 m from the forest boundary to minimize any edge effects.

Within each site, three to five 0.04 ha fixed-radius plots were established so that we could sample for forest stand characteristics and DFTM impact. Plots were established in a transect with approximately 30 m separating plot boundaries. Tree species, tree count, tree status (living/dead, top-kill), diameter at breast height (DBH in cm), level of DFTM defoliation (%), and signs of bark beetle attack were recorded for all trees >12.5 cm DBH within a plot. Total stand and *A. concolor* density (ha^{-1}) and basal area ($\text{m}^2 \text{ha}^{-1}$) were calculated from these plot data. Measurements were recorded from both living and dead trees in the three previously described forest locations.

Douglas-fir tussock moth defoliation was estimated for each tree by recording the percentage of the crown that was consumed based on the seven-point scale (10%, 25%, 50%, 75%, 90%, 99%, and 100%), developed by Wickman (1978). Several people made visual

estimates of defoliation during the field surveys. As a rule, 10% defoliation corresponded to feeding only on new growth confined to the top 10% of the crown, whereas 50% defoliation corresponded to defoliation on all new growth throughout the crown and defoliation of older needles in the top half of the crown. One hundred percent defoliation was associated with feeding throughout the crown that affected old and new needles.

Measurements from the sample plots were synthesized to yield estimates of mean defoliation (%) and density of *A. concolor* top-kill (ha^{-1}) for the three stands. *A. concolor* mortality (%) and top-kill were calculated from the seven-point defoliation scale, corresponding to previous defoliation and tree mortality assessments (Wickman, 1978). Observations of top-killing were limited to the 2012 surveys in the outbreak sites due to the difficulty in differentiating defoliation and death of the main leader in 2011. The density (ha^{-1}) and basal area ($\text{m}^2 \text{ha}^{-1}$) of dead *A. concolor* with DFTM defoliation were calculated for each surveyed forest stand. Previous top-kill and mortality of *A. concolor* were noted by the presence of decaying branches and absence of fading foliage.

We noted bark beetle attack on *A. concolor* by observing the presence of frass in bark crevices, entrance and emergence holes of adult beetles, and by exposing egg and larval galleries by removing the bark (Furniss and Carolin, 1977). Density (ha^{-1}) and basal area ($\text{m}^2 \text{ha}^{-1}$) of dead *A. concolor* correlated with this *S. ventralis* activity were calculated for each forest stand area to differentiate recent tree mortality associated with DFTM defoliation from previous tree mortality not associated with the DFTM injury.

No recent (<10 yr) forest management occurred within either the outbreak or non-outbreak sites in southern California except for (1) a wildfire fuel break that was installed in 2006 on the southern end of the DFTM outbreak, and (2) limited hazard tree abatement and removal of understory trees and shrubs for fuels reduction adjacent to slopes and structures in a high-use recreational ski resort area. No timber harvesting had occurred in the Sierra San Pedro Martir National Park, but limited fire suppression activities had occurred there since the 1970s (Stephens et al., 2003; Stephens and Gill, 2005). Mean annual temperature recorded for the southern California sites was 8 °C with a mean annual maximum temperature of 17 °C and a mean annual minimum temperature of 0 °C (Big Bear, CA; WRCC, 2013). Mean annual precipitation for the outbreak and non-outbreak sites was 56 cm occurring primarily from October to March. Temperature data in the Sierra San Pedro Martir National Park is limited, but over a three-year period annual precipitation ranged from 45.6 to 70 cm at three locations on the plateau in the park (Minnich et al., 2000).

2.3. Risk modeling

To predict the risk of basal area loss from future DFTM outbreaks and to direct future thinning activities in southern California, we applied the U.S.D.A. Forest Service Risk Modeling Application (RMAP) software, which was developed by Krist et al. (2014) to support model development for the 2013–2027 National Insect and Disease Risk Map (NIDRM). The NIDRM utilizes a peer-reviewed, multi-criteria modeling process and integrates multiple insect and disease models to identify the severity and extent of tree-mortality hazard due to insects and diseases (Krist et al., 2010). Criteria were identified from a review of the relevant literature, weighted, and scaled to determine the risk, or more appropriately hazard, for future DFTM outbreaks.

Regions where *A. concolor* is abundant on the four national forests in southern California were included in the risk model [Angeles, Cleveland (only Palomar Mountain), Los Padres, and San Bernardino, i.e., Kern, Los Angeles, Riverside, and San Bernardino, and San Diego Cos.]. The *A. concolor* host layers were modeled at 40 m by utilizing a subset of U.S.D.A. Forest Inventory Analysis

(FIA) and intensified plot data from southern California. This survey system is based on randomly located, but not publically revealed sample plots. The Sierra San Pedro Martir National Park was not included in the risk analysis due to the unavailability of forest inventory data for this region.

Our risk model was adapted from the NIDRM model to account for regional variation and to include additional criteria. Criteria included *A. concolor* basal area ($\text{m}^2 \text{ha}^{-1}$); percentage of *A. concolor* in a stand; tree density (ha^{-1}); quadratic mean diameter of *A. concolor* (cm DBH); terrain position index; and soil drainage index for predicting risk (i.e., basal area loss) from DFTM outbreaks (Krist et al., 2010; Schaetzl et al., 2012). Each criterion was weighted for importance as a predictor in the model (modified from Eastman, 1999) (Table 1). We assigned *A. concolor* basal area and percentage of *A. concolor* the most weight because stands with a large proportion of DFTM host (60–100% host type) are considered to be at highest risk to DFTM (Stoszek, 1977; Williams et al., 1979; USDA PNW, 2000). To calculate conservatively where risk from the DFTM is initiated in the model, *A. concolor* density and basal area were measured on the San Bernardino National Forest from the hypothetical origin of the outbreak (i.e., where defoliation was observed initially in 2009 and the area with the highest level of tree mortality, 80% *A. concolor* host type and $38 \text{ m}^2 \text{ha}^{-1}$, Table 1).

Mature forests with a high density of susceptible hosts and forests located on poor growing and drier sites are at higher risk to outbreaks from DFTM (Dunning, 1942; Stoszek, 1977; Williams et al., 1979). As a result, forest stands on drier slope positions (e.g., higher percentage slope and lower drainage index) were noted as having greater risk to DFTM outbreaks in the risk model (Table 1) and weighted as a contributing factor ($\frac{1}{2}$) in the model.

Each criterion was scaled as having no risk and a beginning, peak, and maximum risk if the parameter was not constrained (Table 1). Risk curves increased linearly for *A. concolor* basal area, *A. concolor* density, percentage of *A. concolor*, and slope position (%), whereas risk followed an inverse linear relationship for drainage index (%) (Table 1). Beginning and peak/maximum risk scaling were obtained either from the current forest stand data or previously published DFTM data (Table 1). Since DFTM outbreaks have never started in smaller diameter trees, quadratic mean diameter of *A. concolor* was constrained to all trees >12.5 cm DBH, such that all trees over this diameter limit were at equal risk to DFTM basal area loss (Table 1).

In the model, maximum basal area loss (%) was constrained by the mean *A. concolor* basal area loss (20%) recorded from the 2008 to 2011 DFTM outbreak in southern California (see Section 3). The predicted basal area loss assumes a single outbreak event in the region over a 15-yr period. Mean predicted basal area loss (20%) was partitioned into three risk categories [low (1–7%), moderate (8–14%), or high (15–20%) risk of basal area loss from DFTM defoliation] to highlight the most susceptible areas.

Individual insect and disease outputs from the U.S.D.A. Insect and Disease Risk Model have not been formally validated.

However, validation of the 2013–2027 National Insect and Disease Risk Map model predictions is underway at the regional level for various insects and diseases (Coleman, unpublished data). Host layers incorporated into the models were reviewed for accuracy by regional vegetation mappers (USDA Forest Service, Pacific Southwest Region) and Forest Health Protection employees (USDA Forest Service, Pacific Southwest Region) and by conducting ground survey checks.

2.4. Data handling and statistical analyses

For all data analyses, a critical value for significance of $\alpha = 0.05$ was used, and all analyses were performed with SAS 9.2 (SAS, 2010). A generalized linear model (PROC GLM) was used to compare differences in forest stand characteristics among the three forest stands (outbreak, non-outbreak, and Sierra San Pedro Martir National Park). Homogeneity of variances was checked by comparison of residuals, and assumptions of normality were checked for all data by using the Shapiro–Wilk test (PROC UNIVARIATE). Those data not meeting assumptions of normality were transformed by using the $[\log_{10}(x + 1)]$ function. Overall tests of significance were determined and means were compared by using the REGWQ procedure (Day and Quinn, 1989). A scatter plot of mean percentage of *A. concolor* mortality versus mean percentage of *A. concolor* defoliation recorded within a stand was fitted with a curvilinear regression to further characterize levels of tree mortality within the outbreak area. The regression was conducted by using SigmaPlot Version 12.0 (Systat Software, Inc., San Jose, CA, USA).

3. Results

3.1. Genetic analyses

The COI gene region was sequenced from 19 specimens, revealing 9 haplotypes. Four haplotypes were identified only from California, 4 ha plotypes were identified only from Washington, and 1 haplotype was identified only from Mexico. The geographic distribution of the haplotypes that we collected is very structured with all San Bernardino National Forest specimens grouped into a single network (haplotypes BCOPO45–BCOPO54) (Fig. 2). The COI sequences of specimens from Mexico differed from the San Bernardino National Forest material by 0.77–0.93%; whereas the COI sequences of specimens from Mexico differed from Washington by 0.46–0.62%. A phylogenetic analysis of the haplotypes revealed that there was no separation among the DFTM populations collected from the San Bernardino National Forest outbreak area, Mexico, Washington, and similar sequences retrieved from GenBank, suggesting that all specimens that we collected were DFTM. The three *Orygia* species used as outgroups segregated from the DFTM populations as separate clades (Fig. 2).

Table 1

Model parameters used to predict the risk of basal area loss in white fir, *Abies concolor*, from the Douglas-fir tussock moth, *Orygia pseudotsugata*, on the Angeles, Cleveland, Los Padres, and San Bernardino National Forests in southern California, USA (Kern, Los Angeles, Riverside, San Bernardino, and San Diego Cos.).

Parameter	Weighted ranking	No risk	Risk begins	Risk peaks	Risk maximum	Progression of risk	References
<i>A. concolor</i> basal area ($\text{m}^2 \text{ha}^{-1}$)	1	0–38	38	56	>56	Linear	Stoszek (1977), data from the current study
Percentage host type (<i>A. concolor</i>)	1	0–80	80	100	–	Linear	Stoszek (1977), USDA PNW (2000), data from the current study
Tree density (ha^{-1})	1/2	0–375	375	750	>750	Linear	USDA PNW (2000), data from the current study
Slope position (%)	1/2	0–45	45	65	>65	Linear	Williams et al. (1979)
Drainage index (%)	1/2	56–99	56	25	<25	Inverse linear	Dunning (1942), Stoszek (1977)
<i>A. concolor</i> quadratic mean diameter (cm)	Constrained	0–12.5	12.5	–	–	Equal	Williams et al. (1979), Wickman et al. (1981)

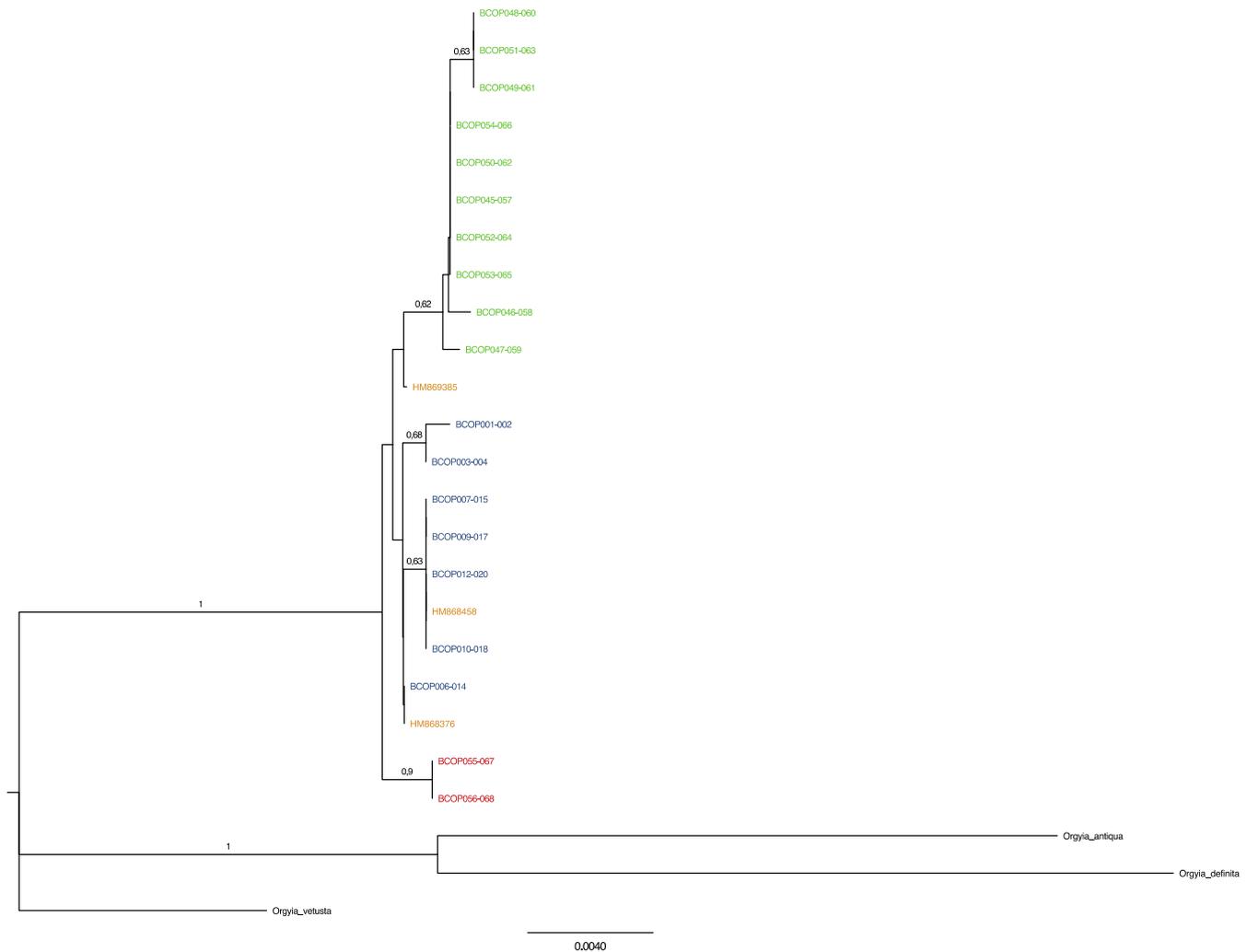


Fig. 2. Phylogenetic tree of mitochondrial DNA COI sequence data from Douglas-fir tussock moth (DFTM), *Orgyia pseudotsugata*, populations from the San Bernardino National Forest, Big Bear Lake, CA (green); the Okanagan National Forest, WA (blue); Sierra San Pedro Martir National Park, Baja California Norte, Mexico (red); three DFTM accessions (HM868458, HM868376 and HM869385) retrieved from GenBank (orange); and three *Orgyia* species used as outgroups [*Orgyia antiqua* Linnaeus (GU707344.1), *Orgyia definita* Packard (GU090644.1), and *Orgyia vetusta* Hampson (DQ116166.1)].

3.2. Forest stand assessments

In California and Mexico, we assessed 2434 trees, comprising ten species. When all three stand types (outbreak, non-outbreak, and Sierra San Pedro Martir National Park) were considered together, *A. concolor* (65% of stems) was the dominant tree species in the survey. Jeffrey pine, *Pinus jeffreyi* Grev. & Balf. (30%), California black oak, *Quercus kelloggii* Newb. (2.5%), Sierra lodgepole pine, *Pi. contorta murrayana* (Grev. & Balf.) Engelm. (1.0%), canyon live oak, *Q. chrysolepis* Liebm. (0.29%), incense cedar, *Calocedrus decurrens* (Torr.) Florin (0.12%), quaking aspen, *Populus tremuloides* Michx. (0.12%), sugar pine, *Pi. lambertiana* Douglas (0.08%), ponderosa pine, *Pi. ponderosa* Douglas ex C. Lawson (0.04%), and white alder, *Alnus rhombifolia* Nutt. (0.04%) comprised the remaining canopy tree species.

Total stand density was significantly higher in non-outbreak stands than in outbreak stands (22%) and the Mexican stands (140% = 1.4x) (Table 2A). Outbreak stands had significantly greater total stand density (94%) than the Mexican stands (Table 2A). *A. concolor* comprised >70% of the total stand density in both the outbreak and non-outbreak stands, but the density of *A. concolor* was not significantly different between the two stand types. *A. concolor* comprised only 4% of the total stand density in Mexico, and this

density was significantly less (97%) than it was in both stand types in southern California (Table 2A). Total stand and *A. concolor* basal area were significantly higher in outbreak (96%) and non-outbreak (97%) stands when compared to the stands in Mexico (Table 2B). *A. concolor* basal area comprised 74%, 69%, and 4% of total stand basal area for the outbreak, non-outbreak, and Mexican stands, respectively.

The stand density of dead trees was significantly higher in the outbreak stands than in the non-outbreak (69%) and Mexican (6.9x) stands (Table 2A). Non-outbreak stands had 3.7x greater density of dead trees than Mexican stands (Table 2A). Basal area of dead trees was not significantly different between outbreak and non-outbreak stands, but it was significantly greater (2.3x and 1.6x, respectively) when compared to Mexican stands (Table 2B). Outbreak stands had significantly greater dead *A. concolor* density (70%) but not basal area (32%) relative to non-outbreak stands (Table 2A and B). Both outbreak and non-outbreak stands had significantly greater dead *A. concolor* density and basal area than the Mexican stands (Table 2A and B). Density and basal area of dead *A. concolor* was 98% less in Mexico in relation to the other two stands. Whether based on density or basal area, dead *A. concolor* comprised >95% of the tree mortality in both forest stand types in southern California and represented a mean 20%

Table 2

Characteristics of Douglas-fir tussock moth (DFTM), *Orgyia pseudotsugata*, outbreak and non-outbreak forest stands with white fir, *Abies concolor*, in the Pacific Southwest region, including the Transverse Mountain Ranges of southern California and the Sierra San Pedro Martir National Park, Northern Baja California, Mexico.

Forest stand parameter		Outbreak	Non-outbreak	Mexico	$F_{2, 48}$	P
A. Density (ha^{-1})	Total stand	395 (± 22.8) b	483 (± 34.3) a	204 (± 21.2) c	21.7	<0.001
	<i>Abies concolor</i>	330 (± 24.6) a	337 (± 35.1) a	8.69 (± 4.18) b	39.0	<0.001
	Total dead tree	129 (± 18.6) a	76.3 (± 12.8) b	16.3 (± 6.46) c	10.9	<0.001
	Dead <i>A. concolor</i>	123 (± 18.5) a	72.5 (± 12.3) b	1.10 (± 0.77) c	13.1	<0.001
B. Basal area ($\text{m}^2 \text{ha}^{-1}$)	Total stand	52.0 (± 2.66) a	60.5 (± 6.00) a	35.4 (± 2.69) b	10.0	<0.001
	<i>A. concolor</i>	38.5 (± 2.93) a	41.8 (± 5.88) a	1.38 (± 0.71) b	27.1	<0.001
	Total dead tree	14.9 (± 2.26) a	11.6 (± 2.72) a	4.46 (± 1.47) b	7.41	0.002
	Dead <i>A. concolor</i>	14.6 (± 2.28) a	11.1 (± 2.57) a	0.12 (± 0.11) b	34.8	<0.001
C. DFTM injury	Mean <i>A. concolor</i> defoliation (%)	39.4 (± 4.22)	0.0 (± 0)	0.0 (± 0)	–	–
	Dead <i>A. concolor</i> density with DFTM (ha^{-1})	76.2 (± 19.5)	0.0 (± 0)	0.0 (± 0)	–	–
	Dead <i>A. concolor</i> basal area with DFTM ($\text{m}^2 \text{ha}^{-1}$)	7.67 (± 1.77)	0.0 (± 0)	0.0 (± 0)	–	–
D. Bark beetle injury ^a	Dead <i>A. concolor</i> density (ha^{-1})	52.2 (± 9.81) a	69.7 (± 12.3) a	0.41 (± 0.41) b	9.7	<0.001
	Dead <i>A. concolor</i> basal area ($\text{m}^2 \text{ha}^{-1}$)	5.56 (± 1.32) b	9.8 (± 2.10) a	0.01 (± 0.01) c	18.6	<0.001

^a Primarily *Scolytus ventralis* LeConte.

basal area loss of the total *A. concolor* component in the outbreak stands associated with DFTM defoliation (Table 2B and C). Dead *A. concolor* comprised <3% of total tree mortality (by basal area) in the Mexican stands; this was an 8.7% basal area loss of *A. concolor* (Table 2B).

Mean defoliation of *A. concolor* was 39% in the outbreak stands, but no detectable defoliation or associated tree mortality were observed from the DFTM in the non-outbreak and Mexican stands (Table 2C). Only 13 instances of *A. concolor* top-kill [mean density of top-kill 4.46 (± 1.32) ha^{-1}] were observed in the outbreak stands; nine instances were observed in the non-outbreak stands [4.39 (± 1.63) ha^{-1}]; and two instances were observed in the Mexican stands [0.06 (± 0.04) ha^{-1}]. Top-kill in the outbreak stands was likely a result of DFTM injury and subsequent attack from *S. ventralis*, whereas top-kill in the other two stands was attributed to *S. ventralis* and fir mistletoe, *Phoradendron pauciflorum* Torr. In the outbreak stands, 3%, 2%, and 4% top-kill of *A. concolor* were observed on trees with 25–49, 50–74, and 75–89 DFTM defoliation levels, respectively (Fig. 3A). In the outbreak stands, 62% of dead *A. concolor* (ha^{-1}) was associated with DFTM defoliation (Table 2A and C); 53% of dead *A. concolor* by basal area was associated with DFTM defoliation (Table 2B and C).

A. concolor mortality and top-kill were highest (98%) when complete defoliation occurred, but mortality and top-kill were only incidental (4% and 2%) when stands were 99% and 75–89% defoliated, respectively (Fig. 3A). *A. concolor* mortality and top-kill were not associated with trees that had been defoliated at the 0–24, 25–49, 50–74, and 90% levels. Stands that had been exposed to three years of consecutive defoliation near the origin of the outbreak were often defoliated >90% and had the highest level of *A. concolor* mortality (Fig. 3B). The percentage of *A. concolor* mortality decreased exponentially with declining levels of defoliation and showed a mean of approximately 22% for stands with <10% mean defoliation (Fig. 3B). In stands with high-levels of defoliation, larval feeding was also observed frequently on *Pi. jeffreyi*, resulting in six instances of mortality.

S. ventralis was the primary bark beetle attacking the main stems of *A. concolor* in both southern California stand types. *S. ventralis* was observed on 42% and 96% of the *A. concolor* snags without DFTM injury in the outbreak and non-outbreak stands, respectively. However, the density of *A. concolor* attacked and killed by *S. ventralis* without DFTM injury was comparable in both outbreak and non-outbreak stands (16% and 20% of the live *A. concolor* component, respectively, Table 2A and D). Density of *A. concolor* attacked and killed by *S. ventralis* in Mexican stands was significantly lower (99%) than in both the outbreak and non-outbreak stands in southern California (Table 2D). The density of dead *A.*

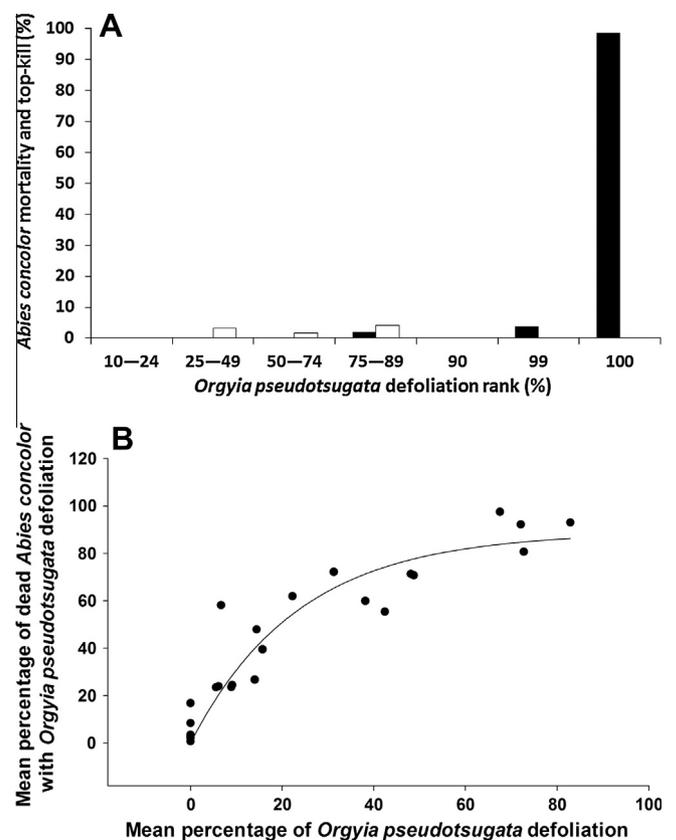


Fig. 3. Percentage of white fir, *Abies concolor*, mortality (black bars) and top-kill (white bars) associated with varying levels of defoliation by the Douglas-fir tussock moth, *Orgyia pseudotsugata*, in the Transverse Mountain Range, San Bernardino National Forest, southern California (A). The relationship of *Abies concolor* mortality and mean DFTM defoliation within a stand was presented as a scatter plot and regressed as the exponential function) where x = mean percentage of *A. concolor* defoliated by *O. pseudotsugata*; y = mean percentage *A. concolor* mortality; coefficient a = 88.8770, $P < 0.001$; coefficient b = 0.0425, $P < 0.001$ with an adjusted R^2 value of 0.8643 (Systat) (B).

concolor with both DFTM and *S. ventralis* injury was low [15.4 (± 4.46) ha^{-1} , 13%] in the outbreak stands. *A. concolor* basal area killed by *S. ventralis*, with no DFTM injury present, in non-outbreak stands was significantly higher when compared to outbreak stands (76%) (Table 2D). *A. concolor* basal area killed by *S. ventralis* was 99% lower in the Mexican stands than in both the outbreak and non-outbreak stands (Table 2D).

3.3. Risk modeling

During a 15-yr projection period, a total of 13,534 ha are predicted to be at risk for basal area loss of *A. concolor* from DFTM outbreaks in southern California (Fig. 4). Forest stands near the Cucamonga Wilderness, San Gorgonio Wilderness, San Jacinto Wilderness, and Sugarloaf Mountain, San Bernardino National Forest; Sheep Mountain Wilderness, Angeles National Forest; and Pine Mountain and Mt. Pinos, Los Padres National Forest have elevated risk of basal area loss from DFTM injury (Fig. 4). The model predicted 11,077 ha at low risk for injury by DFTM, 1,615 ha at moderate risk, and 842 ha at high risk across the region. The greatest risk for basal area loss from DFTM injury was predicted on the San Bernardino National Forest and the model accurately predicted elevated risk at the recent DFTM outbreak sites (Fig. 4).

4. Discussion

In 2011, DFTM was collected from *A. concolor* in the Sierra San Pedro Martir National Park, Baja California Norte, Mexico, representing a new country record for Mexico and expanding the range of this insect coincident with the distribution of *A. concolor* in the Pacific Southwest region of North America (Furniss and Carolin, 1977; Wickman et al., 1981; Burns and Honkala, 1990; Cibrian et al., 1995; USGS, 2014). This documentation of the southern extent of the range of DFTM is not surprising because although the forest structure and relative abundance of tree species differed between the stands in California and Mexico, the presence/absence of the tree species is comparable between southern California and the Sierra San Pedro Martir National Park (Minnich et al., 1995; Stephens et al., 2007). This native pest may have escaped detection previously because the density of *A. concolor* in the area may have been too low to support an outbreak. Surprisingly, the Mexican populations appear to be more related to the northern populations from Washington and British Columbia, from which they have diverged by only two mutational steps in the COI gene. If we assume that the British Columbia populations of DFTM were reared on *P. menziesii* (specimens were collected by light trap), then there appears to be little genetic divergence between DFTM populations collected from *P. menziesii* and those collected from *A. concolor*.

This suggests that the structure of the populations is not related to host of origin, but to geographic locations.

The first recorded DFTM outbreak in the Transverse Ranges of southern CA (2009–2012) caused a significant increase in the mortality of *A. concolor* on the San Bernardino National Forest. With the exception of an isolated, relictual population in western Santa Barbara Co., CA, *P. menziesii* is not native to southern CA (Griffin and Critchfield, 1972), and big-cone Douglas-fir, *Pseudotsuga macrocarpa* (Vasey) Mayr, which is more widely distributed in this area (Griffin and Critchfield, 1972), was not intermixed with *A. concolor* in the outbreak area. Thus, the potential for injury to these tree species near the southwestern limits of their distribution is unknown. The increase in tree mortality was expressed in terms of stem density and basal area lost when compared to non-outbreak stands. Proportional mean tree mortality associated with DFTM injury throughout the outbreak was 20%, which is comparable to previous DFTM outbreaks (21–29% tree mortality) in northern California (Wickman et al., 1973). Higher levels of DFTM-caused tree mortality have been observed in the U.S. interior West (30–40%) (Schaupp et al., 2008), British Columbia, Canada (51%) (Alfaro et al., 1987), and in northern New Mexico (28–97%) (Rogers, 1980). In the New Mexico outbreaks, tree mortality also damaged (20–66%) Douglas-fir saplings (<12.5 cm DBH). In Utah, top-kill by DFTM on *A. lasiocarpa* occurred on nearly half of trees that had been 25 to 89% defoliated (Hansen, 1995). Top-kill of *A. concolor* was not as frequent in our study and in an outbreak in British Columbia, Canada (11%) as on *A. lasiocarpa*, but the injury did correspond to similar DFTM defoliation levels (Alfaro et al., 1987). Following five years of injury, defoliation from the western spruce budworm, *Choristoneura occidentalis* Hübner (Lepidoptera: Tortricidae), on white spruce, *Picea glauca* (Moench) Voss, in northern British Columbia, Canada caused 39% tree mortality (Alfaro et al., 2001). The hemlock looper, *Lambdina fiscellaria* (Guen.) (Lepidoptera: Geometridae), killed 69% of balsam fir, *Abies balsamea* (L.) Mill., in severely defoliated plots in New Brunswick, Canada (MacLean and Ebert, 1999). In contrast to these other native defoliators in North America, outbreaks of the Pandora moth, *Coloradia pandora* Blake (Lepidoptera: Saturniidae), frequently led to reductions in radial growth, but only low-levels of mortality (<2%) in *Pi. ponderosa* in the southwestern USA (Patterson, 1929).

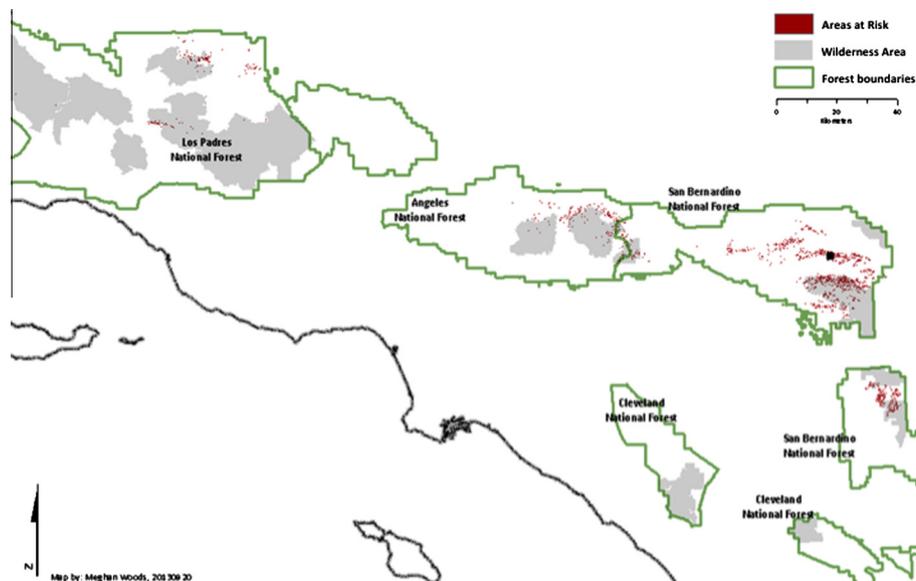


Fig. 4. Predicted basal area loss (red areas, <math><20\% \text{ m}^2 \text{ ha}^{-1}</math>) of white fir, *Abies concolor*, by the U.S.D.A. Insect and Disease Risk Model software associated with Douglas-fir tussock moth, *Orgyia pseudotsugata*, outbreaks in the Transverse Mountain Ranges of southern California (Krist et al., 2013). Location of the recent DFTM outbreak in the San Bernardino National Forest is indicated (■).

Defoliation from the DFTM contributed to 62% of the total density of dead *A. concolor* during the outbreak (Table 2A and C). Larval feeding was also recorded on a non-preferred host, *Pi. jeffreyi*, which has been observed before during outbreak events (Wickman et al., 1981). Three years of consecutive heavy defoliation (>90%) and tree mortality (29%) were located primarily where defoliation was first observed in 2009. Likewise, patches of complete tree mortality were observed during a DFTM outbreak in the Blue Mountains of Oregon (Wickman et al., 1981). Low-levels of defoliation from the DFTM often do not result in tree mortality when DFTM acts as the sole injury agent. In southern California, stands that experienced only one to two years of defoliation had lower rates of mortality of *A. concolor*. Similar low rates of mortality of *A. grandis* was recorded in sites with <90% defoliation in Oregon (Wickman, 1978). In sites with moderate and heavy mortality, *A. concolor* surviving the outbreak were likely to experience increased radial and terminal growth due to the release from competition (Wickman, 1980).

Although *S. ventralis* killed 16% of the *A. concolor* component prior to the outbreak, these stands were still at elevated risk to a DFTM outbreak due to the risk factors described previously. *A. concolor* mortality was attributed primarily to *S. ventralis* in the non-outbreak stands. Prolonged drought during 2002–2003 had led to increased bark beetle activity and elevated levels of *A. concolor* mortality in southern California (Bohne and Rios, 2005). Drought, *S. ventralis*, and *Heterobasidion* root disease, *Heterobasidion occidentale* Orosina & Garbel. (Russulales: Bondarzewiaceae), interact to cause elevated mortality of *A. concolor* in southern California (Coleman, unpublished data); these factors may ultimately prevent DFTM outbreaks by reducing the density and continuity of its primary host (Mason and Wickman, 1991).

Bark beetles and wood borers attack trees predisposed by defoliation, which can increase the rates of tree mortality (Wygant, 1941; Haack and Acciavatti, 1992; Raffa et al., 1998). *S. ventralis* attacked 13% of the *A. concolor* injured by the DFTM. The interaction of the two insect species was limited to severely defoliated trees (>90%) where defoliation was first observed in 2009. In other DFTM outbreaks, 75% of severely defoliated *P. menziesii* were infested with *D. pseudotsugae* (Brookes et al., 1978), whereas low-levels (<5%) of bark beetle attack were reported on trees with light to moderate defoliation in the Blue Mountains of Oregon (Wickman, 1978). Wright et al. (1984) reported that the rates of attack from *S. ventralis* and *D. pseudotsugae* on *A. grandis* and *P. menziesii*, respectively, were highest one to two years after a DFTM outbreak in Washington and then declined thereafter. Ground surveys in January 2013, two years after the decline of the DFTM outbreak in California, did not detect any additional tree mortality. Lower rates of *S. ventralis* injury during the outbreak may be attributed to the normal annual precipitation received in the region from 2010 to 2011 (WRCC, 2013) and low levels of tree mortality in the area before the outbreak (USDA FHM, 2013). The latter is suggestive of a potentially low population density of *S. ventralis* in this general area. Furthermore, newly killed trees were promptly removed in the fall of 2012 in high-use areas and may have reduced local bark beetle populations even more during the DFTM outbreak.

Stand densities were high in both outbreak and non-outbreak stands, suggesting that forested landscapes on national forest land in southern California with dense *A. concolor* are susceptible to future DFTM outbreaks. A total of 11,077 ha, 1615 ha, and 842 ha were predicted to be at low risk (1–7% loss), moderate risk (8–14% loss), and high risk (15–20% loss), respectively, to basal area loss from DFTM outbreaks on national forest lands in southern California. Most of the areas at risk were located in wilderness areas on the Angeles, Los Padres, and San Bernardino National Forests (Fig. 4) where neither forest or fuel management activities are

generally practiced. Cessation of thinning activity and changes in the fire regime in managed forested areas in southern California have led to a shift from pine-dominated stands to a pine–fir mixture with increasing stand densities of *A. concolor*. This is evident when the characteristics of the stands in the Transverse Ranges are compared to those in the Sierra San Pedro Martir (Table 2), and from other studies conducted in these areas (Minnich et al., 1995). Changes in forest management objectives, land-use practices, and fire suppression policies in the USA have been implicated in more frequent and intense outbreak cycles and an elevated threat from several native insects, including the DFTM in the Pacific Northwest, southern pine beetle, *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae), in the southeastern USA, *Ch. occidentalis* in Montana, and *Co. pandora* in Arizona (Williams et al., 1980; Anderson et al., 1987; Landers et al., 1995; Speer et al., 2001). In Europe, human orchestrated low-density plantings as well as thinning operations in pine stands are considered to favor primary defoliators such as the pine processionary moth, *Thaumetopoea pityocampa* Denis and Schiffermüller (Lepidoptera: Thaumetopoeidae), which prefer vigorous and more or less isolated trees (Jactel et al., 2009).

The three-yr DFTM outbreak in the Transverse Mountain Ranges followed a similar temporal pattern as previous outbreaks in western North America and was predicted accurately by egg mass surveys and adult male moth trapping (Daterman et al., 1979; Shepherd et al., 1985; USDA FHM, 2013; Coleman, unpublished data). The DFTM outbreak covered an estimated 261 ha on the San Bernardino National Forest; however, tree mortality was limited primarily to 26 ha (USDA FHM, 2013; Coleman, unpublished data). The outbreak likely subsided from the loss of the preferred host type and build-up of NPV and natural enemies. Future monitoring of DFTM populations would be required in stands predicted to be at moderate to high risk of basal area loss to develop management schemes to reduce impacts caused by this defoliator. DFTM outbreaks occur frequently on a 10–15 yr cycle, but in southern California the duration of the period between outbreaks may be extended due to the lack of dense, contiguous stands of susceptible hosts, as supported by the larger overall area associated with low risk predicted by the risk model. To reduce the risk of DFTM injury in the higher risk stands outside of the wilderness boundaries, silvicultural treatments should be developed to reduce the stem density or replace *A. concolor* with the appropriate *Pinus* spp. for the site (Mason and Wickman, 1991). Thinning dense stands of *A. concolor* does not make these areas resistant to DFTM defoliation, but the stands do recover more quickly than unthinned *A. concolor* stands (Wickman, 1988). We observed that the boundary of the DFTM outbreak coincided with a wildfire fuel break where *A. concolor* was at low densities and defoliation had been negligible. Reducing the densities of at risk stands may limit mortality of *A. concolor* not only from the DFTM, but also from populations of *S. ventralis*. This action would also remove fuels for the high-severity wildfires that occur frequently in southern CA.

Taken together, the collection of DFTM in Baja California Norte and the first recorded outbreak in the southern California Transverse Ranges suggest a southward shift in the outbreak range of this insect. This trend is in contraposition to most geographic shifts in forest insect distributions predicted in response to most global change scenarios (Bentz et al., 2010; Johnson et al., 2010; Weed et al., 2013), suggesting that this effect could be related to local silvicultural and forest compositional changes rather than to climate change. We have not investigated the impact of temperature in the Pacific Southwest region as a direct factor in the new geographic outbreak status of this defoliator, but temperature has been recently reported to positively affect outbreak-level damage by a series of forest defoliators in Hungary (Klapwijk et al., 2013). Nonetheless, the effect of temperature on the genesis of forest insect

outbreaks vs. alternative causes (e.g., changes in stand structure and forest management practices) remains an area of intense interest (Büntgen et al., 2009; Björkman et al., 2011).

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