



Population Ecology

Seasonal life history and impact of *Nepytia janetae* (Lepidoptera: Geometridae): an emerging pest in Southwestern montane forests

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Subject Editor: Darrell Ross

Received on 16 May 2024; revised on 23 August 2024; accepted on 18 November 2024

Nepytia janetae is a previously innocuous non-eruptive species that has recently incurred multiple devastating outbreaks in the American Southwest. We report information on the life cycle, biology, and impact of this species learned during the first 3 known outbreaks in spruce-fir and mixed-conifer forests of the Pinaleno Mountains and White Mountains of Arizona and the Sacramento Mountains of New Mexico. *N. janetae* is a univoltine, autumn- and winter-feeding wasteful defoliator with 3-yr eruptive outbreaks. Outbreaks terminate with parasitism, viral infection, starvation, and in one outbreak with heavy rainfall during egg deposition. Conifer mortality varied between outbreaks but approached 100% in some stands in all three study areas. Only severely defoliated trees died. Mortality was associated with defoliation severity, moisture availability in the last growing season of the outbreak and/or in the first post-outbreak growing season, and bark beetle activity. Other site and stand variables associated with defoliation and mortality varied between outbreaks, highlighting the need to evaluate multiple outbreaks before identifying factors related to susceptibility and vulnerability to a new pest species. The emergence of this insect as a serious pest is probably related to warming climate but the mechanisms are unclear; the only consistent pattern is an association with low or early loss of snowpack in either the year immediately preceding or the first year of the outbreaks. Differences in host specificity and larval coloration between the distant mountain ranges indicate that *N. janetae* may be a complex of multiple species or subspecies.

Keywords: climate change effect, cryptic species, emergent pest, forest defoliator, Janet's looper, spruce beetle, western balsam bark beetle

Resumen en Español

Nepytia janetae es una especie no eruptiva previamente inocua que recientemente ha tenido múltiples brotes devastadores en el suroeste de Estados Unidos. Brindamos información sobre el ciclo de vida, la biología y el impacto de esta especie aprendida durante los primeros tres brotes conocidos en bosques de Picea-Abies y de mixtos de coníferas en las Montañas Pinaleno, las Montañas Blancas de Arizona, y las Montañas Sacramento de Nuevo México. *N. janetae* es un defoliador univoltino que se alimenta en otoño e invierno y que presenta brotes eruptivos de tres años. Los brotes terminan con parasitismo, infección viral, inanición y, en un brote, con fuertes lluvias durante la deposición de huevos. La mortalidad de coníferas varió entre los brotes, pero se acercó al 100% en algunos rodales en los tres áreas de estudio. Sólo murieron árboles severamente defoliados. La mortalidad se asoció con la gravedad de la defoliación, la disponibilidad de humedad en la última temporada

de crecimiento del brote y/o en la primera temporada de crecimiento posterior al brote, y la actividad de los escarabajos de la corteza. Otras variables de sitios y rodales asociadas con la defoliación y la mortalidad variaron entre los brotes, lo que destaca la necesidad de evaluar múltiples brotes antes de identificar factores relacionados con la susceptibilidad y vulnerabilidad a una nueva especie de plaga. La aparición de este insecto como una plaga grave probablemente esté relacionada con el calentamiento del clima, pero los mecanismos no están claros; el único patrón consistente es una asociación con una pérdida baja o temprana de capa de nieve en el año inmediatamente anterior o en el primer año de los brotes. el único patrón consistente es una asociación con una capa de nieve baja o una pérdida temprana de la capa de nieve en el año inmediatamente anterior o en el primer año de los brotes. Las diferencias en la especificidad del huésped y la coloración de las larvas entre las cadenas montañosas distantes indican que *N. janetae* puede ser un complejo de múltiples especies o subespecies.

Introduction

Nepytia janetae, known as Janet's looper, is a previously innocuous non-eruptive species that recently incurred multiple catastrophic outbreaks in the American Southwest. The species was described in 1967 from several specimens collected in 1961 through 1965 at multiple locations in New Mexico and a single specimen collected in 1936 in the White Mountains of Arizona, with the Arizona specimen serving as the type specimen (Rindge 1967) (Supplementary Table S1). Rindge reported collection information and taxonomic descriptions of the adults. He did not report on species biology other than to note that adults were found in July between 2438 and 2743 m elevation with *N. regulata* Barnes and McDunnough. Forest Service records for 1961–1971, when Rindge was collecting, do not indicate any major geometrid activity in either mixed-conifer or spruce-fir in Arizona or New Mexico (USFS 1971). *N. janetae* has been collected in Arizona, New Mexico, and California, but there are no reports of outbreaks or damage prior to 1996.

Isolated *N. janetae* outbreaks occurred between 1996 and 2020 in four Southwestern mountain ranges (Fig. 1). Outbreaks in 1996 to 1999 severely defoliated 4200 ha of spruce-fir forests in the White Mountains and approximately 200 ha in the Pinaleno Mountains of eastern Arizona (USFS 1999, 2000). A third outbreak in 2005 to 2007 defoliated over 4850 ha of mixed-conifer forest in the Sacramento Mountains in southern New Mexico (USFS 2008), and a fourth outbreak in the Sangre de Cristo Mountains in northern New Mexico from 2017 to 2020 defoliated about 2270 ha of mixed-conifer forest (USFS 2021). Outbreaks were detected the year after outbreak initiation due to the insect's seasonal history of feeding through autumn and winter.

Because of the severity of damage caused by an insect not previously observed to incur outbreaks, and the lack of published information on its biology, we initiated studies to learn more about the insect's biology, disturbance ecology, and impact in the Southwest. Our observations from studies of the first 3 outbreaks on the life cycle, seasonal history, outbreak dynamics, and impact are reported here, as well as relevant information from reports regarding the Sangre de Cristo outbreak.

Study Areas and Methods

Study Areas

The outbreaks occurred in high-elevation forests, the first 3 in isolated mountain ranges south of 33° 53' N (Pinaleno Mountains and White Mountains in Arizona and the Sacramento subrange of the Sacramento Mountains (the area south of U.S. Highway 70) in New Mexico), and the fourth in the southern extent of the Southern Rocky Mountains (the Sangre de Cristo Mountains in New Mexico) at ca. 36° (Fig. 1). These ranges are separated from

each other by extensive desert and grassland ecosystems, with ca. 50 to 330 km between ranges (Fig. 1). The Arizona outbreaks were limited to spruce-fir forests and the New Mexico outbreaks to mixed-conifer forests. Southwestern forest types and tree species are distributed along elevation, exposure, and fire-frequency gradients. Generally, spruce-fir occurs above mesic mixed-conifer (mixed-conifer with aspen), which occurs above dry mixed-conifer (mixed-conifer/frequent fire), which transition to pine forests, with elevational placement of the transitions influenced by aspect (Whittaker and Niering 1964, Elmore and Janish 1976, Alexander and Shepperd 1990, Alexander et al. 1990, Dick-Peddie 1993). Engelmann spruce (*Picea engelmannii* Parry ex Engelmann 1863) and corkbark fir (*Abies lasiocarpa* var. *arizonica* (Merriam) Lemmon) dominate above 2700 masl, forming pure spruce or spruce-fir forests, sometimes with minor components of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), southwestern white pine (*Pinus strobiformis* Engelm.), limber pine (*Pinus flexilis* James), and Colorado blue spruce (*Picea pungens* Engelm.) (Dick-Peddie 1993, Vankat 2013, White 2014, O'Connor et al. 2017). Mesic mixed-conifer stands vary in species composition and are usually dominated by shade-tolerant species—Douglas-fir and white fir (*Abies concolor* [Gord. & Glend.] Lindl. ex Hildebr.)—with varying amounts of Engelmann spruce, corkbark fir, and southwestern white pine or limber pine. Quaking aspen (*Populus tremuloides* Michx.) is usually present in both spruce-fir and mesic mixed-conifer, though abundance and patch size vary with site disturbance history. Dry mixed-conifer stands tend to be dominated by fire-tolerant species, particularly Douglas-fir and ponderosa pine (*Pinus ponderosa* var. *brachyptera* (Engelm.) Lemmon), often with abundant shade-tolerant and fire-intolerant species that proliferated during the period of fire exclusion (Margolis and Balmat 2009, O'Connor et al. 2017).

Forest character differs somewhat amongst the four mountain ranges. Colorado blue spruce is absent in the Pinalenos, corkbark fir is less common in the Sacramento mesic mixed-conifer, and Southwestern white pine is replaced by the closely related limber pine in northern New Mexico. Mixed-conifer stands in the southern Sacramento subrange are more homogenous than in the other three ranges, with Douglas-fir and white fir often forming relatively pure single-species or co-dominant stands. Abrupt demarcations between mesic and dry mixed-conifer are common in the Sacramentos, as the range slopes to the east with mostly northeasterly trending drainages, creating ridges that divide the mesic mixed-conifer sites on north-facing slopes from the dry-mixed conifer on warmer drier south-facing slopes (Brown et al. 2001). The spruce-fir type does not occur in the Sacramento subrange (Dye and Moir 1977). Mixed-conifer in the Sangre de Cristos is very diverse (Dick-Peddie 1993, Margolis and Balmat 2009), and perhaps has a greater abundance of pines than the other locations.

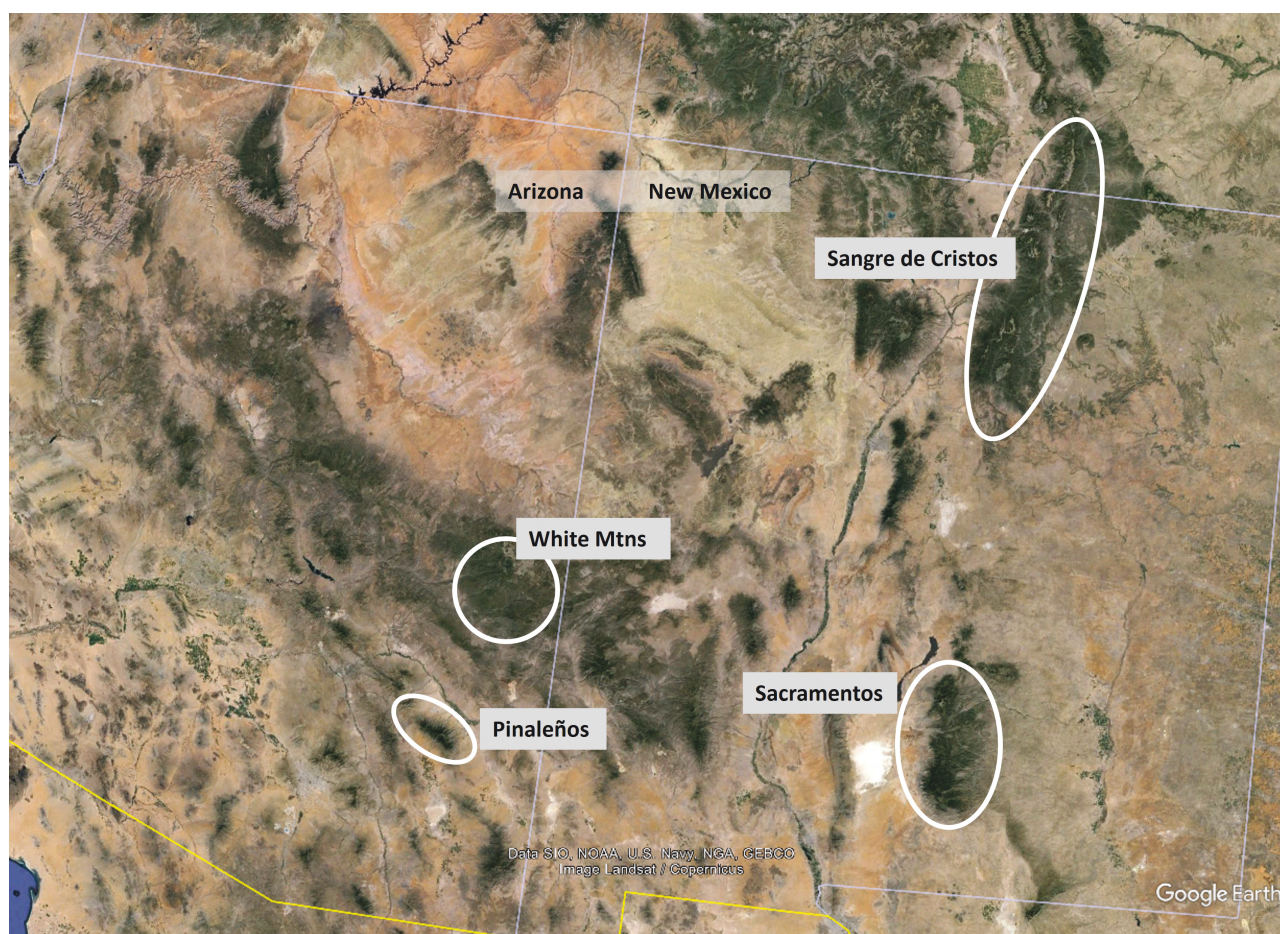


Fig. 1. Location of *N. janetae* outbreaks in Arizona and New Mexico, 1996–2020. The figure was created using Google Earth Pro (2022).

Life History

Life-history observations were made by the second and third authors during multiple site visits and by observing large larvae collected for rearing. Field observations were not limited to the impact assessment plots described later. Arizona specimens were identified by Ron Leuschner, with the Natural History Museum of Los Angeles County, California, and deposited in the University of Arizona Insect Museum. New Mexico specimens were identified by Clifford Ferris with the University of Wyoming.

Meteorological Data

We evaluated meteorological data to identify patterns that might be associated with the outbreaks. Local weather data relative to the period of observations were obtained from several sources which varied in length and quality. Pinaleno data are from the University of Arizona Mount Graham Red Squirrel Research Program's stations at Emerald Peak within the outbreak area, and at Biology Camp just below the outbreak area. White Mountain data are from the National Climate Data Center (NCDC, <https://www.ncdc.noaa.gov>) station at McNary 2 N (NCDC USC00025412) and Alpine AZ (NCDC USC00020159, for snow depth). The McNary station at 2237 m is in the ponderosa pine forest, 700 m below the outbreak zone, and its data are used to evaluate local long-term trends and variability and do not reflect actual temperatures and precipitation in the spruce-fir forest. New Mexico data are from Cloudcroft NM (NCDC USC00291927) at 2689 m within the Sacramento outbreak

zone. Where possible, we evaluated average daily minimum and daily midpoint ($[\text{daily maximum} + \text{minimum}]/2$) or the average of 48 or 96 observations per day (in the Pinalenos) temperatures by month and year, and for the periods September–November and November–February; calendar days of the last spring and first autumn frosts (temperatures at or below 0 °C); frost-free period; precipitation and snow depth for the same periods as above, and calendar date of the first and last measurable snow accumulation and snow pack.

Damage Assessment

Tree defoliation and mortality were evaluated with different plot systems in each mountain range. Damage was assessed in the Pinalenos from 1999 through 2001 using 31 variable-radius plots with basal area factors of 4.59 or 6.89 sq m/ha (20 and 30 sq ft/ac, respectively) (see Schreuder et al. (1993) for a description of variable-radius plot sampling, also known as probability proportional to size). Plots were distributed on a grid with a 200 m spacing, excluding non-forested and excessively steep areas.

The White Mountain outbreak also began in autumn 1996. Here plots are a subset of the Fort Apache Indian Reservation Continuous Forest Inventory (CFI) system, which is designed to provide data on growth, yield, and mortality of the entire forest, and consists of three-plot clusters on a 2012 m grid (Moran-Palma and McTague 1997). Within each cluster, fixed-radius circular plots of 0.0809 ha (0.20 ac) are located on a north-south line, ca. 100 m apart. For this study, individual plots are considered individual observations without regard



Fig. 2. Spruce-fir mortality in 1999 from *N. janetae* in the Mount Baldy Wilderness area of the Arizona White Mountains. Photo by R.A. Fitzgibbon.

to cluster and were assessed annually 1999 to 2001. Half of 30 plots were located within, and half out of, the area mapped as defoliated in 1999 by the U.S. Forest Service Aerial Detection Survey (USFS 2000). The sampled area did not include the most severely damaged area (Fig. 2) in the northeastern quarter of the mountain range (the Mount Baldy Wilderness Area, the Sunrise Park Resort ski area, and the portion within the Apache-Sitgreaves National Forests).

The primary objective in the Sacramento Mountains was to compare damage to what occurred in Arizona. Damage was assessed in 2007, 2008, and 2010 with 22 0.05-ha plots, 19 located randomly, and 3 targeted to include species with low sample depth in the random plots, all in areas confirmed as defoliated by *N. janetae*. Mortality observed in 2010 was attributed to either 2009 or 2010. Some data are missing for 3 plots that were vandalized.

At all locations, tree measurements included species, status (live, dead), diameter at breast height (1.37 m above ground, dbh), relative size (dbh/QMD, used to quantify individual tree size relative to the average tree on the plot), bark beetle activity, bear damage, dwarf mistletoe rating (DMR) (Hawksworth 1977), presence of stem and root pathogens, defoliation, and, in the Pinalenos, tree height, and ring count. Defoliation was assessed by crown third by either 10% classes or by Defoliation Index (similar to DMR, the sum of crown third ratings of 0, 1, 2, and 3 for 0, 1 to 33, 34 to 66, and 67 to 100% defoliated, see Lynch 2004). Crown thirds were partitioned based on the live crown present prior to the outbreaks, rather than partitions based on what was live each year. Defoliation could not be assessed on trees that died prior to plot establishment. Plot-level variables included aspect, elevation, steepness, stand density, stand density index (SDI), basal area, density and basal area of individual species, mean tree dbh, quadratic mean diameter (QMD), coefficient of variation of dbh (CV_{dbh}), proportional representation (dominance) of individual species by density and basal area, relative representation of corkbark fir vs. Engelmann spruce (only in Arizona, quantified as the ratio of

corkbark fir:Engelmann spruce (CF:ES) for both density and basal area), and three extracted descriptive principal components. The first 3 principal components of the topographic and plot character variables were extracted separately for each mountain range using correlation matrices. Variables that would restrict the number of cases in the analyses, such as dbh of frequently absent species, were excluded from the principal components analyses. Conifer species that were not sufficiently represented at the plot level were assessed in tree-level analyses.

Plot-level defoliation, computed as the mean of tree-level defoliation, and mortality were assessed using Pearson's correlation (r) statistics for association with site and plot variables. Plot-level defoliation and mortality associations with aspect were evaluated by examining charted data and with variance-appropriate one-sided t -tests comparing opposing quadrants (ie north vs south is $315\text{--}45^\circ$ vs $135\text{--}225^\circ$). Attributes of dead trees vs. survivors were compared with variance-appropriate one-sided t -tests for means, with variance equality tested using Levene's F -tests. We evaluated all conifers combined and each abundant conifer species individually.

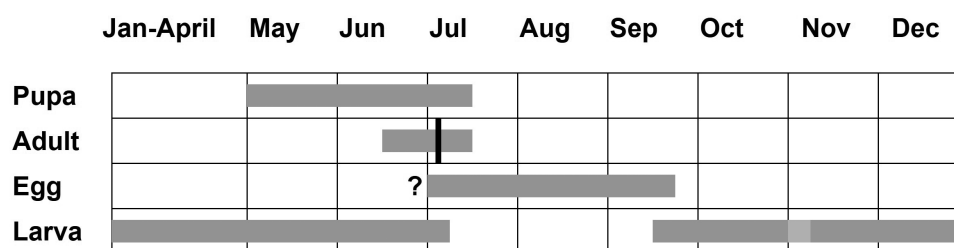
All analyses were completed using SPSS 28.0.0.0 (IBM Corp. 2021).

Results

Host Species

Known hosts include bristlecone pine (*Pinus aristata* Engelm.), Colorado blue spruce, corkbark fir, Douglas-fir, Engelmann spruce, limber pine, ponderosa pine, Southwestern white pine, and white fir, but with distinct differences between Arizona and New Mexico. In both Arizona outbreaks, *N. janetae* fed on and caused serious damage to corkbark fir and Engelmann spruce, but a few Douglas-fir and southwestern white pine within the outbreak areas were either not defoliated or minimally defoliated. Additionally, live large larvae collected in the White Mountains for rearing purposes did

White Mountains & Pinaleno Mountains, 1996-1999



Sacramento Mountains, 2006-2007

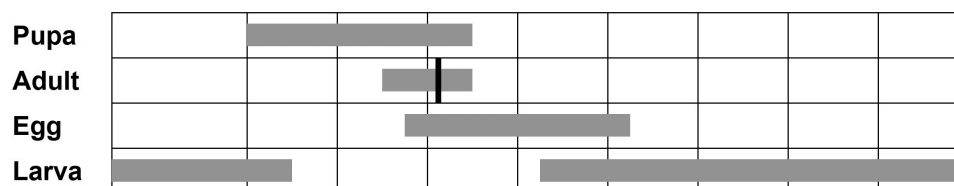


Fig. 3. Life cycle for *N. janetae* as observed during two outbreaks in the 1990s in Arizona and one outbreak in southern New Mexico in the 2000s. The black vertical bars indicate the timing of peak moth flight.

not feed on Douglas-fir foliage when caged with both Douglas-fir and Engelmann spruce foliage. In both New Mexico outbreaks, *N. janetae* fed on and damaged Douglas-fir, Engelmann spruce, ponderosa pine, southwestern white pine (Sacramentos), limber pine (Sangre de Cristos), and white fir, with a strong preference for white fir, Douglas-fir (Allen-Reid 2007a, USFS 2019) and Engelmann spruce. Our data show that Engelmann spruce was more severely defoliated than white fir and Douglas-fir, though the outbreak did not encompass the nearby, but disjunct, spruce-fir forest where Engelmann spruce is much more abundant. The only coniferous species not fed on was common juniper (*Juniperus communis* (Cupressaceae)), a low-growing shrub. Corkbark fir and bristlecone pine were fed on in the Sangre de Cristos (USFS 2019). Corkbark fir is found in the Sacramentos but was absent on our plots; Colorado blue spruce is found in all the ranges except the Pinalenos but was absent on our plots.

Life History, Habits, and Seasonal History

Eggs

The general shape is oblong with a well-defined concave surface or dimple on the distal surface, similar to *Lambdina fuscicollis fuscicollis* (Guenée) (hemlock looper) as shown by Rose and Lindquist (1994), except cream-colored and attached opposite the dimple. Eggs are laid in irregularly shaped clusters of 10 to 50 (usually 25 or less) on the bottom needle surface.

Larvae

Mature larvae are approximately 2.5 cm in length before pupation. The number of instars was not determined. Arizona specimens have a herringbone pattern of gray, dark brown, and green on the upper surface, with irregular pale cream lateral stripes. Head capsules are strongly mottled, with a distinct horizontal black stripe just above the mouthparts. Larvae in the Sacramentos (USFS 2007) are mottled in appearance, without a lateral stripe or distinct pattern, with green, charcoal, and brown color morphs.

There was considerable variability in larval distribution within trees, among trees at a site, and on different dates in the Sacramentos, in part due to larval movement within and between trees (Allen-Reid

2007b). Larvae of all sizes were seen crawling up tree boles from the base during mid-day on sunny days throughout the winter. Larvae are easily dislodged when disturbed, dropping on silken threads, and numerous fallen larvae were often seen crawling on the ground, non-host vegetation, rocks, structures, and snow, and in the Sacramentos were numerous enough to annoy visitors and forest workers. Larvae become inactive during periods of severe cold.

Pupae (Arizona)

In Arizona, the pupae are variable in color but usually lime green or yellow-green, as are *N. freemani* (Klein and Minnoch 1971). Thoracic spiracles are slit-like; abdominal spiracles have brown margins. There are five pairs of cremasters in two sizes. The black stripe seen above the larval mouthparts is also distinct in the pupa. Pupae are webbed onto the foliage near the tips.

Adults

Male and female adults are as described by Rindge (1967). Bodies of the newly eclosed Arizona females were lime green rather than gray. Adult New Mexico females were light gray to white, noticeably lighter colored than the Arizona adults. Photographs of adults, larvae, and pupae are available in USFS (1999, 2007). Moths are active during the daytime and are photopositive.

Seasonal History

Behavior and seasonal activity observations were hindered by travel distances and difficult access to the high-elevation sites during winter. *N. janetae* is univoltine, overwinters as active larvae, with fairly asynchronous development and a great deal of overlap in life stages (Fig. 3). We found no evidence of multiple or overlapping generations per year. Asynchronous development appears to be related to variable autumn-winter temperatures during larval development plus a variable but sometimes prolonged eclosion period (probably from different individuals pupating at different times). Eggs hatch in early autumn and larvae feed from autumn into early summer. In Arizona in the late 1990s, the first instars appeared in mid-September well after the bud set. Several instars were present and actively feeding throughout the winter, with mature larvae found beginning

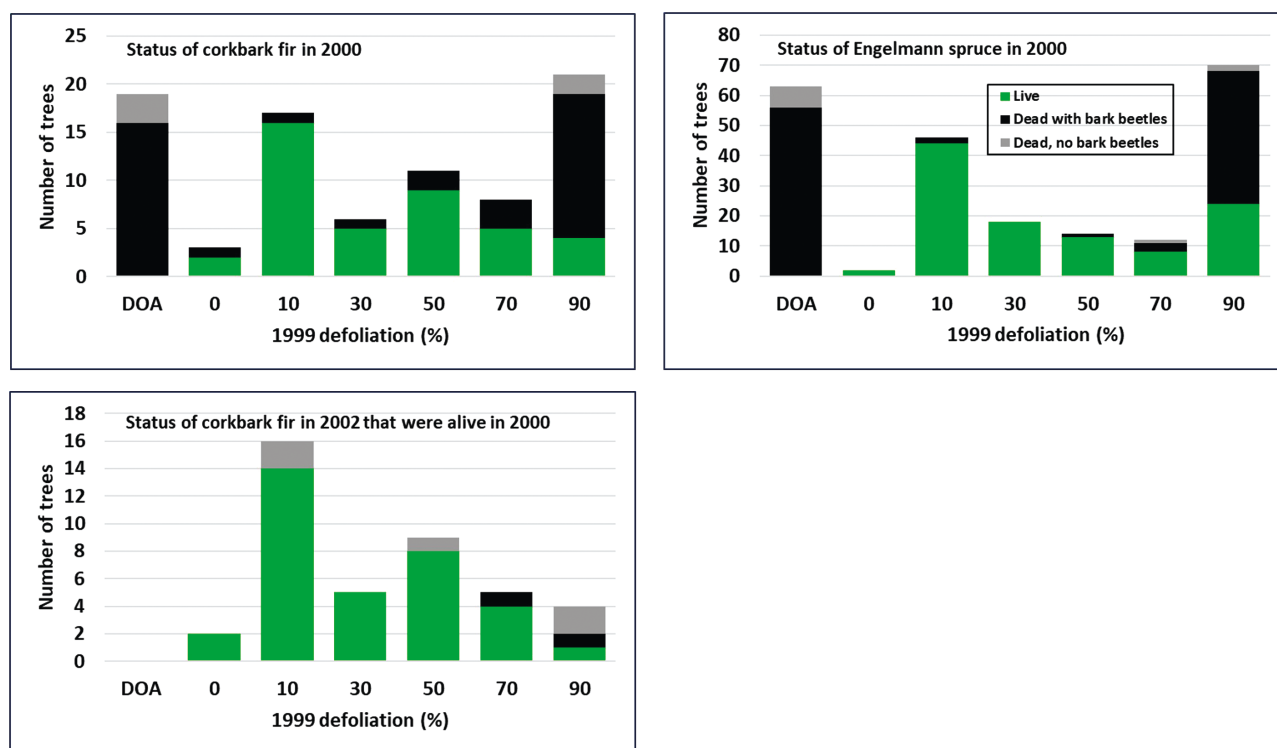


Fig. 4. Status of individual trees (not plot averages) in the Pinalenos in 2000 by defoliation severity and bark beetle activity (top) and status of corkbark fir in 2002 that were alive in 2000 (bottom). The 2002 results are not shown for Engelmann spruce because of severe defoliation in a spruce aphid outbreak in 2000 (Lynch 2009). DOA indicates trees that were dead when plots were installed and are thought to have been severely defoliated.

in November, through the winter and spring, and into July, although numbers diminished after early May. In the Sacramento outbreak, egg hatch began in early August, but most insects overwintered as small larvae.

Small larvae feed on the outer needle tissues, scoring the needle surfaces. In the Sacramento outbreak, where small larvae fed for several months, this caused individual needles to dehydrate and die. Defoliation damage became evident in January, with complete tree defoliation by May. Large larvae are wasteful chewers, though generally feeding first on needle perimeters, leaving needles with ragged edges. Later entire needles are consumed, sometimes leaving the midrib.

Pupae begin to appear in May and are found into July. Moths first appear in late June, peak flight is reached in early July, and then declines rapidly, with few moths found after mid-July. Rindge (1967) collected adults in 1961–1965 in early July, and the 1936 White Mountains' specimen was collected in mid-June. Moths are active during the daytime and are photopositive. Larvae, pupae, adults, and eggs were all found in July in the 1990s outbreaks (Fig. 3).

All years' foliage is consumed, often completely so. Vegetative buds are not fed on. We did not evaluate damage to reproductive buds, flowers, or conelets. In the 1990s Arizona outbreaks, defoliation was primarily caused by needle consumption and wasteful feeding behavior. In the 2000s Sacramento Mountains outbreak defoliation was primarily caused by needle dehydration after scoring of the needle surface, followed by consumption of remaining live needles. All sizes of trees suffer severe damage—complete defoliation of all needles of all age classes. If branches and trees survive, buds flush in the spring, though some trees produce small needles or delay bud flush until the second spring after defoliation.

Outbreak Progression

Outbreak Initiation and Expansion

Outbreaks initiated in the autumn of 1996 in the Pinalenos and White Mountains, in 2005 in the Sacramentos, and in 2017 in the Sangre de Cristos. Each outbreak began in multiple areas scattered within fairly contiguous host type and expanded in subsequent years. Damage in the Pinalenos and Sacramentos was initially reported as caused by different agents in the annual Aerial Detection Surveys but determined to be *N. janetae* in later site visits (USFS 1998, 2007). Defoliation expanded to affect approximately 200 and 4,000 ha in the Pinalenos and White Mountains, respectively (USFS 1999, 2000), 4,900 ha in the Sacramentos (USFS 2008), and 4,300 ha in the Sangre de Cristos (USFS 2020).

Outbreak Termination

Each of the 4 outbreaks lasted 3 autumn–winter periods, though most areas were defoliated only two autumn–winter periods, in the first and second or the second and third autumn–winter periods.

Populations in the Pinalenos and White Mountains declined without intervention in the autumn of 1999 due to several natural control factors (USFS 2000). Collapse of both outbreaks was associated with abundant ichneumonid (Hymenoptera) and tachinid (Diptera) parasitoids, which emerged in abundance from larvae collected in 1998, and a virus that was prevalent in the fall of 1999. There was evidence of parasites and virus in the Pinaleno population as early as spring 1998. Starvation undoubtedly played a role in the collapse of the Pinaleno population. Heavy rains throughout the moth flight and egg-laying period may have contributed to population decline in the White Mountains, a factor related to population declines of *L. fiscellaria lugubrosa* (Hulst) (western hemlock looper) (Furniss and Carolin 1977, Koot 1994).

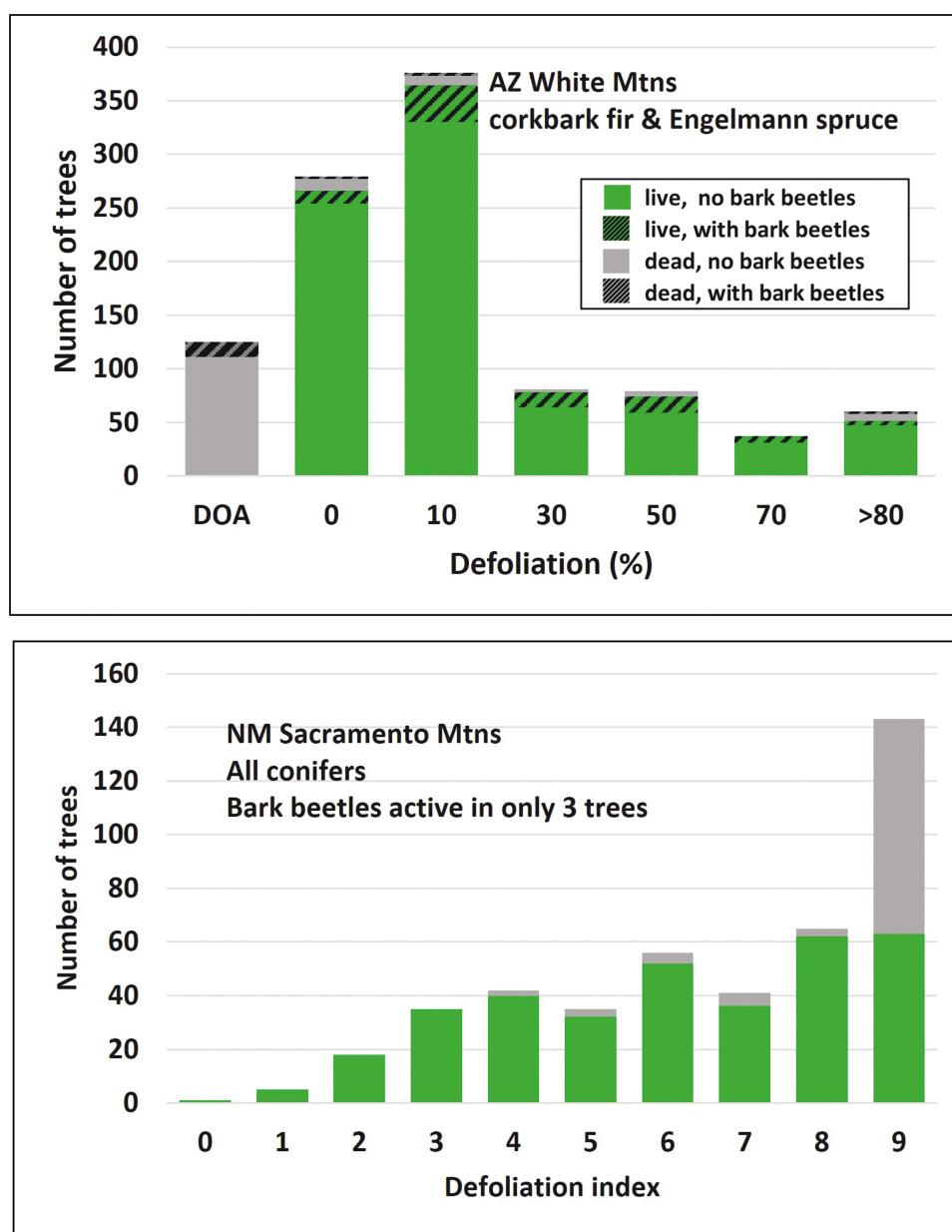


Fig. 5. Status of individual trees (not plot averages) by defoliation severity and bark beetle activity in the Arizona White Mountains (top) and New Mexico Sacramento Mountains (bottom). DOA indicates trees that were dead when plots were installed and are thought to have been severely defoliated.

July precipitation at the White Mountains' McNary weather station included 5 d with heavy rain; the total of 21 cm (NCDC 1999) was 2.5 times the 20-yr average for July (NCDC 1995); a greater amount of precipitation is usually received in the higher elevation host type.

Even though Sacramento populations showed a dramatic decline in September 2007 (Allen-Reid 2007b), parts of the Sacramento defoliated area were sprayed with *Bacillus thuringiensis* var. *kurstaki* (Btk) in early November 2007 due to intense public pressure (eg Albuquerque Journal (2007), Cronin (2007) and similar articles as well as public meetings). Natural enemies, including entomopathogens and parasites, were abundant in autumn 2007 in both treated and untreated areas, with no defoliation detected in summer 2008 (Allen-Reid 2007a, b, USFS 2008, 2009). The Btk application did not alter the course of the outbreak but it is unclear if it affected tree survival.

The area of defoliation in the Sangre de Cristos declined in 2019 after 2 autumn-winter seasons of defoliation, but new areas were defoliated nearby (USFS 2020). There was no defoliation in 2021—a total of 3 autumn-winter seasons but most areas were defoliated only twice (USFS 2020, 2021, 2022).

Weather Associations

Temperature-related variables in the 3 studied mountain ranges show warming trends with considerable year-to-year variation (Supplementary Figs. S1 and S2), but the only pattern found to be associated with the outbreaks relates to snow regimes. Snowpack was either light or gone early in either the year before or the first year of the three studied outbreaks (Supplementary Fig. S3). Maximum snow depth was low during the winter prior to the outbreaks in the Pinalenos and White Mountains, and extremely so in the first

Table 1. Defoliation (% $\pm$ standard deviation) in 1999 and mortality in 2001 at the plot level, by species and mountain range. Values for the White Mountains are from plots within the outbreak area but below the hardest-hit Wilderness Area. In the Sacramentos, Engelmann spruce was present on only 2 plots. Percent mortality is expressed by density (trees per ha, tph) and basal area (BA).

	Engelmann	Corkbark	Engelmann	Ponderosa	White fir	SWW pine	Total
Pinalenos							
defoliation	53.3 $\pm$ 36.3		55.0 $\pm$ 36.2				54.2 $\pm$ 36.1
mortality (% tph)	45.4 $\pm$ 43.2		44.2 $\pm$ 34.0				46.2 $\pm$ 32.9
mortality (% BA)	44.4 $\pm$ 42.4		51.0 $\pm$ 33.2				52.9 $\pm$ 30.8
max defoliation	99		100				100
max mortality (% tph)	100		100				100
max mortality (% BA)	100		100				100
White Mtns.							
defoliation	35.6 $\pm$ 30.0		32.0 $\pm$ 29.3				32.2 $\pm$ 25.2
mortality (% tph)	13.0 $\pm$ 20.4		13.6 $\pm$ 13.2				13.7 $\pm$ 12.9
mortality (% BA)	18.9 $\pm$ 29.5		11.5 $\pm$ 10.3				13.1 $\pm$ 11.0
max defoliation	90		91				86
max mortality (% tph)	67		43				43
max mortality (% BA)	93		36				41
Sacramentos							
defoliation index		6.3 $\pm$ 2.1	7.4 $\pm$ 0.3	5.1 $\pm$ 1.9	6.9 $\pm$ 1.9	8.6 $\pm$ 0.8	6.6 $\pm$ 1.9
mortality (% tph)		13.4 $\pm$ 25.4	8.7 $\pm$ 3.4	10.9 $\pm$ 22.4	30.1 $\pm$ 32.0	24.9 $\pm$ 36.7	19.5 $\pm$ 23.5
mortality (% BA)		8.3 $\pm$ 19.7	3.3 $\pm$ 2.7	10.1 $\pm$ 22.6	25.1 $\pm$ 29.6	20.8 $\pm$ 37.1	16.4 $\pm$ 24.1
max defoliation index		9	9	4	9	9	9
max mortality (% tph)		80	11	50	100	100	90
max mortality (% BA)		74	5	51	100	100	83

year of the Sacramento outbreak. In the White Mountains, there was no snowpack at McNary after 10 February in the spring prior to the outbreak. In the Sacramentos snow depth was extremely and unprecedentedly low the first winter of the outbreak (maximum of 2.5 cm for November-February), so though the last date of snowpack in the first year of the outbreak was unremarkable (16 March) the amount was trivial. Other patterns or thresholds that might be relevant to *N. janetae* were not detected—the first years of the outbreaks and those just prior to the outbreaks were simply not unique compared to earlier years or amongst the outbreaks (Supplementary Figs. S1 and S2).

Minimum temperatures during the outbreaks were -20.6 , -18.3 , and -15.6 °C in the Pinalenos, White Mountains, and Sacramentos, respectively.

Damage Assessments

Pinaleno plots were on elevations between 2878 and 3249 m, on all aspect quadrants, and exhibited wide ranges in mean density (250 to 2463 trees per ha (tph), basal area (14 to 110 m²/ha), stand density index (SDI, 250 to 2463), QMD (18.5 to 45.6 cm), and abundance of corkbark fir and Engelmann spruce, with Engelmann spruce abundance greater than corkbark fir on 25 of 31 plots. White Mountain plots were at higher elevations, between 3038 and 3231 m, on all aspect quadrants, and exhibited wide ranges in mean density (99 to 753 tph), basal area (7 to 50 m²/ha), SDI (18 to 125), QMD (6.8–10.1 cm), and abundance of corkbark fir and Engelmann spruce, with corkbark fir more abundant than Engelmann spruce on only 1 of 15 plots. Sacramento plots were located between 2564 and 2916 m elevation and exhibited wide ranges in mean density (220 to 780 tph), basal area (27 to 73 m²/ha), SDI (472 to 1060), and species composition, but with much larger QMD than in the other mountain ranges (25.2 to 55.8 cm).

Severe defoliation ($> 80\%$) caused 56 to 83% mortality on average, while only 4 to 7% of trees that had less than 80% defoliation died, and bark beetle activity in defoliated trees varied considerably amongst outbreaks (Figs. 4 and 5). Defoliation and mortality

approached 100% on one or more study plots in each of the three study areas (Table 1, Fig. 2). In all three study areas, defoliation was consistently more severe in the lower crown thirds and least severe in the upper crown thirds (data not shown).

Pinaleno spruce-fir

At the plot level, defoliation was $54 \pm 36\%$ and negatively correlated with the CF:ES density ratio and the third Pinaleno principal component, which characterized plots on steeper slopes and lower elevations where the CF:ES basal area and density proportions approached equivalency (0.9 and 0.8, respectively) (Table 2, Supplementary Table S2a). The defoliation pattern reflects species composition at the outbreak origin at the top of the mountain range, with the outbreak not expanding beyond the plateau perimeter where spruce-fir rapidly transitions to mesic mixed-conifer along steep slopes (O'Connor et al. 2015, 2017). Mortality was $46 \pm 33\%$ and $52 \pm 31\%$ by density and basal area, respectively, with 100% mortality on 13% of plots and 80% mortality on an additional 13% of plots (Table 2). Mortality was associated with defoliation severity, elevation, QMD, and average tree height, and negatively correlated with the CF:ES ratios and abundance and size of corkbark fir (Table 2, Supplementary Table S2a). Corkbark fir and Engelmann spruce were comparably defoliated (53 and 35%, respectively) and had similar amounts of mortality (45 and 44% by density, respectively) (Table 1).

At the tree level, defoliation did not differ between corkbark fir and Engelmann spruce and was not correlated with dbh, relative dbh, tree height, or ring count (Table 4). Almost all dead trees were defoliated 80% or more, and 90% of them were attacked by bark beetles (Fig. 4). Dead trees were on average twice as severely defoliated (77 vs 35%) and significantly larger and older than survivors (Table 4); the latter pattern probably reflects bark beetle preference for large trees. Spruce beetle (*Dendroctonus rufipennis* (Kirby) (Coleoptera: Curculionidae)) and western balsam bark beetle (*Dryocoetes confusus* Swaine (Coleoptera: Curculionidae)) attacked severely defoliated trees in the early years of the Pinaleno

Table 2. Plot statistics (mean $\pm$ SD) for the Pinaleno and White Mtns. spruce-fir and the Sacramento mixed-conifer study areas. Significance of variables that are correlated at $P \leq 0.05$ with defoliation are designated as “a”, with mortality by density as “b”, and with mortality by basal area as “c”. Correlation statistics are presented in greater detail in Supplemental Table S1a. Values for the White Mountains are from plots within the outbreak area but below the hardest-hit Wilderness Area. The principal components (PC1, PC2) were derived separately for each mountain range and are described in the text.

Variable	Pinaleno spruce-fir			White Mtns spruce-fir			Sacramento mix-conifer		
	n	Mean $\pm$ SD	Sig.	n	Mean $\pm$ SD	Sig.	n	Mean $\pm$ SD	Sig.
defoliation (%)	31	54 $\pm$ 36	c	15	32 $\pm$ 25				
defoliation index							22	6.6 $\pm$ 1.9	bc
mortality (% tph)	31	46 $\pm$ 33	c	15	10 $\pm$ 10	c	22	20 $\pm$ 24	c
mortality (% BA)	31	52 $\pm$ 31	c	15	13 $\pm$ 11		22	16 $\pm$ 24	
elevation (m)	31	3155 $\pm$ 61	c	15	3126 $\pm$ 67	ab	22	2745 $\pm$ 91	
slope (%)	31	18.8 $\pm$ 10.0		15	17 $\pm$ 11				
density (tph)	31	1147 $\pm$ 825		15	497 $\pm$ 181	b	22	471 $\pm$ 175	
basal area (BA)	31	63.0 $\pm$ 21.2		15	32.1 $\pm$ 9.9	bc	22	43.9 $\pm$ 11.0	b
QMD	31	29.1 $\pm$ 6.2	bc	15	8.6 $\pm$ 1.1		22	35.9 $\pm$ 7.8	b
CVM (dbh)				15	42.6 $\pm$ 5.3		22	49.9 $\pm$ 12.0	b
SDI	31	1193 $\pm$ 470		15	84.8 $\pm$ 25.3	b	22	758 $\pm$ 171	b
PC1	31		a c	15			22		ab
PC2	31			15		b	22		bc
height (m)	31	13.5 $\pm$ 3.0	bc	15	17.1 $\pm$ 2.0				
ratio CF:ES (tph)	31	0.59 $\pm$ 0.56	abc	15	0.28 $\pm$ 0.57				
ratio CF:ES (BA)	31	0.54 $\pm$ 0.66		15	0.20 $\pm$ 0.44				
density (tph) CF	31	363 $\pm$ 322	bc	15	68 $\pm$ 12	c			
BA CF	31	16.3 $\pm$ 12.2	bc	15	3.2 $\pm$ 3.1				
density (tph) ES	31	772 $\pm$ 644		15	362 $\pm$ 153				
BA ES	31	42.1 $\pm$ 20.7	c	15	26.5 $\pm$ 10.7				
ave dbh (cm), CF	26	25.9 $\pm$ 6.4		15	26.6 $\pm$ 17.4	a			
ave dbh (cm), ES	31	27.4 $\pm$ 6.9		15	28.5 $\pm$ 3.9				
ave ht, CF	23	14.5 $\pm$ 2.9		13	15.5 $\pm$ 8.4	a			
ave ht, ES	30	13.6 $\pm$ 3.9	bc	15	17.5 $\pm$ 2.0				
CVM.dbh.CF				9	36.0 $\pm$ 13.8				
CVM.dbh.ES				15	41.1 $\pm$ 5.9	abc			

Table 3. Plot statistics for additional variables for the Sacramento mixed-conifer study area. Significance of variables that are correlated at $P \leq 0.05$ with defoliation are designated as “a”, with mortality by density as “b”, and with mortality by basal area as “c”. Correlation statistics are presented in greater detail in Supplemental Table S1b.

Variable	n	Mean $\pm$ SD	Sig.
density, % Douglas-fir	22	37 $\pm$ 21	a
density, % ES when present	2	68 $\pm$ 5	
density, % ponderosa pine	5	17 $\pm$ 13	
density, % white fir	22	31 $\pm$ 28	a b
density, % SW white pine	22	10 $\pm$ 12	a b c
BA, % Douglas-fir	22	45 $\pm$ 24	
BA, % Engelmann spruce	2	63 $\pm$ 18	
BA, % ponderosa pine	5	17 $\pm$ 13	
BA, % white fir	22	31 $\pm$ 30	a b c
BA, % SW white pine	22	9 $\pm$ 13	

looper outbreak, with a strong preference for severely defoliated trees (Fig. 4). Western balsam bark beetle activity declined in 2002, with residual activity retaining the preference for severely defoliated trees. Spruce beetle activity continued in Engelmann spruce (results not shown) following severe defoliation by spruce aphid (*Elabotium abietinum* (Walker) (Homoptera: Aphididae)) (Lynch 2009, 2019).

White Mountains spruce-fir

At the plot level defoliation was 32 $\pm$ 23% (range from 4–85%), compared to 2 $\pm$ 3% in the non-defoliated area, and much less than in the Pinalenos (Table 2) or higher-elevation Wilderness Area.

Within the sampled defoliated area, defoliation was correlated with elevation, larger corkbark fir, and CV_{dbh} of Engelmann spruce; the latter 2 associations may indicate older stands and/or greater soil moisture availability (Table 2, Supplementary Table S2a). Mortality did not differ between the two sample areas—by basal area it was 13 and 14% within and outside the outbreak areas, respectively, and by density 9 and 10%, respectively. Maximum mortality within the sampled outbreak area was 38 to 41% and approached or reached 100% in the unsampled Wilderness Area (Fig. 2). Within the sampled defoliated area mortality was not correlated with defoliation at the plot level (Table 2); but there were few severely defoliated

Table 4. Comparison of survivor and dead individual-tree characteristics, including defoliation (defol) by crown-third. Significantly different values (live vs. dead) at $p < 0.01$ are indicated by asterisks in front of the paired values, based on one-sided t-tests for individual trees without regard to plot. In the White Mtns, individual-tree defoliation 1999 + 2000 additive values can range from 0 to 200, and in the Sacramentos, individual defoliation index (DI) values can range from 0 to 9 and crown third values from 0 to 3. Note that some statistically significant differences may have little practical relevance.

Variable	Pinalenos spruce-fir				White Mtns spruce-fir				Sacramentos mixed-conifer			
	live	dead	n live	n dead	live	dead	n live	n dead	live	dead	n live	n dead
1999 dbh (cm)	*29.9	36.6	153	174	*26.8	31.1	484	48	30.9	27.7	410	108
plot QMD	*26.8	28.9	153	198	8.4	8.5	519	67	*33.1	36.4	410	108
dbh/QMD	*1.13	1.29	153	174	*3.19	3.73	484	48	*0.93	0.76	410	108
height (m)	*13.7	16.6	78	66								
defol 1999 (%)	*35.1	77.2	121	110	*31.2	57.1	459	20				
defol 2000 (%)					*21.6	59.0	431	10				
defol 1999 + 2000					*50.8	119.6	409	9				
defol 1999 upper-third	*27.4	74.6	121	110	*26.0	52.0	459	20				
defol 1999 middle-third	*38.5	78.6	121	110	*32.6	57.3	459	20				
defol 1999 lower-third	*39.5	78.4	121	110	*35.1	62.0	458	20				
ring count	*119	143	79	58								
DI index 2007									*6.08	8.57	346	95
DI index upper-third									*1.54	2.75	345	95
DI index middle-third									*2.10	2.87	346	95
DI index lower-third									*2.45	2.95	346	94

trees (Fig. 5). Mortality by density was positively correlated with elevation (and thus proximity to the higher-elevation high-mortality Wilderness Area) and variability in Engelmann spruce size, and negatively correlated with density, SDI, basal area, and the second principal component (which characterized plots with high densities and basal area, especially with greater amounts of Engelmann spruce). Basal area mortality was positively correlated with the density of corkbark fir and variability in Engelmann spruce size, and negatively with total basal area of all species combined. Patterns associated with mortality are difficult to discern as death-agent data were not recorded for the 75% of trees that were already dead when plots were first established. However, the proportion of corkbark fir and Engelmann spruce that were dead at plot establishment were similar (70 and 76%, respectively), so we think it likely that *N. janetae* was the mortality agent (spruce aphid would only affect spruce), but we excluded these trees from analyses regarding associations with site and stand variables. Corkbark fir and Engelmann spruce had comparable levels of defoliation (36 and 32%, respectively) and had similar levels of mortality (13 and 14%, respectively) (Table 1).

At the tree level, defoliation in 1999 was correlated with dbh, relative dbh, tree height, and basal area. Though significant due to large sample size of 400+ trees, the shared variability was small ($r = 0.06$ to 0.12). Defoliation in 2000 was also correlated with 1999 defoliation. Defoliation on corkbark fir and Engelmann spruce were very similar (50 and 53%, respectively). Of trees that were alive when plots were established, neither mortality nor bark beetle attack were clearly associated with defoliation severity (Fig. 5). Bark beetles had attacked 16.2% and 14.6% of dead and surviving trees as of 2001, respectively. We do not report later years' mortality data because the causal agent cannot be attributed after a spruce aphid outbreak in 2000 (USFS 2001). Dead trees were significantly larger than survivors, proportionally larger than the average tree on the plot, and more severely defoliated in all crown thirds (Table 4).

Sacramentos Mixed-conifer

At the plot level defoliation index, on a scale from 0 to 9, was 6.6 ± 1.9 , and mortality was $19.5 \pm 23.9\%$ by density and $38 \pm 31\%$

by basal area, with maximums of 90% by density and 83% by basal area (Tables 2,3). Defoliation was correlated with density and basal area of white fir and ponderosa pine dbh (where present) and negatively correlated with Douglas-fir density and the first principal component, which differentiated pine- and white fir-inhabited sites (which are warmer dryer sites) (Tables 2 and 3). The most notable pattern was that defoliation aligned with topography and species composition on the mountain range—defoliation was much greater on north- and east-facing slopes than on south- and west-facing slopes ($DI = 7.5 \pm 1.5$ vs 5.6 ± 1.9 , $t = 2.577$, $P = 0.009$, $df = 20$). North- and east-facing slopes, compared to south- and west-facing slopes, also had more basal area, greater representation of white fir, less Douglas-fir and Southwestern white pine, and negative PC1 values (results not shown), patterns that reflect site moisture and fire history. Of these, the most significant was with the PC1 values. Mortality by density was associated with defoliation, basal area, QMD, CV_{dbh} , SDI, and white fir representation by both density and basal area, and negatively correlated with PC1 (pine vs white fir) and PC2 (which differentiated high-density sites from others) (Tables 2 and 3). Basal area mortality patterns were similar to density patterns but lacked significant correlation with basal area, QMD, and CV_{dbh} .

At the tree level, defoliation was not correlated with dbh or tree basal area but was greater on trees of less-than-average dbh (defoliation was negatively correlated with dbh/QMD). The latter pattern may be related to the diameter distributions of the various tree species. Douglas-fir and ponderosa pine, when present, were the largest trees on the plots. Engelmann spruce, white fir, and Southwestern white pine were more severely defoliated (DI of 7.4, 6.9, and 6.8, respectively) than Douglas-fir and ponderosa pine (DI 6.1 and 5.1, respectively). Overall, dead trees were smaller (27.7 vs 30.9 cm dbh) and proportionally smaller compared to the average tree on the plot, and more severely defoliated in all crown thirds (Table 4). Dead Douglas-fir and Southwestern white pine were significantly ($P < 0.1$) smaller than survivors of the same species (28.2 vs 35.4 cm and 19.8 vs 27.9 cm, respectively); dead white fir were also smaller than survivors (30.9 vs 32.0 cm) but the difference was not significant ($P = 0.331$) (data not shown). Twenty-two percent of trees died

and mortality was strongly associated with defoliation severity (Fig. 5). Overall, 82% of dead trees were very severely defoliated (DI = 9), and there was no mortality in trees with DI values 0 to 3, and mortality in categories 4–8 ranged from 4.6 to 12.2%.

On the 2 plots where it was present Engelmann spruce was the most severely defoliated species (DI = 7.4 ± 1.3 compared to 6.9 ± 2.3 and 6.1 ± 2.5 for white fir and Douglas-fir, respectively) on an individual-tree basis, but incurred less mortality (9.3% compared to 39.5% and 12.1% for white fir and Douglas-fir, respectively) (Table 1). Defoliation of the dead Engelmann spruce was severe, DI of 9.0.

Discussion

Tree mortality related to *N. janetae* defoliation ranged from 56 to 83% when trees were heavily defoliated, reaching 100% in some stands in all study areas, similar to western hemlock looper, *Lambdina fuscicollis lugubrosa* (Hulst) (Lepidoptera: Geometridae) (Koot 1994, Alfaro et al. 1999). Mortality is associated with defoliation severity with or without bark beetle activity. B bark beetle activity and drought increases the level of mortality, and is moderated when there is abundant moisture in the last outbreak year or first post-outbreak year. *N. janetae* is likely to pose further threats to Southwestern forests and possibly to forests in California and areas further north. Emergence of an eruptive disturbance agent is a further destabilizing influence for forests already incurring multiple threats (Koprowski et al. 2005; Lynch 2004, 2009, 2019; O'Connor et al. 2015; Wood et al. 2007).

Life History

Small and large *N. janetae* larvae actively feed from autumn through winter into spring. In general, a distinction is made between loopers with spring and fall larval development (Furniss and Carolin 1977, Rose and Lindquist 1994), a distinction important for life history, host damage (Coulson and Witter 1984, Barbosa and Wagner 1989), and potential management actions. Most *Nepytia* species overwinter in the egg stage (Furniss and Carolin 1977, Rose and Lindquist 1994), but *N. umbrosaria nigrovenaria*, a defoliator of true firs, Douglas-fir, and western hemlock (*Tsuga heterophylla*) in British Columbia, overwinters in the larval stage, though without feeding in the colder months (Ives and Wong 1988, NRC 2015). A winter-feeding life history could have developed as a strategy to avoid natural enemies or competition from other defoliators.

Comparing the Outbreaks

The course of events, associated weather factors, bark beetle activity, and subsequent mortality varied between outbreaks such that we would have drawn different conclusions about factors associated with stand susceptibility and vulnerability had we studied only one outbreak. Our experiences highlight the importance of observing more than one event before drawing conclusions regarding factors associated with outbreak initiation and with stand risk and hazard.

Some patterns that appear contradictory between outbreaks are not. Both Arizona outbreaks occurred in spruce-fir at high elevations and defoliation was associated with mortality in the White Mountains but not in the Pinalenos. The lack of a significant relationship between defoliation and elevation in the Pinalenos may be due to (i) rapid natural enemy responses causing the outbreak to not expand below the fairly flat plateau summit, (ii) distributions of the preferred hosts along elevational gradients, and (iii) the outbreak area (200-ha) may be too small to discern associations between

damage and topographic patterns. The lack of association between plot-level defoliation and mortality in the White Mountains may be misleading, as the most severely defoliated areas with extreme mortality in the Wilderness Area (Fig. 2) were not sampled. At the tree level within the sampled area defoliation of dead trees was 2 to 3 times that of survivors. Associations between defoliation, aspect, and relative size and/or amounts of Douglas-fir and white fir in the Sacramentos, lacking in the other outbreaks, are related to topographically-aligned host-species distributions in that mountain range. The only site and stand factors common to the four outbreaks are “high-elevation mesic forests” and host species distributions—Engelmann spruce and corkbark fir in Arizona, white fir and Douglas-fir in New Mexico, and uncertainty regarding the importance of Engelmann spruce in New Mexico.

Bark Beetle Responses

Bark beetles contributed to the majority of mortality in the Pinalenos but to very little in the White Mountains or Sacramentos. Bark beetle population response in the latter two ranges may have been dampened by abundant precipitation at the ends of the outbreaks. Both spruce beetle and western balsam bark beetle responded quickly to severe defoliation in the Pinalenos, ultimately leading to outbreaks that decimated the spruce-fir forest (Wilson et al. 1999, O'Connor et al. 2015, Lynch 2019). It is not clear how much, or even if, bark beetle population levels were elevated prior to the Pinaleno pre-outbreak. Most spruce beetle outbreaks begin in disturbance-damaged stands (Schmid and Frye 1977) and a 1992 to 1993 winter storm damaged the Pinalenos spruce-fir forest. Material is usually suitable for spruce beetle colonization for 2 yr (Schmid 1977) and the life cycle is completed in 1 to 2 yr (Bentz et al. 2022). Storm damage in the looper-defoliated area was minor, comprised of material less than 8 cm diameter, which is not suitable for spruce beetle, but larger trees (≥ 36 cm dbh) were damaged in areas about 7 km distance (Frank 1993). Spruce beetles can fly long distances but most fly less than 1.2 km (Schmid 1972, Werner and Holsten 1997). No spruce beetle activity was detected until 1998 (Wilson et al. 1999), after 5 post-storm spruce beetle flight periods and after trees were severely defoliated twice. Therefore, we think that bark beetle populations may have been elevated above background levels in the Pinalenos prior to defoliation, but if so not a lot. It is unclear what role bark beetles played in the high level of mortality in the Mt. Baldy Wilderness Area of the White Mountains, but defoliation and drought were undoubtedly important and an aggressive bark beetle outbreak did not develop that progressed to lower elevations. Bark beetle populations were not elevated prior to the White Mountains *N. janetae* outbreak (Lynch 2004) but summer growing season was dry for 11 consecutive post-outbreak years (Palmer Drought Severity Indices (PDSI) for March of -0.5 to -4.8 (obtained from the West Wide Drought Tracker (Abatzoglou et al. 2017))). In the Sacramentos, though defoliation was severe and some sites experienced 90% mortality, average mortality was modest ($20 \pm 24\%$ by density) possibly ameliorated by wet growing seasons in the last (and already declining) outbreak year as well as the next year's growing season (July PDSI of 4.7 and 3.0, respectively).

One species or two?

Differences in adult and larval coloration and host specificity between isolated locations indicate that *N. janetae* may be a complex of 2 or more closely related subspecies or species that diverged geographically or to different host species. The Arizona and New Mexico specimens differed in adult and larval coloration, though

the adult color variability is similar to other *Nepytia* (see photos of false hemlock looper (*N. canosaria* Walker) and other *Nepytia* at <https://www.butterfliesandmoths.org/species/Nepytia-canosaria>, last visited 1 September 2022). Brown and green color phases are common in adults and larvae of other *Lambdina*, *Nepytia*, and *Semiothisa* species (Ives and Wong 1988), but descriptions of Arizona vs. Sacramento Mountain specimens also differ in larval markings (specimens were not compared side-by-side). The populations also had small differences in seasonal histories, but additional study is needed to determine if these patterns are due to differences in seasonal life histories of distinct species, local and yearly weather, or host phenology.

There appear to be differences in host preferences between the Arizona and New Mexico populations, with the former limited to Engelmann spruce and corkbark fir, and disfavoring Douglas-fir and Southwestern white pine, and the latter being a conifer generalist with a preference for Douglas-fir and white fir. Preference for Engelmann spruce in the Sacramentos is uncertain as (i) it was the most severely defoliated species but was found on only 2 relatively low-elevation plots and the outbreak did not encompass the nearby but disjunct higher-elevation spruce-fir forest, and (ii) the amount of prior defoliation by spruce aphid is unknown. Genetic studies show that lepidoptera may have cryptic species that are morphologically indistinct (Janzen et al. 2005, deWaard et al. 2011). Host specificity and larval characteristics can be important indicators of species differences, as adult characteristics can be subtle and blurred by intraspecific variation (Herbert et al. 2004, van Velzen et al. 2007, Burns et al. 2008). If ancestral *N. janetae* diverged according to host specificity then there is the possibility that the reciprocal species or subspecies co-occur. If the populations represent a single species then there is the possibility that spruce-fir forests in New Mexico and mixed-conifer forests in Arizona are at risk once conditions become suitable for population increase.

Recent Change in *N. janetae* Population Dynamics

Given the short history and small number of outbreaks, it is difficult to say anything with certainty regarding causal factors for these unprecedented outbreaks. Our data and analyses do not show clear associations between outbreak initiation and weather in the years immediately before or during the outbreaks except for a possible association with snow regimes. Nonetheless we think that a causal relationship between *N. janetae* outbreaks and climate is likely, but the relationship is indirect, perhaps temporally or spatially distant, or may require multiple climatological and phenological conditions to co-occur or succeed one another. Our reasoning is as follows: First, even allowing for the possibility of *N. janetae* representing more than 1 species with differences in host specificity, the unprecedented outbreaks are so similar and so close in time that it is likely that they have causal factors or conditions in common that are at least regional in scale.

Second, the most likely alternative explanations for the emergence of an outbreaking species in Southwestern montane forests would be the development of novel habitat conditions, or loss of a habitat component or other critical condition for a natural enemy complex, all related to human-induced changes in forest character that are associated with fire exclusion and logging history. We rule this out, with reservation, because (i) the New Mexico outbreaks occurred in forests very different from the Arizona forests, and mixed-conifer forests occur in both Arizona mountain ranges that are similar to the New Mexico mixed-conifer forests, indicating that forest character alone is a doubtful primary factor, and (ii) character

of the Arizona spruce-fir forests has not changed a great deal, but the New Mexico mixed-conifer forests have undergone profound change since European settlement. Species composition has been stable in both Arizona spruce-fir forests, and stand characteristics reflect normal spruce-fir successional patterns in the Pinalenos (O'Connor et al. 2015, 2017) and in the White Mountains reflect normal successional patterns with increased patchiness related to multiple spruce beetle outbreaks, silvicultural treatments (Ragenovich 1982, Moran-Palmer and McTeague 1997) and (outside of the outbreak zone) recent high-severity wildfire (White 2014). In contrast, land use history, particularly intensive grazing and logging followed by fire suppression and more logging, profoundly altered the structure and species composition of the New Mexico mixed-conifer forests, with higher densities and increased representation of white fir and Douglas-fir and less ponderosa pine (Brown et al. 2001, Margolis and Balmat 2009).

Third, failure to detect a relationship doesn't mean that one doesn't exist. Our weather data are a patchwork from sources of variable quality and length, and we lack controlled observations, making it difficult to detect possible relationships. We did not find clear patterns, but a direct cause-and-effect relationship may be too nuanced for our data to detect, perhaps a threshold was surpassed many years ago, or multiple factors need to coincide or occur sequentially for epizootics to erupt.

Furthermore, we think that whatever has changed acts upon the looper population or some aspect of looper-host phenology, rather than on one or more natural enemy populations or their habitats. Rapid population response by multiple natural enemies that terminated all 3 outbreaks shows that effective natural enemies are present. This was the case even in the Pinalenos, where there is no history of conifer defoliator outbreaks, though western tent caterpillar (*Malacosoma californicum* (Packard), Lepidoptera: Lasiocampidae) and large aspen tortrix (*Choristoneura conflictana* (Walker), Lepidoptera: Tortricidae) incur occasional outbreaks on quaking aspen (*Populus tremuloides*), and Douglas-fir tussock moth (*Orgyia pseudotsugata* (McDunnough), Lepidoptera: Erebididae) is present locally. Perhaps a habitat component has been lost for a critical natural enemy, or there is a phenological mismatch between the looper and a predator or parasite (Damien and Tougeron 2019), but it is more likely that there has been a change that more directly influences *N. janetae* population dynamics.

Regardless, either one or more altered conditions have enhanced population dynamics, or one or more population control factors have been lost. This could be temperature factors that we could not discern; disruption of a predator, parasite, or entomopathogen complex; or a snowpack-related factor affecting this autumn- and winter-feeding diurnally tree-to-ground trekking species. Note that we cannot confirm that the insects trek regularly or only when specific weather conditions occur, or if they trek only once food resources have been depleted.

Priorities for Further Work

As with any emergent pest there is considerable need for further research. We place importance on the following: There is a clear need for molecular systematics to identify genetically distinct populations of the *Nepytia* and related genera. This will allow managers to relate research in one geographic area to what has happened in others and to develop effective management strategies, as management options are very different for spruce-fir and mixed-conifer forests. The need is especially crucial with a warming climate and a winter-active pest species, and there are at least 3 coniferophagous *Nepytia* that

overwinter as larvae. Phylogenetic investigations need to be thorough and cover multiple locations, vegetation communities, and seasons within regions. We also note that the species of coniferophagous geometrids are not always identified in the Southwestern records when outbreaks occur, though none of the records indicate winter feeding behavior.

Investigation of the timing and conditions necessary for egg eclosion and small larvae development would increase our understanding of *N. janetae* population ecology and outbreak initiation, and assist managers in developing control tactics that are likely to preferentially target small larvae over large larvae. Our data indicate that the egg eclosion period may be short and fairly well synchronized, but there is a quite variable period when small larvae are abundant. *N. umbrosaria nigrovenaria*, another *Nepytia* that overwinters as a (nonfeeding) larvae also has a very short egg eclosion period (NRC 2015). Development rates of small larvae may be strongly influenced by temperature. Differences in seasonal temperature regimes (in addition to host species differences) may explain the slower development of the Sacramento population, as development was more rapid in the cold high-elevation Arizona spruce-fir than in the relatively warmer lower-elevation New Mexico mixed-conifer. These investigations should also determine if larvae trek regularly or only during certain weather conditions or when food resources are exhausted, if larvae of all sizes trek, and if they return to the same tree. Aside from important biological information, regular trekking behavior would provide opportunities for developing sampling protocols and management strategies.

Damage to tree flowers should be evaluated, as feeding on strobili may explain the possible effect of snow regimes on *N. janetae* population dynamics. *N. semiclusaria* (Walker) feeds on female strobili of *P. echinata* Mill. and *P. taeda* L. as small larvae (Ebel and DeBarr 1973, McLemore 1977). Abundant flowers may provide a nutritious food source that enhances looper survival or reproductive success, thereby initiating outbreaks. Engelmann spruce seed production is associated with low spring snowfall in the year reproductive buds are initiated (Buechling et al. 2016) and flowering is enhanced when root growth coincides with drought (Ross, 1988). Douglas-fir flowering phenology is influenced by cool-season temperatures (Prev  y et al. 2018). A diminished Engelmann spruce cone crop was noted in the Pinal  o defoliated area in 1998 (Wilson and Fitzgibbon 1998), possibly indicating that flowers may have been consumed by *N. janetae*.

Development of sampling protocols to quantify population density and parasitism rates, relate population density to defoliation levels, and more accurately relate defoliation to the likelihood of tree death, are needed to relate life stage developments to temperature, develop an early-warning system or population dynamics model, determine the appropriate timing for potential pesticide applications, determine if treatment in the second year of the outbreak might reduce damage levels, and confirm that treatment in the third year is pointless.

Given the unusual seasonal life history, it is important to identify parasitic species, determine the timing of parasite attacks, and determine how the abundance of a winter-feeding larval population affects the population dynamics of other pest species. Identifying the parasites will help forest health experts and forest managers throughout western North America anticipate the duration and outcome of future outbreaks, including any that might occur outside of the Southwest.

Rodent and bird population responses to the abundance of a winter-feeding larval population should be investigated. The larvae represent a high-fat food resource during a period when

such resources are usually limited. Mount Graham red squirrel (*Tamiasciurus fremonti grahamensis*) was observed feeding on *N. janetae*, and a peak in squirrel population numbers coincided with the Pinal  o outbreak (Koprowski et al. 2005, Lynch 2019). Mice, moles, and shrews probably feed on ground-trekking *N. janetae*s. Resident and migratory winter bird communities may benefit from an abundant larval population, as they do with winter-feeding pine processionary moth populations (*Thaumetopoea pityocampa*) (Barbaro et al. 2013).

Capacity to respond more rapidly to new disturbances would enable researchers and forest health experts to relate mortality to defoliation severity, investigate early-instar behavior in years before starvation and natural enemies affect behavior, and quantify bark beetle response to defoliation. Our studies were seriously hampered by delays in initiating investigations early in the outbreaks. Of the 3 studied outbreaks, impact plot establishment in the first summer following the initial autumn-winter defoliation season was possible only once, and then only because first-year defoliation surrounded the village of Cloudcroft and was reported by residents and because funding was available; no population density or insect behavior observations were made prior to detection. Plots were established to study the Arizona outbreaks just before the third defoliation season, after a 1-yr detection delay and an additional 1-yr funding delay.

We also note the paucity of climate data from high-elevation sites. There is a need for data from permanent weather stations at high elevations, given recent and ongoing increases in insect activity and wildfires, and changes in forest species composition.

Conclusions

N. janetae has emerged as a new disturbance agent in Southwestern high-elevation forests, further destabilizing systems already threatened by large fires of uncharacteristic severity, non-native species, and climate change. Studies reported here will provide baseline data for further research and for land managers in the Southwestern United States.

Acknowledgments

Thanks to Craig Wilcox, Silviculturist (retired) with the Lincoln N.F. for insights into Sacramento Mountain site ecology, to Elaine Lowery for excellent descriptive observations in the Pinal  os, and to Amanda Grady, Entomologist with U.S. Forest Service, Forest Health Protection, for guiding the manuscript through the tribal approval process. Many thanks to the White Mountain Apache Tribe, the Bureau of Indian Affairs, the Cloudcroft Ranger District of the Lincoln National Forest, and the Safford Ranger District of the Coronado National Forest. Comments and suggestions from the reviewers are greatly appreciated. Funding for this work was provided by several U.S. Forest Service sources: the Forest Health Evaluation Monitoring Program, Southwestern Region Forest Health Protection, and the Rocky Mountain Research Station. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official USDA or U.S. Government determination or policy. Insect seasonal life history, behavior observations, and establishment of the Pinal  o and White Mountains damage assessment studies were completed by the second and third authors with assistance from Deborah Allen-Reid (U.S. Forest Service, Southwestern Region, retired). Establishment of the Sacramento damage assessment study, the analyses, and most of the writing were completed by the first author. All authors contributed to the interpretation of results and manuscript preparation.

Author contributions

Ann Lynch (Conceptualization [equal], Formal analysis [equal], Methodology [equal], Writing – original draft [lead], Writing – review & editing [lead]), T. Rogers (Conceptualization [equal], Methodology [supporting], Writing – original draft [supporting]), and Roberta Fitzgibbon (Conceptualization [equal], Methodology [equal], Writing – original draft [supporting])

Funding

Funding for this work was provided by several U.S. Forest Service sources: the Forest Health Evaluation Monitoring Program, Southwestern Region Forest Health Protection, and the Rocky Mountain Research Station. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official USDA or U.S. Government determination or policy.

Conflicts of interest. The authors declare that they have no conflict of interest.

Supplementary material

Supplementary material is available at *Environmental Entomology* online.

Data availability

Data from the Pinaleno Mountains and Sacramentos Mountains that support this article are available in the online supplementary material. Data from White Mountain Apache Tribal lands cannot be shared for privacy reasons.

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