PALEOECOLOGY

Shrub cover declined as Indigenous populations expanded across southeast Australia

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Wildfires in forests globally have become more frequent and intense because of changes in climate and human management. Shrub layer fuels allow fire to spread vertically to forest canopy, creating high-intensity fires. Our research provides a deep-time perspective on shrub fuel loads in fire-prone southeastern Australia. Comparing 2833 records for vegetation cover, past climate, biomass burning, and human population size across different phases of human occupation, we demonstrated that Indigenous population expansion and cultural fire use resulted in a 50% reduction in shrub cover, from approximately 30% from the early to mid-Holocene (12 to 6 thousand years ago) to 15% during the late to mid-Holocene (6 to 1 thousand years ago). Since the start of British colonization to the present, shrub cover has increased to the highest ever recorded (mean of 35% land cover), increasing the risk of high-intensity fires.

We live in a flammable world where forest fires are projected to increase with anthropogenic climate change (*1*). Forested areas of western North America and southeastern Australia are wildfire epicenters, with devastating economic and societal repercussions (*2*). Australia's fires are increasing in frequency and extent (*3*), fueled by anthropogenic warming, droughts (*4*), and increased biomass (*5*). The extreme wildfires of 2019–2020 occurred in the dense *Eucalyptus* woodlands and forests of southeastern Australia (*4*, *6*) during extreme fire weather (*3*). Regarded as "catastrophic" from both a socioeconomic and an environmental perspective (*3*, *4*), the fires burned more than 21% of forest area during this period, in comparison to annual averages of 2 to 3% since 2000 (*7*). Along with climate change, forest management and fire suppression have allowed the accumulation of shrubby biomass, which fuels more intense fires (*8*–*10*). An important component of overall fuel load, known as ladder fuels, is the shrub layer that allows ground fire to spread to the tree layer, causing crown fires (*11*, *12*).

For thousands of years, humans have harnessed fire for various purposes, including fire management itself (*13*). The term "cultural burning" refers to the practice of systematically applying frequent low-intensity fire to the land, as used by many Indigenous groups globally (*14*, *15*). Cultural burning relies on an intimate relationship with the land, creating fine-scale spatial heterogeneity that promotes high biodiversity, improves hunting opportunities, interrupts fuel load connectivity, and serves various cultural and spiritual purposes (*16*, *17*). In North America, suppression of Indigenous cultural burning has had major consequences for forest composition and fuel connectivity (*10*, *18*, *19*). For example, in the Klamath Mountains (California), the cessation of Indigenous cultural burning drastically increased biomass in postcolonial times (*14*). In Australia, Indigenous peoples arrived at least 65,000 years ago (*20*) and likely used fire to care for Country. "Country" is an Indigenous Australian term used to describe relationships and interconnections between lands, waterways, and people (*21*). British colonization disrupted cultural burning in southeastern Australia, and eucalypt-dominated vegetation communities now burn at extreme intensities (*3*), in part because of abundant ladder fuels (*12*, *22*). Colonization of Indigenous lands has suppressed the customary burning practices that maintained open forest structures. This, in combination with the active suppression of forest fires in the 20th century, has caused fuel loads to increase (*5*, *14*).

Although traditional burning practices have important benefits (*23*), quantitative data on Australian vegetation structure under Indigenous management is lacking. Understanding the mechanisms behind extreme wildfires (*6*) under different management approaches, from Indigenous cultural burning to postcolonial practices, can inform better fire management in the future. Paleoecological evidence is becoming an invaluable tool to assess linkages between wildfire extent and changing fuels after colonial invasion of Indigenous lands (*10*, *14*). In this work, we adopted a multidisciplinary approach, compiling multisite data focused on the most densely populated region of Australia, to uncover the regional dynamics of vegetation, fire histories, human activity, and paleoclimates (Fig. 1 and fig. S1).

Previous work focused on past fuel loads [e.g., (*6*)] overlooked the fact that fuel abundance in different vegetation strata and fuel continuity influence fire spread and intensity (*24*). Mariani *et al*. (*5*), focusing on the past 1000 years, hypothesized that the post-European disruption of Indigenous cultural practices led to an expansion of shrubs in the understory of eucalypt forests in eastern Australia, exacerbating recent fire events by providing ladder fuels. In this study, we built further from this hypothesis with a temporally expanded dataset to quantify shrub cover across key periods of human occupation in Australia, gauging changes to the risk of high-intensity crown fires (Fig. 1A). To achieve this, we reconstructed shrub cover during periods of (i) no human activity [Last Interglacial, also known as Marine Isotope Stage (MIS) 5e; 130 to 115 thousand years ago (ka)], (ii) low human activity (early to mid-Holocene, ending at 6 ka), (iii) intensified human activity (mid- to late Holocene, 6 to 1 ka), and (iv) postcolonial cultural burning suppression (from 1788 CE).

Past land cover and ladder fuels

Detecting cultural burning activity in archaeological and palaeoecological contexts is challenging. Previous Australia-wide research combined data from various bioclimatic and cultural areas and failed to detect cultural burning (*25*, *26*). By contrast, local-scale studies, which reflect the scale at which people alter landscapes (*15*), find strong links between historical occupation and vegetation changes, suggesting an increased tree abundance during low-occupation phases (*27*, *28*). Examples of these investigations include coupled archaeological-paleoecological records from Tasmania (*27*, *28*), the Australian Alps (*29*), New South Wales (*30*), and the Bass Strait islands (*31*).

We reconstructed shrub cover using pollen assemblages from 31 sedimentary deposits (from wetlands and lakes) with a minimum age of 1000 years before present (yr B.P.) across

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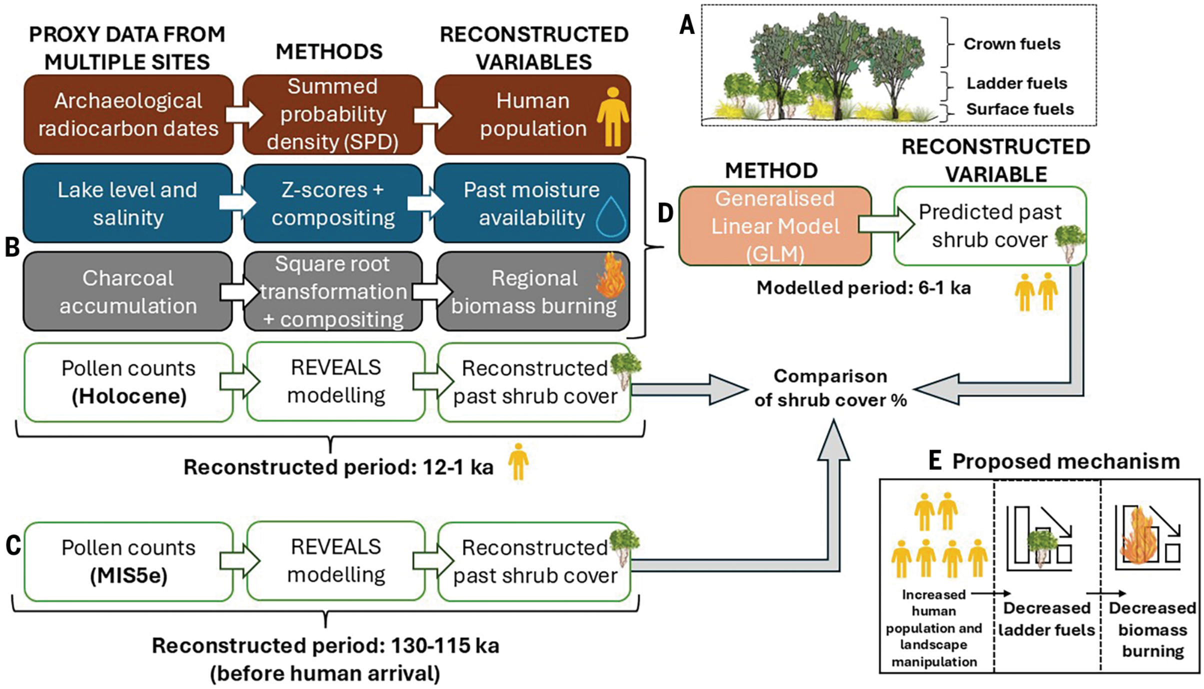

Fig. 1. Flowchart explaining the approach used in the present study to quantify past changes in fuels within the shrub layer (i.e., ladder fuels). (**A**) Schematic illustrating typical fuel layers in Australian sclerophyll forests. (**B**) Approach used to reconstruct Holocene trends in human population, hydroclimate, fire activity, and vegetation cover. (**C**) Approach used to reconstruct prehuman vegetation cover (because no other proxies are available for this period). (**D**) The generalized linear model (GLM) is fitted to predict shrub cover during the period from 6 to 1 ka in a scenario without human influence, with only paleoclimate index and charcoal composite set as predictors. The GLM for the preceding 12-to-6-ka period, which includes paleoclimate index and charcoal as well as human occupation as predictors, is used as the training dataset for the 6-to-1-ka period model. (**E**) Schematic of hypothesized mechanism investigated in the study. All icons used in the illustrations are from Creative Commons.

southeastern Australia (Fig. 2, A and B, and table S1). Two pollen records (Caledonia Fen and Lake Wangoom) covering parts of the Last Interglacial (130,000 to 115,000 yr B.P.) were included to examine vegetation patterns before human arrival and under climates similar to the Holocene (table S1 and fig. S2). The Regional Estimates of Vegetation from Large Sites (REVEALS) model (*32*) provides regional-level reconstructions of aboveground plant cover by structural type (i.e., trees, shrubs, herbs, and grasses) (*5*). REVEALS modeling overcomes biases in pollen production and dispersal that commonly overrepresent trees and underrepresent shrub, herb, and grass cover (*32*). We used the reconstructed cover of shrub taxa to indicate ladder fuel availability across the study area (Fig. 3).

Regional biomass burning was inferred from 108 sedimentary charcoal records (Fig. 2C and table S2). Charcoal influx was calculated, time series were square-root transformed, and min-max transformed series were averaged to create a regional record of paleofire activity for southeastern Australia (*33*) [supplementary materials (SM), material and methods]. Trends in human activity sensu Peros *et al.* (*34*) were tracked by using more than 2000 radiocarbon ages from archaeological sites (Fig. 2C), obtained from the SahulArch database (*35*, *36*). We calculated summed probability density (SPD) to infer past changes in human activity (*34*, *37*). We corrected for detection biases using an exponential-logistic model on the archaeological ages (*37*) (SM, materials and methods). We mapped the distribution of archaeological radiocarbon ages between 9 and 6 ka and 6 and 3 ka (Fig. 2C) to trace changes in population size and landscape use.

To understand interactions between moisture availability and paleofire, five terrestrial paleomoisture records (lake level, salinity, and rainfall) from southeastern Australia were compiled by smoothing z scores (Fig. 2, A and B, fig. S3, and table S3). All trends were then smoothed with generalized additive models (GAMs), and the first derivative was calculated to highlight significant trends in the timeseries. Generalized linear modeling was used to identify the main drivers of change in Holocene shrub cover with climate, paleofire, and human population size as predictors (table S4). A GLM was also used to predict how shrub cover might change if human activity was excluded from the landscape (Fig. 4C).

Reconstructed shrub cover under varying levels of human activity

Our data track major structural changes in vegetation from the Last Interglacial to the postcolonial landscape. In the Last Interglacial, shrub, tree, herb, and grass cover each comprise ~30 to 34% (Fig. 3), with shrub cover ranging from 13 to 80% in this period. Although there is no regional charcoal compilation from the Last Interglacial, owing to the scarcity of records and dating uncertainties, the recently published individual charcoal record from Lake Couridjah spans the Holocene and the Last Interglacial (*30*). This study demonstrated higher levels of charring intensities from biochemical data, most likely reflecting a high abundance of woody fuels that burned at higher intensities (*22*) during the Last Interglacial.

During the early to mid-Holocene, with human presence (Fig. 3), the cover of the three structural plant groups diverged. Comparing this period with the Last Interglacial, median tree cover declined by ~10%, herb and grass cover increased by ~10%, and median shrub cover remained at a similar level. However, there was high variability in cover of each stratum during the early to mid-Holocene, as in the Last Interglacial, ranging from 5 to 55% (Fig. 3). High charcoal influx persisted during the early to mid-Holocene, reaching a maximum at 6 ka (Fig. 4D). From 6 to 1 ka, median shrub cover decreased to <15% (Fig. 4C and fig. S4), accompanied by a gradual decline in charcoal influx until 1 ka (Fig. 4, D and H). The charcoal compilation, interpreted as biomass burning, shows a decline during the period from 6 to 1 ka, which was likely due to limited availability of woody fuels because large particles deriving from wood preserve better in sediment records (*38*). We also found a large increase in herbs and grasses, from <40% before 6 ka to >60% from 6 to 1 ka (figs. S4 and S5). Shrub cover percentage changes observed between prehuman contexts and the Holocene (both from 12 to 6 ka and 6 to 1 ka) are statistically significant (table S5).

During the colonial era (i.e., the past ~200 years), herbs and grasses comprised ~60% of median cover, and tree cover declined to <10%. Over this same period, shrubs increased to ~35%, which is substantially greater than shrub cover in both the Indigenous-managed Holocene landscapes (i.e., in those of both the early to mid-Holocene and mid- to late Holocene) and slightly higher than that in the unpopulated landscapes of the Last Interglacial (Fig. 3). We note a high variability in the postcolonial dataset, which is likely due to the impact of agricultural practices (*5*).

These changes in shrub cover occurred during periods with different underlying levels of human activity and climatic conditions. The SPD of radiocarbon ages indicates increased human activity after 6 ka across southeastern Australia (Fig. 4, B, C, and F, and fig. S6). The distribution of archaeological ages indicates the spatial expansion of human activity during the 6 to 3 ka period (Fig. 2C), suggesting either an increase in population size, an increase in population mobility and extensive land use, or a combination of both during the mid- to late Holocene. This phase of increased human activity occurred after moisture availability peaked at 7 ka, after an initially drier early to mid-Holocene (Fig. 4A). After human activity increased, moisture levels were more stable but drier until ~2 ka (Fig. 4, A and E).

Human activity (SPD of radiocarbon ages) was the strongest predictor ($P < 0.01$) of shrub cover changes in the Holocene up to 1 ka (table S4 and figs. S7 to S10), with declining shrub cover associated with increasing population and/or more extensive land use. Further, the reduction in shrub cover variability from early to mid-Holocene to mid- to late Holocene (Fig. 3) might be reflecting a regional-scale stabilization of cultural burning practices alongside population expansion. When shrub cover for the mid- to late Holocene is predicted without archaeological data (an uninhabited scenario) with an early to mid-Holocene model that includes all predictors as a training dataset, GLM-predicted and observed results diverge by ~50%. Predicted nonanthropogenic median shrub cover was ~30% for the mid- to late Holocene, compared with observed values of ~15% (Fig. 4C, orange line). This suggests that increasing human activity after 6 ka influenced shrub cover.

Discussion

Holocene shrub cover and ladder fuels under intensified cultural burning

For the first time, we have documented a regional-scale decline in Holocene shrub cover across southeastern Australia, which corresponds with evidence for increased Indigenous population size and/or expanded Holocene land use (after 6 ka). Therefore, we suggest that the decline in shrub cover can be attributed to intensified cultural burning practices. The sharp decline in shrub cover from 6 to 5 ka likely reduced vertical fuel pathways because of lower ladder fuels and altered fire behavior. The steady decline in biomass burning up to 1 ka is unlikely related to moisture levels, which remained relatively stable (Fig. 4). Projected shrub cover over the mid- to late Holocene—without considering human population density (28% of land cover; Fig. 4C, orange line)—differs significantly from that we observed (15% of land cover). Shrub cover during the mid- to late Holocene did not return to levels seen during the early to mid-Holocene, with less ladder fuels and lower connectivity likely leading to lower charcoal influx (Fig. 4D). This supports the mechanism hypothesized in this study because cultural burning is generally targeted at fine fuels within the ground stratum, which results in overall lower charcoal production (*39*, *40*). Tree and grass components both increased at this time

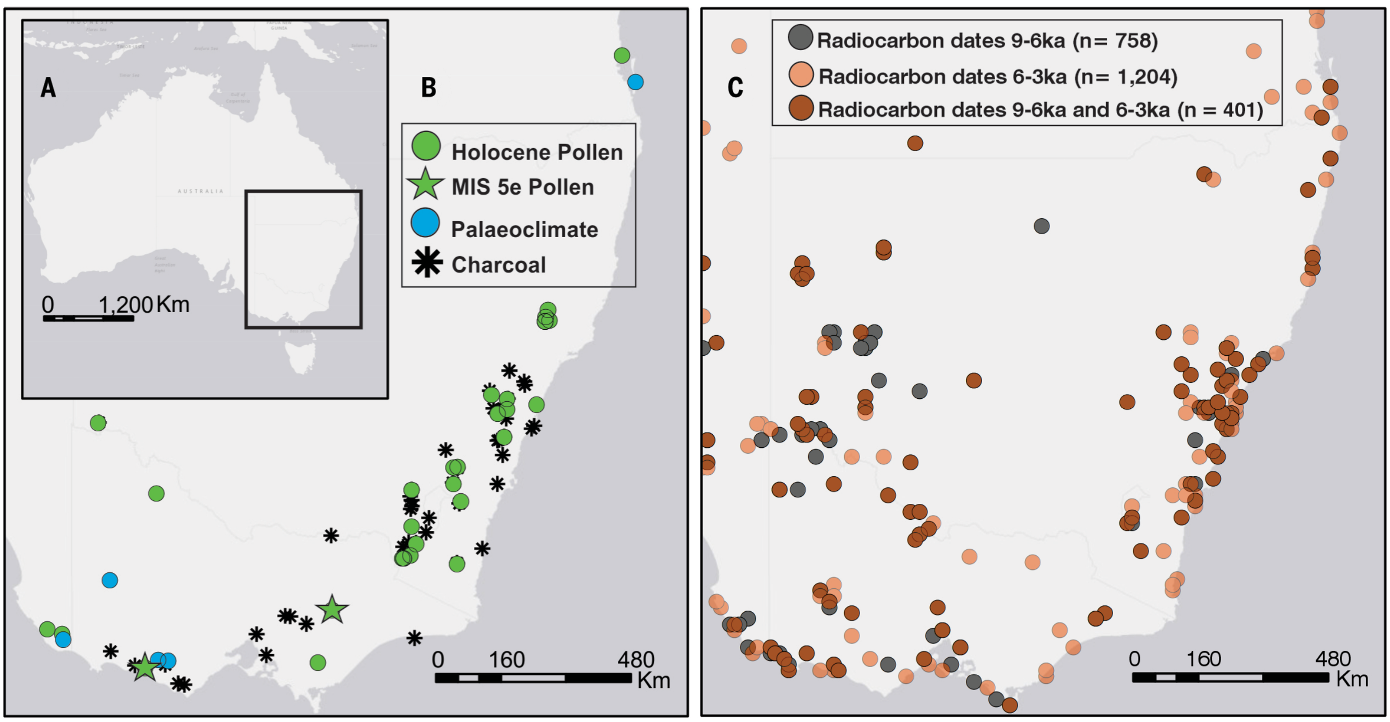

Fig. 2. Map showing site locations. (**A**) Inset, magnified in (**B**) and (**C**), showing locations for (B) pollen, paleoclimate, and charcoal records, and (C), archaeological radiocarbon dates. The light orange dots in (C) are locations only present in the mid- to late Holocene (n = 1204); dark gray dots are locations only present in the early to mid-Holocene (n = 758); and dark orange dots represent locations dated during both early to mid-Holocene and mid- to late Holocene (n = 401). The climatic and vegetation gradients for the study area are presented in fig. S1.

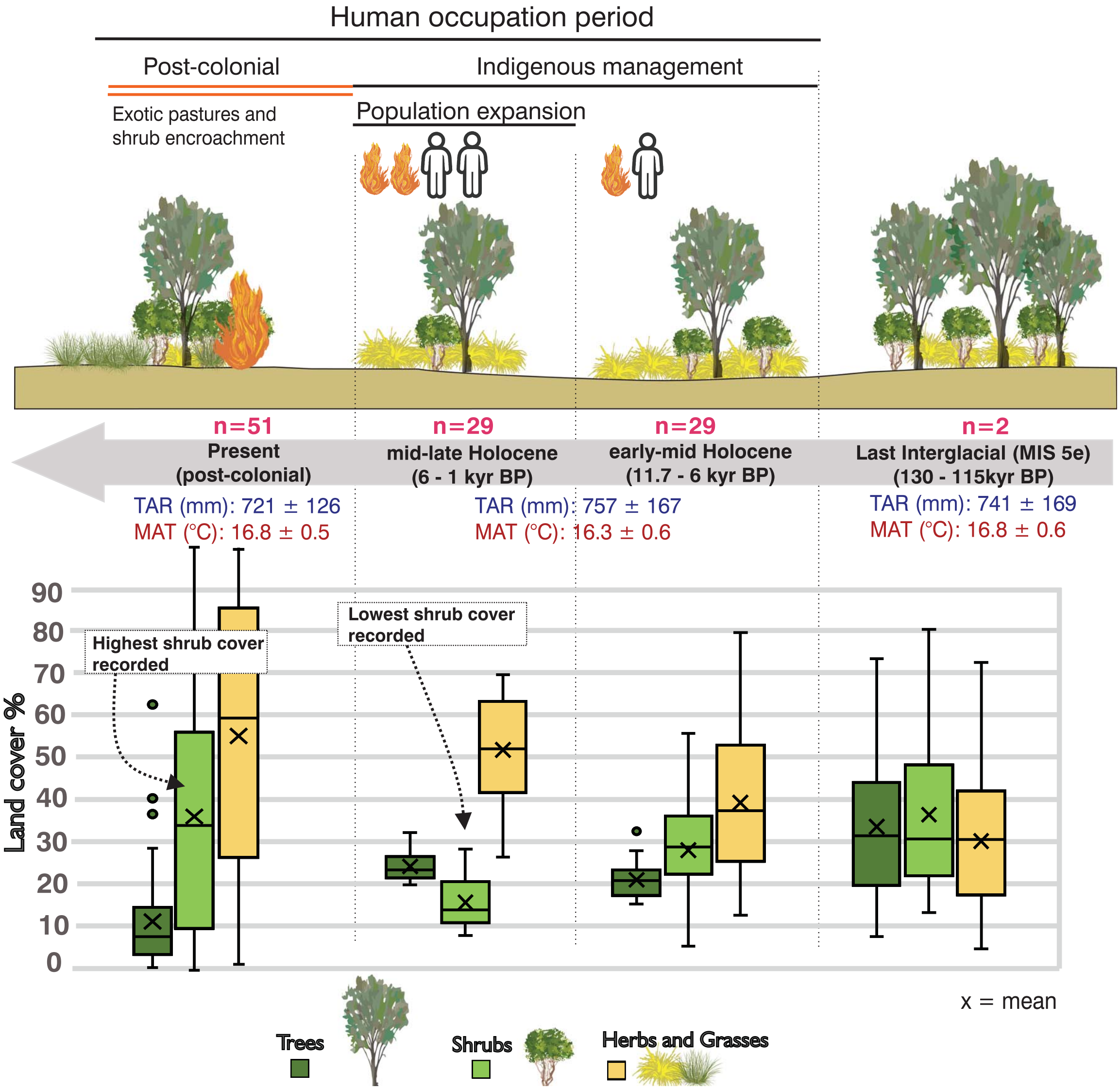

Fig. 3. The lowest shrub cover was found during the mid- to late Holocene (6 to 1 ka), whereas the current postcolonial landscape (0.2 ka to present) hosts the highest median shrub cover. Summary schematic illustrating vegetation changes through time and associated boxplots (*n* = number of sites used in the land-cover estimation performed with REVEALS). The timeline goes from youngest to oldest (left to right). Total annual rainfall (TAR, mm) and mean annual temperature (MAT, °C) modeled for the Holocene (6 ka) and Last Interglacial are shown below the gray arrow (further details provided in fig. S2), alongside present (postcolonial) regional averages.

(fig. S5), suggesting a shift to open savanna-like landscapes with a more open midstory, reducing the risk of crown fires (*24*, *41*).

An increase in population and more extensive land use—including the use of new resource zones—in the mid- to late Holocene is a well-established phenomenon in southeastern Australia (*42*, *43*), although its drivers are contested (*44*). Combined, the results of this multiproxy work suggest a large-scale reduction of shrub cover that altered fuel connectivity and hence fire intensity in southeastern Australia throughout the mid- to late Holocene after population increase, probably through the application of Indigenous management practices, including cultural burning.

Cultural landscapes

Although we recognize that climate modulates vegetation cover and fire regimes in many Australian contexts [e.g., Bowman *et al.* (*45*)], our findings show a decoupling between moisture availability, vegetation, and biomass burning in the mid- to late Holocene (Fig. 4). We suggest that this decoupling is due to an intensification of cultural burning, because the stability in available moisture during this period (Fig. 4A) would not have produced a decline in shrub cover without anthropogenic forcings (Fig. 4C). Moisture levels of the mid- to late Holocene are similar to the conditions existing before the moisture peak at 7 ka, but in this period human activity was lower and shrub cover was higher. This suggests that cultural burning practices may have overridden climatic controls on vegetation structure (Fig. 4, A and C).

As climate would have had similar effects on vegetation dynamics in the early to mid-Holocene and mid- to late Holocene, it seems likely that increased Indigenous cultural burning drove the change in vegetation toward low shrub cover in the latter (Fig. 4C). Indigenous Australians actively and extensively managed Country through cultural burning practices, keeping fuel levels low, until colonial invasion in 1788 CE (*5*). Our evidence corroborates Indigenous oral history and the landscape descriptions recorded by early European colonists (*16*), who both characterized the landscape with widely spaced trees creating open woodlands. These descriptions were likely accurate portrayals of cultural landscapes maintained through cultural burning practices. This also corroborates local-scale evidence from other Australian regions (*28*, *39*).

We recognize that our understanding of vegetation cover at the time of initial human occupation of Australia ~65 ka is limited because of the sparseness of long sedimentary sequences, poor dating quality in older records, and lack of vegetation quantifications [see Florin *et al.* (*46*)]. A recent study from Northern Australia's tropical savanna zone found a clear onset of human-managed fire regimes starting around 11 ka (*47*), predating the human expansion that we observed in southern temperate

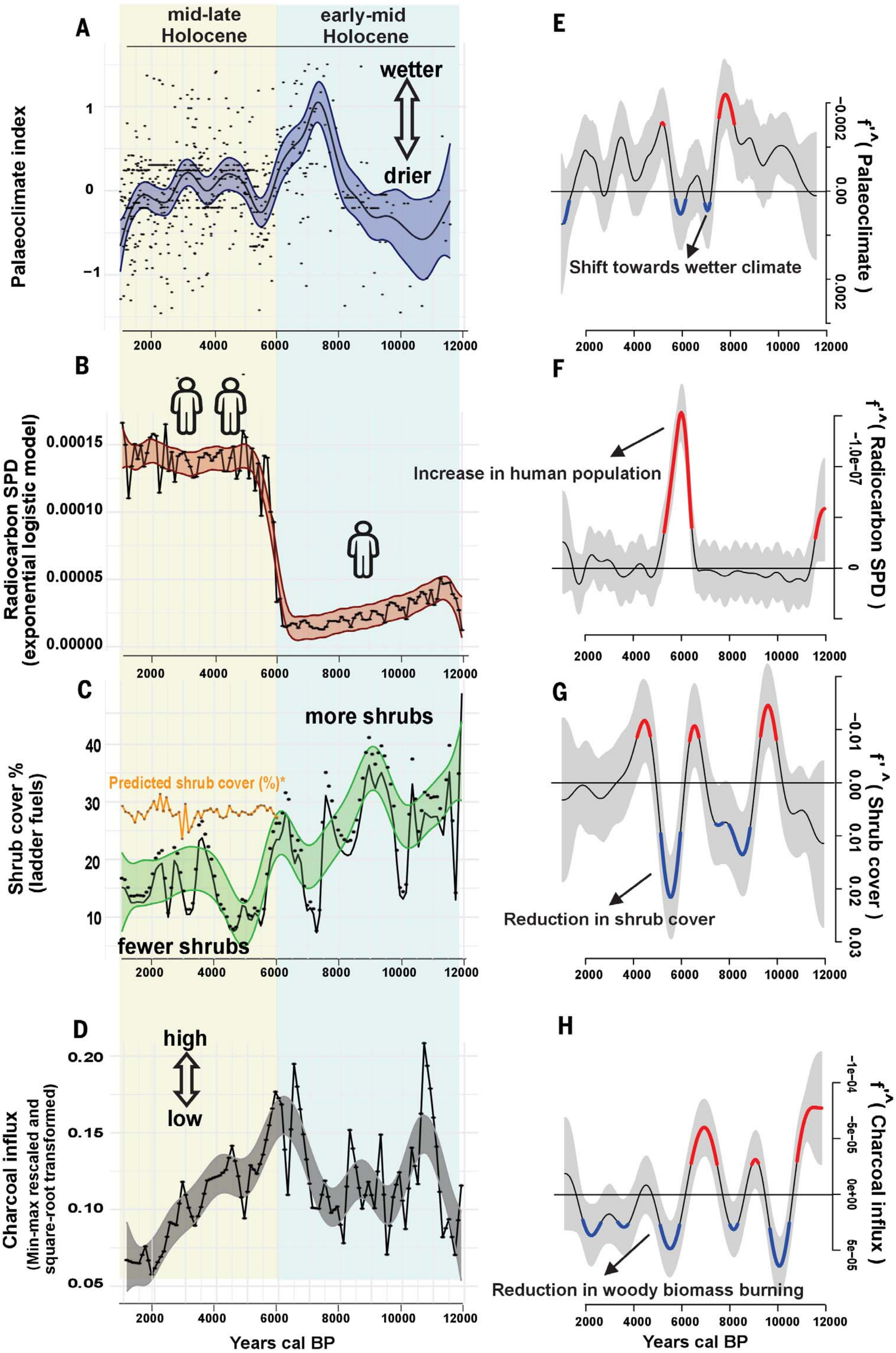

Fig. 4. A ~50% average reduction in shrub cover following expansion of Indigenous populations in the mid- to late Holocene (6 to 1 ka) is concurrent with a reduction in biomass burning. Stacked diagram showing Holocene trends for (**A**) GAM-smoothed palaeoclimate index. (**B**) Summed probability density (SPD) of archaeological radiocarbon dates corrected for preservation and detection biases. (**C**) GAM-smoothed shrub cover percent and (**D**) GAM-smoothed charcoal influx. Asterisk (*) indicates predictive generalized linear modeling result (GLM) in a scenario without human presence (here inferred from SPD) in the landscape [orange dotted line in (C). (**E**) to (**H**) show the respective first derivatives to highlight major significant trends (blue indicates declining trend; red indicates increasing trend). The timeline goes from youngest to oldest.

Australia (this study) by about 5000 years. However, an earlier long record from Lynch's Crater, located at the tropical rainforest–savanna ecotone, suggests that human influence on fire regimes and rainforest landscapes was already in place by around 40 ka (*48*, *49*). This disparity in fire regimes contributes to our growing understanding of cultural burning—and other caring-for-Country practices—as greatly variable and shaped by long-term trajectories of localized human-environment interaction across Australia.

Future outlook: Cultural burning and climate change

Considering the pressing influence of anthropogenic climate change in modulating recent high-intensity and frequent wildfires (*50*), our work suggests that reconstructed postcolonial shrub cover, an important ladder fuel, is unusual from a long-term perspective. The evidence supports the reduction of shrub cover and ladder fuels as an effective way to limit high-intensity crown fires in the flammable forests of Australia and beyond (*22*). Currently, fuel reduction strategies, such as mechanical thinning and prescribed burning, are especially focused on trees

(*51*), but effective fire management also requires targeting ladder fuels (*22*).

This work highlights how cultural burning, over millennia, likely resulted in landscapes with less-intense wildfire activity owing to reduced vertical connectivity of fuels. A wide-scale reintegration of traditional cultural burning, undertaken in combination with Western management techniques (*52*), is crucial in a context where increasing fire weather and expanding population levels intersect (*2*). There are ecological benefits to reintroducing cultural burning, including wildfire prevention and carbon storage, as well as enormous sociocultural benefits for Indigenous communities [e.g., (*25*, *53*)]. However, without more support for Indigenous capacity-building and community-led cultural burns over wider areas, the benefits of cultural burning in the prevention of wildfires are unlikely to be achieved (*15*, *52*). Through detailed histories of Indigenous burning regimes across the world and Indigenous-led collaborations in contemporary wildfire management projects, we can inform sustainable and healthy solutions that "tame the flames" threatening global socio-environmental systems.

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SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.adn8668
Materials and Methods
Figs. S1 to S11
Tables S1 to S5
References (*58*–*82*)
MDAR Reproducibility Checklist

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