A hazards approach towards modelling pandora moth risk

James H. Speer* and Ryan R. Jensen Department of Geography, Geology, and Anthropology, Indiana State University, Terre Haute, IN, USA

Abstract

Aim Pandora moth (Coloradia pandora Blake) is a phytophagous insect that produces a distinctive tree-ring pattern in ponderosa pine (Pinus ponderosa Dougl. ex. Laws.) during outbreak cycles. This paper describes the spatial characteristics of the outbreak regions, determines whether the size of the 1989 outbreak was within the historical range of variability, and constructs a hazard map identifying the forests in Oregon that are susceptible to future pandora moth outbreaks.

Location South-central Oregon along the eastern flank of the Cascade mountain range in the High Lava Plains and Basin and Range Provinces.

Methods We used dendrochronological records of 17 pandora moth outbreaks on 14 sites over 31,200 km² area spanning 433 years. Using the site locations, we calculated minimum bounding polygons of adjacent recording sites to determine the relative size of each outbreak. Published literature on past pandora moth outbreaks and the environmental conditions of locally known outbreaks were used to create an outbreak hazard map using a geographical information system (GIS) model. Vegetation, climate, and soil layers were used to determine the potential susceptibility of Oregon forests to pandora moth.

Results We found the area affected by past pandora moth outbreaks ranged in size from 12.4 to 3,391.5 km². The 1989 outbreak covered 807.9 km², which was well within the historical range of variability. The vegetation and soil layers greatly restricted the area susceptible to pandora moth while the climate layer seemed to have little effect in restricting the susceptible area.

Main conclusions Pandora moth outbreaks did not increase in size over the last century as we have seen with spruce budworm outbreaks in this same region. Analysis of the environmental variables that are known to affect pandora moth outbreaks enabled us to produce a hazard map that predicts the suitable habitat for pandora moth. Temperature at the landscape scale did not restrain the range of pandora moth. The GIS model enabled us to propose areas susceptible to future pandora moth outbreaks providing a predictive model that can now be tested and refined with further sampling.

Keywords Pandora moth, Coloradia pandora, dendrochronology, dendroecology, ponderosa pine, Oregon, geographical information system, hazard map, insect outbreak.

INTRODUCTION

Pandora moth (Coloradia pandora Blake, Lepidoptera: Saturniidae) is a phytophagous insect endemic to the United States whose range includes most western states except Idaho and Washington [most notably in Arizona, California, Colorado and Oregon (Carolin & Knopf, 1968)]. In Oregon the main host species is ponderosa pine (Pinus ponderosa Dougl. ex Laws.) and occasionally lodgepole pine (Pinus contorta Dougl. ex Loud.). Pandora moth has been little studied, but recent interest has arisen due to an outbreak in central Oregon from 1988 to 1996 (Speer, 1997).
In a previous study, Speer et al. (2001) used tree rings to reconstruct 22 pandora moth outbreaks over a 622-year period from 14 sites throughout central Oregon (Fig. 1). Speer et al. (2001) demonstrated that pandora moth outbreaks could be accurately reconstructed and identified a clear tree-ring pattern associated with the outbreaks. In the current study, we use this reconstruction of past pandora moth outbreaks to examine the spatial characteristics of individual outbreaks, examine the regional distribution of outbreaks through time, and parameterize a model developed in a geographical information system (GIS) to determine the potential habitat for pandora moth. The resulting hazard map can be used by managers to plan for future outbreaks and also as a guide to locate samples for future pandora moth reconstructions. Thus, it may be used in forest management planning as well as a sampling tool for future research.

GIS has been used extensively in ecological studies to examine spatial phenomena such as longleaf pine sandhill loss in the south-eastern United States coastal plain (Jensen & Carson, 2001) and forest fragmentation in southern Virginia, USA (Wickham et al., 2000). Specifically, GIS has been used to study historical ecological events. For example, Jensen (2002) used GIS to examine temporal leaf area index dynamics in north-central Florida, USA from 1972 to 1997. Baker & Kipfmuller (2001) used GIS to construct and analyse the spatial ecology of pre-Euro-American fires in a southern rocky mountain subalpine forest landscape. Eeley et al. (1999) used GIS to examine the influence of climate change on forest distribution in South Africa, and Baker (1995) used GIS to simulate the effects of the density of landscape patches to long-term disturbance regimes – global warming and cooling and fragmentation – for a 400-year period. Although, GIS has been used extensively in many ecological studies our application is unique because we use GIS to model insect outbreak hazard and to map the area of past insect outbreaks reconstructed from tree-ring records.

**Pandora moth**

Pandora moth has a 2-year life cycle and spends their first winter in the second instar stage at the base of pine needles. At the end of their second summer the larvae move down the stem of the tree and burrow into the soil to pupate (Massey, 1940; Carolin & Knopf, 1968; Schmid & Bennett, 1988; Fitzgerald, 1992). This insect is also closely adapted to its host species only causing 2% mortality although defoliation is complete every other year. Because of the dependence of this insect on its host tree species, climate factors, and soil type we use these parameters to map the area of Oregon that is susceptible to pandora moth.

Temperature affects the survival of pandora moth, because the larvae are exposed to weather for one whole year. The larvae cease to feed at temperatures below 15.6 °C (Massey, 1940; Schmid & Bennett, 1988), and temperatures at −40 °C have been shown to kill many caterpillars during their first winter (Massey, 1940). Aspect (and most likely the related temperature differences) has been shown to affect pandora moth distributions in Colorado. Massey (1940) found that pandora moth cause greater damage on south-east facing slopes than on north-west facing slopes.

Soil conditions are also a factor in pandora moth outbreaks. Pandora moths occur in areas with immature soils often developed from weathered granite or ash and pumice deposits, which are loose enough to permit the larvae to burrow (Patterson, 1929; Massey, 1940; Carolin & Knopf, 1968; Furniss & Carolin, 1977). In Oregon, pandora moth prefers soils associated with ash and pumice deposits from
et al. (1940) observed that in the absence of such soils, the larvae spend a considerable amount of time trying to burrow searching for a suitable place for pupation. Larvae that make several attempts to borrow into soil that was above 50 °C eventually died from exhaustion and exposure. In areas lacking the proper soil, it is likely that the outbreaks would not be able to maintain sufficient momentum to carry on the outbreak.

In Oregon, ponderosa pine is the main host species to pandora moth, but lodgepole pine is also affected. The ponderosa pine forests of Oregon were heavily logged in the early 1900s, effectively removing much of the moth’s food source. These forests have regrown as ponderosa pine/lodgepole pine forests (Franklin & Dyrness, 1988). In the Blue Mountains of Oregon, the pine trees have frequently been logged and surface fires have been suppressed, resulting in an increase in spruce/fir forests (Mutch et al., 1993). This vegetation change has increased the habitat available to spruce budworm resulting in larger and more damaging budworm outbreaks in the twentieth century (Swetnam et al., 1995). This study will address the issue of whether pandora moth has been similarly affected by 20th century ecosystem change (Morgan et al., 2003). Measurements of past pandora moth outbreaks would be smaller in extent and severity because of removal of a preferred host species.

METHODS

Site description

The study area is located on the east side of the Cascade Mountains in south-central Oregon (43.10 N, 121.75 W). It encompasses 31,200 km² (240 km north-to-south and 130 km east-to-west) (Fig. 1) and ranges in elevation from 1320 to 1670 m. It includes most of the known range of pandora moth in Oregon that was defined from historical outbreaks (Carolin & Knopf, 1968). Each of the 14 insect outbreak sites was a disjunct stand of old-growth ponderosa pine, covering 5–10 ha. The sites are located where remnant stands of old ponderosa pine trees were not logged, therefore the spatial distribution of the sample sites were predetermined by past human land-use.

Determining the area of past outbreaks

Speer et al. (2001) reconstructed 22 outbreaks over the past 622 years (from AD 1373 to AD 1995) by examining increment cores collected from 140 mature ponderosa pine trees. Sample depth decreased further back in time reducing the number of recording sites. In this study, we truncate their record at AD 1563 because the lack of recording sites in the early part of the chronology would bias the site distribution. Six of the 14 sites were still recording outbreaks during the 1563 outbreak.

Speer et al. (2001) demonstrated that the outbreak episodes were not synchronous across the landscape, but instead seemed to spread from one site to another. Because of this starting date ambiguity, we defined the date of the outbreak episode as the period during which the outbreak was most active across the landscape. We used a number of criteria to determine when most of the sample area was experiencing an outbreak. From all of the sites recording each outbreak, we calculated the mode of the first year, the mode of the smallest ring, and the mode of the last year of the tree-ring pattern. When the mode of the first year was followed by the mode of the smallest ring (1 or 2 years later), we were confident that the beginning date of the outbreak was relatively well defined. We used the mode of the last year of the outbreak pattern as the end date of the outbreak. When the end dates did not coincide, we chose an end date that was in the middle of the temporal distribution and did not overlap with the beginning date of a subsequent outbreak.

Nearest neighbour analysis was performed to determine the randomness of the sites affected by each outbreak. This was calculated by comparing the mean of the actual distances between each affected site in each outbreak with the mean of the expected distances if the distribution of sites was random. The difference between these two means was then divided by the standard error of the mean nearest-neighbour distance and compared with a critical value (Z = 1.96; α = 0.05; Earickson & Harlin, 1994).

GIS analysis

The locations of the sites were digitized into ArcView GIS 3.2 to determine the minimum-bounding polygon encompassing pandora moth outbreaks. Individual latitude and longitude values were typed into the GIS to digitize the polygons. These polygons were compiled by including all contiguous sites that were affected by outbreaks. If an intervening site did not record an outbreak, then that polygon was interrupted and separate polygons were used to outline the outbreak regions. For outbreaks that only affected one site, we assumed a circle with a 2.5-km radius. This radius was chosen to account for the spread of pandora moth to adjacent forest stands and approximates the size of the smallest historically recorded outbreak. From these minimum-bounding polygons we estimated the size of past outbreaks. These calculations gave us a conservative estimate of the area affected by past outbreaks. To remain analogous, we calculated the size of the 1989 outbreak using the above method, and then compared it with the size of past outbreaks to determine if the current outbreak was within the historical range of variability. The historical range of variability is defined by the documented past occurrence of some event and may be used to establish acceptable limits of ecosystem change (Morgan et al., 1994).

Hazard mapping of susceptibility to pandora moth outbreaks

We determined the preferred condition of pandora moth outbreaks by using our sample sites with known outbreak histories to identify the soils and vegetation that make a
site susceptible to pandora moth outbreaks. GIS vector data sets of soil (United States Geological Survey (USGS) soils map at the suborder level), vegetation (derived from Advanced Very High Resolution Radiometer (AVHRR) remotely sensed imagery), and climate (National Weather Service) were combined to estimate risk of potential outbreak. Past pandora moth outbreaks in this area were located on Orthent, Cambid, Crypt and Xerent soils, so we used these suborders as parameters in the hazard map (Table 1). We used the vegetation layer designated as ponderosa pine/lodgepole pine from the AVHRR vegetation classification to map the host tree species of this moth. For the temperature constraint we used the criterion that the average temperature had to exceed 15.6 °C for 90 days. This time period was determined based on the assumption that the larvae would need 3 months of intensive feeding to be able to complete its life cycle. Average monthly temperature measurements from four weather stations across Oregon (Bend, Baker, Crater Lake and the Dalles) were used as the base climate data. We then calculated our climate layer from a digital elevation model (DEM) and the dry adiabatic lapse rate of 10 °C/1000 m using AcrView. We tested the model output developed from these parameters against our known pandora moth outbreak sites.

**RESULTS**

Over the 433-year period, the outbreaks appeared spatially dispersed throughout the sample area, affecting only a few of the tree-ring sites at any given time (Fig. 2). The study sites were randomly located throughout the study area, but seven of the 13 eligible sites (two of the outbreaks only affected a single site and were therefore not eligible for the nearest neighbour analysis) were not random ($Z = 1.96; \alpha = 0.05$); 1651 (2.34), 1676 (3.61), 1718 (4.11), 1735 (2.84), 1771 (2.04), 1889 (2.72) and 1989 (6.86). Two of the outbreaks (1794 and 1836) that were randomly located were extreme events affecting at least 75% of the sites.

The modern outbreak was well within the historical range of variability, although it was the fourth largest outbreak of the 15 that were measured. The size of the outbreaks ranged from 12.4 to 3,391.5 km² with a mean of 527.9 km². The 1989 outbreak affected 807.9 km² (Table 2). The histogram of the outbreak sizes describes a reverse J-shaped curve with few large outbreaks and many smaller outbreaks.

The GIS model demonstrated that, based on the host tree species available, pandora moth could affect 43,919 km² in Oregon (Fig. 3). When we included the climate layer, we found that climate did not greatly constrain the model, only restricting the area to 40,140 km² susceptible to outbreaks. Soils appeared to be the most limiting factor, reducing the hazard area to a region along the leeward side of the Cascade mountain range. The combination of these three layers resulted in a predicted affected area totalling 12,523 km² (Fig. 3).

**DISCUSSION AND CONCLUSIONS**

The modern outbreak of 1988–96 was compared with outbreak history to determine if it fell within the historical range of variability. A pattern of change for pandora moth outbreaks is not apparent on the landscape as the modern outbreak was within the historical range of variability and also the fourth largest outbreak recorded. The reverse J-shaped curve of outbreak size (few large outbreaks and many smaller outbreaks) is frequently found in ecological literature and is an expected distribution (Brown, 1995) suggesting that pandora moth has not been affected by recent land use changes. These findings contrast spruce budworm studies that have found an increase in severity and extent of twentieth century outbreaks (Blais, 1983; Swetnam et al., 1995). We expected that pandora moth would respond to logging, which removes its primary food source and fragments ponderosa pine stands, in the opposite manner than that of the spruce budworm, resulting in smaller,
less-severe outbreaks. This is a much more difficult signal to discern than the increased severity and expanse of modern spruce budworm outbreaks, with their higher mortality rates, often as much as 80%, in heavily defoliated stands (Swetnam et al., 1995). Fragmentation by logging and the introduction of roads may not have impacted pandora moth outbreak dynamics because the moths are strong flyers (Massey, 1940) and are able to access the landscape at a broader scale.

We should note the difference in start dates of the modern outbreak. Foresters were able to document the rise of the modern outbreak starting in 1988. The pattern in the wood (as reported in Table 2) runs from 1991 to 1995. The tree-ring record ended in 1995 explaining the early end date of that signature. The beginning date obviously does not record the very early emergence of the pandora moth population. The numbers of larvae have to be great enough to seriously damage the photosynthetic potential of the trees to be recorded in the rings. Because of this and the possibility of not sampling the site from which the outbreak originated, we are not able to record the very first year of the outbreaks. This suggests that, in future work, any climatic trigger that could be explored should come a number of years before the outbreak is recorded in the trees.

We found that the majority of pandora moth outbreaks are significantly spatially autocorrelated, suggesting that

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**Table 2** The area affected by each outbreak episode. The total study area designated the maximum possible area that could be defoliated

<table>
<thead>
<tr>
<th>Outbreak dates</th>
<th>Area affected (km²)</th>
</tr>
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<tbody>
<tr>
<td>1991–95</td>
<td>807.9</td>
</tr>
<tr>
<td>1967–75</td>
<td>13.0</td>
</tr>
<tr>
<td>1923–31</td>
<td>21.0</td>
</tr>
<tr>
<td>1889–03</td>
<td>33.4</td>
</tr>
<tr>
<td>1870–76</td>
<td>25.2</td>
</tr>
<tr>
<td>1840–53</td>
<td>3391.5</td>
</tr>
<tr>
<td>1803–11</td>
<td>1823.8</td>
</tr>
<tr>
<td>1775–83</td>
<td>105.3</td>
</tr>
<tr>
<td>1754–60</td>
<td>62.2</td>
</tr>
<tr>
<td>1735–42</td>
<td>30.9</td>
</tr>
<tr>
<td>1719–25</td>
<td>12.4</td>
</tr>
<tr>
<td>1677–85</td>
<td>71.3</td>
</tr>
<tr>
<td>1661–66</td>
<td>238.9</td>
</tr>
<tr>
<td>1652–57</td>
<td>39.3</td>
</tr>
<tr>
<td>1631–38</td>
<td>1178.4</td>
</tr>
<tr>
<td>1619–24</td>
<td>13.3</td>
</tr>
<tr>
<td>1563–78</td>
<td>80.8</td>
</tr>
<tr>
<td>Total study area</td>
<td>4413.2</td>
</tr>
<tr>
<td>Mean</td>
<td>527.9</td>
</tr>
<tr>
<td>Standard error</td>
<td>246.8</td>
</tr>
<tr>
<td>Minimum</td>
<td>12.4</td>
</tr>
<tr>
<td>Maximum</td>
<td>3391.5</td>
</tr>
</tbody>
</table>
these outbreaks may be spreading from a local source rather than emergent on the landscape as a whole. We noted that it was difficult to specify the beginning year of the outbreaks because it varied from one site to the next. This shows that outbreaks are not being triggered on all of the sites simultaneously as it would be by favourable climate. This does not suggest that climatic factors are not the initial trigger of the nucleus of the outbreak or important in the spread and longevity of the outbreaks. These hypotheses will have to be tested in later work.

We found that the 1794 and 1836 outbreaks were randomly distributed, as were the whole of our sample sites. These two outbreak events were extreme, affecting more than 75% of the sites and probably reflected the random locations of the sample sites. This means that for these two events we sampled a smaller area than the functional area of those particular outbreaks, although, for the majority of outbreaks, the sampling scale was appropriate for testing the tendency of pandora moth outbreaks to be clustered.

The hazard map produced in this study agrees with Caro-
in & Knoll’s (1968) published map of pandora moth outbreak areas in Oregon and also with written accounts of pandora moth outbreaks (Massey, 1940). As we focused on Oregon and used remotely sensed images of the host tree species, our map has greater resolution than previously published maps. This approach examines the mechanisms that drive the distribution of outbreaks and provides a testable hypothesis of the areas susceptible to pandora moth outbreaks. Future research will test this model by collecting tree rings samples located within as well as outside the areas predicted to be susceptible to pandora moth outbreaks. As dendrochronology will be able to determine whether pandora moth outbreaks have ever affected the living stand, we should be able to quickly refine our susceptibility model. These further samples will enable us to explore the full range of soils, vegetation, and climate that are conducive to pandora moth outbreaks resulting in a more accurate model of pandora moth hazard.

We were surprised to find that the climate layer was not a major restraint on the range of pandora moth in our model. A scarcity of climate stations at high elevations hinders the development of a true climate layer based solely on measurements. In future work, we may try to refine our climate layer by using meteorological data from more stations or climate divisions throughout the area. Climate division data extrapolates over the entire divisional area, which is broken down by major topographic barriers and air mass boundaries. This may be the best source of data for future modelling efforts.

One such exploratory analysis has been completed which supports this hazard model. Speer et al. (1997) sampled near

Sisters, Oregon (44.37 N, 121.55 W), c. 100 km north of our northernmost sites but within our predicted area of pandora moth hazard. Nine pandora moth outbreaks were recorded extending back to AD 1610. Foresters have not previously reported the occurrence of pandora moth outbreaks on this site. Speer et al. (1997) found that the most recent outbreak ended in AD 1895, explaining why pandora moth outbreaks had not been recorded this far north.

Spatial analysis of past insect outbreaks could enable forest managers to better understand the outbreak characteristics of an endemic insect in the systems they are managing. This insect has been present for the entire 433 years of this record and the 1988 outbreak was within the historical range of variability. We were able to document that these outbreaks spread from a nucleus and do not affect all sites simultaneously. Future work must be carried out to examine the mechanism driving the spread of pandora moth outbreaks. The GIS hazard model appears to be a useful determinant of areas that are potentially susceptible to pandora moth outbreaks and can be used as a management tool to inform local forest managers of the potential of future pandora moth outbreaks in their forest units. It can also be used as a testable model of where pandora moth has occurred in the past. This model will help drive future sampling and those samples will help to refine this hazard model. This paper has laid the groundwork for the use of GIS to model insect outbreak hazard. Now this work can be expanded to examine the entire range of pandora moth in the western United States and applied to other insects that are dependent upon specific environmental conditions.

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REFERENCES
**BIOSKETCHES**

**Jim Speer** is an Assistant Professor of Geography and Geology. He is interested in environmental reconstruction using tree rings and has worked on projects reconstructing insect outbreaks, fire history, climate, ice storms, and acorn production in oak trees.

**Ryan Jensen** is an Assistant Professor of Geography. He is interested in longleaf pine/turkey oak sandhill fire ecology and habitat loss, tropical deforestation, and urban forestry.