

Historical reconstruction unveils the risk of mass mortality and ecosystem collapse during pan-continental megadrought

Robert C. Godfree^{a1}, Nunzio Knerr^a, Denise Godfree^b, John Busby^a, Bruce Robertson^a and Francisco Encinas-Viso^a

^aCSIRO National Research Collections Australia, GPO Box 1700, Canberra, ACT, Australia 2601; ^b87 Upper Bullawa Creek Road, Narrabri, NSW, Australia 2390
¹Corresponding author: Robert.Godfree@csiro.au

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An important new hypothesis in landscape ecology is that extreme, decade-scale megadroughts can be potent drivers of rapid, macro-scale ecosystem degradation and collapse. If true, an increase in such events under climate change could have devastating consequences for global biodiversity. However, because few megadroughts have occurred in the modern ecological era, the taxonomic breadth, trophic depth and geographic pattern of these impacts remain unknown. Here we use new eco-historical techniques to quantify the impact of a record, pan-continental megadrought period (1891-1903 CE) on the Australian biota. We show that during this event mortality and severe stress was recorded in >45 bird, mammal, fish, reptile and plant families in arid, semi-arid, dry temperate and mediterranean ecosystems over at least 2.8 million km² (36%) of the Australian continent. Trophic analysis reveals a bottom-up pattern of mortality concentrated in primary producer, herbivore and omnivore guilds. Spatial and temporal reconstruction of pre-mortality rainfall shows that mass mortality and synchronous ecosystem-wide collapse emerged in multiple geographic hotspots after 2-4 years of severe (>40%) and intensifying rainfall deficits. However, the presence of hyper-abundant herbivores significantly increased the sensitivity of ecosystems to overgrazing-induced meltdown and permanent ecosystem change. The unprecedented taxonomic breadth and spatial scale of these impacts demonstrate that continental-scale megadroughts pose a major future threat to global biodiversity, especially in ecosystems affected by intensive agricultural use, trophic simplification, and invasive species.

megadrought | ecosystem collapse | mass mortality | trophic impact | Federation Drought

There is growing evidence that under warming scenarios of 1.5-3°C above preindustrial levels, the magnitude and extent of drought, and the occurrence of decade-scale megadrought, is likely to increase across most global land areas (1-3). This is of great concern because megadroughts (4) have a track record of devastating socio-ecological systems worldwide both historically (5-7) and within the past century (1, 8) on a continental scale, particularly when exacerbated by anthropogenic processes such as overgrazing, water extraction, and intensive land use. For example, two multi-annual 20th century droughts, the 1970s-80s Sahel drought and the 1930s US "dust bowl", both caused land degradation, ecosystem decline, and human disruption on a massive scale (1, 9). The severity of these impacts was driven by exceptionally low rainfall and reinforced by coupled edaphic-atmospheric processes linked to intensive agricultural land use and human disturbance (9).

A major question in conservation biology is how native and introduced biota might be affected by increasingly intense, continental-scale megadroughts (CSM) in the future. Recent studies suggest that the ecological impact of such events is likely mediated primarily through rapid shifts in plant and animal populations and the trophic reconfiguration of associated food webs. These changes can be most severe among primary producer

and associated herbivore guilds, such as grazers and browsers of the African savannah (10-12), but may impact predators more than basal species (13) or affect both (14). There is also some evidence that mass mortality events (MMEs) can play a pivotal demographic role during extreme drought, and that these may be responsible for persistent changes in community structure and even transitions between alternate ecosystem states. However, given that CSMs occur very rarely (1, 6), the magnitude of such impacts, the mechanisms through which they manifest across trophic levels, and the implications for biogeography at regional to biome scales remain poorly understood.

One approach is to use historical sources to reconstruct the impacts of major droughts that occurred in the past. Historical reconstructions have successfully been used to investigate the impact of changing climatic regimes and other drivers on insects (15-16), disease (17), marine biota (18-19), bird assemblages (20) and ecosystem transitions in general (21), and the use of such data to guide ecosystem management is growing (22). Newspaper articles are particularly valuable for historical ecology, since they open lines of inquiry about historical events for which little or no other information exists. While data compiled from such sources must be used with caution due to potential bias and non-independence (23-26), they have been successfully used to reconstruct temporal changes in biota (23, 27-28) and physical, hydrological or climatic phenomena (29-30) that occurred decades to centuries ago. They therefore remain a large but mainly untapped resource for in-

Significance

It is thought that extreme, decade-scale megadroughts pose a major future threat to global biodiversity under climate change. However, such events occur rarely and so their capacity to drive ecosystem change remains largely unknown. Here we address this question by reconstructing the impacts of an extreme, historical megadrought period (1891-1903) on plant and animal assemblages across the Australian continent. The geographic extent (≥2.8 million km²) and taxonomic depth (>45 families) of impacts observed during this event were remarkable, and include mass population mortality and broad, bottom-up trophic collapse in multiple subcontinental hotspots. Our work provides new insights into the potential pattern and magnitude of ecological change that can occur during continental-scale megadrought.

Reserved for Publication Footnotes

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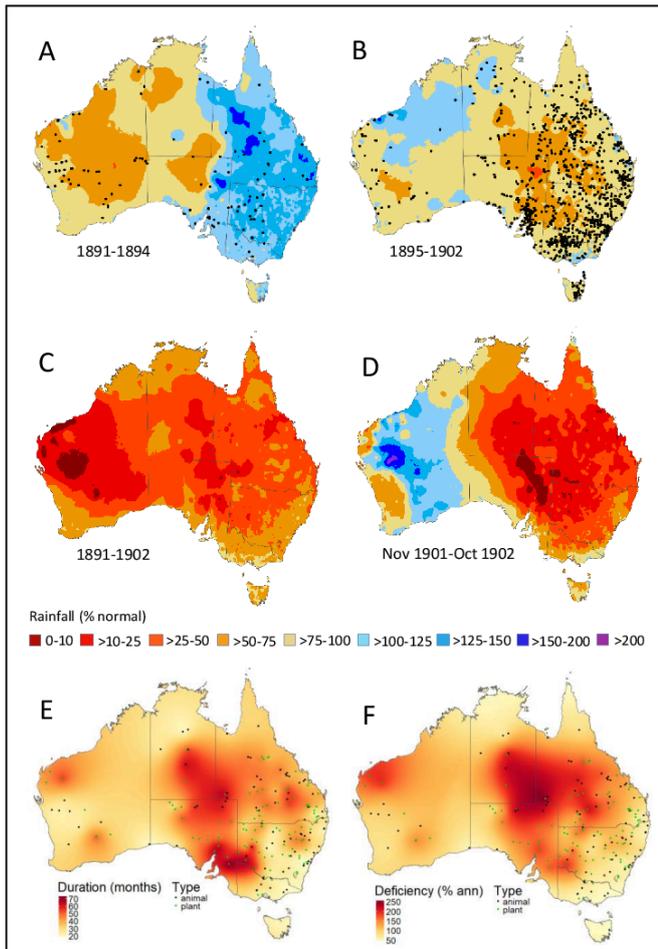


Fig. 1. Rainfall patterns and duration and magnitude of drought during the 1891-1903 study period. (A) Mean rainfall 1891-1894 as a percentage of the 1889-2015 average, showing multi-annual drought in central and western Australia. Black dots indicate geographic locations of drought records during the time period, which partly reflect the pattern of European settlement at the time. (B) As in (A) except for 1895-1902. (C) Minimum annual rainfall as percentage of average, 1891-1902. Most of the continent between 18°S and 32°S experienced at least one calendar year with <50% of average annual rainfall. (D) Hyper-intense drought between November 1901-October 1902, with much of eastern Australia receiving <25% of average rainfall. (E) Reconstructed continental profile of drought duration prior to mortality of biota, defined as the number of preceding months of continuous drought (D_{CON}). (F) Continental profile of drought magnitude (R_{CON}) prior to mortality of biota, defined as the cumulative rainfall deficiency over the period D_{CON} expressed as a percentage of annual mean rainfall P_{AV} . See methods for further details.

investigating the impact of historical drought and other climatic extremes on populations and ecosystems (e.g., 31-32).

In this paper we shed light on these questions by developing an eco-climatic reconstruction of one of the most severe and geographically extensive megadrought intervals of the past two centuries, the Australian Federation Drought Period (1891-1903; FDP). Record low rainfall (see below) and patterns of agricultural land use during the FDP caused catastrophic soil and vegetation loss across large parts of the continental interior (33-34); in eastern Australia, the most intense phase of rainfall deficiencies, now known as the iconic 1895-1903 “Federation Drought” (FD), marked the first major episode (33) in a multi-decadal (1895-1945) “dust bowl” period (35; see *SI Appendix*, Fig. S1) of persistently low rainfall and severe land degradation. The study period also includes preceding intervals of significant drought in Western

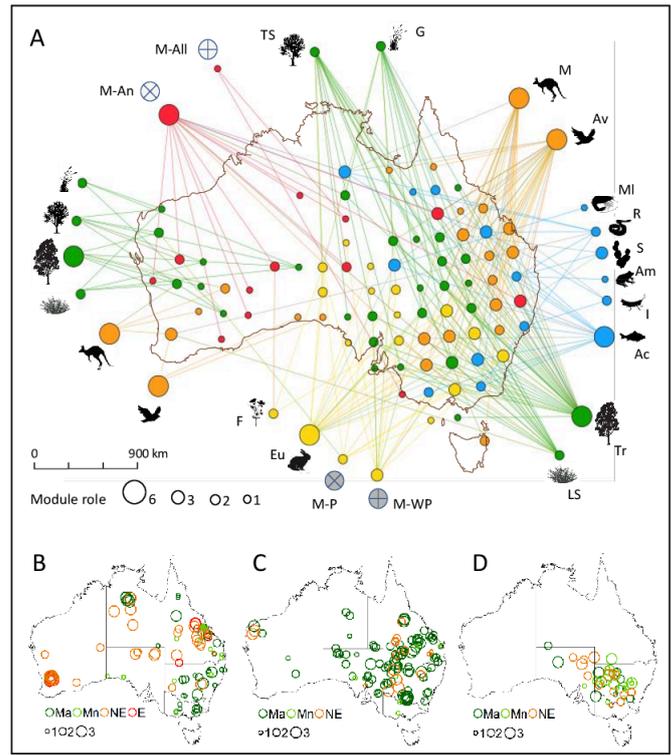


Fig. 2. Spatial distribution of drought impacts on flora and fauna during the FDP. (A) Modularity analysis of taxonomic co-occurrence network based on stress and mortality records. Modules are: red = predominantly arid zone mixed animal and plant assemblages, green = subtropical to arid woodlands, shrublands, savannas and grasslands, orange = inland birds and marsupials, blue = fish and minor animal taxa, and yellow = predominantly mediterranean to arid woody shrubland containing *Oryctolagus cuniculus* (European rabbit). Module roles: 1) ultra-peripheral node, 2) peripheral node, 3) non-hub connector, and 6) connector hub(48). (B-D) Locations of mass mortality by area (Ma) and number (Mn) and population collapse to near-extirpation (NE) and extirpation (E) for native animals (B), plants (C) and *Oryctolagus cuniculus* (D). The categories for Ma, NE and E are as follows: 1 = local (10^2 m-1 km scale), 2 = district (10^1 km) or 3 = regional (10^2 km); the categories for Mn are 1) 10^2 - 10^3 , 2) 10^4 - 10^5 , and 3) 10^6 +. Biotic groups are: Ac = Actinopterygii, Am = Amphibia, Av = Aves, Eu = Eutheria, M = Marsupialia, MI = Malacostraca, I = Insecta, R = Reptilia, F = forbs, G = grasses, LS = low shrubs, TS = tall shrubs, Tr = trees, M-All = mixed all (animal and plant), M-An = mixed animal, M-P = mixed plant, M-WP = mixed woody plant.

Australia (1891-2) and subtropical Queensland (1892-3). Given concerns over the recent return of significant drought-induced ecosystem decline and mortality of native biota in Australia (36-38), and the potential increase in scale and severity of future megadroughts (1-3), historical CSMs such as the FDP provide one of the only sources of information available on which to build broad-scale predictive drought models that capture the genesis and development of such processes.

We begin by constructing a continent-wide dataset consisting of >500 biotic impact records (BIRs) extracted from contemporary newspaper articles and other historiographic sources during 1890-1903. Then, using geocoded data from >60 plant and animal genera, we test for evidence of population mortality and ecosystem collapse during the FDP using trophic reconstruction, statistical modelling, biogeographic network analysis, and spatial models of drought duration and magnitude. We also specifically consider evidence that other landscape-scale processes exacerbated the impact of drought on native and exotic biota, and demonstrate new methods for assessing the reliability of historiographic sources for quantifying drought impacts. The exceptional magnitude and breadth of impacts on the Australian

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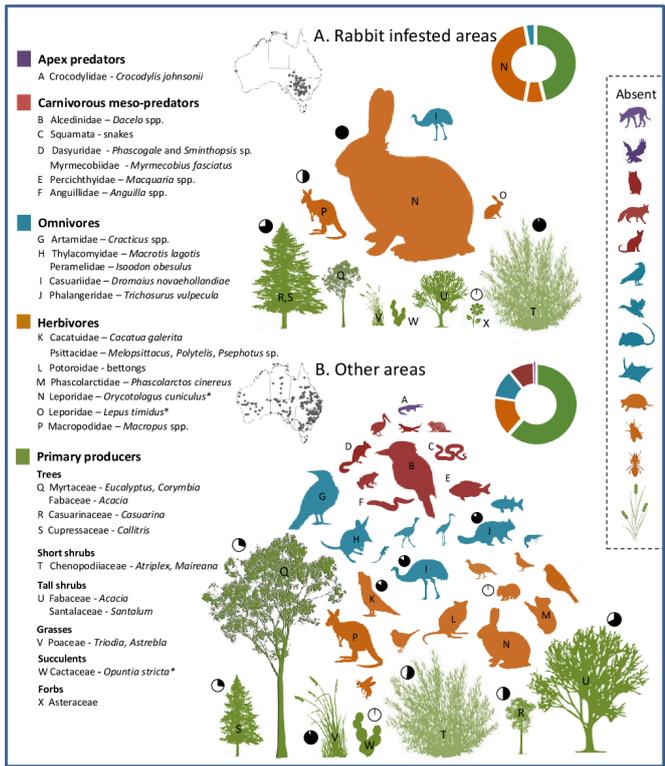


Fig. 3. Trophic structure of drought mortality and stress across plant and animal taxa inside (A) and outside (B) areas infested with large populations of the European rabbit, *Oryctolagus cuniculus*, showing declining impact at higher trophic levels. The size of a minimum circle surrounding each icon is directly proportional to the number of biotic impact records. Pie charts indicate the proportion of mortality records (black) vs. stress records (white). Examples of major groups for which few or no records exist (absent) are provided in each trophic level; from top to bottom: dingo (*Canis familiaris*), raptors, owls, red fox (*Vulpes vulpes*), feral cat (*Felis catus*), crows and ravens (Corvidae), waterfowl (esp. Anatinae), Muridae, gliders, turtles (esp. Cheloniidae), flies, ants, and aquatic and riparian reeds, rushes and other plants (incl. *Phragmites*, *Typha*). *introduced species.

biota revealed in our study provide key insights into the potential implications of pan-continental megadroughts for biodiversity conservation under climate change globally.

RESULTS AND DISCUSSION

Extent and severity of drought

Reconstructed rainfall data (39) show that during the FDP virtually the entire Australian continent was affected by protracted and severe precipitation deficits compared with the long-term average (P_{AV} ; 1889-2015). Semi- to quasi-decadal deficits occurred in all arid, semi-arid and subtropical areas between 18°S and 33°S (Fig. 1A-B) with $\approx 5.5 \times 10^6$ km² experiencing at least one extreme year with total annual precipitation (P_A) less than 50% of the average (i.e., $P_A < 0.5P_{AV}$; Fig. 1C). The most severe deficiencies occurred in the west and north of the continent in 1891-2 and 1894-8 (Fig. 1A-B), the eastern subtropics in 1892-3, and then most of eastern Australia in 1895-1902 (Fig. 1B; *SI Appendix*, Fig. S2). In the latter phase drought severity peaked in Nov 1901 – Oct 1902, when $>1.5 \times 10^6$ km² received less than 25% of P_{AV} and $>2.5 \times 10^6$ km² experienced record low rainfall for the period (Fig. 1D). Below-average rainfall persisted in parts of eastern Australia through 1903 before breaking in 1904. The severity of drought during the FDP was exacerbated by the duration and cumulative magnitude of rainfall deficiencies,

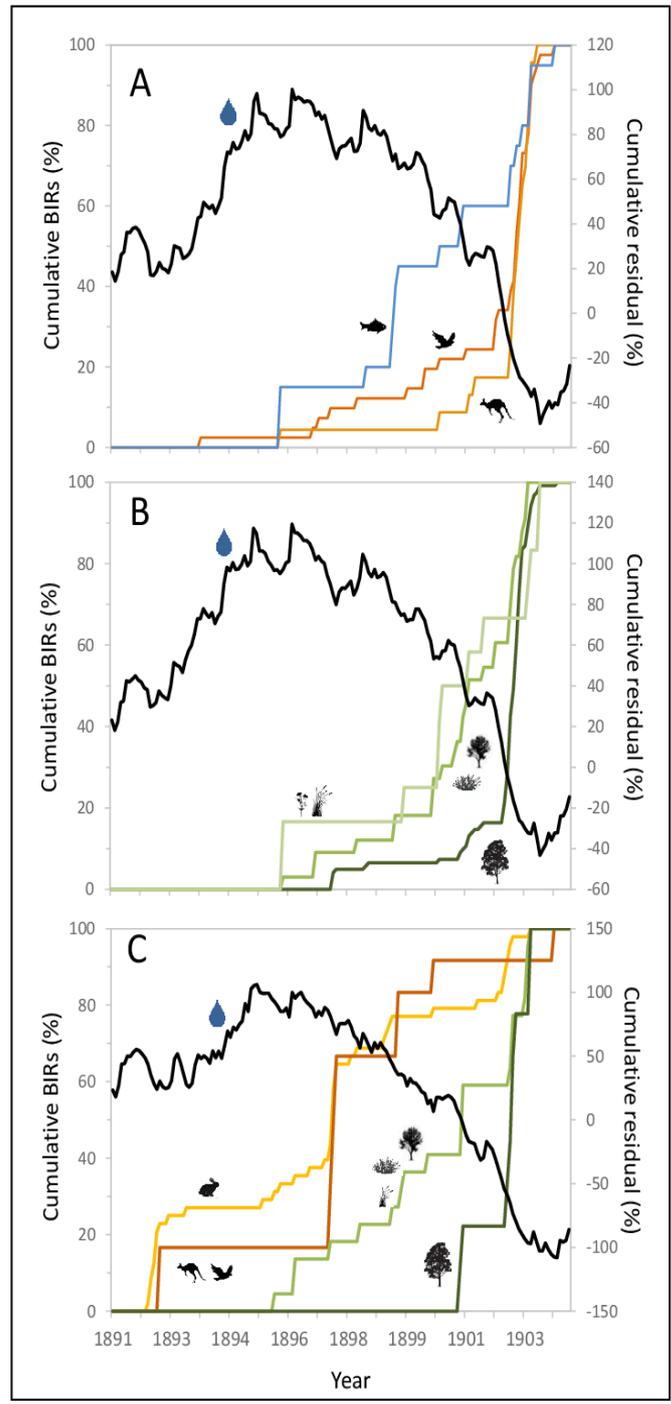


Fig. 4. Relationships between cumulative mortality (percentage of total) of major taxonomic groups and rainfall across eastern Australia during the 1891-1903 study period outside (A-B) and inside (C) areas heavily infested by European rabbits. Cumulative rainfall residuals (heavy black lines) show above average rainfall between 1891 and 1894 in all areas, apart from a short period in late 1891-early 1892, followed by establishment of semi-continuous drought in 1895 and continuous drought from 1898- to early 1903 (the Federation Drought; see methods). The cumulative rainfall residual (relative to the 1889-2015 mean) is expressed as a percentage of mean annual rainfall; for example in panel C the cumulative rainfall residual for the period 1895-1903 was close to 200% of mean annual rainfall. Icons are as in Figure 2.

which reached 7+ years and $>200\%$ of P_{AV} in some arid and semi-arid areas (see below).

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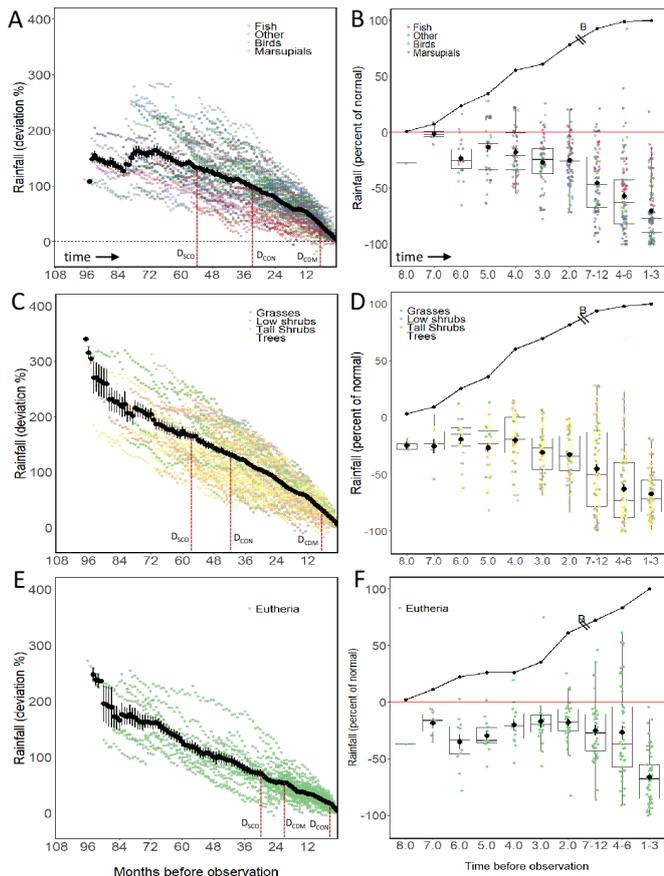


Fig. 5. Reconstructed rainfall patterns prior to mortality in native animals, native plants, and the European rabbit (*Oryctolagus cuniculus*). (A) Cumulative rainfall deficit as a percentage of mean annual precipitation prior to mortality in birds, fish, marsupials and other native animals outside of rabbit-infested areas. Shown are mean values of D_{CDM} = months of consecutive below average precipitation, D_{CON} = months of continuous drought and D_{SCO} = months of semi-continuous drought. (B) Rainfall deficits for birds, fish, marsupials and other native animals in months 1-3, 4-6, 7-12 and years 2-8 prior to observed mortality. The solid black line indicates the cumulative count of BIR records as a percentage of the total at each time period. (C-D) as in (A-B) but for native plant groups (grasses, low shrubs, tall shrubs, trees). (E-F) As in (A-B) but for *Oryctolagus cuniculus* inside heavily rabbit infested areas. Data for each BIR extend back in time only to terminal D_{CDM} , D_{CON} , or D_{SCO} dates. The mean cumulative rainfall deficit value (y axis) can be determined for any period prior to the BIR observation.

Recent reconstructions (37, 40) indicate that three major decade-scale drought epochs have occurred in the instrumental record: the (1892-) 1895-1903 “Federation Drought”, the (1935-) 1937-1945 “World War II Drought”, and the (1997-) 2000-2009 “Millennium Drought” (MD) (*SI Appendix*, Fig. S1; 41; dates in brackets used by some authors). Pre-instrumental (pre-1900) and instrumental reconstructions (40) indicate that the FD (esp. 1895-1902) was the most geographically extensive of the three, with more intense rainfall deficiencies across most of the eastern half and north of the continent (the exception being far southern regions; 37, 40) and a combined intensity and spatial footprint that exceeds that of any Australian drought for at least the past two centuries and possibly longer (40). In contrast to the MD, rainfall deficiencies were concentrated in spring and summer (37, 40), when many biota are especially sensitive to the combined effects of drought and heat stress (42), and were particularly extreme during 1896, 1899, 1900, 1901 and 1902 (40). Notably, cool-season deficiencies were also extreme during 1902 (40), which was probably the driest year across the continent during

the instrumental record. Rainfall deficiencies during the FD were associated with a sustained period of El Niño activity (the warm mode of the El Niño/Southern Oscillation; 37, 40) combined with the positive phase of the Inter-decadal Pacific Oscillation (IPO; 37) and probably neutral to positive values of the Indian Ocean Dipole (37, 40, 43).

Secondary indicators confirm the magnitude of drought impacts on hydrological, edaphic and agricultural systems, with more than 3×10^6 km² of pastoral land denuded of groundcover, extremely low river levels, tens of millions of livestock dying from starvation and thirst (34), and wind erosion affecting $> 1 \times 10^6$ km² of the arid and semi-arid pastoral zone [*SI Appendix*, Fig. S3 and Table S1.1-14 (the number after the decimal refers to the account number in Table S1)]. In the south-eastern inland severe dust storms and soil drift occurred regularly, burying fences, buildings, and livestock, and even mobilising formerly stable sand dunes in parts of the arid zone (44). Social and economic impacts were also severe (*SI Appendix*, Table S1.15-18). Collectively, these data support the view that the scale and severity of the FDP meets or exceeds that of other major global droughts of the past century, such as the Sahel (45) and US “dust bowl” droughts (9).

Structure and reliability of biotic impact records

A total of 541 BIRs were extracted from historical sources between 1891 and 1903. The temporal distribution of spatially unique BIR observations (see methods) was strongly associated with drought severity in north-eastern (NE), south-eastern (SE) and western (W) continental areas (*SI Appendix*, Fig. S4A). Overall, BIRs occurred most frequently in very dry years, especially 1902 (66% and 49% of all records in NE and SE areas respectively) and 1891-92 (42% of records in W areas; *SI Appendix*, Fig. S2 and Fig. S4A) and very rarely if ever in wet years (NE = 0%; SE = 0.4%, W = 3.2% of records). The periods of very high BIR counts in the NE (1899-1903) and SE (1897-1902) are consistent with intensifying drought conditions during these years (*SI Appendix*, Fig. S2). On the other hand, the large number of counts in 1892 in the SE is anomalous based on the comparatively mild rainfall deficiencies occurring at this time (Fig. 2C).

We constructed a simple index (PR_R) to determine association between the timing of a BIR observation and the magnitude of the preceding cumulative 12-month rainfall relative to average (R_{12} ; %). Here, PR_R is the percentile rank of the R_{12} prior to the observation month of given BIR relative to all R_{12} values in the 1890-1903 study period ($n = 157$). Across all BIRs the mean PR_R of spatially unique records (see methods) was 15.6, or in the driest 16% of R_{12} intervals. Mean PR_R was also extremely low in the extreme years of 1902 (mean $PR_R = 5.3$ and 8.7 in the northeast and southeast) and 1891 (5.8 in western parts of the continent). The mean preceding cumulative 12-month rainfall across all BIRs ($R_{12} = -45.6\%$) was significantly ($P < 0.001$) below the null expectation of -4.2% (90% confidence interval = $-5.0, -3.3$), also confirming that BIRs were positively associated with extremely low preceding rainfall. Both are consistent with observer attribution of drought causality. However, the spatial distribution of PR_R values also reveal a cluster of higher values ($PR_R > 40$) across western New South Wales (NSW) (*SI Appendix*, Fig. S4B). As we discuss below, high PR_R values identify BIRs in which additional factors may influence the relationship between biotic impact and drought severity.

Impacts on animal and plant assemblages

Taxonomic and spatial aggregation of BIR data show that the FDP caused mortality and extreme stress in a minimum of 50 families (67 genera) of animals and plants (*SI Appendix*, Table S2) over at least 2.76×10^6 km² or 36% of the Australian continent (*SI Appendix*, Fig. S5), including in eight of Australia’s broad terrestrial ecoregions (46) and 45 of 89 large geographically distinct bioregions (47). Evidence of local (10^2 m-1 km scale), district (10^1 km) or regional (10^2 km) population collapse and mass

mortality involving hundreds to millions of individuals occurred across much of the continent, with all major animal and plant groups affected (*SI Appendix*, Table S3). To our knowledge the spatial and taxonomic breadth of these impacts exceeds that of any drought yet reported in the Australian or global ecological literature.

We built a co-occurrence network derived from aggregating BIRs into a continental-scale 100 km x 100 km co-occurrence grid (48, 49), which is shown in Fig. 24. Biogeographic patterns within the network helps us to detect geographical hotspots where taxa have been impacted by the drought. Analysis of this network reveals three important findings. First, the majority of BIRs were concentrated in drier subtropical, semi-arid and arid parts of the continent (mean annual temperature and precipitation of approximately 15-24°C and 150-800 mm respectively). All major plant and animal groups except for fish and trees display this basic pattern (*SI Appendix*, Fig. S5A-B), although the total area of impact (A_T) for fauna extended slightly further into mesic northern subtropical and southern temperate environments than plants ($A_T = 2.2 \times 10^6 \text{ km}^2$ vs. $1.8 \times 10^6 \text{ km}^2$; *SI Appendix*, Fig. S5). Few impacts were reported in more mesic eastern coastal and cool far southern temperate areas of the continent (Fig. 24), where rainfall deficiencies were less severe (Fig. 1), and also in the monsoonal north, which rainfall reconstructions (Fig. 1; 40) indicate did suffer periods of intense drought. These regions contain numerous centres of high biodiversity and paleo- and neo-endemism among major plant and animal lineages (50-52), which suggests that recent megadroughts continue to reinforce continental-scale phylogeographic patterns established during more arid phases of the Pleistocene (53-55).

Second, the high modularity of the network ($Q = 0.33$, $P = 0.02$) indicates strong spatial synchronicity among drought impacts on specific groups of taxa. Here (Fig. 24), mixed communities (red colouring), woodland, shrubland and grassland (green), bird and marsupial assemblages (orange) and fish and minor animal taxa (blue) broadly partition along the strong aridity gradient that extends from coastal through dry temperate and subtropical to semi-arid and finally arid central parts of the continent. Semi-arid to arid woody shrubland containing invasive populations of *Oryctolagus cuniculus* (European rabbit) form a discrete module (yellow; see below). The biome-scale geographic extent ($\geq 100,000 \text{ km}^2$) of each of these modules suggests that during megadroughts local refugia are likely to play a vital role in maintaining the viability of plant and animal populations, especially in more topographically homogeneous landscapes (56).

Third, the presence of impacted areas involving multiple biotic groups (i.e., non-hub connectors; 48) and local to regional population collapse or mass mortality (Fig. 2B-D) reveals the presence of two major subcontinental-scale impact hotspots during the FDP. The most distinct comprised $\approx 650,000 \text{ km}^2$ of south-eastern arid, semi-arid and mediterranean ecosystems that contained hyper-abundant populations of *O. cuniculus* (57) (*SI Appendix*, Fig. S5A). A trophic reconstruction of BIRs from this hotspot (Fig. 3) shows mortality among herbivore and primary producer guilds, including woody vegetation and herbs, *O. cuniculus*, and native herbivores (*Macropus* spp.). Here, impact records showed a lower level of association with rainfall deficiencies than elsewhere, with the mean PR_R of mortality records inside this hotspot being significantly higher than outside (back-transformed adjusted mean $PR_R = 16.8$ vs. 8.5; $F_{1,218} = 6.5$, $P = 0.01$), indicating relatively higher rainfall in the preceding 12 months (viz., driest 17% vs. 9% percentile). However, this mainly reflects differences among animal records (mean $PR_R = 21.6$ vs. 7.3; $P < 0.001$) and not plants (mean $PR_R = 9.3$ vs. 7.4; $P > 0.1$). Areas inside this hotspot also had a much higher frequency of impacts attributed to the synergistic effects of drought and overgrazing than outside (26% vs. 6%; *SI Appendix*, Fig. S4C).

These data support the conclusion that in this hotspot a classical boom-bust dynamic (58) developed during the FDP, which involved a recurring cycle of growth and subsequent collapse and near-extirpation of immense (e.g., $10^6 - 10^7$) rabbit populations (Fig. 2D; *SI Appendix*, Table S1.36-38) linked to food and water supply and competition with domestic livestock and native herbivores. In more arid areas, severe drought combined with overgrazing by rabbits and livestock resulted in regional-scale ($10^2 + \text{km}$) mass mortality and collapse of edible shrubs and grasses, especially *Atriplex*, *Maireana* and *Acacia* spp.. The wind erosion, soil drift and land degradation that followed is a clear case of ecosystem meltdown (59) caused by the interactive effects of an invasive species, extreme drought, predator control, and poor land management (33, 34, 57, 60).

A second area of especially high mortality occurred in central eastern to western Queensland, which experienced record rainfall deficits in 1901-02 (Fig. 1D, *SI Appendix*, Fig. S2). In this region a diverse native fauna including large terrestrial macropods, possums, the koala (*Phascolarctos cinereus*), emu (*Dromaius novaehollandiae*) and predatory birds (kookaburra and magpies) suffered apparent population collapse (Fig. 2A; *SI Appendix*, Table S1, S3). Mass mortality of vegetation occurred in stands of vegetation dominated by *Acacia*, *Callitris* and *Eucalyptus* tens to hundreds of kilometres wide (Fig. 2B; *SI Appendix*, Table S1.45-62). Again, the trophic pattern of these impacts and elsewhere (see Fig. 3) indicates a bottom-up, ecosystem-wide cascade of mortality focused on vegetation (62% of BIRs) and attenuating across herbivore (16%), omnivore (12%) and meso-predator (10%) guilds. Very few BIRs in this hotspot report overgrazing as a factor leading to biotic stress or mortality (*SI Appendix*, Fig. S4C), indicating that record rainfall deficiencies (up to 75-90% below average) were likely the primary driver of mortality. The main exception to this was the catastrophic decline of passerine and some predatory bird populations in central eastern Queensland, which was observationally linked in part to reduced availability of grasses, seeds and small prey (61), consistent with the response of avian assemblages to drought and livestock overgrazing elsewhere (62).

Mortality in a broad range of taxa was also reported across the western and central arid zone (Fig. 2), although since these areas were sparsely inhabited (see *SI Appendix*, Fig. S3), such events were probably underrepresented in our data. Less is known about these impacts, although mass vegetation mortality and severe wind erosion certainly occurred in some areas (e.g., the Gascoyne region of Western Australia; Fig. 2; *SI Appendix*, Fig. S3C), and native animal populations in the northern deserts (Fig. 2) were apparently so reduced that the food supply of local indigenous human populations was affected (*SI Appendix*, Table S1.24). Livestock grazing was not usually invoked as a causal factor (*SI Appendix*, Fig. S4C), although it probably, along with disease, played a contributing role in the sudden decline of native animal populations in the southwestern wheatbelt in 1898-1903 (63), and in vegetation loss across the Gascoyne.

Significant fish-kill events were noted in watercourses and lakes across parts of eastern Australia. Many involved the drying of ephemeral waterholes and lakes, but major inland and coastal rivers were also affected. The magnitude of mortality was often very large, as evidenced by a report that the first steamer to navigate the Darling River in western NSW after it resumed flowing in 1903 pushed up tons of dead fish (*SI Appendix*, Table S1.42). Extremely low water levels, contamination and eutrophication all probably contributed to mortality (*SI Appendix*, Table S1.5-9), as in more recent drought-driven fish kill events in the Murray-Darling basin (64).

The nature of historical observations, which are often qualitative or semi-quantitative, do not usually allow for a strict test of population or ecosystem-level change and recovery over time.

681 However, while acknowledging these limitations, a basic evaluation of the hypothesis that ecosystem collapse occurred across 682 parts of the continent during the FDP is possible. Consistent 683 with recent approaches (65-67), we use three general criteria 684 for identifying collapse: 1) a perceived abrupt or drastic decline 685 in biotic populations across multiple trophic levels relative to 686 pre-drought abundance, 2) a widespread area of impact, not 687 restricted to localised populations associated with local habitat 688 heterogeneity, and 3) decadal-scale (or longer) persistence of 689 these changes. Contemporary articles provide evidence for 1) and 690 2), while more recent publications referring to the FDP provide 691 data relevant to post-drought recovery (criterion 3). 692

693 Collectively, evidence for collapse of semi-arid and mediterranean 694 ecosystems in western NSW, southwest Qld and eastern 695 South Australia during the FDP is unequivocal. The mass mortality 696 of perennial vegetation (Fig. 2C) and associated loss of soil, 697 biodiversity and ecosystem function were clearly understood at 698 the time to be catastrophic (*SI Appendix*, Table S1: 74-76), and 699 prompted a review of degrading processes in the semi-arid Crown 700 Lands of western NSW in 1901 (68). These events are now seen as 701 the first major episode (33, 34) of a longer period of "dust bowl" 702 conditions and degradation in these regions, which lasted until the 703 mid-1940s (35), when rainfall improved. Only partial recovery has 704 occurred in most affected areas, despite significant improvements 705 to land management practices.

706 The collapse of bird, mammal, shrub and tree populations in 707 central eastern to western Queensland (Fig. 2B-C) are also 708 indicative of broad-scale ecosystem collapse. Reports at the time 709 indicate extensive mortality of trees and shrubs from the mesic 710 eastern ranges to the arid interior, many of which appeared to 711 result in the loss of entire cohorts for decades (e.g., *SI Appendix*, 712 Table S1: 77). Similarly, there is strong evidence that components 713 of the avifauna in central regions had become rare by 1902, with 714 many taking years or even decades to recover (61, 69; *SI Appendix*, 715 Table S1: 78). Local to regional extinctions of several species 716 have also been attributed to the event (e.g., 70). Due mainly 717 to remoteness and a low human population at the time, less is 718 known about the magnitude and permanence of FDP impacts in 719 central and western Australia. However, there is strong evidence 720 of severe, widespread decline among faunal assemblages, some 721 apparently permanent, and significant land degradation and soil 722 erosion (typical of ecosystem collapse in eastern Australia) in at 723 least some locations (*SI Appendix*, Table S1: 45).

724 **What trophic levels were mostly affected by FDP?**

725 In contrast to other studies (13), our data do not support 726 the hypothesis that drought impacts manifest predominantly at 727 higher trophic levels. Indeed, the near-absence of reported 728 mortality among large, conspicuous terrestrial apex and meso- 729 predators, such as dingoes (*Canis familiaris*), feral cats (*Felis 730 catus*), quolls (*Dasyurus* spp.), raptors and corvids, is striking 731 (Fig. 3). Newspaper accounts are unlikely to reflect unbiased 732 reporting of underlying ecological phenomena or events, and 733 here we cannot rule out the possibility that mortality in these 734 groups was under-reported due to negative social perceptions 735 associated with livestock predation. Indeed, many species, and 736 dingoes particularly, were subjected to population control via 737 bounties and other programs throughout the FDP (60). It is also 738 possible that low reporting rates in these groups reflect lower 739 overall population sizes compared to those in lower trophic levels, 740 or perhaps that drought impacts manifest in predator guilds 741 through reduced fecundity instead of mortality. 742

743 On the other hand, numerous accounts attest to the abundance 744 of many predatory species at the time. For example, dingo 745 numbers in parts of inland Australia were reported to be very 746 high due to the availability of rabbits (71), and corvids (i.e., 747 ravens and crows), which attack the eyes and soft tissues of weak 748 livestock, were clearly abundant throughout rabbit-infested and

749 sheep-raising areas. More generally, there is strong evidence that 750 a major pulse in availability of carrion, drought-weakened native 751 animals, rabbits and livestock supported predator numbers in 752 drought-affected areas (*SI Appendix*, Table S1.63-73), many of 753 which are also facultative scavengers. The lack of mortality among 754 reptiles (especially large taxa such as monitors) may reflect their 755 relatively low metabolic rate per unit body weight and ability to 756 survive for weeks or months without food or water (72, 73), but, 757 again, at least some were significant predators of rabbits (e.g., 758 monitors) and livestock or scavenged carrion (*SI Appendix*, Table 759 S1).

760 Our data also show that vegetation impacts were concentrated 761 in dry terrestrial ecosystems (91% of BIRs) and were especially 762 prevalent on ridges, hills, and sloping terrain with shallow 763 soils (e.g., *SI Appendix*, Table S1.59). This pattern of topographic 764 development of drought symptoms is consistent with the typical 765 expansion of soil drought from rainfall-dependent habitats 766 of higher relief to lower drainage areas as rainfall deficiencies 767 progress (56), but strikingly different to that observed during the 768 Millennium Drought, which caused extensive mortality of riverine 769 floodplain and wetland species across south-eastern Australia 770 (74). These differences are probably linked to the more recent 771 development of hyper-drought associated with anthropogenic 772 water extraction, which now poses a significant additional threat 773 to Australian biota during periods of low rainfall (75, 76). 774

775 **Temporal development of ecosystem impacts**

776 The strongly nonlinear accumulation of mortality among 777 birds, mammals and woody vegetation (Fig. 4A-B) indicate that 778 populations of these taxa are prone to sudden drought-induced 779 collapse rather than gradual decline (38, 56). Spatial interpolation 780 of pre-impact cumulative rainfall data reveals that this typically 781 occurs after 2-4 years of continuous drought (drought duration, 782 D_{CON} ; Fig. 1E) during which cumulative rainfall deficiencies 783 (drought magnitude, R_{CON}) total ≈ 80 -200% of annual mean 784 precipitation (i.e., $P_A \approx 0.5$ - $0.6P_{AV}$ for the period; Fig. 1F), with 785 the longest and deepest droughts prior to mortality occurring 786 in arid, central-northern parts of the continent. Similarly, linear 787 models show that D_{CON} and R_{CON} were both inversely related to 788 mean annual precipitation (P_{AV}) at the BIR impact site ($P < 0.01$; 789 *SI Appendix*, Table S4) with D_{CON} and R_{CON} varying from ≈ 29 790 months and 80% of P_{AV} in high rainfall areas ($P_{AV} = 1000$ mm) 791 to 36 months and 120% of P_{AV} in semi-arid ecosystems ($P_{AV} = 792 430$ mm; *SI Appendix*, Table S4). These data indicate a higher tolerance 793 among arid-zone species for intense, prolonged drought 794 compared with those found in wetter areas around the continental 795 periphery (Fig. 1E-F), consistent with observed phytogeographic 796 patterns in drought tolerance (77).

797 In contrast, there was only weak evidence that D_{CON} and 798 R_{CON} were lower for native terrestrial animals than for plants (i.e., 799 generally < 10 -20%; *SI Appendix*, Table S4), indicating that during 800 the FDP these groups tended to undergo mortality following 801 rainfall deficiencies of similar duration and magnitude. A possible 802 exception to this occurred in more peripheral, mesic temperate 803 and subtropical areas, where animal but not plant mortality was 804 recorded (Fig. 2). However, sample sizes in these habitats were 805 small and associated models significantly affected by spatial 806 autocorrelation (c.f., non-spatial and spatial models; *SI Appendix*, 807 Table S4), and so a clear understanding of associated broad 808 taxonomic differences in drought impacts awaits further study. 809 Similarly, differences among specific plant or animal groups were 810 also minor (*SI Appendix*, Table S5), except perhaps for fish, which 811 appeared sensitive to the rapid drying of ephemeral waterbodies, 812 and rabbits (see below).

813 Temporal analysis of drought magnitude (depth)-duration 814 curves data also reveals a pattern of nonlinear intensification of 815 continuous rainfall deficits prior to mortality of native plants and 816 animals (Fig. 5A-D). These rise from 15-30% below normal in

years 2-4 to $\approx 50\%$ in months 7-12 and finally to $\approx 70\%$ in the last three preceding months (Fig. 5B,D). This terminal period of sharply intensifying rainfall deficits contained, on average, 5-8 consecutive months of below average rainfall immediately prior to mortality (D_{CDM} ; Fig. 5A-D; *SI Appendix*, Table S4). For a substantial proportion of BIRs, the period of continuous annual rainfall deficiencies (D_{CON}) prior to mortality occurred at the end of period of semi-continuous drought (D_{SCO}) 5-8 years long during which mean cumulative rainfall deficits reached 150% of P_{AV} or more (Fig. 5A-D). This mainly reflects the high number of BIRs observed during 1902 across eastern Australia following seven to eight prior years of generally below average rainfall (i.e., since 1895; Figs. 4-5). In northern parts of the continent (-16 to -26°S) impacts occurred at a similar frequency throughout the year (Jun-Aug = 29%, Sep-Nov = 29%, Dec-Feb = 21%, Apr-May = 20% of records; $\chi^2_{(3)} = 1.89$, $P > 0.05$). In contrast, BIRs in southern regions (-26 to -42°S ; excluding rabbits, see below) were most frequent in summer (Dec-Feb = 27%) and autumn (Apr-May = 34%) and least in winter (21%) and spring (18%; $\chi^2_{(3)} = 14.3$, $P < 0.01$). This is consistent with the summer-dominated nature of rainfall deficiencies during the FDP in this region (40).

Collectively, these data indicate that ecosystems exposed to rapid drought intensification following a semi-to quasi-decadal period of persistently accumulating rainfall deficits are at high risk of collapse. Indeed, megadroughts may differ in a fundamental way from droughts of shorter (e.g., annual) duration, with chronic, multi-year rainfall deficiencies allowing the development of meso-scale hydrological and land-cover feedback mechanisms (9) that ultimately render populations and ecosystems more sensitive to intensification of abiotic stress during subsequent extreme years. Examples noted by observers during the FDP include the decline of food resources, development of extreme temperatures and plant-soil feedback loops caused by the progressive loss of perennial vegetation cover, and the increasingly concentrated impacts of native animals and livestock in refugial waterholes of drying river systems. Such processes indicate that megadrought-landscape interactions exhibit many characteristics of complex adaptive systems, a concept that has proved fruitful in the investigation of other ecological and social phenomena (78).

In our study, habitats containing hyper-abundant rabbit populations exhibited a different pattern of impact than elsewhere. Here, mortality profiles for most native animal groups, *O. cuniculus* and woody shrubs (which are herbivorised by rabbits during drought) show punctuated development, beginning after only one year of low-intensity drought (1892; Fig. 4C), consistent with a lower degree of association with severe rainfall deficiencies (*SI Appendix*, Fig. S4B). Only trees predominantly suffered mortality in the latest stages of the drought (Fig. 4C). Linear models also support the view that severe rabbit infestation reduced mean D_{CON} and R_{CON} for some co-occurring native plant and animal groups (by 10-12 months and 30-45% respectively) compared with non- or less-infested areas (Fig. 1E-F; *SI Appendix*, Tables S4-5), although spatial models indicate that the impact of other variables (e.g., vegetation, soil types, stocking regimes) cannot be ruled out as contributing to these differences. The frequency of rabbit mortality BIRs in this region was least during winter (Jun-Aug = 5%) and spring (Sep-Nov = 14%) and highest in summer (Dec-Feb = 26%) and autumn (Mar-May = 56%; $\chi^2_{(3)} = 25.6$, $P < 0.001$), suggesting that rabbit populations, which grew during the very wet years of 1889-1891 (and probably 1894) to levels vastly in excess of the long-term carrying capacity, collapsed (in 1892-3 and 1895-6; Fig. 4C) following progressive summer-autumn drying and a lack of cool-season herbage growth on which they depend (57).

More generally, these data indicate that assemblages dominated by a hyperabundant, highly fecund herbivore guild are extremely sensitive to drought-induced meltdown, as in other

systems lacking robust top-down control (59). This suggests that the progressive trophic downgrading of ecosystems under modern anthropogenic land use regimes globally (79) now poses a significant additional risk to biodiversity in megadrought-prone areas.

CONCLUSIONS

This study shows, for the first time, that it is possible to reconstruct the spatial, taxonomic, trophic and demographic impacts of historical droughts on biota using analysis of data compiled from contemporary written accounts. The unprecedented geographic extent, taxonomic breadth and temporal distribution of population mortality and ecosystem collapse that occurred during the Australian Federation Drought Period show that extreme, semi-to decadal megadrought events can have serious demographic and biogeographic consequences for plant and animal populations on a pan-continental scale. These include rapid, broad scale mass biotic mortality and collapse of both agriculturally modified and natural ecosystems. Importantly, our study also indicates a clear bottom-up effect where lower trophic levels (e.g. plants and herbivores), and not higher trophic levels, can be most affected by decadal droughts of this magnitude and duration.

The longest and most intense droughts in eastern Australia (e.g., Federation, WWII and Millennium droughts) can be largely explained by the modular states of a relatively small set of underlying climatological drivers (e.g., ENSO, IOD, IPO and the southern annular mode, SAM), albeit manifesting with different spatial and seasonal footprints (37, 40, 43). The periodic recurrence of such events during the 20th century, combined with an apparent shift towards reduced moisture availability across eastern Australia since the mid-19th century (40, 80) and the return of generally drier conditions, rising temperatures and reduced water availability and runoff in parts of Australia over the past two decades (81-83) all suggest that the likelihood of a similar, or possibly even more extreme bioclimatic event occurring in the future is high. More generally, our study shows that an increase in the frequency and severity of megadroughts clearly poses a serious threat to global biodiversity conservation, especially in trophically downgraded and overgrazed ecosystems.

MATERIALS AND METHODS

Database development

The primary source of data consisted of digitised newspaper articles contained in the National Library of Australia's Trove platform (www.trove.nla.gov.au). We conducted a series of searches of Trove that contained the terms *drought*, *dead* OR *dying*, followed by one of 296 terms or phrases relating to geographic locations or features across all six Australian states and two territories (mainly towns, rivers, major geographic regions, and telegraph or private stations) or broad vegetation groups, plant genera, and colloquial plant names. Based on these searches we screened >35,000 relevant newspaper articles (and a small number of related explorer journals and other sources) for those documenting either an impact of drought on plants or non-domestic animals (biotic impact records; BIRs) or a significant event or attribute of drought-affected areas (drought impact record; DIR). A total of 1748 DIRs and 541 BIRs with suitable geographic information were identified.

For BIRs we then extracted information for the following data fields (e.g., *SI Appendix*, Fig. S6): 1) estimated observation date (usually last full calendar month before each report's publication date), 2) broad morpho-taxonomic group (8 animal and 6 plant groups, see *SI Appendix*, Table S2), 3) taxonomic identity (family, genus or species), 4) impact type (mortality, stress or absence), 5) geolocation (latitude, longitude), 6) estimated extent of impact (circle of radius r in km), 7) IBRA bioregion (47), 8) ecosystem type (aquatic, terrestrial, mixed, other), 9) presence of livestock-related factors contributing to the stated impact, 10) location relative to area of severe rabbit infestation in 1891 (RIA; based on 57), and 11) evidence of population collapse or mass mortality. This was classified into one of four categories: 1) extirpation of population (E), 2) near-extirpation (NE), 3) mass mortality based on area (Ma), and 4) mass mortality based on numerical estimate (Mn). Categories 1-3 were then classified as local (hundreds of m to < 10km radius), district (10 - <100 km radius), or regional (>100 km radius). We classified the Mn category into 1) hundreds to thousands (10^2 - 10^3), 2) tens to hundreds of thousands (10^4 - 10^5), and 3) millions or more (10^6 +).

For DIRs we estimated the geolocations of observations of 1) dust storms, sand storms and drift, 2) livestock death, 3) hydrological impacts (low

953 water levels in rivers, lakes, etc.), 4) bare understory and 5) general drought
954 conditions. Further methodological details are provided in the *SI Appendix*
955 *SI Text*.

Rainfall data and association with BIRs

956 Rainfall data were obtained from the public SILO enhanced climate
957 database (daily rainfall 1889-) hosted by the Science Delivery Division of
958 the Department of Science, Information Technology and Innovation (DSIT)
959 found at <https://legacy.longpaddock.qld.gov.au/silo/>. We then determined,
960 for Australia, 1) mean annual precipitation (P_{AV} ; 1889-2015), 2) total annual
961 precipitation P (all years 1890-1903), 3) percentile annual P , 4) total P as a
962 percentage of the mean, and 5) lowest annual P as total and as percentage
963 of P_{AV} . We compared numbers of BIRs across "wet" years and "other" years in
964 three continental regions (western, north-eastern and south-eastern; *SI Ap-*
965 *pendix*, Fig S4A) using simple χ^2 contingency analyses. To avoid dependency
966 among data points we included only BIRs with unique spatial coordinates
967 and observation dates ($n = 339$) in these analyses.

968 We used analysis of cumulative sum of monthly rainfall residuals (R)
969 to quantify the depth and magnitude of drought for each BIR between
970 the last full calendar month before each report date and January 1889.
971 We determined the preceding duration (in months) of 1) consecutive below
972 average monthly rainfall (D_{CDM}), 2) continuous drought (D_{CON} ; no unbroken
973 12-month period of above average rainfall), and 3) semicontinuous drought
974 (D_{SCO} ; no unbroken 24-month period above average rainfall). Drought mag-
975 nitude after D_{CON} was defined as the total cumulative rainfall residual over
976 the period (R_{CON} ; percentage of mean annual rainfall). A worked example is
977 provided in *SI Appendix* Fig. S7.

978 We also developed a percentile-based index, (PR_R), to determine the
979 strength of association between the magnitude of cumulative 12-month
980 rainfall (R_{12} , percentage deviation relative to the 1889-2015 average) and the
981 estimated observation date of a given biotic impact record. We determined
982 PR_R as the percentile rank of R_{12} prior to the BIR observation date relative
983 to all cumulative 12-month rainfall intervals between Jan-Dec 1890 and
984 Jan-Dec 1903 ($n = 157$; details provided in *SI Appendix* *SI Text*). PR_R was
985 also compared (using BIRs with unique spatial coordinates) both within
986 and outside the primary rabbit infested area (RIA) using generalised least

987 squares linear model analysis. Spatial autocorrelation was accounted for by
988 incorporating an exponential correlation structure which had the lowest
989 Akaike information criterion (AIC) among tested structures (see *SI Appendix*
990 *SI Text*). We also tested whether the mean R_{12} across all BIRs differed from a
991 statistical null model using the standard z statistic.

992 We also compared the frequency of BIRs citing livestock
993 impact across rabbit-infested and other areas, and across winter, spring,
994 summer and autumn seasons in the RIA and other northern and southern
995 regions using simple χ^2 contingency analyses.

Density and network analyses, spatial interpolation, and statistical modelling

996 Kernel density analysis with a bandwidth (H) of 5 was performed on
997 geocoded mortality records for key animal and plant groups using the R pack-
998 age GISTools (v. 0.7-4). Modularity network analysis of the network based on
999 spatial co-occurrence of broad impacted plant and animal groups was con-
1000 ducted based on stochastic simulated annealing algorithm using the package
1001 netcarto (see 48 for details). Significance of the observed modularity was
1002 tested using a randomisation test with $N=1000$ replicates implemented in the
1003 netcarto command line program ([https://bitbucket.org/amarallab/network-](https://bitbucket.org/amarallab/network-cartography)
1004 [cartography](https://bitbucket.org/amarallab/network-cartography)). Spatial interpolation of D_{CON} and R_{CON} was performed using
1005 variogram fitting and ordinary kriging approaches (84, 85) and relevant
1006 functions in R packages gstat v. 1.1-6, sp v. 1.2-4 and raster v. 2.5-8.

1007 We determined mean values of D_{CDM} , D_{CON} , R_{CON} and D_{SCO} prior to mor-
1008 tality for key animal and plant groups. Each parameter was then modelled
1009 using generalised least squares linear model analysis with broad biotic group
1010 (native animals vs. plants), RIA, and mean site precipitation as predictor
1011 variables. Three model types were used: 1) full, non-spatial containing all
1012 observations (FNS), 2) full, but incorporating spatial autocorrelation (FS),
1013 and 3) restricted non-spatial model using only BIRs with unique geolocations
1014 (RNS). For FS models we tested five autocorrelation structures (exponential,
1015 Gaussian, linear spatial, rational quadratic and spherical) and selected the
1016 model with the lowest Akaike information criterion (AIC). Model param-
1017 eters including adjusted means and tests of main effects were constructed
1018 and extracted using R packages stats v. 3.4.2 and nlme v. 3.1-139. Further
1019 information is provided in the *SI Appendix* *SI Text*.

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