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Geographical distribution of an 18th-century heart rot outbreak in western juniper (*Juniperus occidentalis* spp. *occidentalis* Hook.)

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Between 1749–1730 a widespread occurrence of fungus-caused heart rot affected western juniper in the interior Pacific Northwest, U.S.A. In this study 12 *Juniperus occidentalis* spp. *occidentalis* chronologies collected from various sites throughout the western juniper range were examined. The presence of heart rot precluded dating many of these samples prior to the 1730s. Subsequently, sample size decline in these chronologies was examined and it was found that a substantial decrease in chronology sample size was present in nine chronologies, with no other periods exhibiting a decline of equal magnitude. Since heart rot requires open wounds to establish, and the major heart rot episode was confined to a short period, we suspect that a regional–scale climatic event such as a windstorm or icestorm was the initiating cause of this outbreak.

Keywords: heart rot; *Juniperus occidentalis* spp. *occidentalis; Antrodia juniperina;* tree-ring chronologies

Introduction

Western juniper (*Juniperus occidentalis* spp. *occidentalis* Hook.) is a long-lived conifer that is the dominant tree species of the semi-arid inland woodlands of the Pacific Northwest, U.S.A. (Fowells, 1965; Franklin & Dyrness, 1988). Although there are 'relatively' few wood-rotting fungi that affect the genus *Juniperus (*Gilbertson & Lindsey, 1975, p. 288), four important fungi species may cause heart rot in western juniper (Gilbertson, 1997, pers. comm.). These are *Antrodia juniperina* (Murrill) Niemela & Ryvarden, which is a brown rot fungus, and *Pyrofomes demidoffii* (Lev.) Kotl. & Pouzar, *Diplomitoporous rimosus (*Murrill) Gilb. & Ryvarden, and *Phellinus texanus* (Murrill) A. Ames which are white rot fungi (Gilbertson & Ryvarden, 1987). The fungi typically enter trees via openings in the heartwood or in dead sapwood openings near the heartwood (Scharpf & Goheen, 1993). While these openings may be caused by extreme weather events such as wind and ice which break branches, the chief means of entry is through wounds caused by fire (Scharpf & Goheen, 1993). Once established at a host

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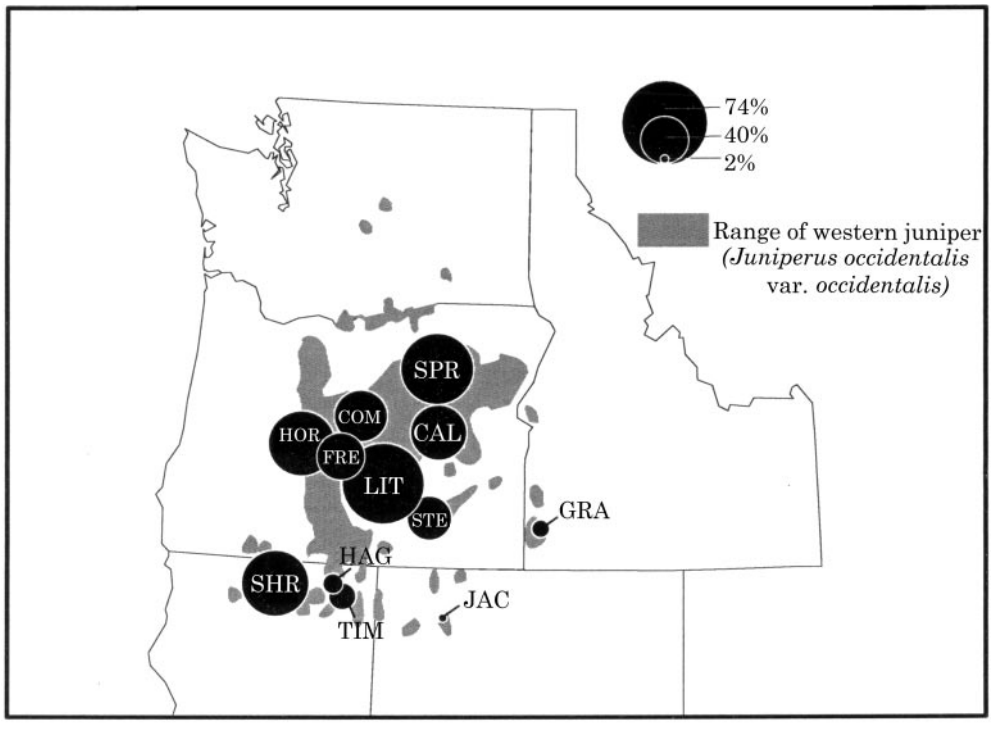


Figure 1. Sample population decline (%) of 12 selected chronologies (1749–1730), identified by sample site. Full names for chronologies are listed in Table 1. Native range of western juniper (*Juniperus occidentalis* var. *occidentalis*) is shown as lightly shaded area. Source: Fowells (1965); Holmes *et al.* (1986).

site, the fungi attack the heartwood, converting both the carbohydrate and lignin heartwood components into food, expanding primarily vertically in the tree (Wagener & Davidson, 1954; Scharpf & Goheen, 1993).

These heart rot fungi are not pathogenic since they do not attack either the sapwood or cambium of living trees. Thus, trees often survive heart rot infestations but, because of the loss of heartwood, become structurally less sound and more susceptible to climatic elements such as wind-throw (Wagener & Davidson, 1954). Decay rates vary considerably between trees and may be affected by the presence of gases (oxygen and carbon dioxide) and moisture in the heartwood, as well as heartwood temperature (Wagener & Davidson, 1954). Additionally, older heartwood appears more susceptible to decay than heartwood formed closer to the sapwood, possibly because of a decline in the presence of fungicide or fungistatic volatile oils and/or tannins that decrease towards the pith (Wagener & Davidson, 1954). Heart rot is rare in young trees and its frequency increases substantially in older trees as the percentage of heartwood increases and the ability to seal wounds where the fungus gains entry decreases (Wagener & Davidson, 1954).

The four wood-rotting fungi identified for western juniper are all widespread (Gilbertson & Ryvarden, 1987) and may affect junipers within their distribution in Oregon, Idaho, California, Nevada, and Washington (Fig. 1). In the mid 18th century, a widespread occurrence of heart rot affected western juniper throughout much of this range. The purpose of this paper is to describe the geographical pattern of the mid 18th-century heart rot occurrence and to discuss its potential causes and spatial pattern.

Methods

Twelve of the *Juniperus occidentalis* var. *occidentalis* chronologies collected by Holmes *et al.* (1986) in Oregon, Idaho, California, and Nevada were selected for analysis (Table 1). The trees selected by Holmes *et al.* (1986) were primarily strip-bark trees since their goal was to core old age trees (R.K. Adams, 1998, pers. comm.). All chronologies were collected in the 1980s and dated back at least several hundred years. Increment core samples were gathered from 16 to 50 trees at each site, with multiple core samples from each tree. Information based on the standardized chronologies was used in interpretation of the data. Holmes *et al.* (1986) mentioned that the presence of heart rot in many of their samples from the 1730s and 1740s inward precluded dating past this point, thus their sample sizes decreased. To determine the temporal and spatial pattern of this heart rot episode, changes in sample size were plotted over the length of each chronology to check for any discernible periods of sample size decline. After examining the plotted chronologies, a two-decade period (1749–1730) that best represented the greatest widespread decline in sample size was selected. Sample size decline, shown as percentage decrease between 1749–1730, was mapped to show spatial patterns. Correlation between mean maximum summer temperature (°C [June, July, August]) and sample size decline (%) between 1749 and 1730 was determined using Spearman's rank order (*Rs*). A correlation (*Rs*) also was obtained between mean site elevation and sample size decline. Temperature data were obtained from Western U.S. Historical Climate Summaries (Western Regional Climate Center, 1998). Temperatures for each chronology site were determined by adjusting mean maximum summer temperatures by mean lapse rates (0·65°C 100 m^{-1}) based on data from the nearest climate station.

Table 1. *Selected characteristics of western juniper tree-ring chronologies**

Site code	Site name	State	Lat. (°N)	Long. (°W)	Altitude (m)	Mean max. summer temp. (°C)	Trees sampled	Heart rot†
SPR	Spring Canyon	OR	44 54	118 55	1340–1610	23·4	39	Y
COM	Committee Creek	OR	44 10	120 14	1486–1518	25·6	31	Y
CAL	Calamity Creek	OR	43 59	118 48	1433–1494	24·8	40	Y
HOR	Horse Ridge	OR	43 58	121 04	1109–1183	25·7	43	Y
FRE	Frederick Butte	OR	43 35	120 27	1433–1554	25·4	50	Y
LIT	Little Juniper Mountain	OR	43 08	119 52	1524–1768	26·8	49	Y
STE	Steens Mountain	OR	42 40	118 55	1625–1686	25·5	48	Y
GRA	Grasshopper Trail	ID	42 31	116 48	1689–1713	26·0	49	N
HAG	Hagar Basin	CA	41 46	120 45	1518–1530	27·5	27	N
SHR	Sharp Mountain	CA	41 44	121 49	1335–1500	25·6	42	Y
TIM	Timbered Mountain	CA	41 43	120 45	1555–1616	27·1	16	Y
JAC	Jackson Mountains	NV	41 18	118 26	2024–2170	25·6	43	N

*Information taken from Holmes *et al.* (1986), except for mean maximum summer temperature (Western Regional Climate Center, 1988). Data from Holmes *et al.* (1986) were extracted from the International Tree-ring Data Bank.

†Y = heart rot is mentioned in site description summary for that chronology; N = not mentioned.

Results

The number of datable samples declined substantially for 9 of the 12 chronologies between 1749–1730 (Fig. 1). In general, declines were greater for chronologies gathered in the north-west portion of the study area, with little decline in the Idaho and Nevada chronologies. Percentage decline ranged from 74% at Little Juniper Mountain, showing that nearly three-quarters of the trees datable to 1749 could not be dated in 1730, to only 2% at Jackson Mountain (Fig. 1). No other time period within the chronologies illustrated a significant widespread decline in sample population size (Fig. 2), although smaller declines (perhaps minor heart rot outbreaks) do exist in the 1850s for the Sharp Mountain, CA and Spring Canyon, OR chronologies. The correlation between mean maximum summer temperatures and sample size decline was $R_s = -0{\cdot}03$ ($p = 0{\cdot}91$). Conversely, there was a significant relationship between mean site elevation and sample size decline, $R_s = -0{\cdot}64$ ($p = 0{\cdot}03$).

Discussion

There is only one major widespread heart rot infestation evident in the chronologies, and although the fungus causing the heart rot was never identified, we believe *Antrodia juniperina* is the most likely candidate. Wood decayed by brown rot fungi such as *A. juniperina* leave a 'residue of amorphous, crumbly, brown cubical chunks', as opposed to a bleached and paler color plus stringy or spongy appearance typical of white rots (Gilbertson & Ryvarden, 1987, p. 35). Personal communication with one of the collectors of the western juniper chronologies (R.K. Adams, 1997, pers. comm.) describes the heart rot as fitting the criteria for a brown rot. Additionally, in winter 1998, R.K. Adams presented several core samples from the Holmes *et al.* (1986) collection to R.L. Gilbertson (Professor Emeritus, Department of Plant Pathology, University of Arizona) who agreed that the samples were most likely affected by brown rot (e.g. *Antrodia juniperina*).

Although species confirmation is only possible when either fresh samples or fruiting bodies are present, neither of which are available from the 1980s collections, we do know that the effects of the mid 18th-century heart rot episode were most substantial in Oregon and two of the California sites, while less substantial at the Idaho, Nevada, and third California sites. Differences in rates of infection are unlikely to be a function of the disjunct range of western juniper to the Idaho or Nevada chronologies, since heart rots, as suggested by paleobotanical records, have existed for western juniper throughout its range since the late Tertiary (Wagener & Davidson, 1954). Because *Antrodia juniperina* is found on junipers throughout the United States (Gilbertson & Ryvarden, 1987), it is likely that other causes have limited the impact of heart rot in some of these *Juniperus occidentalis* chronologies.

The widespread occurrence of western juniper heart rot and its synchronous timing suggest some macroscale feature such as climate may have been the initiating trigger (R.K. Adams, 1997, pers. comm.). In northern California, Page (1981) concluded that the 1975–1977 drought was largely responsible for accelerating the effects of the fungus *Fomes annosus*, causing root disease and widespread mortality in ponderosa pine (*Pinus ponderosa* Laws.). Similarly, we suspect that a widespread climatic event, particularly an ice or wind storm, would be sufficient to break off branches and thus create a pathway for the heart rot fungus to enter heartwood. We cannot reconstruct single climatic events in the 1700s, but historical records, beginning in the late 1800s, show that destructive and widespread windstorms have impacted the interior Pacific Northwest from Washington State to northern California and Nevada. For example, from 13–15 November 1981 the entire Pacific Northwest was impacted by a severe windstorm, with gusts exceeding 160 k.p.h. as

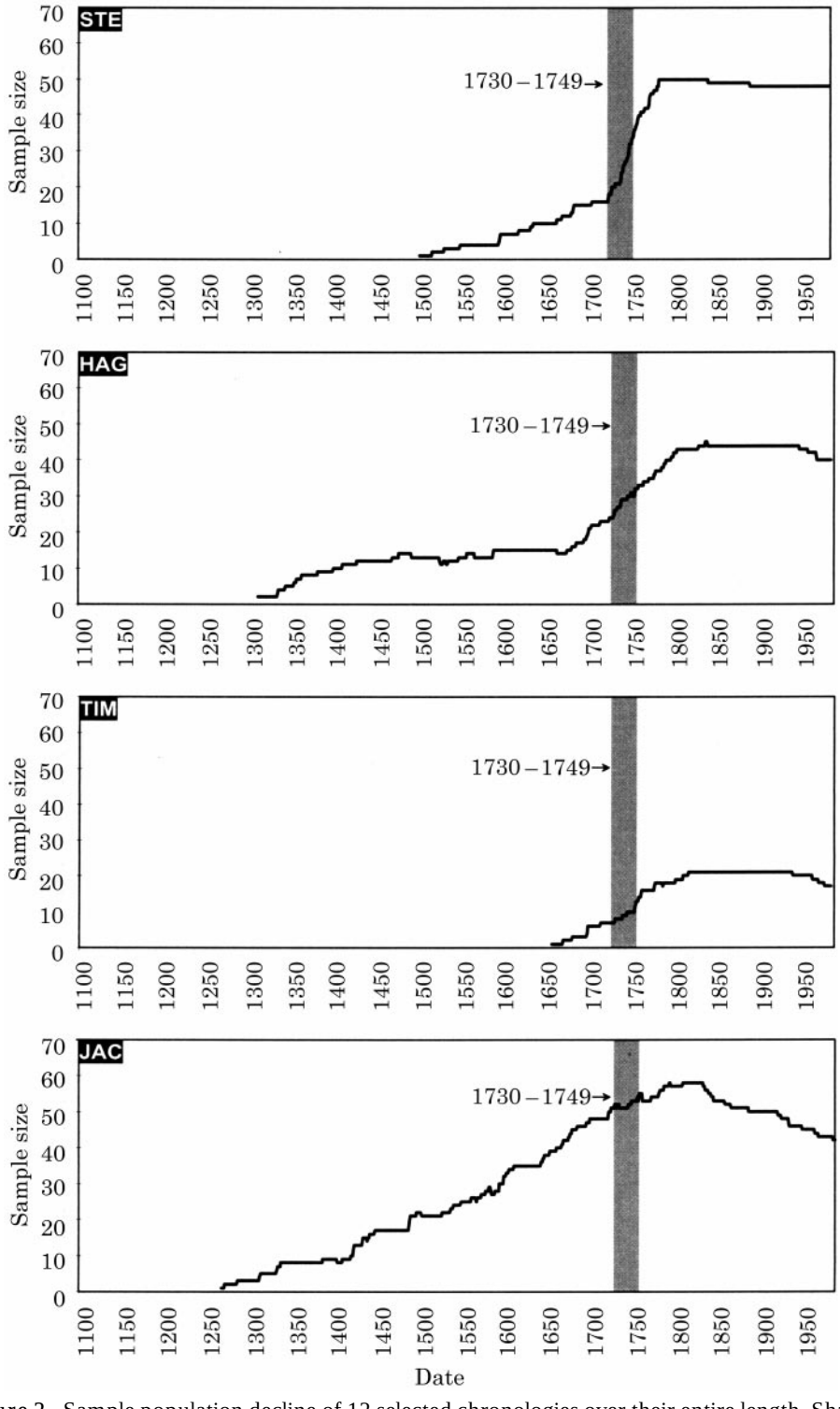
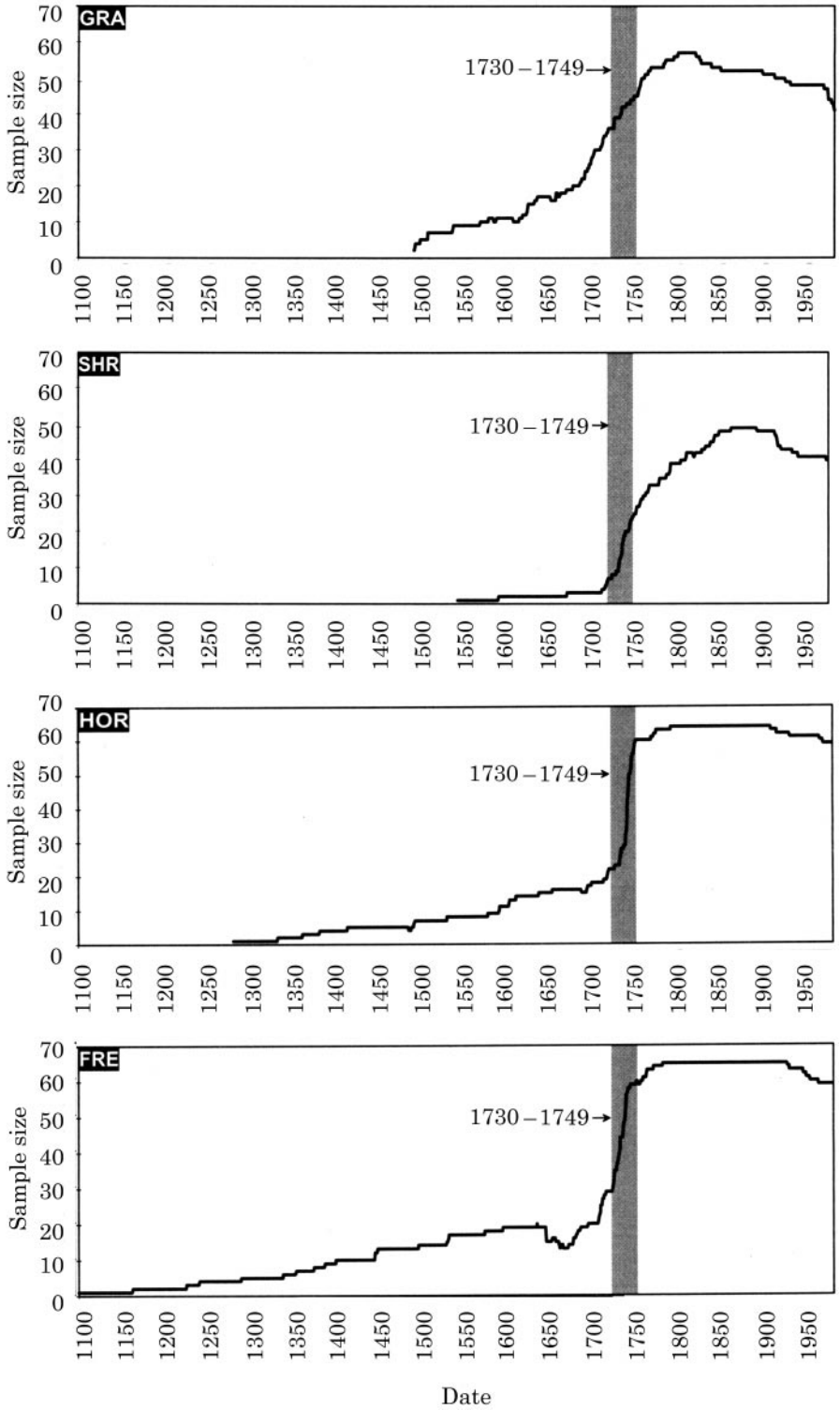


Figure 2. Sample population decline of 12 selected chronologies over their entire length. Shaded vertical bars represent the 1730–1749 time period, while the solid black lines represent sample size by year. The chronology code name is in the upper left corner (see Table 1). Source: Holmes *et al.* (1986). (Cont.)



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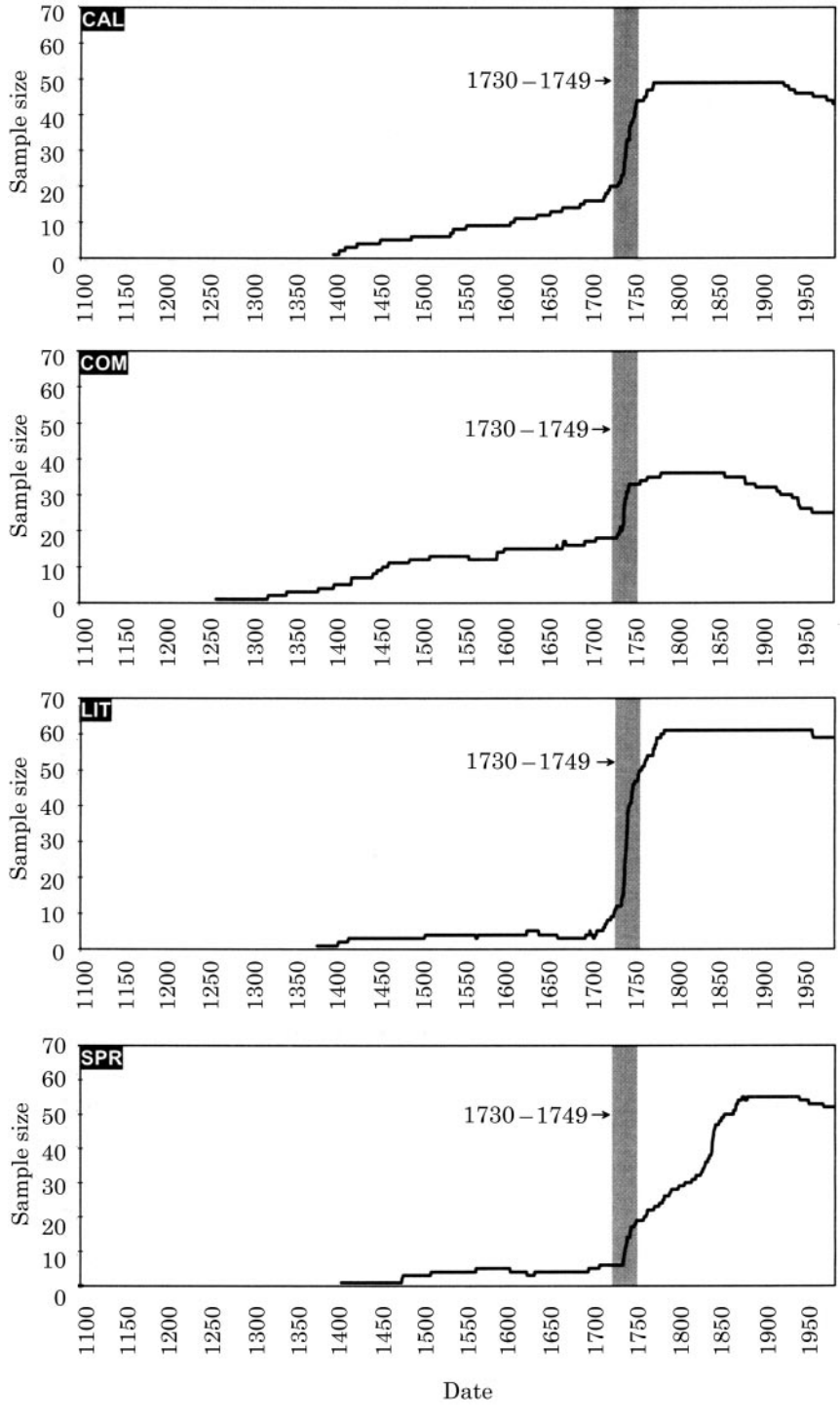

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far inland as Boise, ID and Reno, NV (National Oceanic and Atmospheric Administration, 1998).

Ice storms periodically affect the Columbia River Basin region with their effects ranging as far south as south-eastern Idaho, north-western Nevada, and north-eastern California (Robbins & Cortinas, 1996). These storms are generated by mild and humid Pacific-type frontal systems over-riding cold dense air trapped in the Columbia River Basin/northern Great Basin (Robbins & Cortinas, 1996), and can sufficiently ice trees to the point of branch failure. Since neither ice storms nor wind storms are exceptionally rare (e.g. there were > 40 freezing rain observations in south-eastern Oregon between 1982–1990 (Robbins & Cortinas, 1996)), this raises the question of why there have not been other widespread heart rot outbreaks related to branch failure caused by ice buildup. Perhaps a rare combination of events, such as an ice storm coupled with high winds, worked synergistically to cause the heart rot episode from 1749–1730.

The activity of heart rot-causing fungi in the mid latitudes is temperature dependent, with optimal internal tree temperatures ranging between 24°C and 30°C (Wagener & Davidson, 1954). Below optimal temperatures appear to inhibit or stop fungus growth. We have no knowledge of optimal temperatures for *Antrodia juniperina*, but our correlation test shows that no significant relationship exists between mean maximum summer temperatures and sample size decline. Alternatively, the significant negative correlation between elevation and sample size decline, that is lower elevation sites experienced greater heart rot infections than higher elevation sites, may be reflective of additional temperature or precipitation variances, such as cold air drainage (potentially enhancing the effects of an ice storm) or short-term summer temperature extremes that favor fungal growth.

Wagener & Davidson (1954) suggest that the majority of heart rot infestations (approaching 70%) are initiated by fire. Fire spread within western juniper communities is favored when grass is the dominant fuel type (Agee, 1993). Paleobotanical records from Diamond Pond in south-eastern Oregon (Miller & Wigand, 1994), however, suggest that the 1700s was a period less conducive for large-scale fires. Grass pollen/sagebrush pollen ratios were below the mean for the 5500-year record (indicating less grass cover), and large charcoal–small charcoal index values do not indicate this was a period of exceptional fire activity (see Figures 3 and 5 in Miller & Wigand, 1994). Further, since site-specific characteristics (e.g. topography, fuel availability) of juniper woodland locations impact fire intensity and frequency (Agee, 1993), a widespread fire event affecting nearly the entire range of western juniper is improbable, given the variable site conditions where the tree exists (Fig. 1).

Two studies on fire histories of western juniper, however, do not exclude the possibility of fire-initiated heart rot. Young & Evans (1981), examining frequency of fire scars in western juniper in northern California, identified a period of peak fire frequency sometime between 1750 to 1760 that was preceded by a 100-year fire-free period. In south-western Idaho, Burkhardt & Tisdale (1976) examined the fire history of western juniper since the late 1600s and determined that fire frequency declined markedly beginning in the 1870s. These results suggest this was only a 100-year, as opposed to 200-year period following the 1740s when fire may have been a dominant widespread feature in the Intermountain West. Thus, a lack of other sufficiently widespread intense fires may explain why there appears to be only one major widespread heart rot episode in the chronologies examined.

We recognize that arguing for a singular event as the cause for a heart rot outbreak can be problematic. First, wounded trees undergo a dynamic compartmentalization process that enables them to seal off micro-organisms introduced via wound openings (Shigo, 1984). Fungi spread is restricted by a ‘barrier zone’ of unique cells produced by the cambium that ‘isolate injured tissue’ (Shigo, 1984, p. 193) and limit subsequent wood decay. Thus, the concept of dynamic compartmentalization suggests that it is only

possible to confirm the latest date (as opposed to the earliest) when decay occurred since wood formed between 1730–1749 could undergo decay because of wounding as early as 1730–1749, but all dates (i.e. wounding events) afterwards. Second, time lags exist between the introduction of wood-decaying fungi (via a wound) and their subsequent detection as decayed wood. Since wood decay progresses fastest in attenuated columns both above and below the wound (Shigo & Hillis, 1973), its time of detection also would be a function of the distance between the wound site (e.g. a fire scar or broken limb), the decay rate of the fungi (Shigo & Hillis, 1973), and the core extraction height. The second point, however, could also help explain the two-decade period (1749–1730) where the detection of heart rot became so prevalent, since a singular wounding event would have taken different time periods to be manifested as decayed wood at coring height.

In conclusion, heart rot affected much of the western juniper range at least once in the last 250 years. Because the majority of trees with heart rot dated to the 1730s–1740s, and the lack of similar magnitude infestations during other periods of the tree ring chronologies, we theorize that a rare combination of events (i.e. windstorms, ice storms) may be necessary for the fungus to attack the heartwood of western juniper, although the exact cause is unknown. Further, chronologies gathered from higher sites were impacted less by heart rot than samples gathered at lower elevation sites, suggesting that some climatic variable may influence the development of *Antrodia juniperina* growth. Regardless, our results show that high-impact regional scale events do occur if even only at infrequent intervals, and have the ability to affect many trees over a large geographic range.

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