ECOSYSTEM ENGINEERS

Equids engineer desert water availability

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Megafauna play important roles in the biosphere, yet little is known about how they shape dryland ecosystems. We report on an overlooked form of ecosystem engineering by donkeys and horses. In the deserts of North America, digging of ≤2-meter wells to groundwater by feral equids increased the density of water features, reduced distances between waters, and, at times, provided the only water present. Vertebrate richness and activity were higher at equid wells than at adjacent dry sites, and, by mimicking flood disturbance, equid wells became nurseries for riparian trees. Our results suggest that equids, even those that are introduced or feral, are able to buffer water availability, which may increase resilience to ongoing human-caused aridification.

Terrestrial large herbivores (henceforth megafauna) have undergone extensive extinctions and range contractions beginning during the late Pleistocene (100,000 to 12,000 years before the present) and continuing today (*1*, *2*). Although climate change at the end of the last glacial maxima may have played a contributing role (*3*), emerging consensus indicates that most prehistoric losses were driven by human activity (*1*, *2*). In tropical and temperate ecosystems, megafauna declines are linked to the formation of closed woodlands, increased wildfire, and reduced dispersal of large-seeded plants (*4*). Less is known, however, about how megafauna may have shaped dryland ecosystems, which comprise a third of Earth's surface (*5*).

Water is the main limiting resource in dryland ecosystems. It determines species composition, food web structure, and vegetation dynamics (*6*, *7*). Yet, the capacity for animals to enhance water availability by exposing subsurface water has received little attention. Wild donkeys (*Equus africanus asinus*) and horses (*E. ferus caballus*), as well as most other equids and all elephant species, regularly dig wells of up to 2 m in depth (Fig. 1, A to D; see table S1 for review). We evaluated well digging and its associated ecosystem effects in a North American system where equids have established feral populations.

We surveyed four Sonoran Desert groundwater-fed streams every 2 to 4 weeks over three summers (table S2). At each site we mapped "background" (e.g., already present) and "equid well" water [data S1 and (*8*)]. Streams were 7 to 32 km apart and were ~300 to 1800 m long (table S2). Like many desert streams, site hydrology was highly variable, as was the relative contribution of equid wells. Equid wells were particularly important to provisioning water in midsummer as temperatures increased and water tables receded (Fig. 1E). At one fully intermittent stream that lost all background water, equid wells provided 100% of surface water. Even at sites which remained perennial (background water retained at headwater springs), wells provided up to 74% of surface water by accessing the water table in dry reaches (Fig. 1E). Likewise, equid wells increased water density relative to background water by an average of 332% (SD = 416%) and by as much as 1450% (Fig. 1F).

Isolated water features can be areas of heightened antagonistic interactions among wildlife, including predation, disease transmission, competition, and herbivory (*9*–*11*). Equid wells strongly reduced the isolation of water features, reducing average nearest-neighbor distances between water features by an average of 65% (an 843-m reduction, SD = 798 m) and by as much as 99% (a 2.3-km reduction) (Fig. 1G). Thus, in addition to increasing the total amount of water available (Fig. 1E), we argue that equid wells may relax the potential for strong antagonistic interactions and reduce the distances that animals must travel to reach water.

To understand whether equid wells have value for other species, we deployed camera traps at five sites in the Sonoran and Mojave Deserts, sampling over 3258 trap nights (table S2). We calculated daily species richness and the duration and frequency of visits as measures of vertebrate activity, which we compared between equid wells, background waters, and adjacent dry controls. We excluded the equids themselves and species <100 g to control for poor detection probabilities for small animals.

Overall, we detected 59 vertebrate species at equid wells, of which 57 were recorded drinking [Fig. 2, A to D; table S3; data S2; and (*8*)]. Daily species richness was 64 and 51% higher on average at equid wells and background waters, respectively, than at dry controls (post hoc test: t ratio = −7.6 and −10.3, $p < 0.0001$; Fig. 2E). Likewise, visit duration was 274 and 620% longer at equid wells and background waters than at dry controls (t ratio = −7.8 and −9.7, $p < 0.0001$; Fig. 2F), and visit frequency was 91 and 60% higher on average (t ratio = −11.3 and −16.32, $p < 0.0001$; Fig. 2G). These effects increased with temperature at both water types (Fig. 2G; see table S4 for omnibus test results). There was no difference between equid wells and background waters in terms of richness (post hoc test: t ratio = −1.6, $p = 0.25$) or duration (t ratio = 1.9, $p = 0.14$), but background waters had higher visit frequencies than equid well waters (t ratio = −3.4, $p = 0.002$).

Responses were similar across vertebrate body sizes (fig. S1), and species composition did not vary between resource types [permutational multivariate analysis of variance (PERMANOVA): $F = 0.9$, $p = 0.7$; fig. S2]. Domestic cattle activity showed a similar pattern but was analyzed separately, because cattle densities were determined by humans and fluctuated during the study period (fig. S3 and table S4).

Some of the species detected drinking from equid wells are free-water dependent, such as mule deer (*Odocoileus hemionus*), whose summer distribution is shaped by surface water [table S3 and (*12*)]. Other desert species, such as javelina (*Pecari tajacu*), are capable of extracting sufficient water from food and thus can be free-water independent (table S3). However, this requires increased food consumption rates, especially at high temperatures (*13*). By maintaining water availability, equid wells may both enable the persistence of free-water–dependent species and prevent transitions from "food web" to "water web," thereby reducing the potential for oscillatory population dynamics (*14*).

Well digging also influences vegetation. On a dammed perennial Sonoran Desert river, abandoned equid wells host numerous riparian trees (primarily *Populus fremontii* and *Salix gooddingii*; Fig. 3A), members of a small-seeded, fast-growing, flood-adapted functional group whose germination requires moist substrate without competing vegetation and whose conservation is considered a regional and global priority (*7*, *15*, *16*). We collected data on germination and establishment of these trees across available habitats and found higher seedling density in equid wells than in adjacent moist riverbank zones (89% of seedlings, Wilcoxon signed rank test: $W = 109$, $p = 0.007$; Fig. 3B), a difference which persisted after typical summer mortalities [generalized linear mixed-effect model: $\chi^2 = 54.6$, $p < 0.0001$; Fig. 3B, data S2, and (*8*)].

Although riverbanks provided the moist substrate necessary for germination, they were

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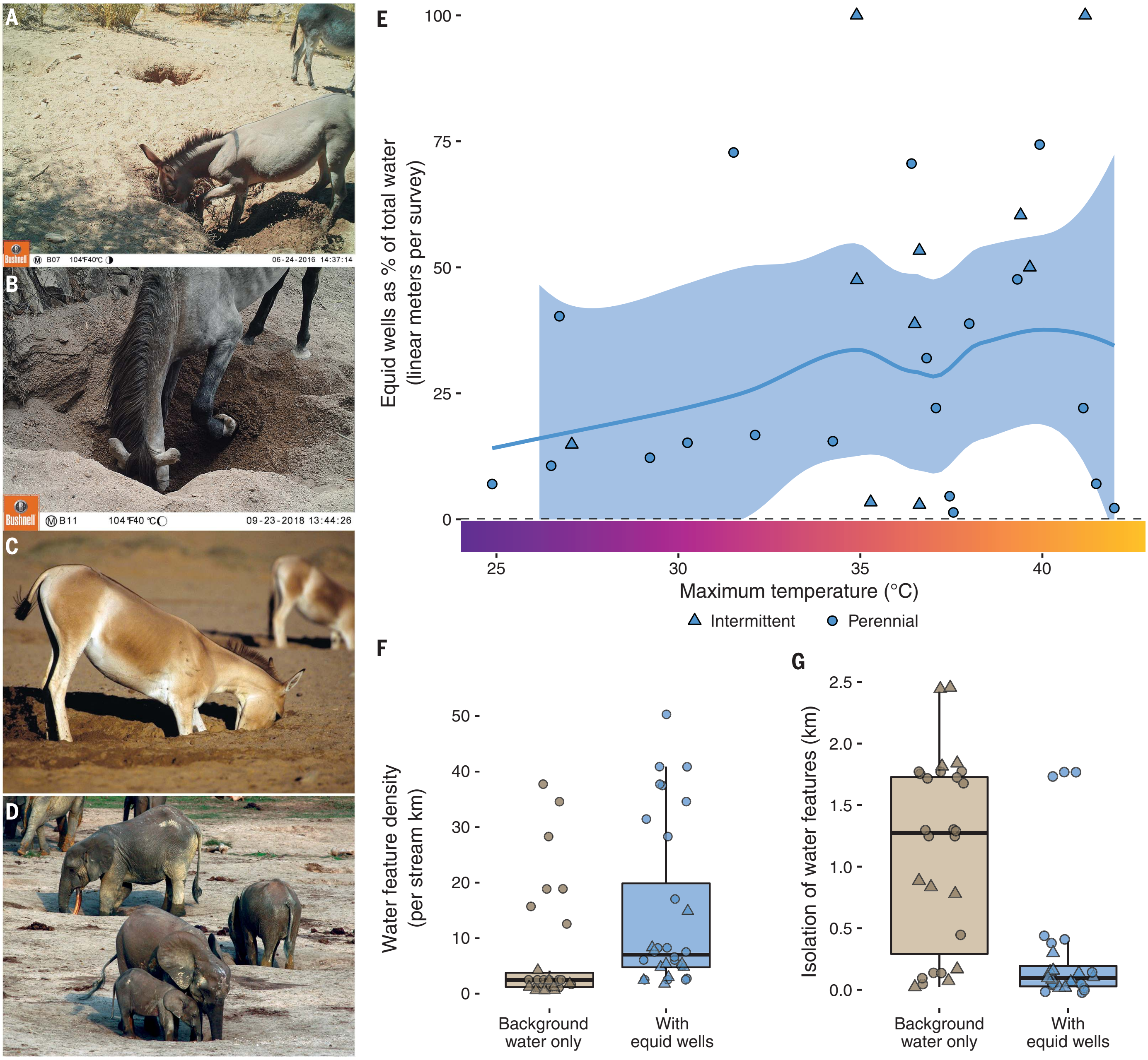

Fig. 1. Well digging increases water availability in desert streams. (**A** to **D**) Well digging by (A) wild donkeys (*E. africanus asinus*) and (B) wild horses (*E. ferus caballus*) in the Sonoran Desert, USA; (C) khulan (*Equus hemionus*) in Mongolia; and (D) African elephants (*Loxodonta africana*). (**E**) The contribution of equid wells increases with temperature. Each point shows the percentage of total water provided by equid wells at each survey and site, measured in meters parallel to the direction of stream flow. Line and fill show loess regression and confidence intervals. Maximum daily temperatures were obtained from PRISM (*23*). (**F**) Equid wells increase the density of water features (per km). (**G**) Equid wells reduce the isolation of water features, measured as average nearest-neighbor distances between waters. For (F) and (G), boxplots indicate median (central line), interquartile range (bottom and top of box), and minimum and maximum values excluding outliers (lines). [Photo credits: E.J.L. [(A) and (B)], P. Kaczensky (C), and R. Ruggiero (D)]

significantly more herbaceous ($p < 0.0001$; fig. S4A), and seedling density showed a strong negative relationship to herbaceous cover ($p < 0.0001$; fig. S4B). This suggests that riverbanks are less competitively suitable for these small-seeded pioneer trees, a relationship shown in previous work (*7*, *16*). Thus, by exposing moist substrate free of competing herbaceous vegetation, we argue that equid wells can serve as flood-mimicking nurseries. The importance of megafauna for the dispersal of large-seeded, high–wood density functional groups is well known (*4*), yet facilitation of pioneer trees through megafauna disturbance is less recognized. Further research is necessary to understand how these nurseries may contribute to long-term riparian forest dynamics.

Equid well digging was limited by water-table depth, with equids unlikely to dig deeper than 2 m (table S1). Well digging was also constrained by substrate, primarily occurring in flood-disturbed systems of loose sand and gravel ($p < 0.0001$; fig. S5). The ecological relevance of this behavior also appears to be shaped by the availability of alternative water sources in the broader landscape and by stream intermittency. Intermittent streams, the most common stream type across nearly half of Earth (*17*), were where equid wells had the strongest effects on water availability. Stream intermittency is projected to increase as currently perennial streams lose yearlong flows (*18*) and as drylands expand [Fig. 4 and (*19*)] as result of groundwater mining, agriculture, and climate change (*17*). These reductions in water availability, coupled with rising temperatures, are projected to have strong effects on biodiversity and ecosystem function

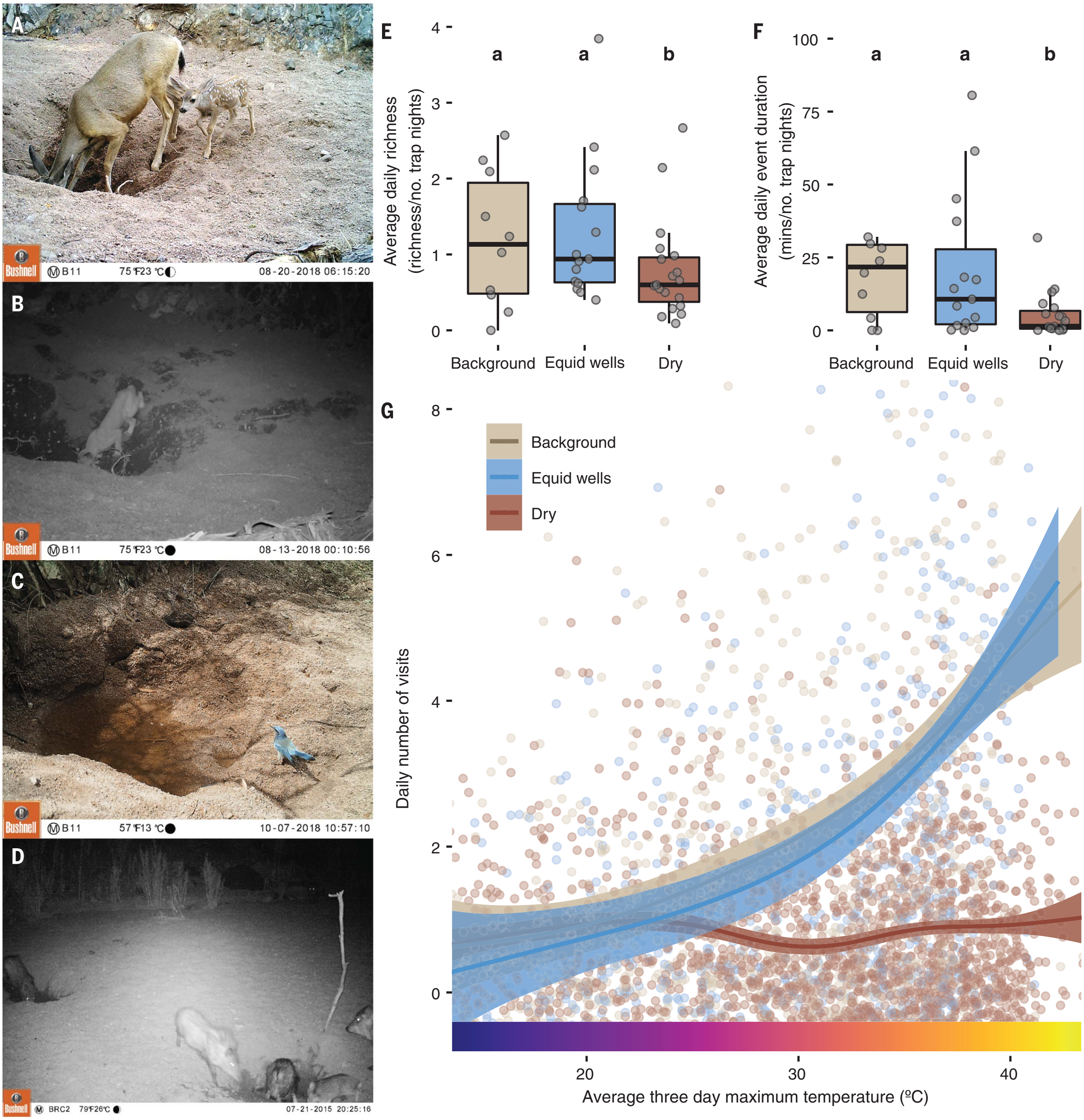

Fig. 2. Use of equid wells by vertebrates. (**A** to **D**) Use of equid wells by select species: (A) mule deer (*O. hemionus*), (B) bobcat (*Lynx rufus*), (C) Woodhouse's scrub-jay (*Aphelocoma woodhouseii*), and (D) javelina (*P. tajacu*). (**E** and **F**) (E) Average daily species richness and (F) daily visit duration, by camera station, relativized by number of trap nights. Letters (a and b) indicate significance groupings ($p < 0.001$). Boxplots indicate median (central line), interquartile range (bottom and top of box), and minimum and maximum values excluding outliers (lines). (**G**) Daily visit frequency by average 3-day maximum temperature (°C). Points indicate days. Line and fill illustrate generalized linear model of relationship between temperature and visit frequency. Equids and vertebrates <100 g (e.g., small passerines and mice) were excluded from analyses, the latter because of poor detection probabilities for small species. Domestic cattle were analyzed separately because of high, but inconsistent, stocking rates throughout the season (fig. S1). [Photo credits: E.J.L. [(A) to (D)]

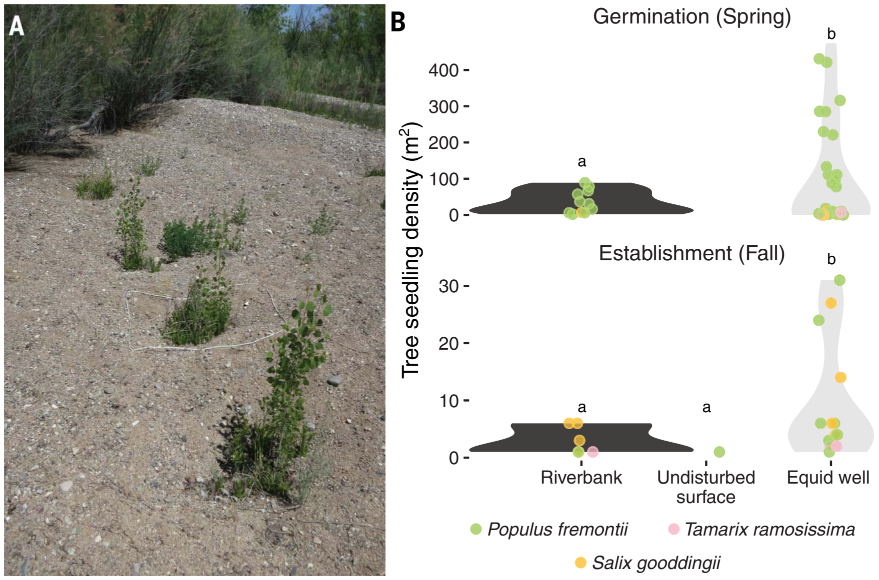

Fig. 3. Equid wells function as germination nurseries for riparian pioneer trees. (**A**) Fremont cottonwood (*P. fremontii*) in a series of abandoned equid wells. (**B**) Seedling density between riverbank germination zones, undisturbed surfaces, and equid wells. Filled intervals behind points indicate density distribution of seedlings. Letters (a and b) indicate significance groupings ($p < 0.01$). [Photo credit: E.J.L.]

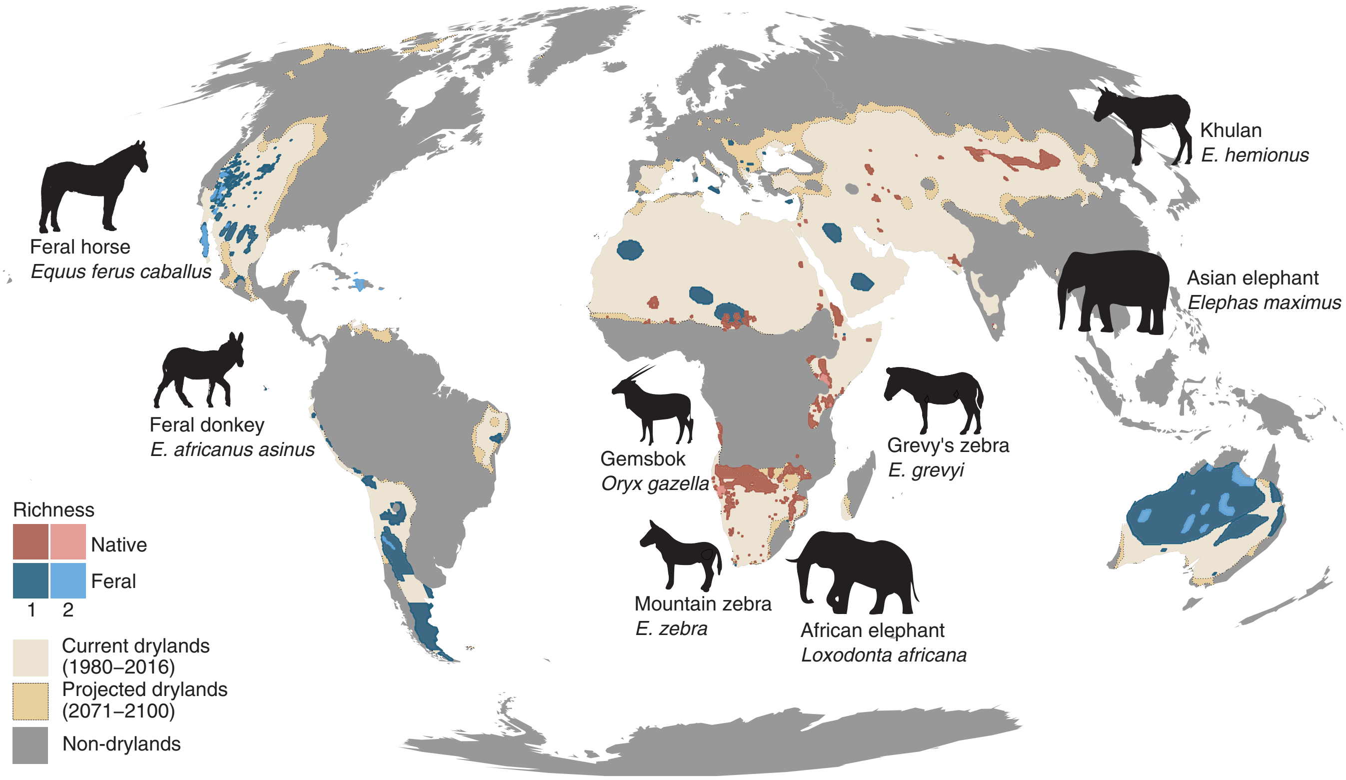

Fig. 4. Well-digging megafauna contribute the capacity to buffer water availability across many drylands. Species richness (number of species) of native and introduced megafauna known to regularly dig wells ≥0.5 m in depth overlaid on current (beige) and projected (yellow ochre) global drylands [semi-arid plus arid Köppen-Geiger climate zones (*19*)]. Gray fill indicates non-drylands. Feral equids (blue) have been documented regularly digging wells in suitable terrain in North America and Australia [table S1; ranges from (*24*, *25*)]. Projected dryland expansion is based on business-as-usual emissions [Representative Concentration Pathway (RCP) 8.5].

(*6*). Our results suggest that equids and other well-digging megafauna have the potential to mitigate these changes, whether native or introduced (Fig. 4).

Recent and ancient extinctions and range contractions of megafauna, and the loss of their distinct ecological functions, has led to highly modified modern landscapes (*4*). Although introduced megafauna have primarily been studied as threats to conservation goals (*20*), growing evidence suggests that they present a countercurrent to ancient losses (*21*) and may replace lost ecological functions (*22*). Specifically, we show that feral equids can increase water availability in drylands, with associated effects on a variety of species and ecosystem processes. We suggest that well digging by feral equids may replace a function lost with the extinctions of large vertebrates across the world's drylands.

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ACKNOWLEDGMENTS

This work is dedicated to the memory of co-author Nathan C. Nieto, a dear friend and mentor. We thank M. Schlaepfer, M. Davis, P. B. Shafroth, D. C. Allen, H. Greene, and five anonymous reviewers for their constructive feedback. We thank M. Lundgren, C. Lundgren, A. Willis, R. O'Leary, C. Alexander, A. Varela, J. Givens, M. Thuan Nhut Cao, M. Riffle, M. Clyne, A. Riley, and E. Anderson for their assistance with fieldwork. **Funding:** This work was supported through crowdfunding and two Arizona State University fieldwork grants. **Author contributions:** All authors conceptualized and designed the research. E.J.L. collected and analyzed the data. All authors contributed to the interpretation of the data and writing of the manuscript. **Competing interests:** The authors declare no competing interests. **Data and materials availability:** All data and scripts used for analyses are available on Figshare (*8*).

SUPPLEMENTARY MATERIALS

science.sciencemag.org/content/372/6541/491/suppl/DC1
Materials and Methods
Figs. S1 to S5
Tables S1 to S4
References (*26–74*)
Data S1 and S2

5 July 2020; resubmitted 27 October 2020
Accepted 25 March 2021
10.1126/science.abd6775

Science

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Science **372** (6541), 491-495.
DOI: 10.1126/science.abd6775

Digging for water

Water is scarce in dryland ecosystems. Some larger animals in these regions dig wells that may provide water to other species. This behavior may have been common among megafauna that are now extinct, especially in North and South America, where megafaunal extinctions were the most severe. Lundgren *et al.* tested whether feral equids (horses and donkeys) reintroduced to desert regions in the North American southwest dig wells that provide ecosystem-level benefits. They found that equid-dug wells increased water availability, were used by a large number of species, and decreased distance between water sources. Abandoned wells also led to increased germination in key riparian tree species. Such equid-dug wells improve water availability, perhaps replacing a lost megafaunal function.

Science, this issue p. 491

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