Legacies of Indigenous land use shaped past wildfire regimes in the Basin-Plateau Region, USA

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Climatic conditions exert an important influence on wildfire activity in the western United States; however, Indigenous farming activity may have also shaped the local fire regimes for millennia. The Fish Lake Plateau is located on the Great Basin–Colorado Plateau boundary, the only region in western North America where maize farming was adopted then suddenly abandoned. Here we integrate sedimentary archives, tree rings, and archeological data to reconstruct the past 1200 years of fire, climate, and human activity. We identify a period of high fire activity during the apex of prehistoric farming between 900 and 1400 CE, and suggest that farming likely obscured the role of climate on the fire regime through the use of frequent low-severity burning. Climatic conditions again became the dominant driver of wildfire when prehistoric populations abandoned farming around 1400 CE. We conclude that Indigenous populations shaped high-elevation mixed-conifer fire regimes on the Fish Lake Plateau through land-use practices.

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Fire is one of the most important disturbance processes in the western United States (hereinafter referred to as the west). Many modern terrestrial ecosystems reflect this long evolutionary history, requiring fire to maintain species composition and structure. However, fire activity has increased significantly in the last three decades in the west, with a twofold increase in the cumulative area burned since 1984 as a result of human settlement and human-caused climate change, compounded by twentieth century fire suppression legacies. Recent wildfire activity has been more pronounced at mid- to high-elevations in response to changes in temperature and precipitation, fuel density, and increases in human-caused ignitions. Although climate, specifically drought, is considered to be the dominant driver of fire in the west, recent research in the Sierra Nevada Mountains illustrates that human-caused fire, not lightning-caused fire, best approximated changes in forest composition during prolonged periods of cool and wet conditions. These data suggest that Indigenous people may have played an important role in shaping mountain fire regimes in the past. To date, little is known about the extent and influence of past Indigenous fire use in western US forested environments. Today, fire regimes in these forests are assumed to be climatically driven and not considered to be influenced by pre-European human activity. A better understanding of how Indigenous peoples used fire and the subsequent legacies Indigenous fire use had within forested ecosystems is particularly important for fire management in the west. Here we examine how high-elevation, mixed-conifer/subalpine forests (above 2700 m), within the Great Basin–Colorado Plateau Region of the western United States, were shaped by changing human land use over the past 1200 years.

The legacy of Indigenous fire use has gained increased attention in the Southwest and other regions of the Americas, where the effect of pre-European fire on modern flora is more pronounced than previously thought. However, the influence of pre-European Indigenous populations on fire regimes in North America remains controversial. Part of the controversy is linked to the lack of integrative studies that examine fire–human–climate dynamics in the past. As a result, there is a persistent paradigm that low-density human populations had minimal impacts on ecosystems at the landscape scale in the Americas. This is particularly true in remote regions such as mountainous environments, where lightning has been considered to be the main ignition source. However, there is increasing archeological and ethnographic evidence for Indigenous fire use for a variety of farming, hunting, and foraging purposes from the Great Plains, Great Basin, Sierra Nevada, and Rocky Mountains, illustrating that climate and human activities are not mutually exclusive.

By altering ignition patterns to clear vegetation for fields, forage production, enhance regrowth of edible plants, drive game, and ease travel, Indigenous fire use may have altered the fire frequency and fuel availability. Human-driven changes in fire regimes may have, in turn, altered forest composition and structure, potentially superseding the natural (climatic) controls on fire regimes. It is possible that Indigenous fire use may have had long-lasting legacies on modern mountain forest ecosystems.

Long-term, high-resolution, multidisciplinary records combining paleoecological and archeological archives, also known as applied historical ecology, are vital for disentangling the drivers of past fire and subsequent ecological effects. To begin to distinguish human-caused from naturally caused fire regimes, paleoecological records must demonstrate that observed changes in vegetation and fire are in response to changes in human activity rather than driven by natural climate–fire relationships. To address this issue, we implement a multidisciplinary approach combining paleoecology, paleoethnobotany, and archeology, to reconstruct vegetation change, fire activity, drought, and the chronology of human activity over the last 1200 years of central Utah (Fig. 1). The novel model integration of these multiproxy paleoecology, archeology, and paleoclimate data enables us to disentangle the relative roles climate and human land use had on past fire regimes. We used sieved sedimentary charcoal accumulation rates (grains cm$^{-2}$ yr$^{-1}$) as an indicator of changes in regional (>10 km) vegetation composition. Summed probability distributions (SPDs) of calibrated radiocarbon-dated archeological sites in the vicinity of Fish Lake, Utah, are used as a proxy for pre-European human activity. We also use a tree-ring reconstruction of drought, which is a potentially important driver of fuel availability, fuel moisture and subsequent fire activity, and a record of the El Niño Southern Oscillation (ENSO) variance, which is the main teleconnection thought to drive fire activity in the west.

Results

Study area. Sedimentary proxies were collected from Fish Lake, located in south-central Utah on the boundary between the Great Basin and Colorado Plateau (i.e., the Basin-Plateau Region (Fig. 1)). Fish Lake is an ideal study site to investigate fire–climate–human interactions given the coupled records of past fire activity and vegetation change through sedimentary archives alongside tree-ring reconstructions of drought, combined with a well-documented Late Holocene archeological record that was used to generate past human activity estimates (Fig. 1). Fish Lake is a high-elevation (2700 m asl) mountain lake located in Fishlake National Forest, Sevier County, Utah. Fish Lake is a large, deep (average depth = 27 m, maximum depth = 37 m), natural graben-filled lake situated on the southern end of the Fish Lake Plateau, flanked by the Mytoge Mountains to the southeast, and has a high lake area to watershed ratio (~73.8 km$^2$). Contemporary forests surrounding Fish Lake are strongly controlled by aspect, characterized by ecolonal mixed-conifer to spruce–fir. Overstory tree species, including Engelmann spruce (Picea engelmannii), subalpine fir (Abies lasiocarpa), and Douglas-fir (Pseudotsuga menziesii), are dominant on the northerly aspects, whereas the southerly aspects contain a mixture...
of quaking aspen (*Populus tremuloides*), including the famous "Pando" aspen clone, considered to be the world’s single largest living organism⁴⁷,⁴⁸, ponderosa pine (*Pinus ponderosa*), piñon (*Pinus edulis*), Rocky Mountain juniper (*Juniperus scopulorum*), and curlleaf mountain mahogany (*Cercocarpus ledifolius*).

**Proxy-based climate–human–fire relationships.** High fire activity (i.e., biomass burning) between 900 and 1400 CE (Fig. 2A) is concomitant with a peak in human activity (i.e., human population densities; Fig. 2B). Both fire activity and human activity decrease after 1400 CE and remain low until 1900 CE when fire activity increases simultaneously with Euro-American settlement and the end of the Little Ice Age (LIA; 1500–1850 CE). Droughts occurred over the past 1200 years with extreme amplifications in maximum and minimum soil moisture conditions (Palmer Drought Severity Index (PDSI)) between 1100 and 1300 CE (Fig. 2C). ENSO variance declines during the Medieval Climate Anomaly (MCA; 900–1200 CE) (i.e., more La Niña-like conditions) and increases during the LIA and into the present, consistent with more El Niño-like conditions (Fig. 2D; from ref. ⁴³). Increasing arboreal pollen (AP) and non-AP (NAP) influx values are evident during periods of increasing farming activity between ~1050 and 1200 CE (Fig. 2E, see Supplementary Table 1 for a complete list of taxa classified as AP, NAP, and paleoethnobotanically significant pollen). AP influx stays relatively stable until Euro-American settlement ~1900 CE (Fig. 2E), when it increases dramatically compared to NAP post Euro-American settlement (Fig. 2F). NAP increases relative to AP during peak farming, followed by a general decline in post-farming occupation ~1400 CE, and does not increase again until Euro-American settlement. Paleoethnobotanical influx shows similar trends as NAP with a peak in paleoethnobotanical species relative to NAP that occurred during the apex of farming between 900 and 1400 CE (Fig. 2E, G).

![Fig. 2 Summary figure differentiating climatic, anthropogenic, and ecological drivers of fire activity at Fish Lake and the surrounding region. A Fire activity (i.e., biomass burning) was strongly associated with prehistoric farming activity (B). The “+” symbol shows the median ages of the summed probability distribution of calibrated archeological radiocarbon dates that were sampled for the time-series. C Fire activity was not related to tree-ring-reconstructed drought (z-scored PDSI 30-year running average), nor was it related to tree-ring-derived ENSO variability during the apex of prehistoric farming (D; from ref. ⁴³). E Arboreal pollen, non-arboreal pollen, and paleoethnobotanically (PalaeoEthno.) important taxa (see ref. ⁵⁷) illustrate changes in pollen influx values over time. F Mixed-conifer/subalpine forests were dominated by AP with the highest abundance of NAP taxa during the apex of prehistoric farming. G Farming populations, as well as foragers, likely used fire to increase paleoethnobotanically (PalaeoEthno.) significant taxa compared to other herbaceous taxa (NAP). Pink shaded box in the background indicates the prehistoric farming period, whereas the tan shaded box indicates Euro-American settlement.](https://doi.org/10.1038/s43247-021-00137-3)
MODELED CLIMATE–HUMAN–FIRES RELATIONSHIPS. We assessed each of the paleoecology, paleoethnobotany, paleoclimatology, dendrochronology, and archeology time-series datasets using a generalized additive model. Comparing these continuously sampled time-series in a multivariate generalized additive model shows that prior to European settlement, climate (drought and ENSO) and fuel (AP : NAP) explain over 74% of the variability (deviance) in fire activity (Fig. 3). However, of the four explanatory variables, human activity has the only significant effect ($p = 0.00109$; Table 1) with a sharp positive slope, indicating that fire activity increases as a function of past human activity. A pairwise Pearson’s correlation test further demonstrates a positive correlation between fire activity and population density (Table 2). The model residuals do not show meaningful temporal autocorrelation (Supplementary Figs. 5 and 6), indicating that the results are not biased by lagged values in the time-series.

DISCUSSION

The archeological record captures a peak in Indigenous human activity between 900 and 1400 CE associated with the northward expansion of maize (Ze a mays) agriculture from the Southwest proper into the Basin-Plateau region. During this time, sedentary farming populations often referred to as the Fremont (hereinafter referred to as farmers), established major villages in lower-elevation settings and increasingly made seasonal forays into high-elevation environments such as Fish Lake. The combination of increasing population density and changing land-use practices towards more intensive subsistence strategies likely contributed to an overall increase in the number of ignitions and subsequent increase in fire activity documented at Fish Lake.

Pollen and macrofossils found within archeological hearths at Fish Lake indicate the use of wild resources primarily from the sunflower (Asteraceae), grass (Poaceae), Amaranth (Amaranthaceae), and sedge (Cyperaceae) families, as well as skunkbush berries (Rhus spp.). Wild resources in the Asteraceae, Amaranthaceae, Cyperaceae, and Poaceae families are economically important and common Indigenous food resources throughout the Great Basin. Many ruderals in the Amaranthaceae family such as Amaranth and Chenopodium are fire-responsive plants that typically colonized and thrived in human-caused disturbances including fire. Charred Z. mays kernels were also present, providing evidence that maize was likely grown in nearby settlements found at lower elevations. Burned faunal remains from the same archeological hearths illustrate farming populations were also consuming porcupine, deer, hares/rabbits, squirrels, birds, fish, and other mammals at Fish Lake. Charred quaking aspen macrofossils suggest it was one of the primary sources of fuel.

During the apex of prehistoric farming, modeled fire–climate–human relationships illustrate that fire activity was more strongly correlated with human activities than drought and ENSO. These data suggest that farming populations were not only burning at high elevations such as Fish Lake, but that human-caused ignitions impacted high-elevation fire regimes on the Fish Lake Plateau (Table 1). The apex in prehistoric farming overlaps with the MCA, a period of increased aridity in the US desert southwest and Basin-Plateau region, which has previously been attributed to more persistent La Niña-like conditions. Modern high-elevation wildfires in the southwest United States

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**Fig. 3 Model response plots showing the relationship between fire activity and population density, vegetation, and climate.** Model response plots show a strong relationship between fire activity (charcoal influx; particles cm$^{-2}$ yr$^{-1}$) and population density (summed probability distribution; top left). Model response plots show no significant relationship with drought (Palmer Drought Severity Index (PDSI); top right), vegetation type, i.e., the ratio of arboreal pollen (AP) to non-arboreal pollen (NAP) influx (grains cm$^{-2}$ yr$^{-1}$; bottom left), and El Niño Southern Oscillation Index (ENSO) variability (bottom right).
are highly correlated to drought, ENSO, and the Pacific Decadal Oscillation\textsuperscript{65}. The onset of the MCA witnessed exceptionally large fires in high-elevation spruce–fir forests of northern Colorado, but burning did not persist throughout the MCA as a result of fuel limitations\textsuperscript{66}. However, unlike in northern Colorado, relatively high levels of CHAR persisted at Fish Lake until \textless{}1400 CE when farming populations collapsed and abandoned agriculture. The elevated levels of CHAR is suggestive of an increased incidence of human-caused ignitions, a well-documented phenomenon associated with Aboriginal burning in Australia\textsuperscript{67}.

The presence of increased levels of CHAR, increased paleoethnobotanical species relative to other NAP (Fig. 2G), and climate (i.e., drought (PDSI) and ENSO), and fuels (AP : NAP ratio).

### Table 1 Results of generalized additive model.

| Response variable | EDF | Ref.df | F statistic | P value |
|-------------------|-----|--------|-------------|---------|
| Population        | 1.86| 2.3    | 8.652       | 0.00109 |
| Drought           | 1.00| 1      | 0.462       | 0.50323 |
| Fuels             | 1.00| 1      | 0.15        | 0.70172 |
| ENSO              | 1.00| 1      | 0.978       | 0.33235 |

Results of generalized additive model reporting the estimated degrees of freedom (edf), reference degrees of freedom (ref.df), F statistic, and p value for each variable in the model. Results demonstrate a positive partial covariance between fire activity and population density even when holding all other variables constant, and negligible relationships between fire activity and climate (drought (PDSI) and ENSO), and fuels (AP : NAP ratio).

### Table 2 Pairwise Pearson’s correlation coefficients.

| Pearson’s correlation | Charcoal influx | Population density | AP : NAP | PDSI | ENSO |
|-----------------------|----------------|--------------------|----------|------|------|
| Charcoal influx       | 1              | -                  | -        | -    | -    |
| Population density    | 0.88           | 1                  | -        | -    | -    |
| AP : NAP              | -0.62          | -0.65              | 1        | -    | -    |
| PDSI                  | 0.12           | 0.05               | 0.07     | 1    | -    |
| ENSO                  | -0.63          | -0.62              | 0.37     | 0.005| 1    |

Pairwise Pearson’s correlation coefficients demonstrating a positive correlation between fire activity and population density, a negative correlation between fire activity and the ratio of arboreal to non-arboreal pollen (AP : NAP), and negligible relationships between fire activity, climate (i.e., drought (PDSI), and ENSO), and arboreal to non-arboreal pollen (AP : NAP).
of soil quality, which have been proposed as explanations for the collapse of farming populations in the region.\(^{35}\) The decline in farming populations in the Basin-Plateau Region at this time is part of a broader regional trend that occurred across climatic zones in the Intermountain West.\(^{36}\) At Fish Lake, no archaeological artifacts have been found dating to the foraging period, further illustrating a decline in farming populations in the immediate vicinity of the lake.\(^{37}\) The LIA experienced cooler and wetter conditions compared to the MCA, with an overall decrease in fire activity across the west according to regional sedimentary charcoal records.\(^{37}\) Conversely, local and regional fire-scar records from lower-elevation fuel-limited sites illustrate a more frequent, low-severity fire regime during the LIA.\(^{42}\) These records of frequent, low-severity fire are not recorded at Fish Lake, likely because these fires were either too small or were too far away to contribute to the Fish Lake CHAR record. Despite the low CHAR levels in the Fish Lake record, local Indigenous farming populations likely continued to use fire to increase foraging returns\(^{44,47}\) during the LIA at high elevations, as evidenced by the continued persistence of paleoethnobotanically significant taxa (Fig. 2G). The combined influence of lower foraging population densities and decreased human-caused ignitions, coupled with the cooler–wetter conditions of the LIA, likely dampened the extent and severity of fires resulting in less biomass burned around Fish Lake compared to the farming period (Fig. 4b). As a result of less biomass burned and/or cooler–wetter LIA conditions, the forest composition and structure changed at Fish Lake, including more arboreal fuels (i.e., increasing forest density and fuel moisture). The change in fuels coupled with cooler–wetter conditions likely hindered the incidence of natural lightning-caused ignitions as well, enabling the establishment of the infrequent (~100–150-year fire return interval).\(^{73}\) High-severity fire regime characteristic of the modern high-elevation mixed-conifer/subalpine forest on the Fish Lake Plateau. We suggest that during the LIA, lower foraging population densities around Fish Lake resulted in fewer human-caused ignitions, which resulted in climate becoming the dominant driver of the fire regime at Fish Lake.

Relatively low CHAR levels persisted from 100 CE until Euro-American settlement in the late 1800s (Fig. 2). The modern, post-European settlement ecosystem (1850 CE to present) is strikingly different from the pre-European era (Fig. 4c), with the highest values of both AP and NAP (Fig. 2E), an absence of paleoethnobotanical taxa (Fig. 2G), and a threefold increase in CHAR (Fig. 2A). In February 1899, the Fish Lake Forest Reserve (later formally known as the Fishlake National Forest) was established to protect the Fish Lake watershed after the Ute tribe sold its water rights to the Fremont Irrigation Company.\(^{74}\) Shortly thereafter, active fire suppression efforts went into effect with local fire-scar-based research indicating the absence of local wildfires after the late 1890s.\(^{73}\) Since then, repeat photography has captured the dramatic increase in conifers, sagebrush (Artemisia), and piñyon-juniper, and decrease in grasslands and quaking aspen.\(^{74}\) This increase in conifers documented in historic photographs correlates with the highest values of AP relative to herbaceous pollen (Fig. 2F), and is likely the result of modern fire suppression and the absence of frequent, low-severity Indigenous fires in the Fish Lake basin, as well as natural successional trends and densification documented for high-elevation forests.\(^{74}\) In the twentieth century, fires (generally small, <0.10 ha)\(^{75}\) have persisted in the Fish Lake region. Since the 1970s, CHAR values have experienced a fourfold increase compared to the last 1200 years, which is a similar trend recorded nearby on the Aquarius Plateau ~60 km away.\(^{76,77}\) Since 1984, ~16 large (>400 hectares) fires, both wild and prescribed, have occurred within 50 km of Fish Lake, well within the airshed of macro-charcoal for Fish Lake, including one wildfire within the Fish Lake watershed, which burned 682 ha in 2002.\(^{77}\) Utah’s largest wildfire (141,143 ha) on record burned in 2007 ~70 km from Fish Lake and may have also contributed to the charcoal deposition found at Fish Lake. The record high levels of CHAR in the Fish Lake record is attributed to combined natural and human factors resulting in larger, more severe fires. This is the result of the accumulation of fuels in response to fire suppression efforts over the past century, which is being exacerbated by warming temperatures and a lengthening in the fire season,\(^{36}\) and by intentional and unintentional human-caused ignitions. These results illustrate that in the last century, the combined effect of climate and human factors influencing fire regimes at Fish Lake are unlike anything recorded in the last thousand years.

Our approach integrating model-based evaluations of multiproxy time-series datasets enabled the detailed examination of a millennium of human-fire use in the high-elevation forests of the Fish Lake Plateau located in the Basin-Plateau Region. The data presented here challenge the notion that high-elevation mixed-conifer/subalpine fire regimes are exclusively climate-driven and contribute to a growing body of evidence suggesting that humans have the ability to use fire to modify forest structure and composition, thereby reducing the role of climate as the dominant driver of past fires in high-elevation ecosystems.

In the coming decades, annual wildfire area burned is likely to increase in response to natural and anthropogenic drivers.\(^{78}\) Our findings suggest the Indigenous use of frequent, low-severity fire likely reduced fuel loads and the risk for large-scale wildfire activity in mountain environments on the Fish Lake Plateau, even during periods of drought more extreme and prolonged than today. Given the change in forest structure and composition over the last century, contemporary management strategies may benefit from implementing pre-European Indigenous burning practices to mitigate the potential for large-scale wildfires in a warming world. As climate change continues to push fire outside the historical range of variability, it is increasingly important to understand the role of fire in forested environments, which will help avoid or minimize catastrophic social and economic impacts. Our results provide new insights into the legacy of prehistoric farming populations that may help to inform fire management efforts in ecosystems previously thought to be shaped by climatically driven wildfire alone.

**Materials and methods**

**Sedimentary proxies.** Two sediment cores 5 m apart were collected through the ice in February 2014 in 32 m of water. The first core (49 cm; FLF2C_17_14; 38°32’N, 111°43’W; elevation 2700 m.s.a.l.) was taken using a wedge freeze corer. The second core (11 m; D14) was taken using a 9 cm diameter UWITEC surface corer. Core D-14 was extruded in the field at 0.3 cm intervals. Each core was subsampled at contiguous 0.5–1 cm intervals for loss-on-ignition (i.e., L.O.I 550 °C)\(^{79}\) to correlate the cores and to create a composite age-depth model (Supplementary Fig. 1). Organic matter content showed a strong correlation and was used to produce an age-depth model combining 210Pb series from D14 and two accelerator mass spectrometry radiocarbon dates from FLF2C (Supplementary Table 2). Radiocarbon ages were calibrated with the IntCal13 dataset\(^{80}\) and a chronological model was developed using the software BACON\(^{81}\) (Supplementary Fig. 2). Because of the high temporal variability within each of the time-series, we used the constant median sampling interval (30 years per sample) of the charcoal in flux, developed using the software BACON.\(^{81}\) The SPDs are generated by calibrating and summing all fossil records and to create a composite age-depth model (Supplementary Fig. 1). A detailed description regarding each of the time-series used in this study is provided in the Supplementary Discussion section.

**Reconstructing human activities.** We reconstruct human activities by generating a SPD of calibrated radiocarbon dates from archeological sites\(^{45–48}\) (see Supplementary Data File 1). SPDs are generated by calibrating and summing all 308 available radiocarbon dates from 46 archeological sites in Sevier County using IntCal13 curve\(^{82}\) in the rCarbon package.\(^{83}\) The SPD specifies a 100-year moving average to smooth over stochastic variation introduced by the radiocarbon calibration curve and different radiocarbon sampling strategies. We applied a 100-year
binning parameter using the binPrep function following reference13. This binning parameter combines different radiocarbon ages from the same archeological site that are within 100 calibrated years from each other, which reduces biases caused by oversampling at specific sites or specific occupation events on sites. Although we recognize that several processes can bias the relationship between the number of dated sites and population size27, we feel confident in this case given that we are quantifying the local expression of a major demographic event representing the well-known collapse of farming populations in the study region.

Reconstructing local drought (PDSI). We reconstruct local, summer (May through August) drought conditions by modeling the relationship between historical drought measurements and tree-ring width from trees that occur in environments sensitive to hydroclimatic conditions. A multiple regression model that incorporates newly collected and previously published tree-ring chronologies as independent variables exhibits high skill (R² = 0.57; see Supplementary Table 3). Sampling depth among the tree-ring chronologies was sufficient for reconstructing drought as far back as 800 AD. Detailed tree-ring-based climate reconstruction is provided in the Supplementary Information Discussion section.

Generalized additive models. To model the effect of each predictor variable on charcoal influx through time (see Supplementary Data File 2), we use multivariate generalized additive models implemented in the mgcv library in the R environment28. We used a Poisson error distribution with a log link and fit the data using quasi-likelihood estimation. Population activity used a knot value of 4. We report the estimated degrees of freedom, reference degrees of freedom, F statistic, and p value for each variable in the model, and we report the proportion of deviance explained for the whole model. We evaluate residual temporal auto-correlation with an auto-correlation function on the model residuals (Supplementary Figs. 4 and 5).

Data availability
The data used in this study are presented in the Supplemental Material and in the Supplemental Data Files. The ENSO (https://www.ncdc.noaa.gov/paleo-search/study/11194) and PDSI data (https://www.ncei.noaa.gov/metadata/geoportal/rest/metadata/item/noaa-tree-12373html) are available from the NOAA Paleoclimatology Database. The new tree-ring data used in this study (ITRDB; site u549) is available from the International Tree-Ring Data Bank (https://www.ncdc.noaa.gov/paleo/study/32774). The new sedimentary proxy data is available from the Neotoma Database (https://apps.neotomadb.org/explorer/?datasetid=49854).

Code availability
The statistical analyses were carried out using the R packages cited in the Methods section.

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V.A.C., A.B., M.J.P., R.J.D., I.H., and B.F.C. designed the research. V.A.C., A.B., M.J.P., M.A., I.H., R.J.D., M.F.B., E.R., I.S., and B.F.C. collected the data. V.A.C., A.B., M.J.P., R.J.D., M.B., S.B., J.S., E.R., M.A., S.Y.M., and B.F.C. analyzed the data and wrote the manuscript.

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