Biodiversity and ecological function in an age of biotic redistribution

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Thesis submitted in fulfilment of the requirements for
the degree of Doctor of Philosophy

under the supervision of Daniel Ramp and Arian Wallach

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Certificate of Original Authorship

I, Erick Joseph Lundgren, declare that this thesis is submitted in fulfilment of the requirements of the award of Doctor of Philosophy, in the School of Life Sciences, Science at the University of Technology Sydney.

This thesis is wholly my own work unless otherwise referenced or acknowledged. In addition, I certify that all information sources and literature used are indicated in the thesis.

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Thesis Abstract

The human-assisted dispersal of species through introductions is a form of anthropogenic change that has received significant attention in conservation biology research and in conservation policy. Until recently, introduced biodiversity has been considered by most to be synonymous with anthropogenic harm. However, the empirical premises supporting this have been criticized as evidence has falsified or qualified the claims about introduced species as biodiversity threats and as the underlying normative value of *nativism* has come increasingly into focus. This thesis asks how suspending the value of nativism might alter how we understand biodiversity change, the ecology of introduced species, and conservation policy. This thesis focuses primarily on introduced herbivores, a globally endangered functional group that has experienced significant human-caused declines since prehistoric extinctions in the Late Pleistocene.

I begin by analyzing how the twin anthropogenic forces of extinction and introduction have shaped herbivore functional diversity since the Late Pleistocene, finding that introduced herbivores restore many lost ecological functions and make assemblages more similar to the pre-extinction past than native ones. I then describe ecosystem engineering by introduced equids, who dig wells to groundwater in desert drainages. In doing so, introduced equids restore a capacity to buffer desert water availability and facilitate plant and animal communities. While introduced herbivores are functionally similar to extinct species and can have facilitative relationships with native species, little is known about whether the small-bodied predators that survived the Late

Pleistocene extinctions can influence them. In Chapter 4, I report on a trophic cascade driven by cougar (*Puma concolor*) predation on wild donkeys (*Equus africanus* asinus) which significantly altered their behavior and their effects on desert wetlands.

Finally, I synthesize this work by asking to what extent broadening our value systems changes conservation priorities. I empirically test several value scenarios, including *nativism* and more inclusive alternatives, by conducting spatial prioritization simulations to find optimal solutions to protect threatened species. I find that while the scale of global endangerment overshadows the scale of introductions, including introduced species as biodiversity provides new opportunities to prevent extinctions and shifts conservation priority into overlooked landscapes.

Like any applied scientific discipline, conservation biology is comprised of both normative values and empirical facts. It is, however, imperative that conservation biology interrogate its values as robustly as its facts. This thesis suggests that expanding conservation values offers new understandings of ecological change, reveals unseen ecological relationships, and provides new solutions to prevent global extinctions.

Chapter 1: Introduction

Conservation biology in an age of biotic redistribution

The human-assisted dispersal of species across biogeographic barriers is a form of anthropogenic change that receives significant attention in conservation biology research and in conservation policy. While many introductions are known to have occurred in ancient times (Gippoliti and Amori 2002, 2006, Trucchi and Sbordoni 2009, Carden et al. 2012), their rate and scale in our globalized economy has alarmed many conservationists because of concern over their potential to suppress native populations and to alter ecosystem properties. Introduced populations are largely considered parallel forces to other anthropogenic pressures, such as pollution, habitat loss, development, industrial extraction, wildlife exploitation, and climate change (Vitousek et al. 1997, Chew 2015).

However, the empirical premises underlying the positioning of introduced species as anthropogenic harms has come under increasing scrutiny (Davis 2003, Davis et al. 2011, Wallach et al. 2015b, Cassini 2020), leading to many heated discussions about the reality of ‘nativeness’ as a measurable, biological phenomenon (Sagoff 2018, Munro et al. 2019). Furthermore, the normative values underpinning conservation’s concern with introduced species are increasingly coming into focus. *Nativism*, in particular, is a normative value driving many of conservation biology’s research agendas, rhetoric, and decision-making–particularly regarding introduced species. In the conservation field, nativism consists of a belief that species belong in the place in which they evolved or immigrated to on their own volition. Nativism thus reflects a desire to return the world to the ecological configurations present prior to European colonization or to industrial development, as these reflect the way the world *ought* to be (Pollan 1994, Gould 1998, Peretti 1998, Hettinger 2001, Wallach et al. 2018). Thus, the value of organisms is defined by whether or not modern humans have had a hand in their dispersal history (e.g. see Box 1 in Russell and Blackburn 2017).

All applied scientific disciplines (e.g. medicine) are founded on a mixture of empirical facts and normative values, as values are how we decide what we ought to do. However, interrogating these values is imperative for producing quality science and for making ethically-transparent and empirically-robust decisions (Yanco et al. 2019). In this introductory chapter I review empirical concerns about the utility of 'nativeness' as a biological and ecological concept and discuss how the normative value of *nativism* can interfere with conservation science and decision-making. I then provide an overview of the following chapters, which together ask what the world looks like if we relax the value of *nativism*.

Nativism in conservation biology

Conservation biology's concern with introduced species is a relatively recent development, primarily supported by the oft-cited claim that introduced species are the second leading cause of extinction (Chew and Hamilton 2011, Chew 2015). However, historical analysis of this claim finds that it was inappropriately extrapolated from the effects of introduced predators on select islands and does not reflect the outcomes of introductions in the vast majority of cases (Davis et al. 2011, Chew 2015). Indeed, causative evidence tying introduced species to extinctions remains elusive because of confounding concurrent anthropogenic pressures, such as overharvesting, modification of disturbance regimes, habitat loss, and the persecution of apex predators (MacDougall and Turkington 2005, Stromberg et al. 2007b, Wallach et al. 2015b, Doherty et al. 2019). In most cases, introductions have increased species richness without corresponding losses of native species (Sax et al. 2002, Sax and Gaines 2008, Vellend et al. 2013, Thomas and Palmer 2015, Wallach et al. 2019). Despite increasing recognition that introduced species play only a minor role in driving extinctions, this claim is still regularly repeated (e.g. Gallien et al. 2017, Melotto et al. 2020).

The proposed mechanism underlying conservation’s concern with introduced species is that long-term community-wide coevolutionary history (e.g. only shared between native species) is responsible for the coexistence of species and the functioning of ecosystems. However, there is little to no conclusive evidence to indicate that this kind of dispersed, community-wide coevolution actually happens. Although perhaps seeming ‘coevolved’, paleoecological evidence indicates that modern ecological communities are but the current face of independently shifting species distributions, as most organisms have moved independent of each other through climatic cycles, forming only fleeting associations with other species (Williams and Jackson 2007).

As Janzen (1985), pointed out, even what appear to be classic examples of pairwise coevolution–say between a caterpillar and its host plant–may be artifacts of dispersal and ecological fitting. As such, the complex interactions observed in novel ecosystems composed of numerous introduced and native species are most likely impossible to distinguish from interactions within historically native ecosystems (Wilkinson 2004a, b). While the concept of a Clementsian, super-organismic ecological community has long since left the vogue of ecological thought, it has found a new home in ideas of the native, coevolved community (Sagoff 2019).

Introduced species do indeed cause ecological change. These changes affect other species, often in complex ways. However, the value of *nativism* posits that human-caused deviations from pre-European conditions is a violation of how the world *should* be. Thus, any measurable effect of an introduced species becomes by definition ‘harmful’. This can prevent empirical understandings of introduced species and their effects. For example, grazing by introduced wild donkeys and other megafauna in North America and Australia is key to the maintenance of freshwater desert springs: when removed by land managers, many springs became anaerobic or lost surface water completely, causing the extinction of several endemic fish populations (Kodric-Brown and Brown 2007) and likely the endangerment of at least one amphibian whose abundance is closely linked to wetland disturbance by introduced donkeys (Bradford et al. 2004).

Under the lens of nativism these phenomena are ignored or are reframed: these very same influences (trampling, herbivory) are being used as justifications for removals and eradications of the same megafauna populations, regardless of inadvertent consequences (Death Valley National Park 2020). This also has implications for the advancement of basic science. As Tschinkel and Wilson (2014) argue, studying introduced organisms exclusively in the context of invasion biology, instead of studying their natural history on their own terms, ignores the very biological complexity responsible for generating breakthroughs in ecological and evolutionary theory in the first place.

Introduced species are also increasingly recognized for provisioning ecosystem services in their new homes (Schlaepfer et al. 2011, Mascaro et al. 2012), often in response to novel anthropogenic pressures for which native species lack adaptations (Hobbs et al. 2017). For example, introduced trees were the only trees able to establish on nutrient-leached, abandoned agricultural lands in Puerto Rico. By creating closed canopy forests and stabilizing soils, these introduced trees facilitated native trees, which began recruiting into these now favorable abiotic environments (Lugo 2004).

In Southwestern North America, tamarisk (*Tamarix* spp.) has been widely blamed for the loss of riparian gallery forests and population declines among some bird species. However, mechanistic research on the factors engendering riparian forest dynamics reveals that tamarisk happens to be preadapted to the modified flow-regimes stemming from widespread damming (Shafroth et al. 2002, Stromberg et al. 2007a, Stromberg et al. 2007b, Andersen and Shafroth 2010). These tamarisk forests now provide habitat for endangered bird species and vegetation structure unavailable from the few native plants that can tolerate the same flow conditions (Shafroth et al. 2005, Ellis et al. 2008). Attempts to revert these emergent, novel communities of introduced and native species to their historic states is often impossible and undesirable, especially without addressing underlying anthropogenic drivers (Lugo 2004, Mascaro et al. 2012, Hobbs et al. 2017).

Nativism is also limited in its temporal dimension, as it denies long-term ecological changes stemming from prehistoric and historic human-caused extinctions and range contractions. For 35 million years until the Late Pleistocene (beginning ~100,000 years ago), the world was dominated by a diversity of large-bodied terrestrial herbivores and their predators. These megafauna went extinct as humans spread from Africa, which led to profound changes in ecosystems, including increases in wildfire, nutrient cycling, nutrient and seed dispersal, vegetation structure, albedo, and primary productivity (Zimov et al. 1995b, Gill et al. 2009, Rule et al. 2012, Bakker et al. 2016, Doughty et al. 2016a, Doughty et al. 2016b, Malhi et al. 2016, te Beest et al. 2016, Zhu et al. 2018). The ecosystems that resulted from this size-selective filtering of large-bodied animals (Smith et al. 2018) are now enshrined as the native world, yet are functionally divergent to compositions reflective of the last ~35 million years of terrestrial life (Alroy 1998, Svenning et al. 2016, Smith et al. 2018, Lundgren et al. 2020).

The very act of defining a species as native or not further illustrates the ambiguity and intrinsic instability of the concept. For example, supposedly introduced monitor lizards on islands in Micronesia, whose impacts were sure to lead to catastrophic extinctions and whose eradication has been the focus of island conservation campaigns, turn out to have arrived on their own thousands of years before humans did and are in fact endemic species (Weijola et al. 2020). If introduced species are harmful because they are introduced, what becomes of the alleged harms when we find out they are native? It remains unlikely, if not impossible, if a researcher could determine the nativeness of a species by measuring its actual effects, without historical knowledge.

This contradiction has been described as the genetic fallacy of invasion biology (Sagoff 2018).

Nativism asserts rules of belonging–that species belong to the places they were at the time of European colonization–a belief which necessitates the eradication of introduced populations. However, eradication is mostly unattainable, often has unexpected and undesirable outcomes (Zavaleta et al. 2001), and may divert resources from anthropogenic pressures that have far greater current or anticipated effects on the living world, such as habitat loss, exploitation, and climate change (Ramp and Bekoff 2015, Wallach et al. 2015a, Díaz et al. 2019).

Lethal control and eradication of introduced populations also comes in conflict with other conservation values, including that life itself possesses intrinsic value. The belief that life has intrinsic value and should be treated with respect is shared by much of the public and likely motivates most conservation professionals (Vucetich et al. 2015, Wallach et al. 2020), especially given growing understandings of sentience and sapience among most, if not all, animals (Low et al. 2012). Killing sentient organisms in order to reconstruct historic species compositions produces a dissonance in a field otherwise dedicated to cherishing non-human life and reinforces notions of human supremacy–notions that got us into this situation in the first place (Wallach et al. 2020). This dissonance has led to numerous conflicts with the public and may erode people's trust in and support of the very project of conservation biology (Crowley et al. 2017).

The lack of empirical evidence supporting the claim that nativeness has a biological reality, the non-universality of the value of *nativism* among conservation practitioners and the public (Sandbrook et al. 2011, Sandbrook et al. 2019), the increasing reality that species will not be able to live in their historic native ranges because of climate change (Williams and Jackson 2007), and the need to find conservation approaches that are both pragmatic and ethical (Ramp and Bekoff 2015) suggests that relaxing the value of nativism may provide new insights into ecological change and new approaches for conservation. This thesis thus asks how our understandings of the world change if we suspend the value of nativism.

Thesis overview

I focus here on mammals, and, in particular, herbivores, which are the most endangered functional group across vertebrate life (Atwood et al. 2020) and which are particularly sensitive to habitat loss and overexploitation (Duffy 2003, Ripple et al. 2015). Herbivores also play important metabolic roles in the Earth System by cycling and pumping plant nutrients across the Earth's surface (Zimov et al. 1995a, Doughty et al. 2016a, Malhi et al. 2016, Doughty 2017, Zhu et al. 2018). Using both macroecological and field methods, this thesis addresses the extent to which studying introduced herbivores without the lens of *nativism* changes the way we understand modern ecological change. This work is relevant to broad-scale understandings of biodiversity trends from prehistoric time (100,000 years ago) to the present; to understanding how introduced herbivores affect modern ecosystems; and to understanding how introduced herbivores fit into modern food webs. Finally, I synthesize these projects by analyzing the extent to which changing our value systems changes conservation priorities and policy recommendations.

In Chapter 2, now published in *Proceedings of the National Academy of Sciences,* I begin by analyzing how mammalian herbivore (≥ 10kg) assemblages have changed from the twin anthropogenic forces of extinction and introduction since the pre-extinction Late Pleistocene. I pursue this question from the perspective of herbivore functional traits: measurable traits that influence how an organism affects their environment (McGill et al. 2006, Petchey and Gaston 2006, Luck et al. 2012). Analyzing ecological change in terms of functional trait compositions yields insights that cut across species identity and can allow comparisons of community composition and ecosystem function across space and time (Pimiento et al. 2017). To conduct this research, I assembled an international collaborative team, with whom I collected traits for all mammalian herbivores ≥10kg over the last 130,000 years. This dataset is now itself in revision with *Nature Scientific Data.*

Using this dataset, we quantified the functional trait structure of herbivore assemblages through time, mathematically assessing the degree to which both extinctions and introductions have shaped the capacity of herbivores to affect the environment. We found that the majority of introduced herbivores restore lost trait combinations and that modern herbivore assemblages are more similar to those of the past than native-only ones are. Although seemingly novel, the trait combinations of introduced taxa, and thus their potential ecological effects, are more similar to those of the pre-extinction Late Pleistocene than those of native-only assemblages. By dropping the value of *nativism* and expanding our conception of Earth's history we find that the apparently novel influences of introduced herbivores have deep precedents and that introductions can play countercurrent to global extinctions. This work suggests that instead of forcing ecosystems back into recent historic states, the real work is in interrogating our ideas of naturalness.

In Chapter 3, currently in revision with *Science*, I report from fieldwork on ecological engineering by introduced horses (*Equus ferus caballus*) and donkeys (*Equus africanus asinus*). While considered pests across their expansive introduced range, these animals dig wells up to 2m in depth to groundwater in the deserts of Australia, and North and South America. By maintaining access to groundwater in intermittent streams, introduced equids sustain water availability through dry seasons, provide resources used by numerous other species, and create germination nurseries for foundational riparian tree species. This behavior is common across these species' ranges yet has remained unexamined in the scientific literature and has been described as a harm to justify their eradication (see Texas Parks and Wildlife). Well digging by megafauna is likely an ancient function, ubiquitous until the extinctions of the Late Pleistocene, and which may have played a vital role in buffering water availability across climatic cycles. The restoration of this ecological function by introduced equids has the capacity to buffer against ongoing aridification and increasing rates of intermittency among currently perennial streams (Datry et al. 2017, Beck et al. 2018).

The effects of organisms on the environment are driven not only by their traits but also by the ecological contexts within which these organisms live. For herbivores, one particularly salient context is predation (Ripple et al. 2014). Predation drives trophic cascades both by regulating populations through direct mortality but also by altering prey behavior, including spatial and temporal activity patterns and foraging rates. These behavioral changes can have cascading effects on vegetation, soils and other species (Laundré et al. 2010). However, the majority of introduced herbivores have been studied as if their effects are context-independent under the oft-stated claim that they have ‘no natural predators’. This premise–that introduced herbivores are not components of modern food webs–justifies culling and removal programs and turns a blind eye towards the potential inadvertent consequences of these actions.

In Chapter 4, I report on the first documented predations of introduced wild donkeys by cougars (*Puma concolor*) in the Sonoran and Mojave Deserts of North America. I analyzed ~2,500,000 trail camera images and vegetation data from field surveys and found that the presence of cougars significantly alters the temporal activity patterns of wild donkeys and restructures their effects on desert wetland vegetation and soils. These results have important implications for how we treat both organisms. This emerging eco-evolutionary relationship suggests that ongoing removals of wild donkeys and the continued persecution of cougars may have unintended consequences on the ecological effects and demographics of donkeys, and on cougars and their historic prey.

In Chapters 2-4 I found that dropping the value of nativism alters our understandings of prehistoric and modern ecological change, uncovers overlooked ecological functions that play important roles in modern ecosystems, and reveals the entanglement of introduced herbivores in modern food webs. In Chapter 5, I take this question to the next step, asking the extent to which including introduced taxa under the umbrella of conservation concern changes conservation policy priorities for the protection of threatened mammals.

One particularly challenging question has been raised in recent years in response to a paradoxical phenomenon (Marchetti and Engstrom 2015): what should conservationists do if an introduced species is threatened in its native range? The oft-stated aim of conservation biology is to prevent the extinction of species, yet to the best of our knowledge, there has been no coordination of conservation activity across regions to ensure that introduced threatened species are protected at least somewhere. Likewise, there has been little consideration for how this conservation paradox may provide unexpected conservation opportunities (but see Bradshaw et al. 2005), particularly if the native populations are threatened by processes over which we have little control, such as exploitation and land-use change driven by extreme poverty.

In prior work on this paradox, most authors (Pascual and Ciancio 2007, Marchetti and Engstrom 2015, Gibson and Yong 2017) concluded that these populations should be considered refuge populations for future repatriation to their native ranges, or that those populations introduced by the wildlife trade should be used as source populations for said trade, to reduce pressure on native populations (Gibson and Yong 2017). These suggestions grow in the soil of nativism. However, if we suspend this normative value, how else could we consider these populations?

In Chapter 5 I consider what would happen if we valued these populations in their introduced ranges. To do so, I mapped distributions for the world's introduced threatened mammals which I compiled with IUCN native range data (IUCN Red List 2018). I then employed the latest in spatial prioritization methods to assess global conservation solutions to maximize the protection of threatened species. We analyzed four scenarios based on different interpretations of how to include introduced populations under the umbrella of conservation concern. This work, to the best of our knowledge, is the first to test how value systems, such as nativism and its alternatives, can alter empirical conservation policy recommendations. Our results indicate that altering the values driving conservation provides new opportunities to protect species– particularly in currently overlooked landscapes, such as central Australia and the southwestern United States. However, we also affirm that the scale of introductions pales in comparison to the scale of global endangerment.

In summary, conservation biology, like medicine or any other applied scientific discipline, requires values. Values are how we make decisions to act and are how we compose arguments to, for instance, not cut down rainforests or kill rhinos for their horns or blow up mountaintops for coal. However, conservation biology has largely adopted the value of *nativism* as if it were a universal value and empirical fact, despite the lack of evidential, measurable proof of the existence of such a thing. This thesis suggests that interrogating nativism, and other underlying values, presents new opportunities to understand and respond to our changing world.

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Chapter 2: Introduced herbivores restore Late Pleistocene ecological functions

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Abstract

Large-bodied mammalian herbivores dominated Earth’s terrestrial ecosystems for several million years before undergoing substantial extinctions and declines during the Late Pleistocene (LP) due to prehistoric human impacts. The decline of large herbivores led to widespread ecological changes due to the loss of their ecological functions, as driven by their unique combinations of traits. However, recently, humans have significantly increased herbivore species richness through introductions in many parts of the world, potentially counteracting LP losses. Here, we assessed the extent to which introduced herbivore species restore lost—or contribute novel—functions relative to pre-extinction LP assemblages. We constructed multidimensional trait spaces using a trait database for all extant and extinct mammalian herbivores ≥10kg known from the earliest LP (~126,000 ybp) to the present-day. Extinction-driven contractions of LP trait space have been offset through introductions by ~39% globally. Analysis of trait space overlap reveals that assemblages with introduced species are overall more similar to those of the LP than native-only assemblages, because 64% of introduced species are more similar to extinct rather than extant species within their respective continents. Many introduced herbivores restore trait combinations that have the capacity to influence ecosystem processes, such as wildfire and shrub expansion in drylands. Though introduced species have long been a source of contention, our findings indicate that they may in part restore ecological functions reflective of the last several million years before widespread human-driven extinctions.

Significance Statement

Humans have caused extinctions of large-bodied mammalian herbivores over the last ~100,000 years, leading to cascading changes in ecosystems. Conversely, introductions of herbivores have in part numerically compensated for extinction losses. However, the net outcome of the twin anthropogenic forces of extinction and introduction on herbivore assemblages has remained unknown. We found that a primary outcome of introductions has been the reintroduction of key ecological functions, making herbivore assemblages with non-native species more similar to those that existed before LP extinctions than native-only ones are. Our findings support calls for renewed research on introduced herbivore ecologies in light of paleoecological change and suggest that shifting focus from eradication to landscape and predator protection may have broader biodiversity benefits.

Introduction

Global extinctions and range contractions of large-bodied mammalian herbivores have occurred across the world beginning ~100,000 years ago and peaking towards the end of the Late Pleistocene (LP) (Martin and Wright 1967). Emerging consensus indicates that LP losses were primarily driven by prehistoric human impacts (Barnosky et al. 2004, Sandom et al. 2014), either alone or synergistically with climate change (Metcalf et al. 2016). On the other hand, recent introductions of herbivore taxa outside their native ranges has increased species richness across much of the world, in some continents to levels approaching the LP (Lundgren et al. 2018).

The prehistoric declines of large-bodied herbivores led to widespread ecosystem changes, including reduced nutrient cycling and dispersal, reduced primary productivity, increased wildfire frequency and intensity, and altered vegetation structure (Zimov et al. 1995, Doughty et al. 2016, Malhi et al. 2016). Likewise, introduced herbivores have been found to drive changes in vegetation structure (Werner et al. 2006), to increase water availability in deserts through grazing and disturbance (Kodric-Brown and Brown

2007), and to reduce fuel loads and thus wildfire (Werner et al. 2006, Johnson et al. 2018).

These effects emerge from the distinct ecological functions of large herbivores. Here, we define 'function' as the capacity of organisms to affect their environment, as determined by their combinations of traits, such as body mass, fermentation type, and diet (Luck et al. 2012) (SI Appendix, Fig. S1). For example, large-bodied hindgut grazers have the unique capacity to bulk-graze large quantities of low-nutrient grasses (Demment and Van Soest 1985, Owen-Smith 1988, Doughty et al. 2016). However, the downstream ecological effects of this function vary with ecological context (e.g. precipitation, soil type, predation pressure). For example, bulk-grazing can lead to the formation of high productivity grazing lawns, but this process is shaped by interactions between soil nutrients, rainfall, and herbivore densities (Hempson et al. 2015b).

Most extant plant and animal species evolved in the context of diverse large-bodied herbivore assemblages, from the early Cenozoic (30-40 million ybp) until the LP extinctions (Smith et al. 2018). However, most research on introduced large-bodied herbivores has been conducted under the premise that they are ecologically novel and thereby disadvantage resident species (e.g. Barrios-Garcia et al. 2014). The possibility that introduced herbivores may in part restore the ecological functions that characterized the last several million years until LP extinctions has been suggested (Martin 1970, Janzen and Martin 1982, Donlan et al. 2006, Davis 2017), but has not been rigorously evaluated.

Here, we analyze how the twin anthropogenic forces of prehistoric extinction and recent introduction have shaped herbivore functional diversity and the extent to which introduced herbivores restore lost, or introduce novel, ecological functions relative to pre-extinction LP assemblages. We do so by comparing *native-only* and *inclusive* (native and introduced) herbivore species assemblages of the present-day to *LP* assemblages in terms of trait structure across the continents.

Results

We compiled native-only, inclusive (native and introduced), and LP species lists for continental assemblages for all herbivore species ≥ 10kg recorded over the last ~ 126,000 years, i.e. since the last interglacial (Data S1). Globally, LP extinctions resulted in a loss of 160 of 427 (35%) herbivore species ≥ 10kg, particularly in North America (67% lost), South America (65%), Australia (64%), and Europe (56%) (Fig. 1A). Thirty-three herbivore species were introduced into new continents, replacing lost species richness by 50% in Australia and Europe, 46% in North America, 42% in Africa, 27% in South America, and 11% in Asia (Fig. 1A).

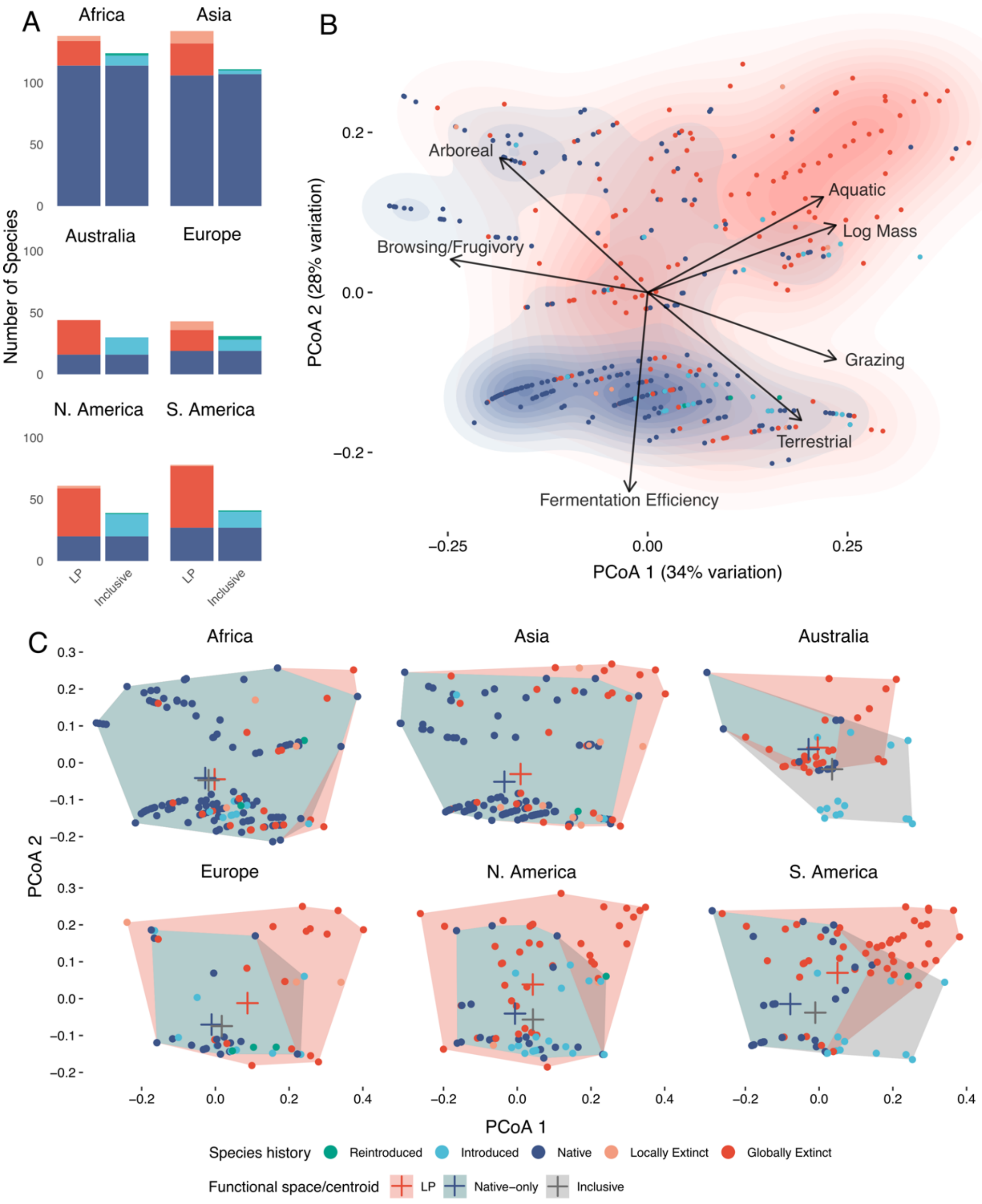

Figure 1. Trait space changes resulting from Late Pleistocene (LP) extinctions and recent introductions. (**A**) Species richness per continent. Introductions have numerically replaced lost species richness by between 11% (Asia) and 50% (Australia and Europe). Fill color indicates species fate, with the legend shared with panel c. *Inclusive*=native+introduced modern assemblages. (**B**) Global herbivore trait space. Arrows indicate how particular traits shape trait space axes. The first two PCoA axes (~62% of variation) of trait space are shown (see SI Appendix, Fig. S1 for PCoA axes 3 and 4). Points indicate species and the fill density indicates their density distribution, with the legend shared with panel c. (**C**) Changes in continental trait space (PCoA 1 and 2) from extinctions and introductions. Crosses indicate centroids of the first two PCoA

axes. Locally extinct species went extinct within the respective continent but survived elsewhere. *Native*-only=modern native assemblages; *inclusive*=native+introduced modern assemblages.

To understand how extinctions and introductions affected the capacity of herbivores to influence their environments, we compiled a trait dataset of body mass, fermentation type (simple gut, hindgut, foregut non-ruminant, ruminant), diet (graze, browse), habitat (aquatic, terrestrial, arboreal), and limb morphology (plantigrade, digitigrade, unguligrade) (Table S1). Fermentation type was recorded in terms of fermentation efficiency, with ruminants scoring highest. Limb morphology was included as a trait due to its influences on soil disturbance (Cumming and Cumming 2003), locomotion (e.g. cursoriality, fossoriality) and habitat constraints, which can otherwise be difficult to infer for extinct species (Brown and Yalden 1973, Polly 2007, Kubo et al. 2019).

To analyze changes in trait combinations, we constructed multidimensional trait spaces using Principal Coordinates Analysis (PCoA) to describe the primary axes by which herbivores differ from each other in terms of their traits and thus encapsulate the overall functionality of herbivore assemblages. Collectively, the first four axes of global herbivore trait space accounted for 78% of interspecific trait variation (Fig. 1B, SI Appendix, SI Appendix, Fig. S2). PCoA 1 (34% of total variation) was primarily shaped by body mass (r = 0.87) and diet (grazing r = 0.78; browsing r = -0.66), while PCoA 2 (28% of total variation) primarily reflected fermentation efficiency (r = -0.93). Changes along these axes revealed that, as expected, LP extinctions of herbivores led to substantial contractions in overall trait space, shifting the balance towards smaller-bodied species with more efficient fermentation strategies (e.g. ruminants) (Fig. 1B).

To understand how the overall diversity of species trait combinations has changed from extinctions and introductions, we compared the *volume* of occupied multidimensional trait space for LP, native-only, and inclusive assemblages. Trait space volume is a metric of functional diversity also known as *functional richness* (Villeger et al. 2008). LP extinctions reduced the total volume of occupied multidimensional trait space by 62% globally, particularly in Australia (99% contraction in richness), North America (83%), and South America (83%) (Fig. 2A). In contrast, introduced herbivores replaced lost trait space volume by an average of 39% globally, particularly in Australia (100% replaced and 30% expanded over LP levels), South America (47% replaced), Europe (22%), Africa (18%), and North America (17%) (Fig. 2A).

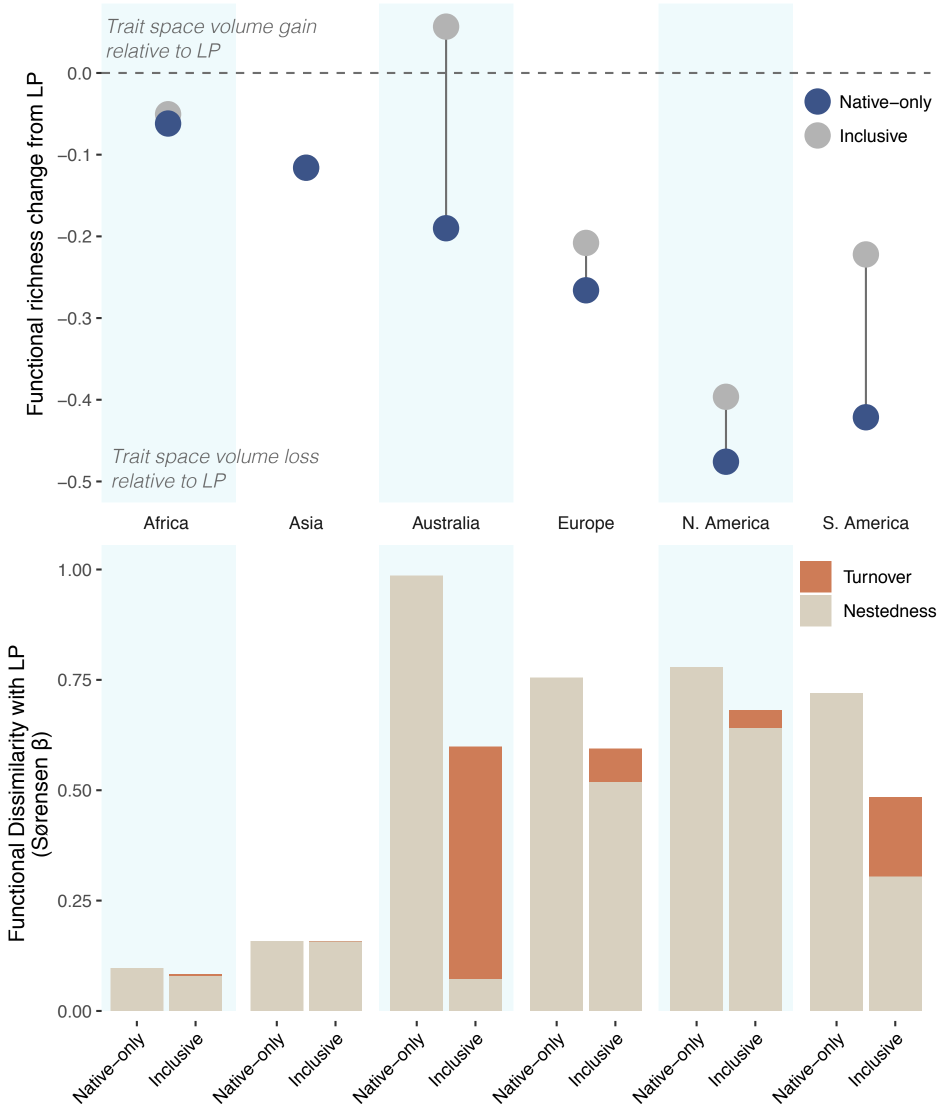

Figure 2. Change in trait space volume and functional dissimilarity (**A**) Difference between native-only and inclusive trait space volumes from the LP volume for each continent. Trait space volume is the 4-dimensional volume of each trait space (also known as functional richness). Contractions in trait space volume following LP extinctions (native-only points) have been offset by introductions in inclusive assemblages. The dashed line indicates no change from LP. *Native*-only=modern native assemblages (blue); *inclusive*=native+introduced modern assemblages (gray). (**B**) Total functional dissimilarity to the LP, calculated from the overlap of 4-dimensional trait spaces. Functional dissimilarity (measured as Sørensen's β) is composed of two additive components: *nestedness* is dissimilarity caused by being a subset of another trait space, while *turnover* is the degree to which assemblages do not overlap (e.g. novelty).

While introductions substantially replaced lost trait space volume, to understand whether inclusive assemblages with introduced species are more or less similar to the LP than native-only ones, we calculated functional dissimilarity (Sørensen's β) from the overlap of native-only and inclusive trait spaces with LP ones. Functional dissimilarity, like other beta diversity measures, is comprised of two additive components: nestedness, the overlap of assemblages in trait space (e.g. the degree to which one is a subset of the other), and turnover, the degree of non-overlap in trait space (e.g. novelty) (Baselga 2010). We found that introduced taxa make inclusive continental assemblages more functionally similar to the LP than native-only assemblages, by 39% in Australia, 33% in South America, 21% in Europe, and 13% in North America. However, introductions contribute turnover to inclusive assemblages, driven by the unique traits and trait combinations of some introduced taxa (Fig. 2B). Australia had the highest turnover, with 88% of the remaining dissimilarity with the LP comprised of turnover. This is due to the introduction of ruminants and larger-grazers than those present in its LP marsupial-dominated fauna (Fig. 2B).

To understand how introduced species relate to other taxa, we examined whether their nearest neighbors in trait space are extant or extinct. To avoid comparing species with different thermal tolerances (e.g., tropical versus arctic), we restricted comparisons by Köppen-Geiger climate zones (Kottek et al. 2006) and by body mass bins. Body mass bins were calculated using the Sturges algorithm (Sturges 1926), which finds natural breaks points in continuous data distributions, thus reducing analytic bias.

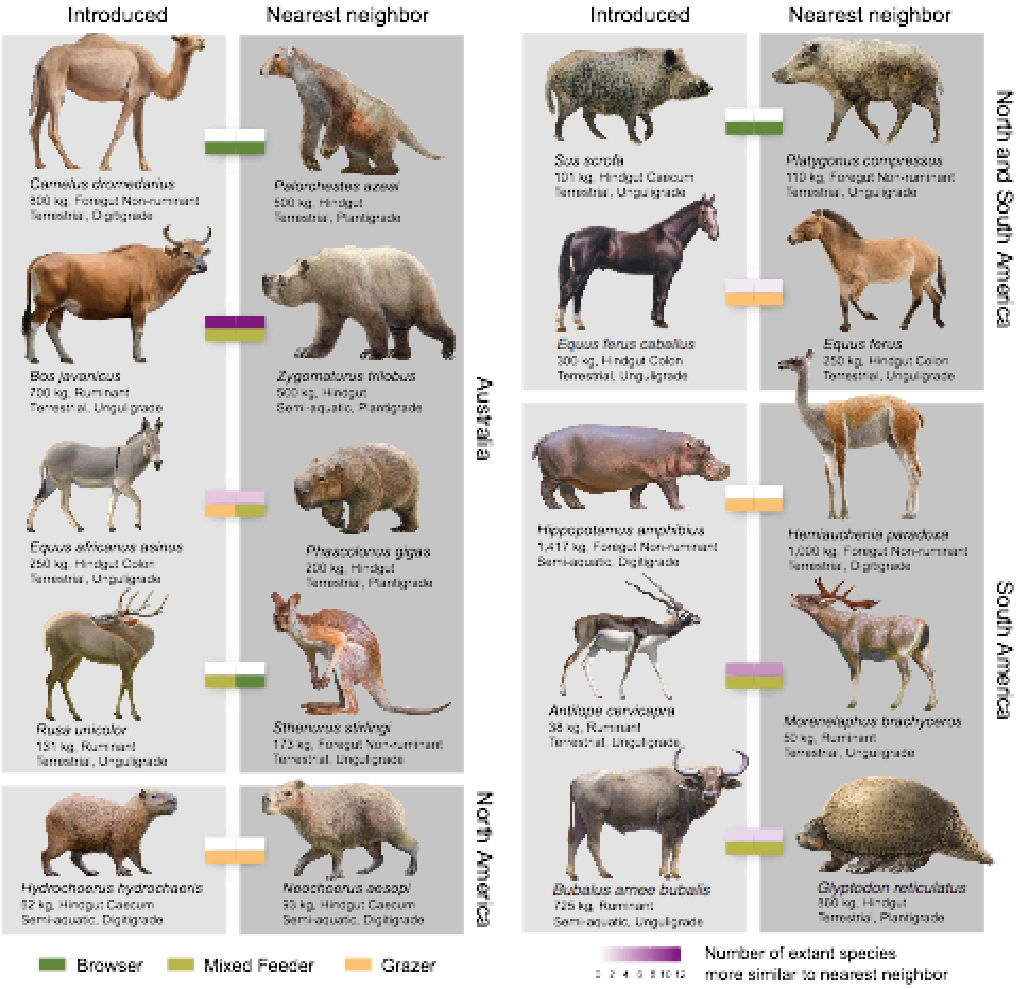

Figure 3. Select introduced herbivores and their extinct nearest neighbors in those continents most impacted by extinctions and introductions. The color of the top bar indicates the number of extant species (per body mass bin and climate zone) that are more similar to the nearest neighbor than the introduced species is, while the lower bar color indicates dietary guild. For a full list of pairs see SI Appendix, Fig. S3.

Overall, 64% of introduced species are most similar to extinct LP species rather than extant species. This is most apparent in those continents with high LP extinction rates: in Australia 93% of introduced species are most similar to extinct taxa; followed by 86% in South America, 74% in North America, and 50% in Europe (Fig. 3, SI

Appendix, Fig. S3). In Africa and Asia, which experienced few extinctions, 90% and 75% of introduced taxa are most similar to extant species (SI Appendix, Fig. S2).

The similarity of introduced herbivores to extinct ones indicates that introductions have restored lost trait combinations and thus functions. To better understand which functions have been restored, we focused on key 'metabolic' functions herbivores contribute in ecosystems by consuming plant biomass and by cycling and redistributing nutrients (Doughty et al. 2016). These functions are primarily influenced by body mass and dietary guild—traits that control the *quality*, *quantity*, and *type* of vegetation consumed, with larger herbivores prone to greater dispersal distances and capable of digesting larger-quantities of fibrous, low-nutrient vegetation (Demment and Van Soest 1985, Owen-Smith 1988, Doughty et al. 2016). To understand how extinctions and introductions have affected these key metabolic functions, we categorized species into *functional groups* by combinations of body mass bins and dietary guilds.

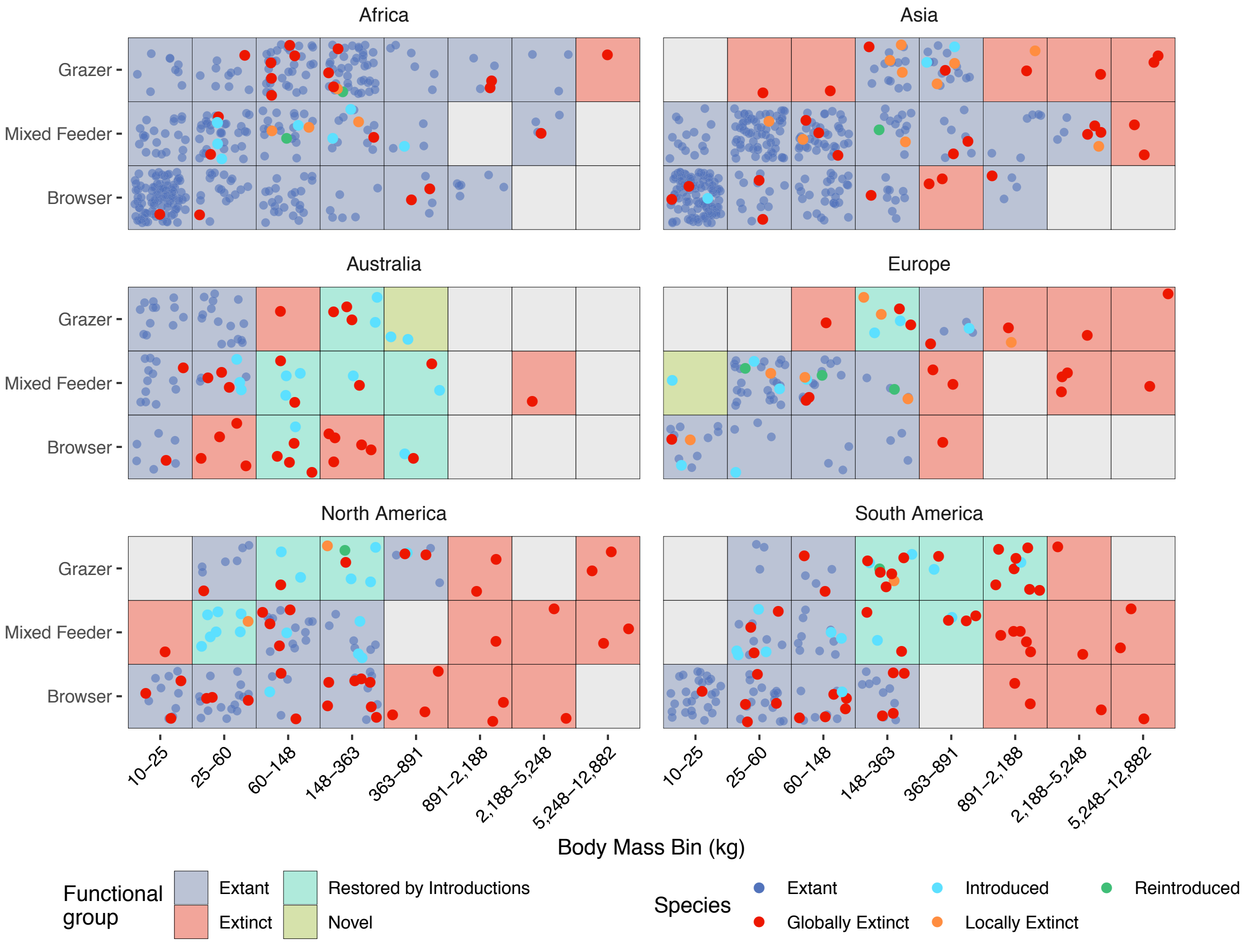

Figure 4. The loss and restoration of key metabolic ecosystem functions. Forty-four percent of introductions restore extinct functional groups, restoring 14 of 51 extinct dietary body mass groups across continents. Body mass groups were determined analytically with the Sturges algorithm, which finds natural breakpoints in continuous distributions. Three species introduce novel groups to Australia and Europe. Points indicate species and are jittered randomly for visualization within each cell.

We found that 42% of introduced herbivores restore extinct functional groups, particularly in Australia (60% of lost functional groups restored) and in South America (42% restored) (Fig. 4). Three introduced herbivores (5%) contribute novel functional groups: two species introduced to Australia contribute a grazing functional group larger than any present in the LP (by ~200 kg), while in Europe the introduction of a small-bodied mixed-feeder (*Macropus rufogriseus*) contributes one novel functional group.

Discussion

The redistribution of species through human introductions is primarily perceived as an environmental harm. However, our results indicate that one consequence of introductions has been to counteract global patterns of human-caused extinction by replacing lost functional diversity and making modern trait compositions more similar to those of pre-extinction LP assemblages. In doing so, the majority of introduced species are functional surrogates for extinct species and many restore ‘metabolic’ functional groups, particularly in those continents most impacted by LP extinctions.

Many of these restored functions have the potential to affect ecosystems. For example, large-bodied browsers were severely impacted by LP extinctions in Australia (Fig. 4). The restoration of these functional groups may reduce shrub cover and promote grasslands, with implications for albedo, carbon storage, and wildfire (Cromsigt et al. 2018). Likewise, the widespread restoration of extinct large-bodied grazing functional groups, which are capable of bulk-grazing large quantities of low-nutrient grasses compared to smaller grazers, could reduce wildfire intensity (Cromsigt et al. 2018).

In some cases, introduced taxa have close phylogenetic relationships with extinct species. For example, in North and South America, introduced equids (*E. africanus asinus, Equus ferus caballus*) are related or conspecific to extinct taxa (*E. francisci, E. ferus*) and have restored lost trait combinations, such as large-bodied hindgut grazing. The effects of these species are poorly understood (e.g. Abella 2008) but some evidence suggests that the restoration of these trait combinations can have facilitative effects on other species. In North American desert wetlands, disturbance and grazing by wild burros (*E. a. asinus*) of fast-growing, emergent vegetation maintains open water habitat to the benefit of endemic fishes (Kodric-Brown and Brown 2007) and an endangered amphibian (Bradford et al. 2004). Likewise, grazing by wild horses (*E. f. caballus*) in North American salt marshes favors higher diversity of foraging birds and increased crab density, while reducing fish density and diversity (Levin et al. 2002).

In other cases, introduced taxa are unrelated to extinct species in their new homes yet show strong functional similarities, although often in novel trait combinations. For example, introduced hippos (*Hippopotamus amphibius*) in South America present a chimera of multiple extinct species' trait combinations. While they are most similar to a giant extinct llama (*Hemiauchenia paradoxa,* Fig. 3) in all assessed traits bar habitat use, our analysis revealed that they are nearly as similar to an extinct semi-aquatic notoungulate (*Trigonodops lopesi*) in all traits but fermentation type. While the ecological effects of hippos in South America remain unknown, their trait combinations suggest that their ecological effects may overlap with extinct species in certain ecosystem components (e.g. grazing and disturbance in riparian zones) and diverge elsewhere (e.g. direction of nutrient transport).

The apparent novelty of some introduced traits is tempered when compared to the trait compositions of the LP. For example, the disturbance-related effects of Australia's introduced hoofed ungulates on soils and vegetation appear novel (Johnson et al. 2018). Yet the extinct short-faced kangaroos (sthenurines) possessed monodactyl hoofs and an unguligrade morphology similar to 'open-plains' horses (Prideaux et al.

2009). However, rumination remains a novel trait in Australia, where macropods' non-ruminant foregut fermentation is less thorough (Hume 2002). It is therefore possible that some of Australia's plants lack seeds capable of surviving ruminant digestive systems, which could lead to shifts in seed dispersal efficacy and possibly to vegetation structure. Australia also received two grazers larger than any LP grazing species (by ~200 kg). The introduction of large-bodied bulk-grazing may have strong effects on Australia's uniquely fire-driven ecosystems (Orians and Milewski 2007). In a long-term experimental system in Northern Australia, seasonal bulk-grazing by introduced water buffalo (*Bubalus bubalis*) of fibrous, low-nutrient grasses, reduced wildfire and promoted tree establishment and survivorship through wildfire (Werner et al. 2006). Whether these ecological effects are novel or overlap with those of extinct mixed feeders is unknown.

Many important traits remain unknown for extinct taxa, such as sociality, movement patterns, foraging behavior, and vulnerability to predators. All could be factors affecting similarity with LP species and thereby shaping how introduced herbivores interact with extant native species. Yet, the diversity of LP herbivores makes it likely that many of these introduced traits have precedents. For example, although the seemingly novel rooting behavior of wild boar (*Sus scrofa*) is thought to disadvantage native species across their extensive introduced range (Barrios-Garcia and Ballari 2012), several extinct species likely had similar foraging strategies, including *Platygonus compressus* (Koch and Barnosky 2006) in North and South America, and *Zygomaturus trilobus* (DeSantis et al. 2017) in Australia. Indeed, rooting by wild boar increases tree growth rates by mixing leaf litter into upper soil layers, enhancing decomposition rates and thus nutrient availability in eastern North American forests (Lacki and Lancia 1986); and increases bird abundance by increasing accessibility of food resources in northern Australia (Natusch et al. 2017).

While the trait combinations of herbivores drive their functional capacity to affect ecosystems, their actual effects emerge in interaction with ecological contexts, such as predation (Wallach et al. 2015) and landscape connectivity (Boone and Hobbs 2004). Many apex predators continue to face declines (Ripple et al. 2014). Likewise, ongoing landscape fragmentation restricts herbivore movements and can lead to concentrated herbivory (Boone and Hobbs 2004). Therefore, while introductions make herbivore assemblages more functionally similar to the LP, they do not necessarily restore ecosystems to LP conditions due to ongoing anthropogenic pressures.

Introduced species have been primarily studied in the context of recent historic states under the premise that their ecological functions are novel. However, presumed novelty yields to functional similarity when compared to the LP, a time period largely reflective of the last ~40-30 million years of terrestrial ecosystem evolution (Smith et al. 2018). Compared to these pre-anthropogenic conditions, introduced herbivores replace lost functional diversity, make modern herbivore assemblages more similar to LP ones, and restore key metabolic functional groups in the Earth system. Our results indicate that introductions are an inadvertent counterpoint to prehistoric and historic anthropogenic defaunation and that future research on the ecologies of introduced herbivores would benefit from incorporating deep-time perspectives.

Materials and Methods

We included all extant and extinct herbivore species ≥10 kg that lived the last 130,000 years, following taxonomy in the PHYLACINE v1.2 dataset (Faurby et al. 2018). Many analyses of LP extinctions have focused on species ≥44kg or 100kg, however, given that Australia lost all but one herbivore ≥44kg during the LP extinctions, we included herbivores ≥10kg to ensure that modern, native-only assemblages would have sufficient numbers of species for analysis. Herbivores were selected from PHYLACINE as species with >50% plant in their diet, thereby including some carnivorans (e.g., bears). Alternative species lists for the LP exist, varying in their taxonomy of extinct and extant species. To verify that our results were robust to differences in taxonomy we conducted all analyses using the species list in Smith et al. 2018 (Smith et al. 2018) (SI Appendix, SI Text, Figs. S3-S6).

To determine how modern (native-only) and inclusive (native and introduced) herbivore assemblages compare to LP ones, we compiled three datasets of herbivore species ranges. We drew continental LP assemblages from ‘present-natural’ ranges of herbivores from Faurby et al. (2018), which primarily used fossil co-occurrence records to reconstruct modern-day herbivore ranges in the absence of anthropogenic extinction and range contraction. Native-only assemblages were drawn from spatial distributions in the IUCN Red List V6.1 (Schipper et al. 2008). Introduced species distributions, compiled from IUCN spatial distributions and numerous peer-reviewed sources and databases (see Data S1), were added to native assemblages to establish inclusive assemblages. Only self-sustaining populations that have been moved across continents were included (e.g. intra-continental introductions were excluded). Domestic herbivores were excluded from analysis as these populations are not necessarily ecologically viable without human intervention, and their behavior and interactions within ecosystems are heavily modified by human management. However, wild populations of domestic species were included.

Given different types of error in each of these scenario's distribution maps (e.g. ranges estimated using different methods and with different degrees of certainty) we used these range maps to create continental species lists for LP, native-only, and inclusive assemblages. We chose to conduct analyses at the continental scale as they reflect the long-term dispersal-limits of herbivores and the plants and other animals they interact with, thus setting the eco-evolutionary context of modern ecosystems. We limited our analyses to large landmasses, excluding smaller islands because they have unique evolutionary histories owing to their isolation. Additionally, this avoids the inclusion of small populations of functionally unique and geographically restricted introduced species (e.g. giraffes *Giraffa camelopardalis* introduced to a small island in Southeast Asia).

Traits

We collected data for traits that drive herbivores' interactions with other species and the environment: body mass, diet, fermentation type, habitat type, and limb morphology. Body mass (kg) was collected as a continuous variable from Smith et al. (2003) and PHYLACINE v1.2 (Faurby et al. 2018) and was analyzed as log base 10. We collected dietary data as two ordinal variables for graminoid and browse consumption respectively from the peer-reviewed literature, each ranging from 0-3, following the method of MammalDiet (Kissling et al. 2014). While coarse, these two dietary categories remain paradigmatic to herbivore ecology in both ancient and modern systems, and reflect key evolutionary and ecological differences in herbivore dietary adaptations (Gordon and Prins 2019) (SI Appendix, Table S1, Text S1).

Fermentation type further influences the quality and quantity of vegetation herbivores consume, and the nutrient stoichiometry of resulting excreta (Demment and Van Soest 1985, Hume 2002). Fermentation type was collected as a categorical variable for five fermentation types following Hume (2002): simple gut, hindgut colon, hindgut caecum, foregut non-ruminant, and foregut ruminant. However, this variable was ranked in terms of fermentation efficiency when constructing trait spaces, and hindgut caecum and colon were lumped because that degree of distinction was unavailable for some extinct taxa. Habitat use was collected as three binary and non-exclusive variables (arboreal, terrestrial, and aquatic) (Table S1).

Limb morphology was included as it influences disturbance-related impacts on soils (Cumming and Cumming 2003) and is therefore frequently mentioned in relation to the non-analogy of introduced herbivores in Australia (e.g. Bennett 1999, Johnson et al. 2018). Furthermore, limb morphology is correlated with other ecological attributes such as cursoriality, fossoriality, and habitat constraints, which can otherwise be difficult to infer for extinct species (Brown and Yalden 1973, Polly 2007, Kubo et al. 2019), Limb morphology was obtained from a variety of peer-reviewed literature sources (primarily, Kubo et al. 2019) and was inferred based on family and order for extinct taxa if specific morphological studies (e.g. Janis et al. 2014) were unavailable. Limb morphology and was treated as three binary variables: digitigrade, plantigrade, and unguligrade (Table S1).

All trait data were cross-referenced with the primary literature or handbooks (e.g. Wilson and Mittermeier 2009-2019). Diet data was unavailable for 14 extinct species (of 427 total). We imputed their diets based on their phylogenetic relationship to other species with known diets and traits using the R package “Rphylopars” v. 0.2.9 (Goolsby et al. 2017) and PHYLACINE phylogeny. “Rphylopars” was run with all default parameters including a Brownian motion evolutionary model.

Analytic Methods

We calculated a Gower distance matrix that evaluated pairwise functional similarity between species. Gower distance is a flexible distance-based measure that can incorporate multiple variable types and has been widely used in analyses of community trait composition and structure (Safi et al. 2011, Mazel et al. 2014).

We weighted traits when calculating Gower distance, with mass weighted by two; diet, fermentation, and habitat weighted by one; and limb morphology weighted half (Table S1). Mass was weighted by two as it is correlated with many other life history traits, such as reproductive and metabolic rate. Limb morphology was weighted half because, although it captures morphological diversity and disturbance-related effects, the relationship between it and ecosystem effects is less well established. Other weighting methods produced similar results but trait spaces were less biologically interpretable (e.g. body mass had no visible correspondence to trait space axes, see sensitivity analyses in SI Appendix, Fig. S8 & S9).

Multidimensional trait spaces were constructed using the function *dbFD* in the R package “FD” (Laliberté et al. 2014).This conducts principal coordinates analysis (PCoA) on the Gower’s distance matrix to produce synthetic traits which become the axes of the multidimensional trait space. We used the first four axes of the PCoA after reviewing axis quality (SI Appendix, Fig. S10) and because including more than four axes has been shown to distort functional relationships across a variety of real and simulated datasets (Maire et al. 2015). The relationship between PCoA axes and traits was determined using the R function *envfit* in the R package “vegan” with 1000 iterations (Oksanen et al. 2019).

A number of functional diversity metrics exist to describe different attributes of the structure of trait spaces. Since we were primarily interested in the range of functions present, we focused on functional richness, which is a measure of the multidimensional volume of trait space (Villeger et al. 2008). To understand if introduced herbivores restore lost LP trait combinations or contribute novel ones by introducing traits without LP analogs, we calculated trait space overlap with the function *beta.functional.pair* in the R package “betapart” (version v1.5.1) (Baselga et al. 2018), which returns a

Sørensen dissimilarity metric decomposed into its primary components of nestedness and turnover.

To understand if introduced species are functionally most similar to native or extinct taxa we identified the nearest neighbor of each introduced species from the Gower distance matrix. We filtered pairs by Köppen-Geiger (Kottek et al. 2006) climate zones to prevent comparing species with different physiological tolerances (e.g. arctic species with desert species). We further constrained pairs by body mass bins to prevent spurious pairings between species with identical diet and morphological traits but gross differences in body mass (e.g. without body mass filtering, the 800 kg *Camelus dromedarius'* nearest neighbor is a 166 kg kangaroo because of convergence in all other traits, see SI Appendix, Fig. S11). Body mass bins were calculated using the Sturges algorithm (Sturges 1926), which finds natural break points in continuous distributions and reduces analytic bias. To assess the quality of functional analogy between introduced herbivores and their nearest neighbors, and to accommodate the intrinsic distinctiveness of certain species, we calculated the number of extant species, per body mass bin and climate zone, that are more similar than the introduced analog. To understand whether introduced species restore key metabolic functions in their new homes we classified herbivores into functional groups, as unique combinations of dietary guild and body mass bins (as determined above). Dietary guild (grazer, browser, and mixed feeder) was classified from the twin ordinal diet scores for graze and browse (see Table S1).

Supplemental Information

Species List Sensitivity

We conducted our analyses using the dataset published in PHYLACINE (Faurby et al. 2018). However, other species lists for the LP exist and can differ drastically. One such dataset, published by Smith et al. 2018 (Smith et al. 2018), contains 3 fewer total species than PHYLACINE, but 26 more extinct species and 33 fewer extant species (Fig. S4). These differences show a taxonomic signal, with Smith et al. 2018 reporting more extinct perissodactylas and diprotodons, and PHYLACINE reporting more extant cetartiodactylas and primates (Fig. S4)

To understand if discrepancies between PHYLACINE and Smith et al 2018's species lists and others could affect our results, we conducted all major analyses using the species list published in Smith et al. 2018. However, unlike Smith et al. 2018, who analyzed Europe and Asia as Eurasia, we chose to analyze our data with Europe and Asia separate, given their divergent socio-biogeographic histories since the LP.

Overall, we found strong concordance between the results using either PHYLACINE or Smith et al. 2018's datasets (Fig. S5-S7). Changes in species richness from extinction and introduction remained largely the same (Fig. S5), as did changes in functional richness (e.g. volume of trait space) (Fig. S6A and C). The functional beta diversity results (e.g. whether change in trait space reflects increasing similarity or dissimilarity) were qualitatively the same except for in Eurasia, where total dissimilarity *increases* slightly from introductions (Fig S6B and D). This is because of the absence of certain extant species in Smith et al. 2018's dataset, leading to the introduced rednecked wallabies (*Macropus rufogriseus*) falling outside of native-only functional space. Finally, the percent of introduced species most similar to extinct taxa varied only by decimal points between datasets, remaining at ~64%. This final analysis was not fully comparable between datasets as we did not have climate distributional data to constrain pairings for the Smith species list.

Trait Resolution

We chose traits that are strongly supported by empirical literature to influence the ecology of herbivores. All studies have inherent scales, meaning that the ecological patterns that emerge are dependent upon the scale chosen (Levin 1992). Our interest was to encapsulate herbivore trait variation over the last 100,000 years of Earth's history, which drives the emergent functional capacity of herbivore assemblages. Unwarranted precision in trait estimates at these broad spatiotemporal scales could lead to an artificial over-emphasis of ecological difference (e.g. every species becomes functionally unique), given the broad ranges of variation within species (Asevedo et al. 2012, Davis and Pineda-Munoz 2016, Rivals and Lister 2016). Likewise, organismal responses (e.g. of plants to herbivory) are unlikely to be so tightly coevolved with herbivore traits (e.g., lock-and-key coevolution) but rather driven by diffuse coevolution with suites of species (Jablonki and Sepkoski 1996). We therefore used categorial variables to capture fermentation type, limb morphology, and habitat use (SI Appendix, Table S1).

We collected two ordinal variables to describe diet, varying from 0-3 in importance, for browse and graze. While, diet is often treated categorically (e.g. Smith et al. 2015), our ordinal diet scores allowed a higher degree of resolution than in most studies to distinguish between obligate grazers, mixed-feeders, and browsers. Given the impossibility to separate fruit consumption from browsing among fossil taxa, frugivores were considered browsers. The consumption of bamboo was considered browsing, as its heavy lignification makes it more chemically similar to wood than to grass (Van Soest 1996). Dietary data was collected from a variety of peer reviewed sources and either collapsed into the ordinal scale from continuous data (e.g. stomach contents, isotope values) or from expert estimates (e.g. a "specialized grazer" would receive a 3 for graze and a 0 for browse). These two ordinal scores provided a high degree of resolution in dietary trait values, while still encapsulating intra-specific variation.

Grazing and browsing remain paradigmatic axes of dietary differentiation among herbivores, involving a suite of evolutionary adaptations in cranio-dental morphology, tooth-enamel hardness, and skull morphology that have appeared independently in all major herbivore lineages (Gordon and Prins 2019). Likewise, these axes of dietary differentiation control the capacity of herbivores to affect broad components of vegetation and drive downstream effects on global processes, such as climate (Cromsigt et al. 2018). The differentiation between grazers and browsers are keystone to many studies of herbivore ecology, both in extant and extinct systems (Janis et al. 2000, Hempson et al. 2015a, Cromsigt et al. 2018, Faith et al. 2019).

Table S1. Functional traits used in analyses, with descriptions on variable types, weightings used in the calculation of Gower distance, the primary types of sources, and notes on trait collection and analysis.

Trait	Type	Value	Weighting	Primary sources	Notes
Mass	Continuous	Log 10 kilograms, based on average species mass	2	PHYLACINE 1.2	Analyzed on log base 10 scale. Discretized into bins using Sturges algorithm for the dietary-mass group analysis and the filtering of nearest neighbors.
Diet: graminoids / browse	2 ordinal variables	0 (insignificant) – 3 (heavy consumption)	Each weighted 1/2; total weight of 1	Isotope analyses; micro and mesowear studies; eco-morphometrics; coprolites	Graminoid and browse consumption were treated as separate ordinal variables following MammalDiet (Kissling et al. 2014). Each dietary element was weighted by 1/2 in the calculation of Gower distance. Fruit consumption was included with browse. Grass seed and bamboo consumption were considered browse (following Van Soest 1996).
Fermentation Type / Efficiency	1 categorical / ordinal variable	Simple gut (efficiency = 0), Hindgut Colon (1), Hindgut Caecum (1), Foregut non-ruminant (2), Ruminant (3)	1	Peer reviewed literature; phylogenetic inference	Fermentation type was collected as a categorical variable with 5 levels but was ranked as an ordinal variable in terms of efficiency (0-3) for the calculation of Gower distance.
Habitat use	3 binary variables	Aquatic (0 or 1), Terrestrial (0 or 1), Arboreal (0 or 1)	Each weighted 1/3; total weight of 1	Eco-morphometrics, isotopes	Use of particular habitats (aquatic, terrestrial, arboreal) was given a 0 or 1 and were not exclusive (e.g. an herbivore with 1 for arboreal and 1 for terrestrial would then be semi-arboreal).
Limb morphology	Categorical	Plantigrade, Digitigrade, Unguligrade	1/2	Peer reviewed literature, phylogenetic inference	Limb morphology was treated as an unranked categorical variable in calculation of Gower distance.

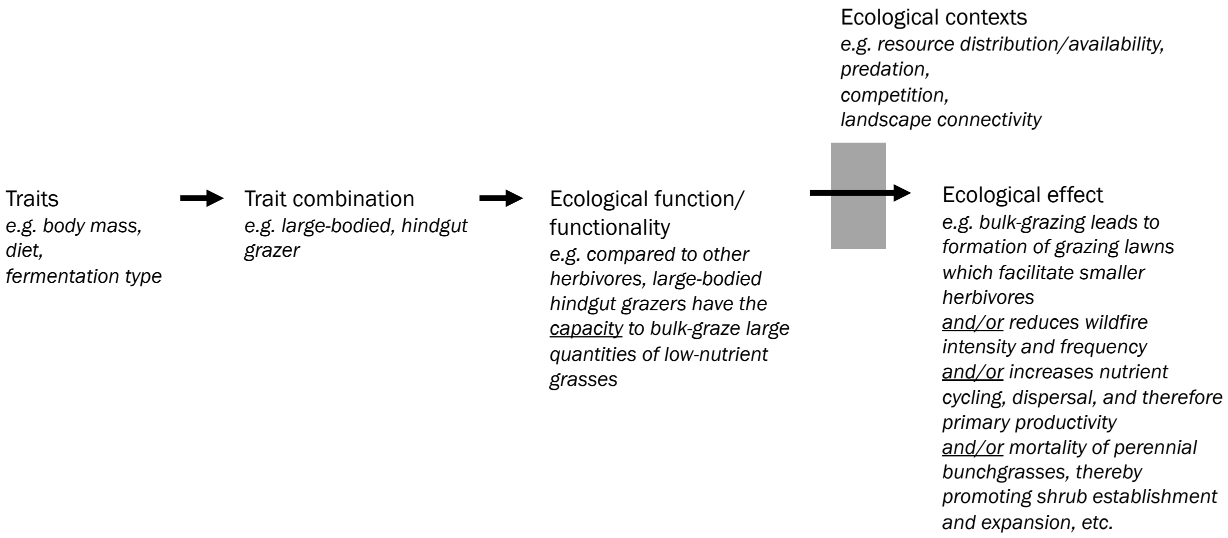

Figure S1. Schematic glossary of key functional ecology terms as used in text. The term ‘function’ has a diverse usage, particularly between the fields of functional ecology and ecosystem services. We here define ‘function’ as the capacity of organisms to affect their environment. The actual effect of an organism’s ‘function’ is emergent and depends on ecological contexts, such as resource distribution and availability, soil type, predation pressure, competition, or landscape connectivity.

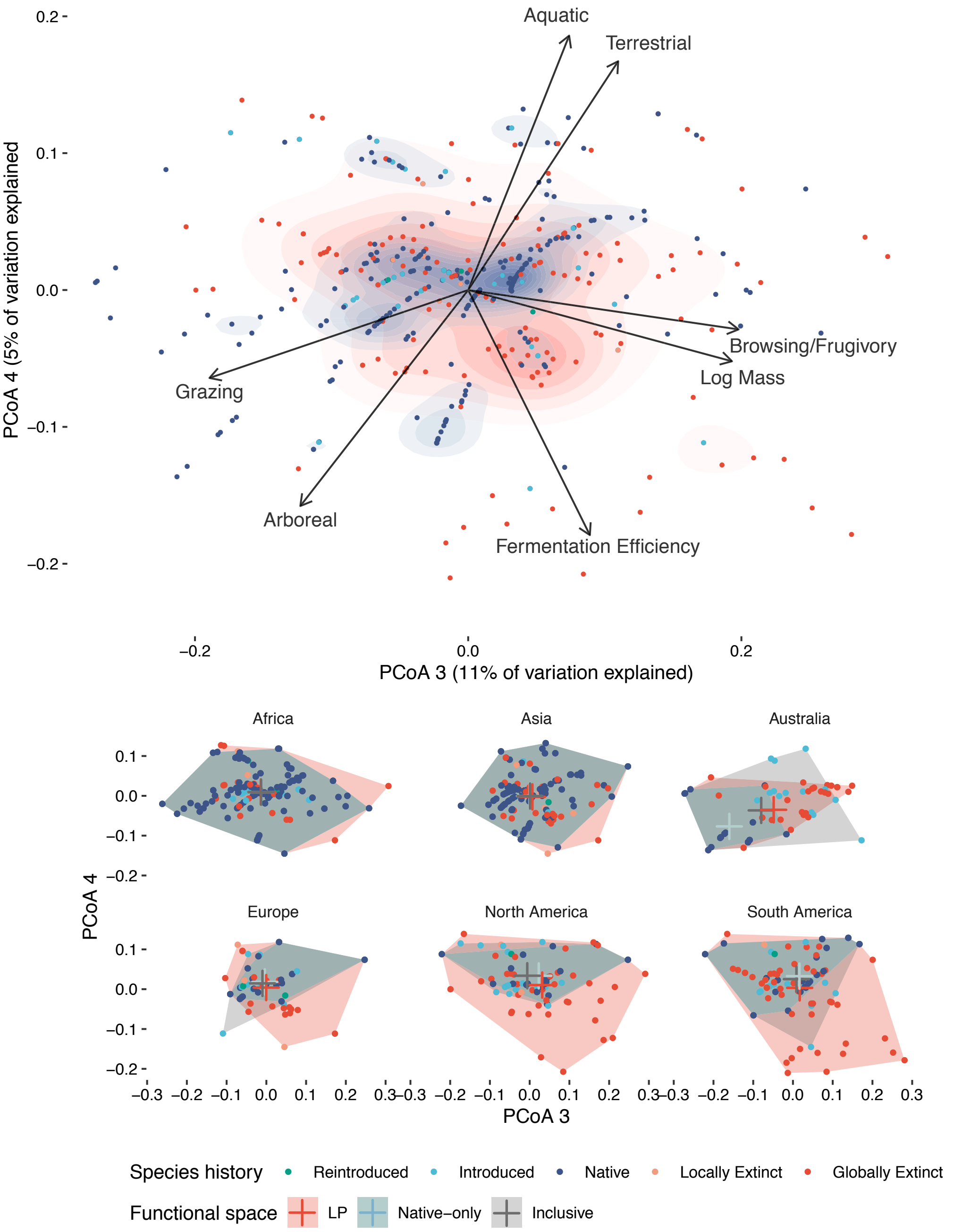

Figure S2. The third and fourth axes of herbivore trait space. PCoA 1-4 were used in subsequent beta diversity and functional richness analyses. (**A**) PCoA 3 (11% of total variation explained) and PCoA 4 (5% of total variation explained) were primarily shaped by grazing (r = -0.53), browsing (r = 0.46), log10 body mass (r = 0.45), and unguligrady (r = 0.34). (**B**) Trait space change for PCoA 3 and 4 across continental assemblages.

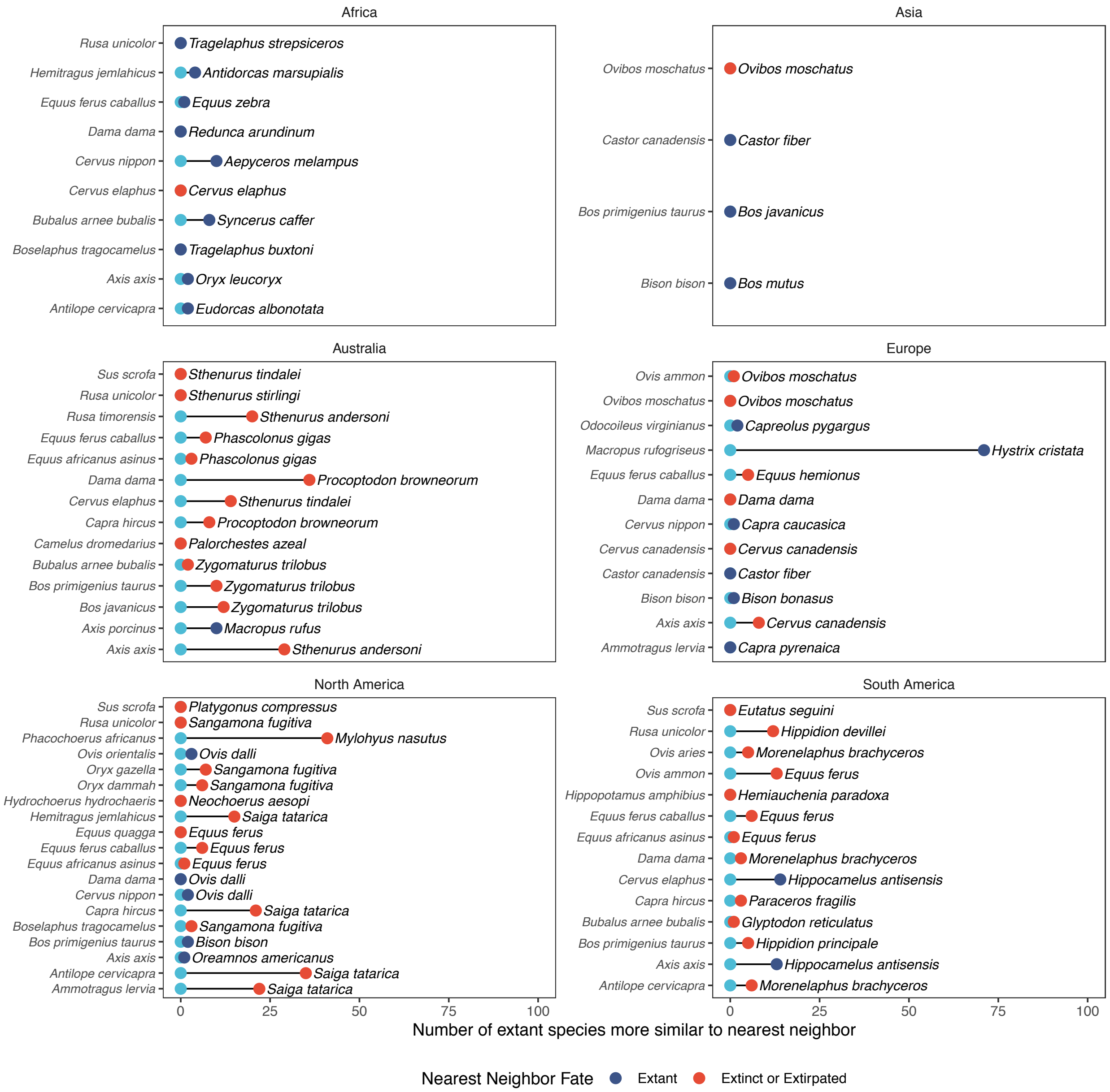

Figure S3. Introduced taxa and their nearest neighbors. Point color indicates if nearest neighbor is extant or extinct. The x axis shows the number of extant species (per body mass bin and climatic tolerance) that are more similar than the introduced analog.

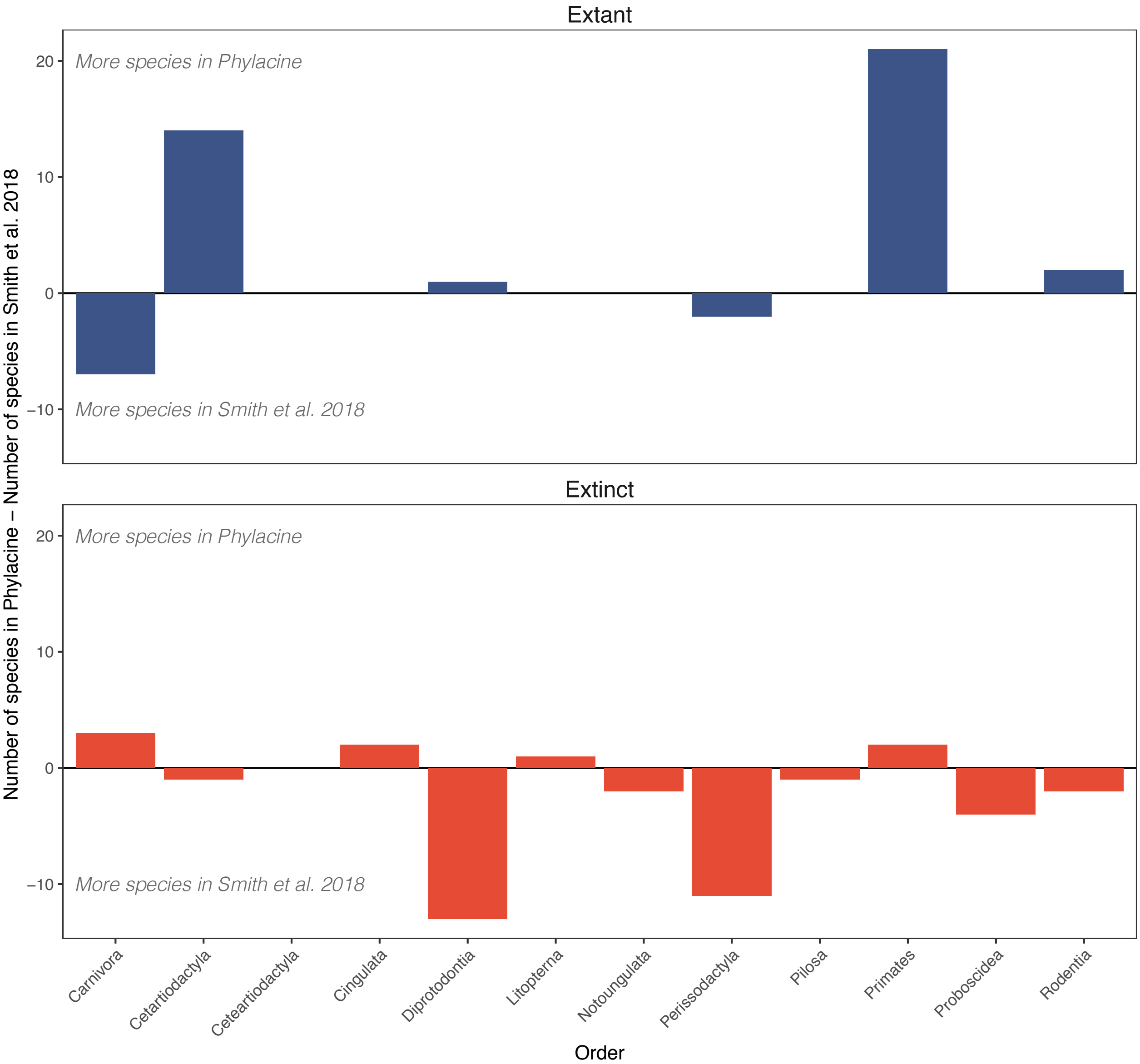

Figure S4. **Discrepancy between the Phyacine species list and Smith et al. 2018 species list.** The Phylacine species list contains 419 total species and 149 extinct species, while Smith et al. 2018's species list contains 416 species and 175 extinct species. Biases between the number of species included, and inter-order biases, could lead to different functional outcomes of extinction and introduction.

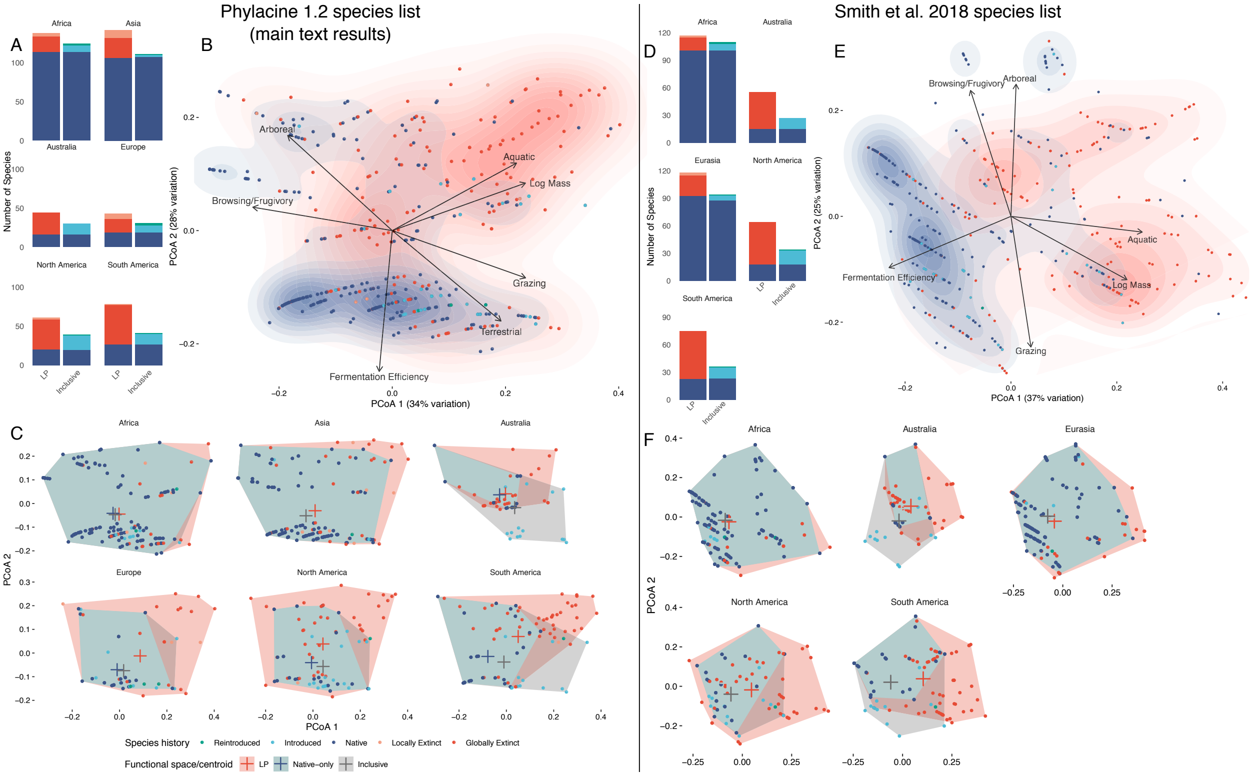

Figure S5. Primary analysis of species changes and trait space changes when using Phylacine's species list (A-C) and Smith et al. 2018's species list (D-F). Although results differ qualitatively, overall patterns and degrees of species richness replacement and trait space change remain similar.

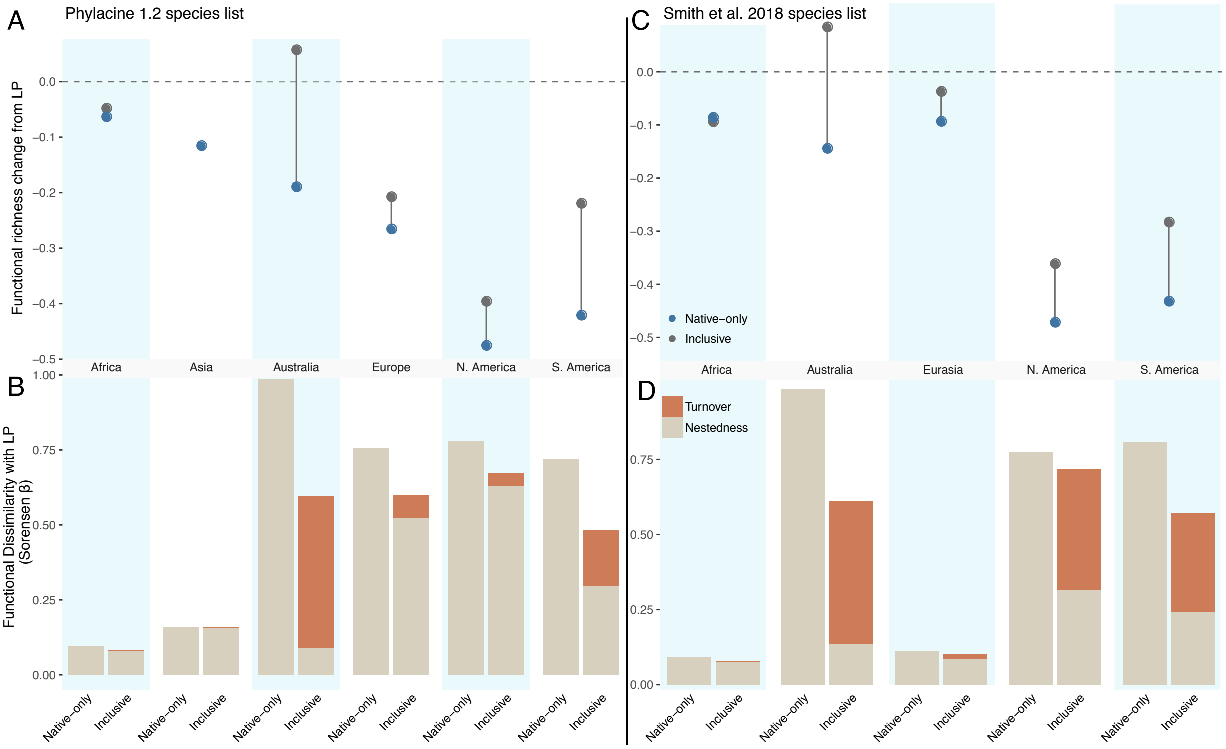

Figure S6. Functional richness and beta diversity results with Phylacine species list and Smith et al. 2018's species list. Subplots (**A**) and (**C**) show trait space change (functional richness) since the LP, while (**B**) and (**D**) show beta diversity change between LP and native-only and inclusive assemblages. Overall, results are qualitatively the same, with one exception. Inclusive assemblages in Eurasia are *more* dissimilar to the LP than native-only ones. This is driven by a discrepancy in the inclusion of extant species in Smith et al 2018's dataset, towards which the introduced *Macropus rufogriseus* is most similar.

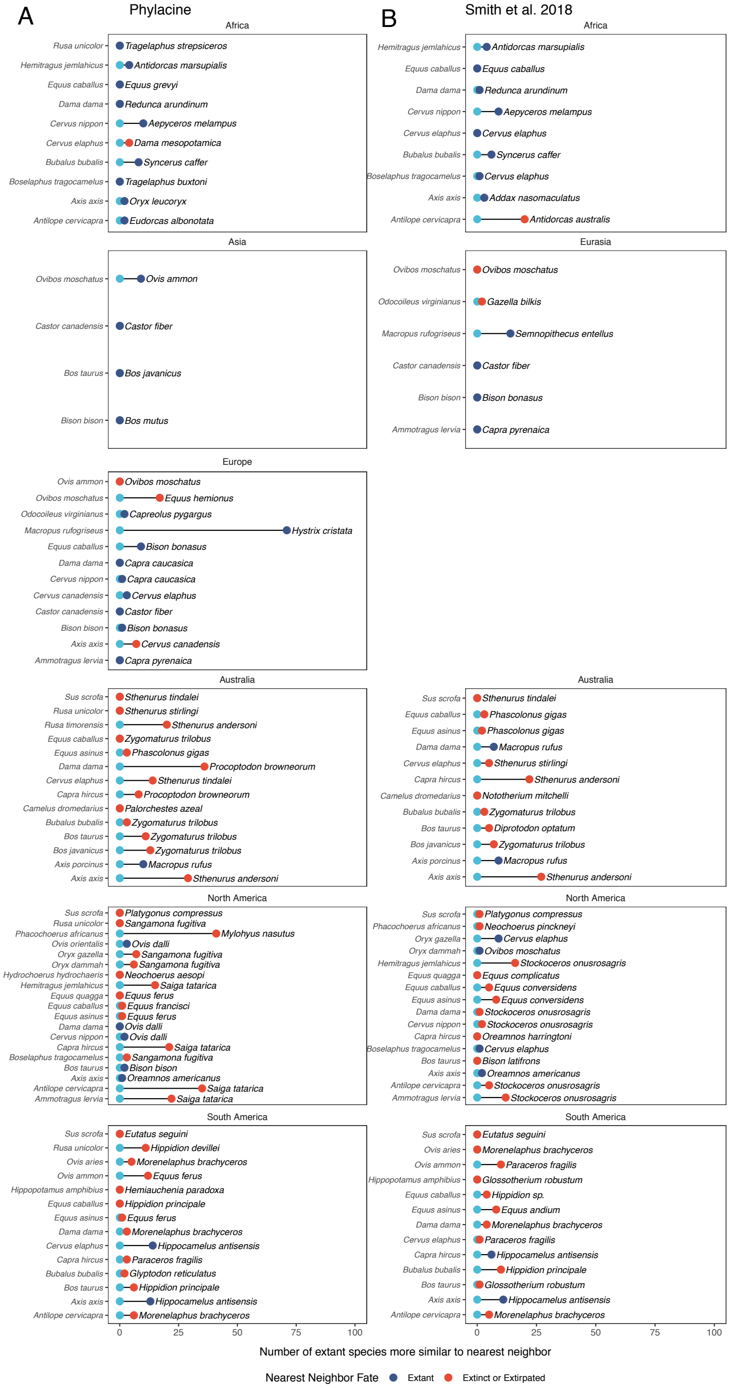

Figure S7. Nearest neighbor analysis sensitivity between Phylacine and Smith et al. 2018 species lists. Using either species list, 64% of introduced species' nearest neighbors are extinct. Note that some introduced species are not in the Smith et al. 2018 dataset and are thus excluded (e.g. *Rusa/Cervus unicolor* and *Rusa/Cervus timorensis*).

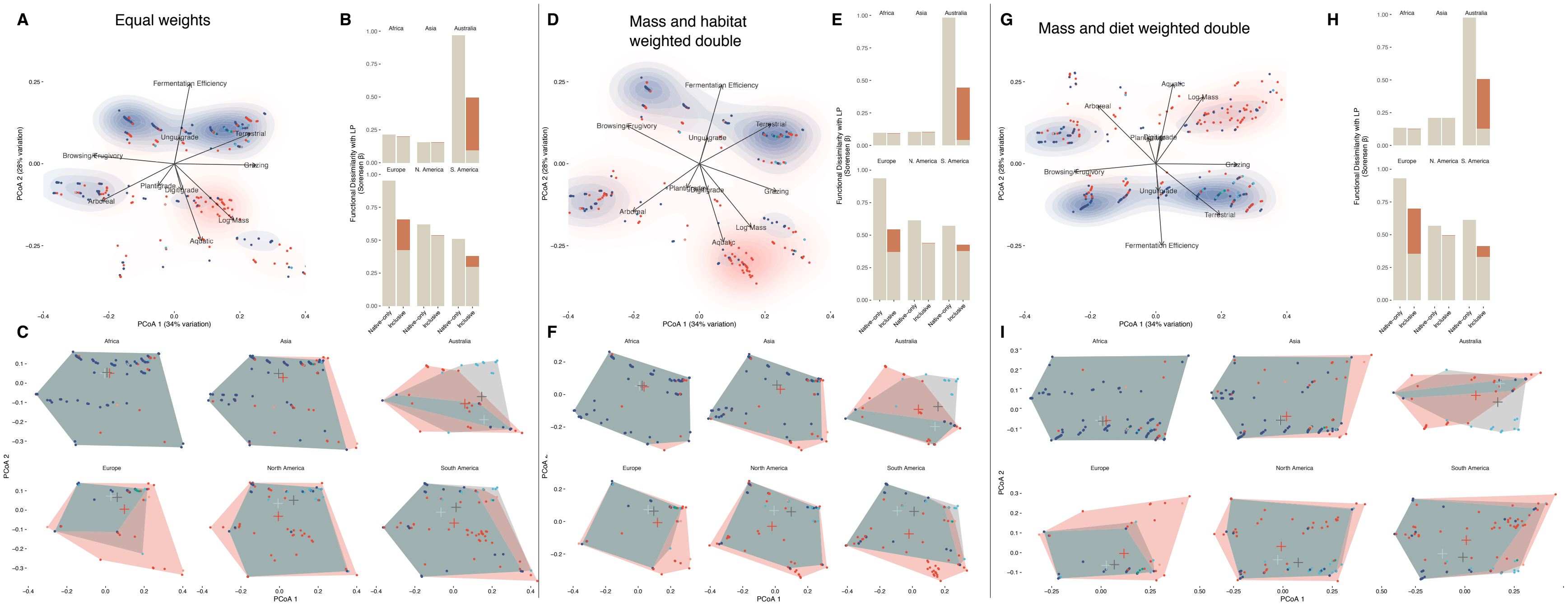

Figure S8. Key trait space results under different weighting scenarios. We did sensitivity analyses by trying 3 additional, biologically defensible weighting scenarios to the one reported in the main text: all traits weighted equally (A-C); *mass and diet weighted double any other* (D-F)*; mass and habitat weighted double any other* (G-I). The interpretability of global trait space (e.g. panel a) vary under different weighting scenarios, but key results do not.

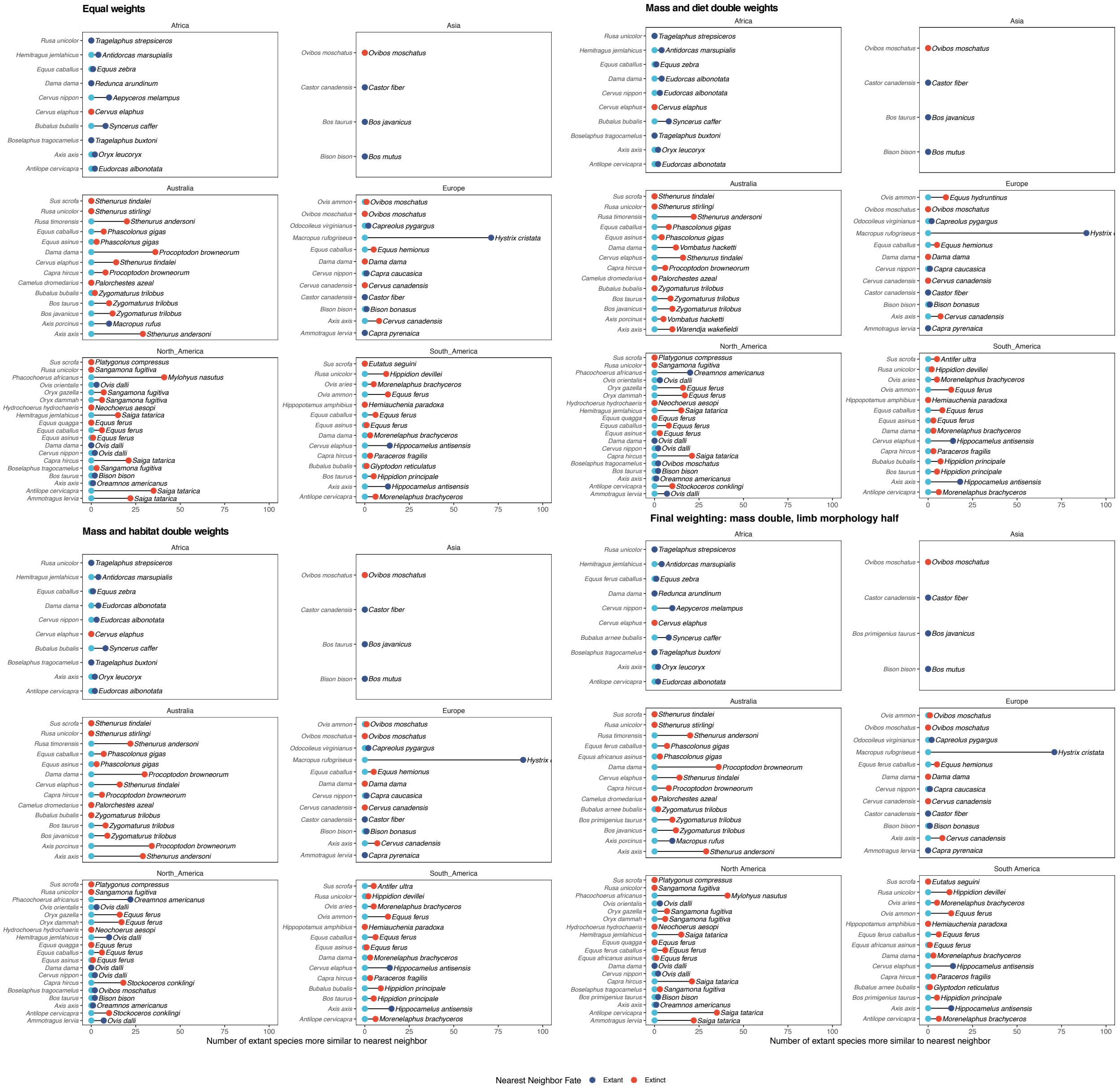

Figure S9. Change in nearest neighbor results under different weighting scenarios. The four scenarios used were: all traits weighted equally; mass and diet weighted double any other; mass and habitat weighted double any other; and the final, main text, weighting of mass double, foot half, all others equal. Under the different weighting scenarios, the percent of introduced species most similar to extinct species changes by no more than 4% (ranging from 60% to 65%): equal weights = 62%; mass and habitat double = 60%; mass and diet double = 62%

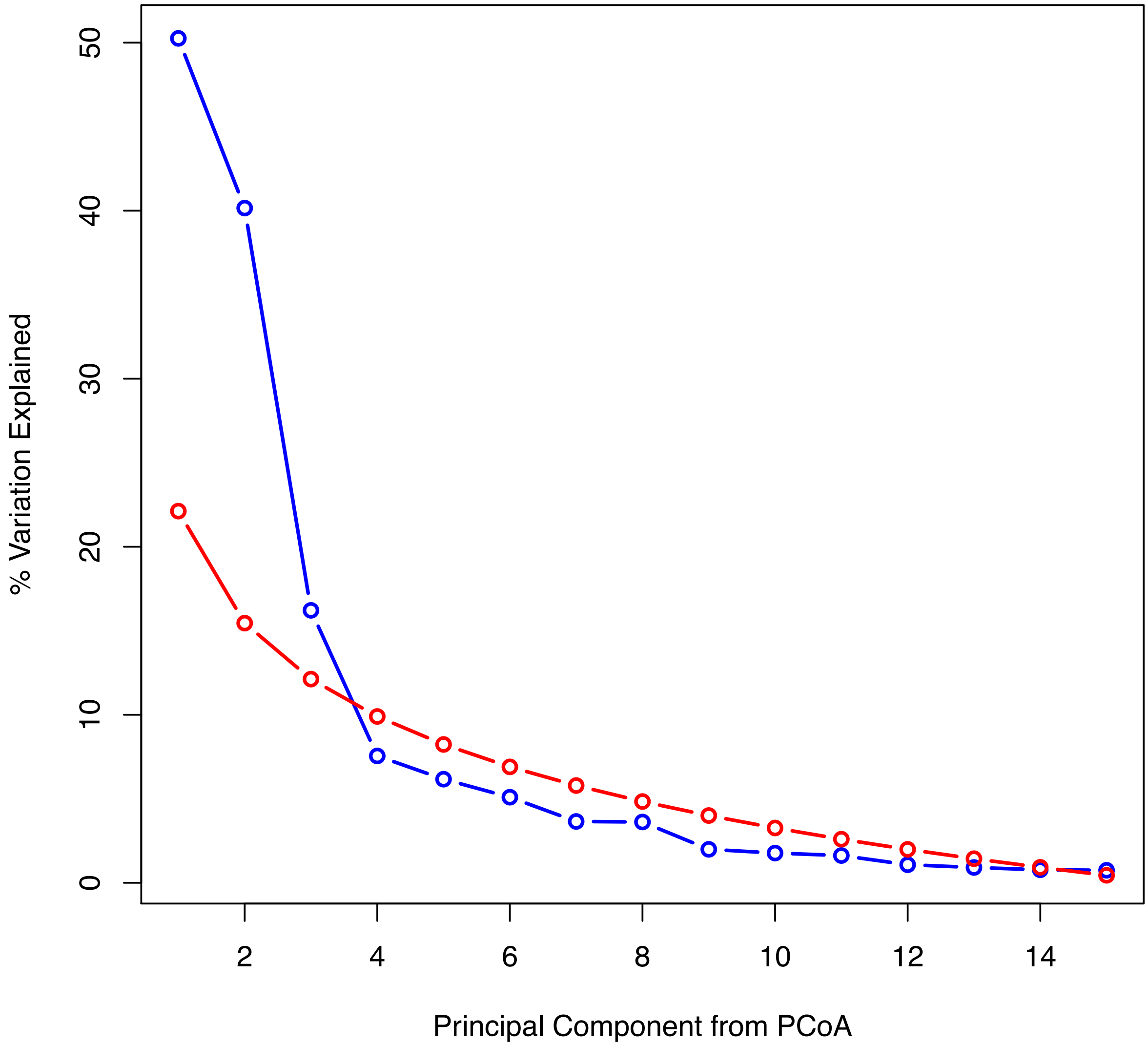

Figure S10. Eigenvalues from PCoA on Gower's distance matrix. Y-axis indicates percent of inter-species trait variation explained by each axis. Blue lines indicate axis quality of actual data, whereas red lines indicate simulated broken stick values. Given that the two intersect near axis 4, we retained 4 PCoA axes in all subsequent trait space analyses.

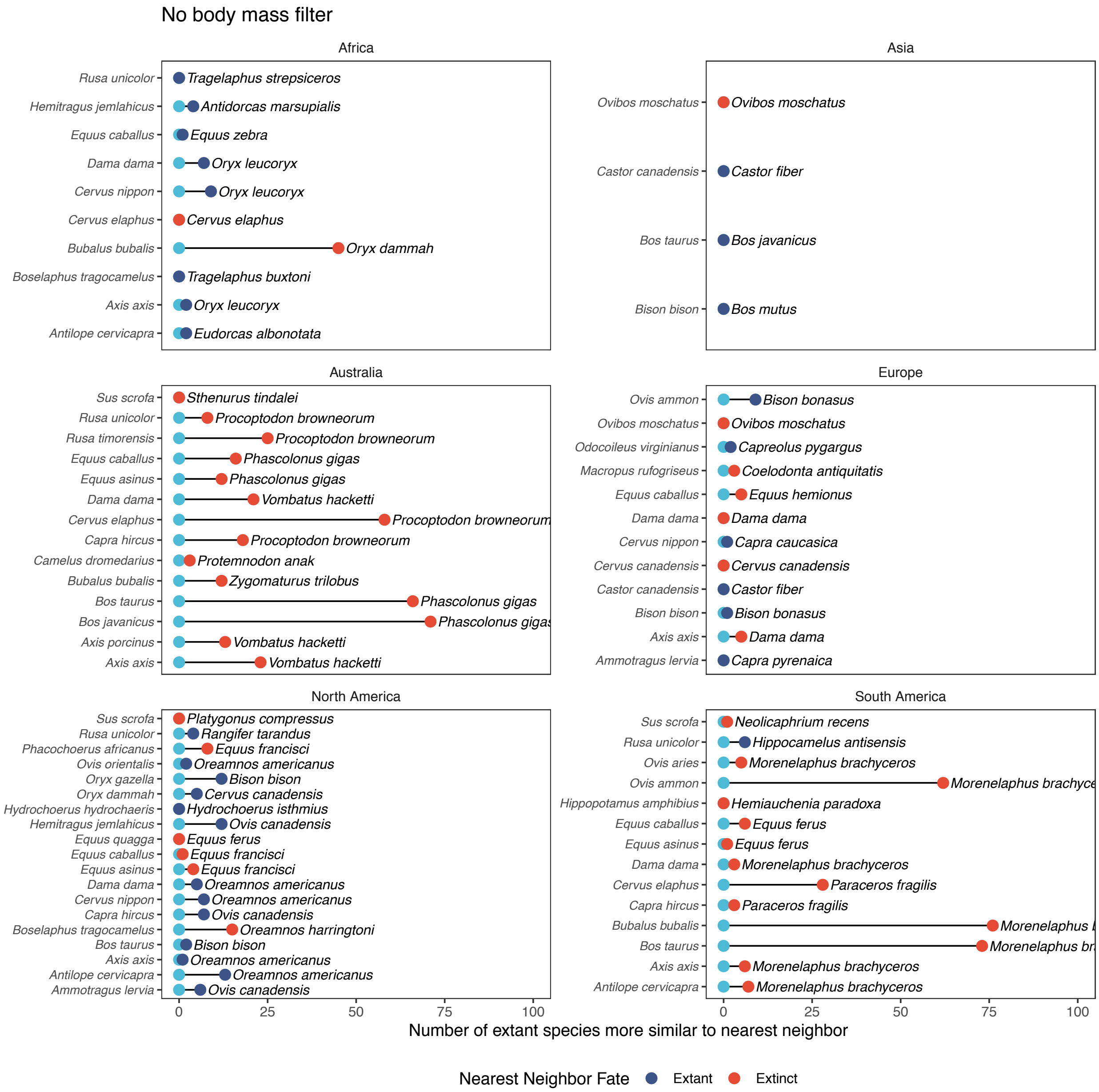

Figure S11. Introduced taxa and their nearest neighbors when not filtered by body mass. Although overall statistics remain nearly the same (58% of introducd species most similar to extinct species without body-mass filtering, versus 64% with filtering), comparisons become non-intuitive, as small-bodied species became paired with large-bodied ones due to strong convergence in other traits.

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Chapter 3: Equids engineer desert water availability

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Abstract

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 m 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 adjacent dry sites and by mimicking flood disturbance equid wells became nurseries for riparian trees. Our results suggest that equids, even those that are reintroduced or feral, are able to buffer water availability, which may increase resilience to ongoing human-caused aridification.

Main Text

Terrestrial large herbivores (henceforth megafauna) have undergone extensive extinctions and range contractions beginning during the late Pleistocene (100,000-12,000 ybp) and continuing today (Barnosky et al. 2004, Ripple et al. 2015). While climate change at the end of the last glacial maxima may have played a contributing role (Metcalf et al. 2016), emerging consensus indicates that most prehistoric losses were driven by human activity (Barnosky et al. 2004, Ripple et al. 2015). In tropical and temperate ecosystems, megafauna declines are linked to the formation of closed woodlands, increased wildfire, and reduced dispersal of large-seeded plants (Malhi et al. 2016). Less is known, however, about how megafauna may have shaped dryland ecosystems, which comprise a third of the Earth's surface (Schlesinger et al. 1990).

Water is the main limiting resource in dryland ecosystems. It determines species composition, food web structure, and vegetation dynamics (Stromberg et al. 2007, McCluney et al. 2012). 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. 1A-D, see Table S1 for review). We evaluated well digging and its associated ecosystem effects in a North American system where equids have been inadvertently reintroduced as feral populations.

We surveyed four Sonoran Desert groundwater-fed streams every 2-4 weeks over 3 summers (Table S2). At each site we mapped 'background' (e.g., already present) and 'equid well' water (Data S1, Lundgren et al. 2021a). Streams were 7-32 km apart and were ~300-1,800 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 1,450% (Fig. 1F).

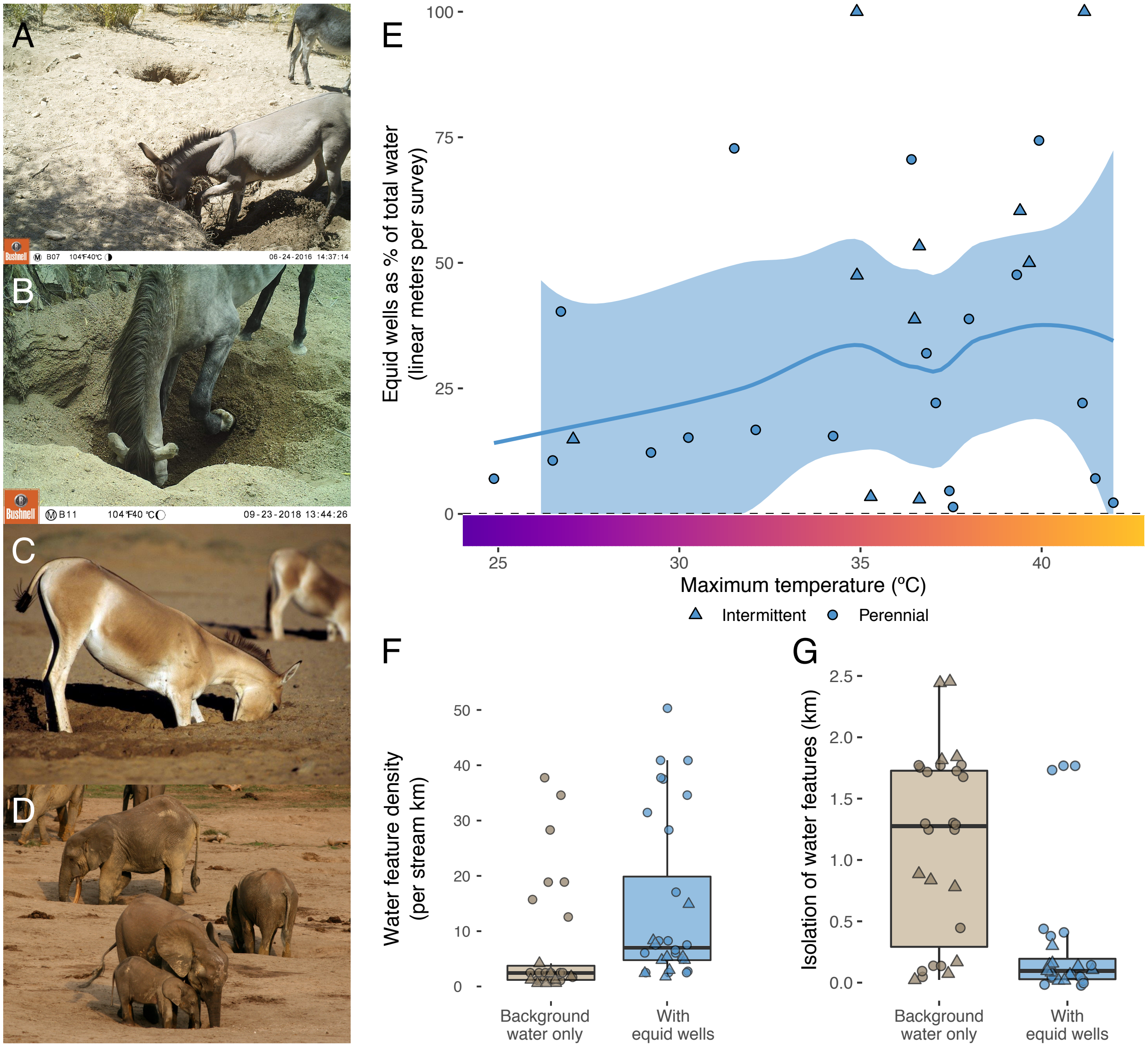

Fig. 1. Well digging increases water availability in desert streams. Well digging by: **A.** wild donkeys (*Equus africanus asinus*) and **B.** wild horses (*Equus ferus caballus*) in the Sonoran Desert, USA; **C.** kulan (*Equus hemionus*) in Mongolia; and **D.** African elephants (*Loxodonta africana*). **E.** The contribution of equid wells increases with temperature. Each point shows the percent of total water provided by equid wells at each survey and site, measured in meters parallel to direction of stream flow. Line and fill show loess regression and confidence intervals. Maximum daily temperatures from PRISM (PRISM Climate Group 2020). **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. **A** and **B** by EJL, **C** by P. Kaczensky**, D** by R. Ruggiero.

Isolated water features can be areas of heightened antagonistic interactions among wildlife, including predation, disease transmission, competition, and herbivory (Thrash et al. 1993, Rogerson et al. 2008, Atwood et al. 2011). 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 animals must travel to 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 3,258 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 <100g in body mass to control for poor detection probabilities for small species.

Overall, we detected 59 vertebrate species at equid wells, of which 57 were recorded drinking (Fig. 2A-D, Table S3, Data S2, Lundgren et al. 2021a). 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, $p<0.0001$), and visit frequency was 91% and 60% higher on average (t ratio=-11.3 and -16.32 $p<0.0001$, Fig. 2E-G). 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).

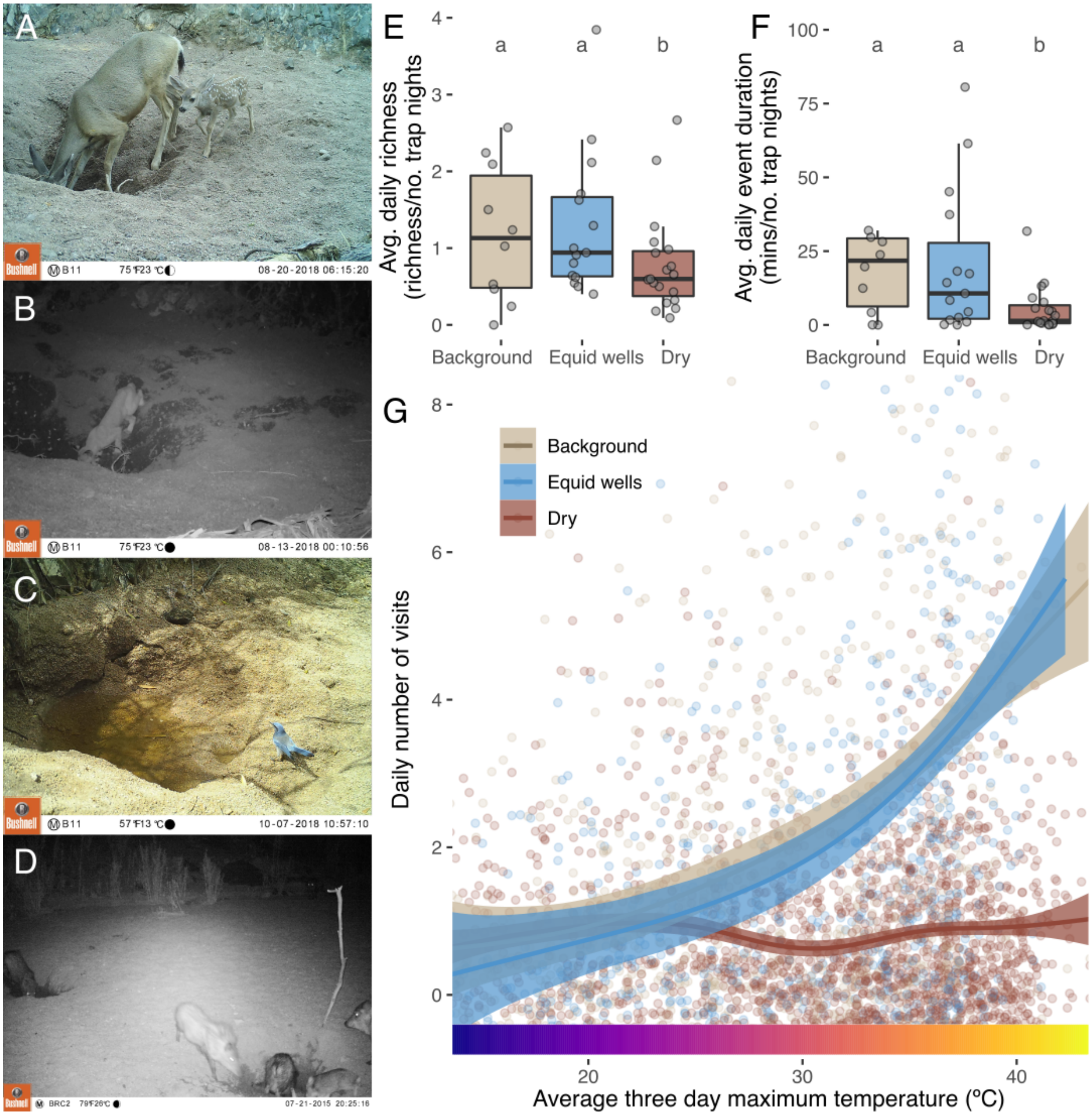

Fig. 2. Use of equid wells by vertebrates. A-D. Use of equid wells by select species: **A.** mule deer (*Odocoileus hemionus*), **B.** bobcat (*Lynx rufus*), **C.** Woodhouse's Scrub-

Jay (*Aphelocoma woodhouseii*), and **D.** javelina (*Pecari tajacu*). **E.** Average daily species richness and **F.** daily visit duration, by camera station, relativized by number of trap nights. Letters (a, b) indicate significance groupings ($p<0.001$). **G.** Daily visit frequency by average three-day maximum temperature (°C). Points indicate days. Line and fill illustrate generalized linear model of relationship between temperature and visit frequency. Equids and vertebrates <100g (e.g. small passerines and mice) were excluded from analyses, the latter due to poor detection probabilities for small species. Domestic cattle were analyzed separately because of high but inconsistent stocking rates through the season (Fig. S1).

Responses were similar across vertebrate body sizes (Fig. S2) and species composition did not vary between resource types (PERMANOVA: $F=0.9$, $p=0.7$, Fig. S3). Domestic cattle activity showed a similar pattern but was analyzed separately, as cattle densities were determined by humans and fluctuated during the study period (Fig. S1, Table S4).

Some of the species drinking from equid wells were free-water dependent, such as mule deer (*Odocoileus hemionus*), whose summer distribution is shaped by surface water (Table S3, Rautenstrauch and Krausman 1989). 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 (Allen et al. 2014). 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 (McCluney and Sabo 2009).

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 (Stromberg et al. 2007, Shafroth et al. 2017, González et al. 2018). We collected data on germination and establishment of these trees across available habitats and found higher seedling density in equid wells than adjacent moist riverbank zones (89% of seedlings, W=109, p=0.007, Fig. 3B), a difference which persisted after typical summer mortalities (χ2=54.6, p<0.0001, Fig. 3B, Data S2, Lundgren et al. 2021a).

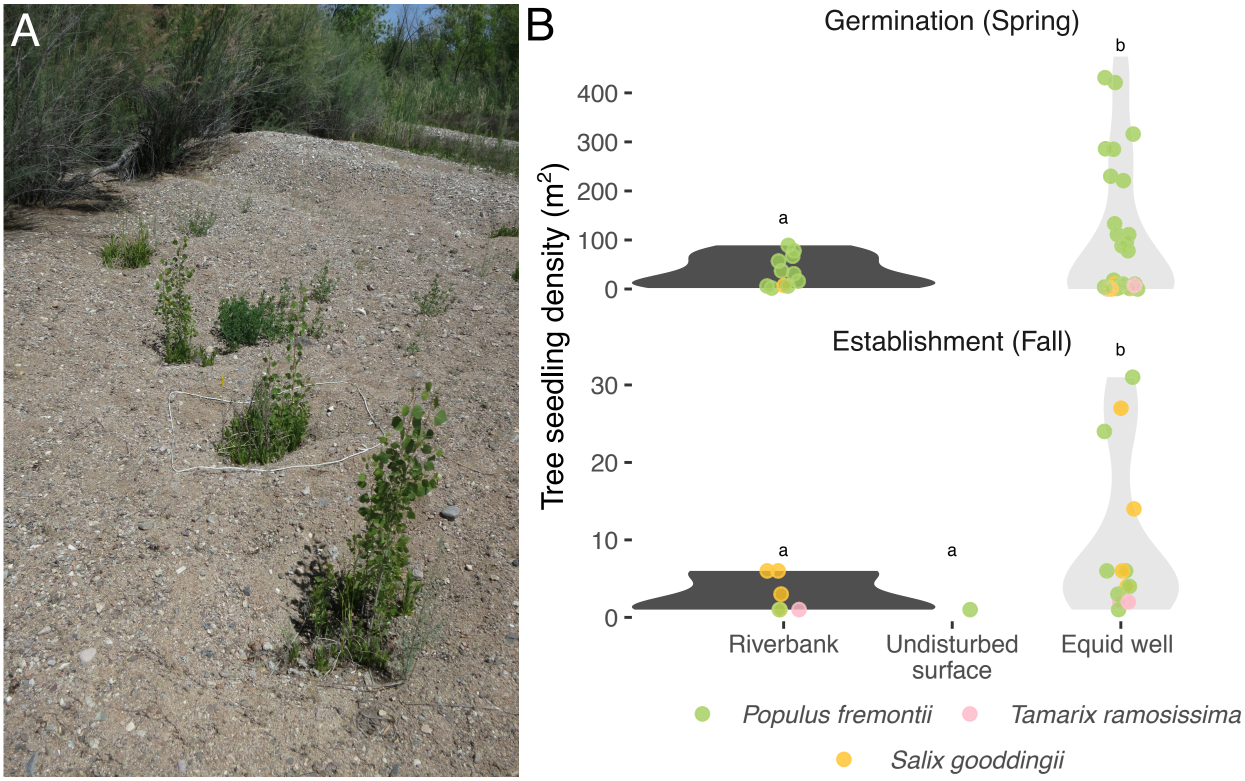

Fig. 3. Equid wells function as germination nurseries for riparian pioneer trees. A. Fremont cottonwood (*Populus fremontii*) in a series of abandoned equid wells. **B.** Seedling density between riverbank germination zones, undisturbed surfaces, and equid wells. Filled intervals behind points indicates density distribution of seedlings.

While riverbanks provided the moist substrate necessary for germination, they were 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 (Stromberg et al. 2007, Shafroth et al. 2017). 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 (Malhi et al. 2016), 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 ($p<.00001$, 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 the Earth (Datry et al. 2017), were where equid wells had the strongest effects on water availability. Stream intermittency is projected to increase as currently perennial streams lose yearlong flows (Burrell et al. 2020) and as drylands expand (Fig. 4, Beck et al. 2018) as result of groundwater mining, agriculture, and climate change (Datry et al. 2017). These reductions in water availability, coupled with rising temperatures, are projected to have strong effects on biodiversity and ecosystem function (McCluney et al. 2012). Our results suggest that equids and other well-digging megafauna have the potential to mitigate these changes, whether native or introduced (Fig. 4).

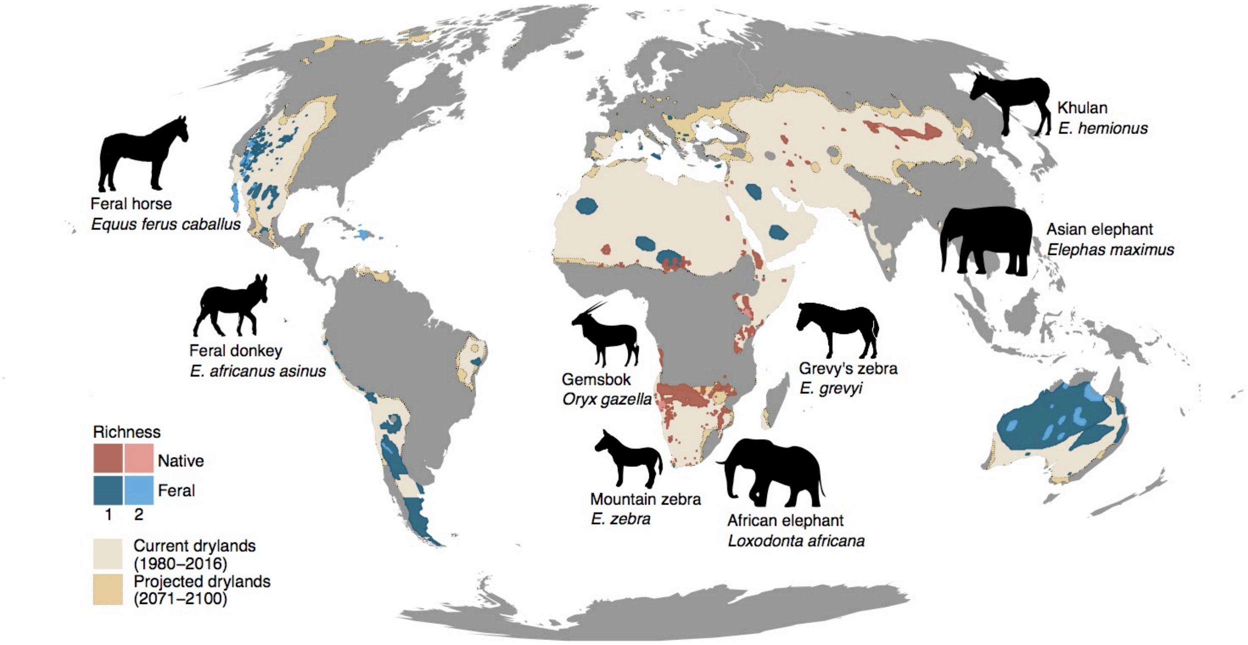

Fig. 4. Well-digging megafauna contribute the capacity to buffer water availability across many drylands. Species richness of native and introduced megafauna known to regularly dig wells ≥0.5 m in depth, overlaid on global drylands, which are highlighted in light brown (semi-arid + arid Köppen-Geiger climate zones, Beck et al. 2018). 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 IUCN Red List 2018, Wallach et al. 2019). Projected dryland expansion is based on business-as-usual emissions (RCP 8.5).

Recent and ancient extinctions and range contractions of megafauna, and the loss of their distinct ecological functions, has led to highly modified modern landscapes (Malhi et al. 2016). While introduced megafauna have primarily been studied as threats to conservation goals (Wallach et al. 2018), growing evidence suggests that they present a countercurrent to ancient losses (Lundgren et al. 2018) and may replace lost ecological functions (Lundgren et al. 2020). 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.

Supplementary Materials

Materials and Methods

Well digging by feral equids has been documented in North America and Australia, but has never been formally studied. On the Flinders River in northern Queensland, Australia, wild horses (*Equus ferus caballus*) have been described digging wells deeper than their own height (~2m, Rolls 1969). We have documented well digging by wild donkeys in southern Australia, in the Painted Desert. Well digging has been documented in mesic ecosystems as well, where surface water availability may be limited by edaphic or geologic factors even with abundant precipitation. In particular, wild horses on Sable Island, Novia Scotia, Canada, have been reported digging wells to groundwater on the dry side of the island (Rozen-Rechels et al. 2015).

We conducted our study in the Sonoran and Mojave Deserts, North America, where feral donkeys and one band of feral horses were both observed digging wells. In our study sites, equid wells reached just over one meter in depth, though in one ephemeral, rainwater-fed system wild donkeys were observed digging wells deeper than their own height (~1.5-2 m deep) to water captured in sediment-filled stone basins. Equid wells were common in ephemeral rainwater-fed desert drainages and stone water catchments, and in groundwater-fed systems, including in the channels of intermittent streams and on the floodplains of perennial rivers, where they created water access points outside the density of streamside vegetation. Equid wells generally occurred in clusters of 5-30 wells, in open, unvegetated areas up to 3 km^2, and were observed year-round.

Effect of well digging on water availability

We selected four groundwater-fed streams to survey the effect of well digging on water availability. All sites were in separate drainages, 7-32 km apart (average 14.7 km), and 1-8 km (average 3 km) from other unmonitored streams. Sites were 0.3-1.8 km long (average 1 km) (see Table S2 for site descriptions, Fig. S5). All four sites had the potential to become intermittent (e.g. losing surface water as the water table becomes subsurface), however, like many dryland groundwater-fed springs, flow variability led to three of the four sites retaining perennial headwater springs during the survey periods. All sites had extensive downstream intermittent reaches, containing surface water only seasonally.

The full length of each site was surveyed every 2-4 weeks during the summers of 2015, 2016 and 2018 (Table S2). We followed water mapping protocols of The Nature Conservancy (Turner and Richter 2011). This consisted of georeferencing and measuring the length each water feature parallel to the direction of stream flow. From this, we were able to calculate the total linear meters and spatial distribution of ‘background’ (e.g. already present without well digging) and ‘equid well’ water features (Data S1).

The spatial pattern and density of distinct water features affects the distances animals must travel to drink, and the types and intensity of interactions that occur (e.g. Thrash et al. 1993, Bright and Hervert 2005, Whiting et al. 2009). We therefore calculated how equid wells increased the density of water features (per survey km) and the isolation of water features using the R package ‘sf’ (v0.8-0). Isolation was calculated by averaging nearest neighbor distances (i.e. the distance of each water feature to only its nearest neighbor) with equid wells included and excluded. To avoid inflating isolation metrics we only included features >10 m apart from any other (thus only counting equid wells if >10 m from background water, and counting equid wells <10 m apart as a single feature). Metrics were calculated using the R package ‘geosphere’ v1.5-10. Since these metrics could not be calculated on surveys where background water was absent, the nearest two perennial water sources to each site, outside the survey area, were included in each calculation.

Equid wells as vertebrate resource points

To understand the value of equid wells to other vertebrate species we installed camera traps (Bushnell Trail Cam Pro) >100 m apart, at the same four Sonoran Desert water availability survey sites, and at an additional site in the Mojave Desert (Mojave National Preserve, permit MOJA-2018-SCI-0050, Table S2). At each site we monitored three resource types: equid wells, background waters, and dry controls. Dry controls were established randomly in similar vegetation, at least 100 m away from any water source. Overall, trail cameras recorded 446,817 images of vertebrate species, sampling a total of 957 trap nights at background water sources, 686 at equid wells, and 1,749 at dry controls (Data S2).

We visually identified all vertebrates to the best of our ability, using field guides as necessary (Sibley 2000, Reid 2007). Five taxa could only be identified to genus and one only to family. We excluded species <100 g from statistical analyses, due to inconsistent detection probabilities and because of uncertainty identifying mice and small passerines during low light conditions in camera trap images. We excluded wild equids as we were interested in the utilization of equid wells by other species. Cattle were analyzed separately because high but variable stocking rates would influence patterns of resource use across the study period.

We classified images into ‘visits’ based on contiguous activity by the same species, with no more than a fifteen-minute interval between images. We then quantified vertebrate activity patterns in terms of daily visit frequency, total daily visit duration, and daily species richness (number of unique species per day). Given that the importance of surface water is shaped by precipitation and temperature, we collected an ensemble of climate variables from PRISM, an interpolated 4 x 4 km climate dataset for North America (PRISM Climate Group 2020). Variables included daily maximum temperature, daily mean temperature, and daily precipitation. Since organismal responses to temperature and precipitation often exhibit lag periods (e.g. responding to conditions over prior days) (Rocklov et al. 2012) we derived eight lag variables: days since any precipitation ≥1 mm; days since precipitation ≥1 cm, total cumulative precipitation over the prior 3, 7, and 14 days; and average maximum temperature over the prior 3, 7, and 14 days.

We then used generalized linear mixed effect models in the R package 'glmmTMB' v1.0.1 to analyze how resource types (i.e. equid wells, background waters, and dry controls) and environmental variables influenced vertebrate activity. We chose distributions appropriate for each response variable and nested date within site as a random effect. We employed multi-model inference techniques to eliminate spurious and correlated environmental variables (Burnham and Anderson 2003). Across all analyses, omnibus tests were conducted with the 'Anova' function in R package 'car' v3.0-8 (Fox and Weisberg 2019), while post-hoc tests were conducted using the 'emmeans' package v1.4.7 (Lenth 2020).

To understand if resource use patterns differed by vertebrate body size, we compared the same response variables (daily richness, duration, and event frequency) by three body size classes, consisting of <1 kg, 1 kg – 10 kg, and ≥10 kg. Furthermore, we conducted a PERMANOVA on a Bray-Curtis dissimilarity matrix to test if species composition was significantly different between resource types. We visualized the dissimilarity in species composition between camera stations with a Principal Coordinates Analysis (PCoA). The PERMANOVA was conducted in the R package 'vegan' v2.5-6 (Oksanen et al. 2019) while the PCoA was performed in the R package 'ape' v5.4 (Paradis and Schliep 2019).

Equid wells as vegetation nurseries

The recruitment of riparian trees in abandoned equid wells was observed on the Bill Williams River in the Sonoran Desert of Arizona. Unlike the partially or fully intermittent study sites above, the Bill Williams River is a dammed perennial desert river characterized by a stable, flow regulated water table, multiple channels and extensive beaver ponds. Riverbanks are densely vegetated with cattails (*Typha* spp.) and other herbaceous plants.

Fremont cottonwood and Goodding's willow (*Salix gooddingii*) are important riparian, groundwater-dependent plants of the Bill Williams River and many dryland rivers. These trees possess adaptations reflective of many global ecologically important, early succession riparian tree species (henceforth 'pioneer' trees) including copious production of small seeds released in concurrence with seasonal flood events and low wood density and thus fast growth rates (Stella et al. 2006, Cooper and Andersen 2012, Stromberg and Merritt 2015). These traits are adapted for scouring floods which remove competing vegetation and deposit germination beds of bare moist mineral substrate (Shafroth et al. 2017). In the absence of floods, germination is limited to the moist soil of riverbanks: zones densely vegetated with herbaceous plants. As the Bill Williams River is a dammed system, it receives managed floods released to stimulate the germination of cottonwoods and willows if there is sufficient water in the upstream reservoir. At the time of the study, the last flood pulse had been released the year prior (2014) (gage #09426000, United States Geologic Survey 2020).

Based on observations of cottonwood recruitment in abandoned equid wells, we investigated whether these features provided a substitute for flood disturbance by creating access to bare moist mineral substrate and removing competing vegetation. We randomly selected five well clusters for spring germination surveys and follow-up fall establishment surveys. At each cluster, 10-15 1m^2 plots were randomly distributed among 3 potential germination zones: abandoned equid wells, undisturbed surfaces, and the nearest riverbank. Riverbank zones and undisturbed surfaces differ in their combinations of key variables important to pioneer tree germination and establishment. Riverbank zones have moist substrate but are densely vegetated, while undisturbed surfaces lack herbaceous vegetation but are dry. Undisturbed surfaces were not sampled during the spring germination survey, as they lacked seedlings, but were added in the fall establishment survey (n=9). Riverbank zone plots were 10-50 m from well clusters while undisturbed surface plots were placed randomly on the same geomorphic surface (e.g. sandbar) as the equid well cluster. All woody seedlings were counted and the percent cover of each herbaceous plant species was recorded (Data S2).

We compared spring germination rates between riverbank (n=24) and equid well (n=24) plots with non-parametric, paired Wilcoxon signed rank tests. To analyze fall survivorship data, we used zero-inflated Poisson mixed effect models, with site as a random effect. To understand the relationship between herbaceous cover and habitat type and between woody seedlings and herbaceous cover, we used zero-inflated negative binomial mixed effect models with season nested within site as a random effect. All analyses were conducted in R with the ‘glmmTMB’ v1.0.1 (Brooks et al. 2017). Omnibus tests were performed by the ‘Anova’ function in the ‘car’ package (Fox and Weisberg 2019) while post-hoc tests were conducted with the package ‘emmeans’ v1.4.7 (Lenth 2020).

Constraints on equid well digging

We surveyed for equid wells in the Southwestern USA and in Northwestern Mexico from 2015-19 by searching Google Earth for riparian vegetation, which is indicative of a water table within 1.5-2 m of surface (Lite and Stromberg 2005). To understand the constraints of well digging, we classified riparian systems based on substrate and general topographic position: (1) steep, mountainous cobble-dominated systems; (2) flood-prone systems with loose unconsolidated gravel and sand substrates; (3) silt and clay dominated systems; and (4) systems with compacted, mixed soil types with low flood disturbance (as indicated by lack of debris-wrecks and high organic matter in soils). We then conducted a mixed effect logistic regression using the R package ‘lme4’ v1.1-23, to understand how substrate type influenced the probability of well digging.

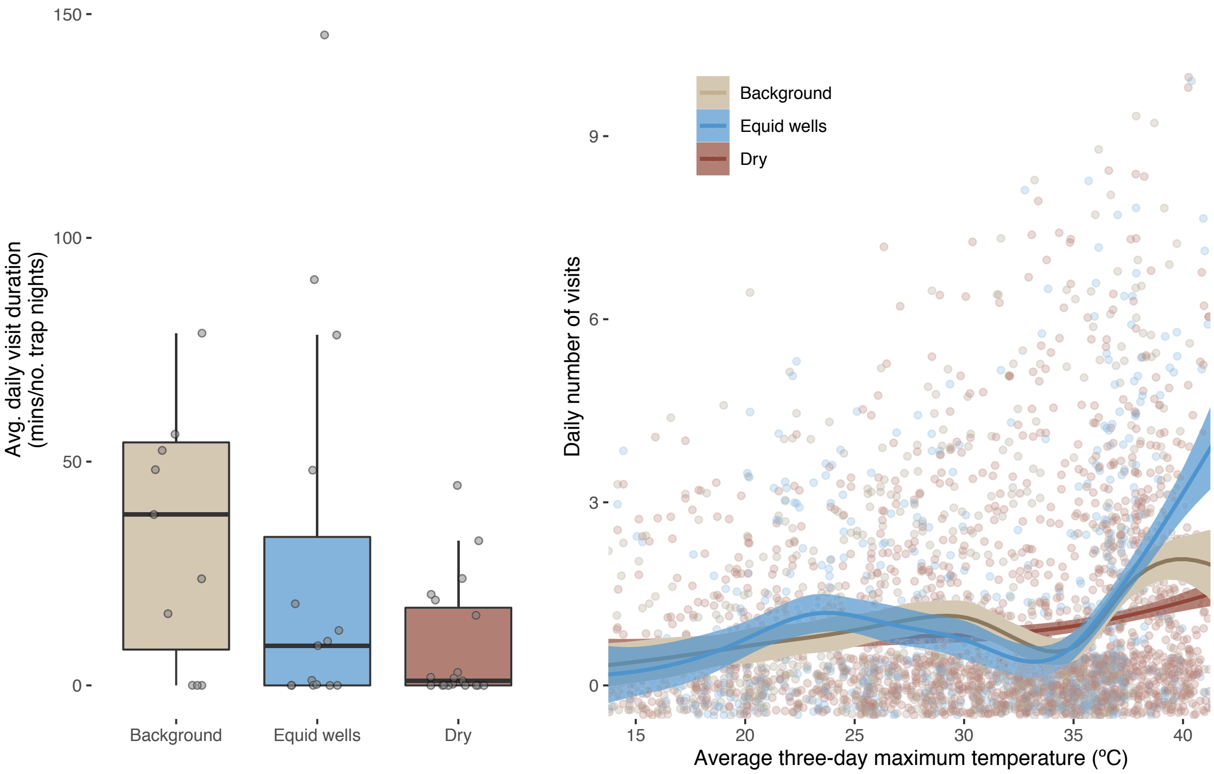

Fig. S1. The response of domestic cattle to background waters, equid wells, and dry controls. Cattle stocking densities were variable during the season, reflecting local husbandry practices.

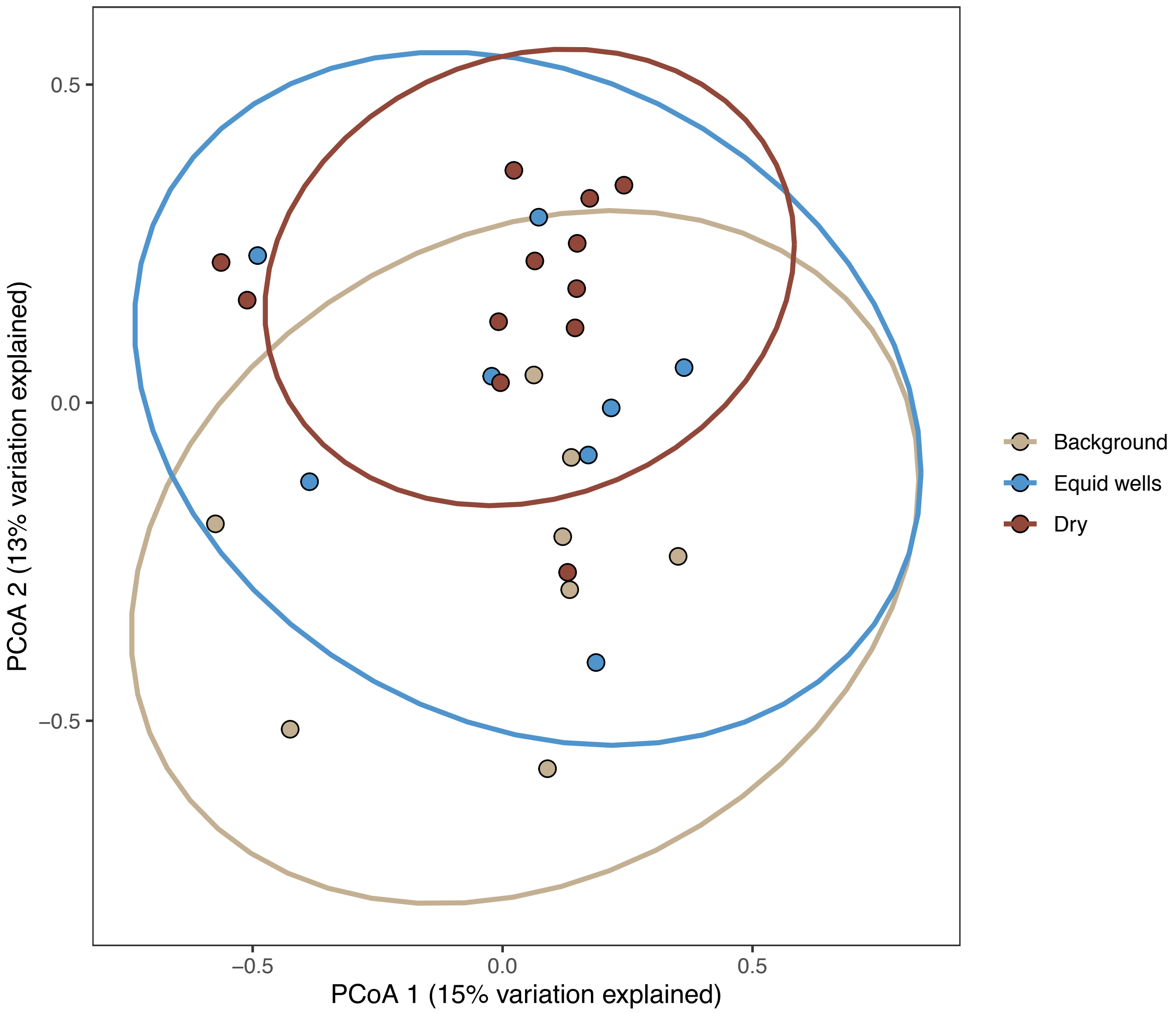

Fig. S2. First two axes of a Principal Coordinates Analysis (PCoA) describing differences in species composition between camera stations. Points are individual camera stations, colored by resource type. There was no significant difference in species composition based on water type (PERMANOVA: F=0.9, p=0.7).

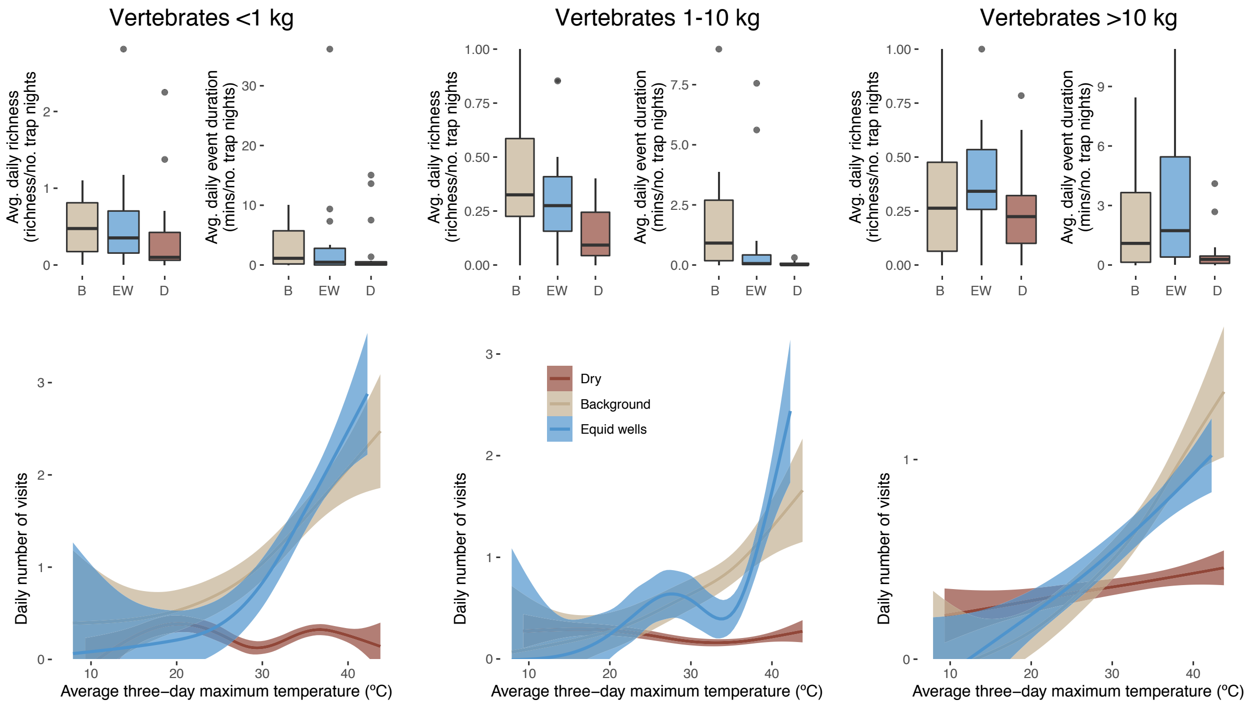

Fig. S3. Patterns of resource use were similar across vertebrate body size classes. Vertebrates <100 g were excluded from the smallest body size class. B=background water, EW=equid well water, D=dry controls.

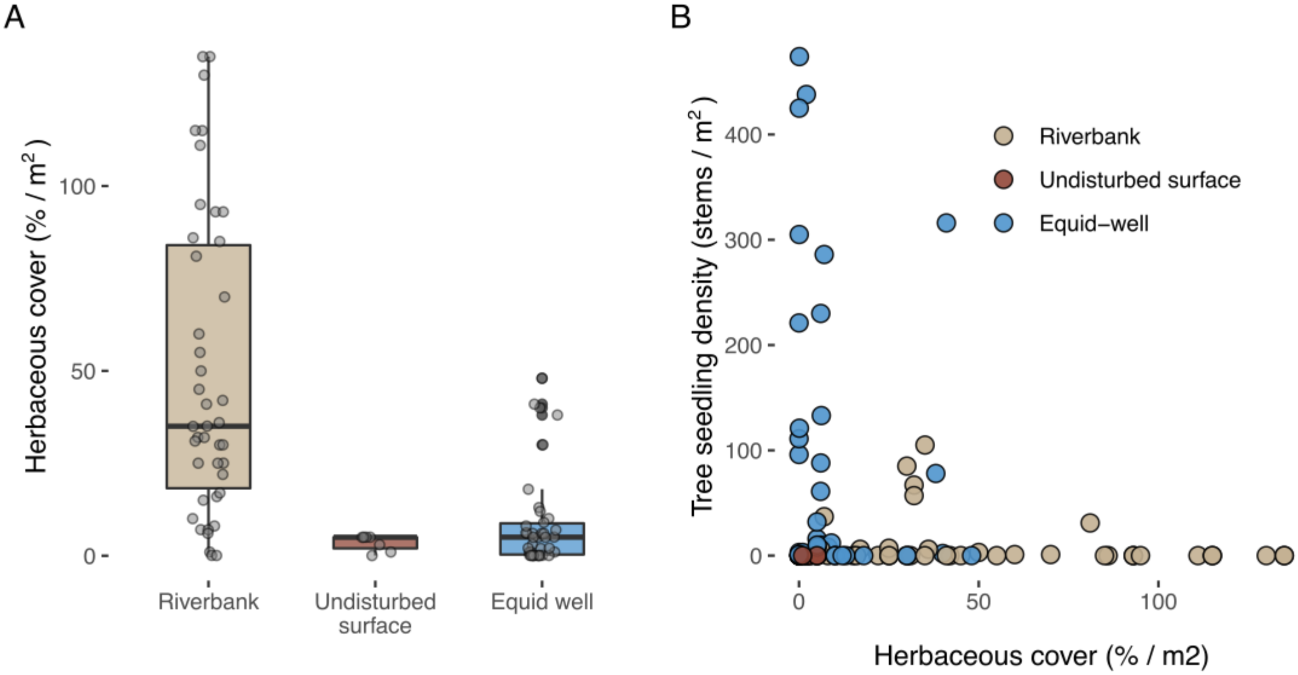

Fig. S4. Relationship of herbaceous cover to landform and tree germination. **A**. Herbaceous cover was significantly higher on moist riverbank zones than on undisturbed surfaces or equid wells (zero-inflated negative binomial mixed effect model: $\chi^2 = 60.2$, $p < 0.0001$, post-hoc $p < 0.0001$) and was not significantly influenced by season (e.g. spring or fall, $\chi^2 = 1.3$, $p = 0.7$). **B**. A strong negative relationship existed between tree germination and establishment and herbaceous cover (zero-inflated negative binomial mixed effect model: $\chi^2 = 16.9$, $p < 0.0001$).

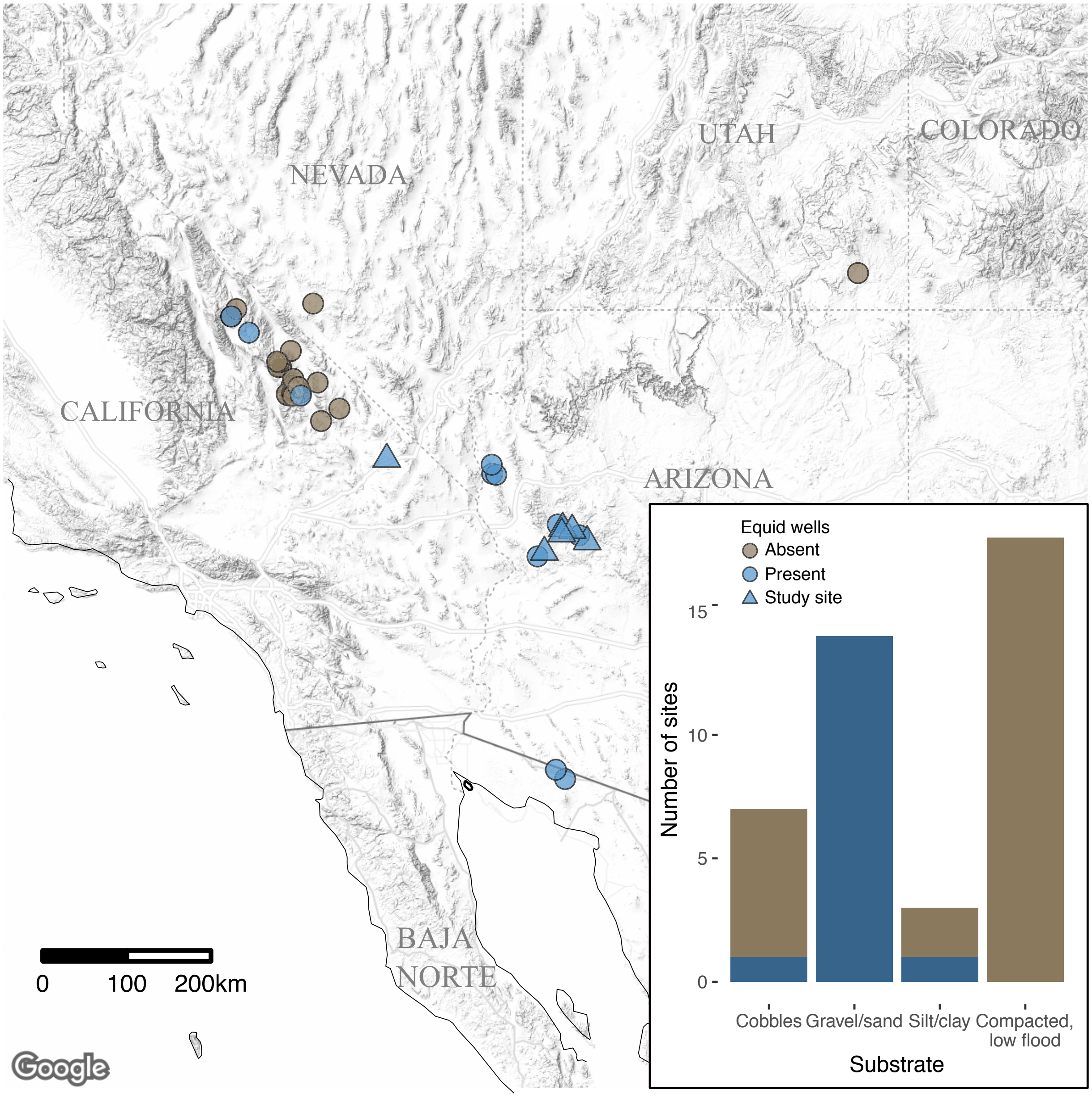

Fig. S5. Distribution of equid well digging locations across the Southwestern United States and Northern Mexico (this study). Color indicates the presence or absence of wells. Triangles indicate study sites. The absence of wells at certain sites is explained by substrate (logistic regression: X^2=27.7, p<.00001), indicated in the inset. Equid wells were largely absent in systems with coarse cobble substrates over bedrock and in low-flood systems with compacted substrates of mixed materials. Equid wells were likewise absent from all but one silt and clay dominated system, such as found in the beds of ephemeral lakes.

Table S1. Species known to dig wells to groundwater, with sources, depth, and notes. As a largely overlooked behavior, we here review all current published knowledge about well digging among extant vertebrates. Well digging, particularly to depths significant for maintaining water availability in drylands, appears to primarily be a megafauna function. Smaller bodied animals, listed below, dig more irregularly and to shallower depths, thus limiting their ability to maintain access to subsurface water.

Species	**Source**	**Depth**	**Description**
African elephant (*Loxodonta africana)*	Payne 1999 (Payne 1999); Haynes 2012 (Haynes 2012); Ramey et al. 2013 (Ramey et al. 2013)	1.5 m. Maximum depth unknown	African elephants dig large clusters of wells, of 0.5-1.5 m in depth, but are likely capable of digging deeper. Forest elephant wells sustained water presence during the summer dry season and were used by numerous animals (Payne 1999). Elephant-well water has reduced bacterial loads, suggesting a reason for digging even when background water is present (Ramey et al. 2013).
Asian elephant (*Elephas maximus*)	Joshi 2009 (Joshi 2009)	Unknown	Joshi 2009 (Joshi 2009) reported well digging by Asian elephants during the dry season. These elephant wells were reported in use by spotted deer (*Axis axis*), sambar (*Rusa unicolor*), mongoose (species unreported), Bengal foxes (*Vulpes bengalensis*), jackals (*Canis aureus*), boar (*Sus scrofa*), and various birds.
Feral horse (*Equus ferus caballus*)	This study; Rolls 1969 (Rolls 1969); Rozen-Rechels 2015 (Rozen-Rechels et al. 2015)	Observed (this study) up to 1.5 m. Reported up to ~2 m (Rolls 1969)	In the Flinders River in northern Queensland, Australia, wild horses have been reported digging wells deeper than their own height (~2 m, Rolls 1969). On Sable Island, Canada, wild horses create the only sources of surface water on one half of the island (Rozen-Rechels et al. 2015).

Feral donkey (*Equus africanus asinus*)	This study; McKnight 1958	Observed up to 1.2 m (this study). Reported up to ~1.5-2 m	McKnight (1958) mentions wild donkeys digging ≥5 feet (~1.5 m) to groundwater in North America, location undisclosed. We have also documented well digging by wild donkeys in ephemeral washes in the Painted Desert of Southern Australia.
Khulan (*Equus hemionus kulan*)	Feh et al. 2002; Payne et al. 2020; Association GOVIIN KHULAN	0.5 m, maximum depth unknown	Khulan regularly dig wells, generally ~0.5 m in depth, though likely capable of reaching similar maximum depths as donkeys and horses. Khulan wells are used by domestic and wild animals, including the endangered Gobi Desert Grizzly Bear (*Ursus arctos gobiensis*) (Chadwick 2016) and argali (*Ovis ammon*) (Association GOVIIN KHULAN).
Grévy's zebra (*Equus grevyii*)	Klingel 1974	0.5 m, maximum depth unknown.	Grévy's zebras regularly dig wells in dry sandy streambeds during the dry season, which have been documented in use by Grant's Gazelles (*Nanger granti*), giraffes (*Giraffa campelopardalis*), and elephants (*Loxodonta africana*) (Klingel 1974).
Mountain zebra (*Equus zebra*)	Klingel 1968	0.5 m, maximum depth unknown.	Klingel 1968 reported on mountain zebras digging wells of 0.5 m in depth, which were subsequently utilized by giraffes (*Giraffa campelopardalis*), kudus (Tragelaphus strepsiceros), gemsbok (*Oryx* gazella), hyena (*Crocuta* crocuta), elephants (*Loxodonta africana*), springbok (*Antidorcas marsupialis*), plains zebra (*Equus quagga*), lions

			(*Panthera leo*), and cheetahs (*Acinonyx jubatus*).
Gemsbok (*Oryx gazella*) & chacma baboons (*Papio ursinus*)	Hamilton et al. 1977	~ 1 m	Gemsbok and chacma baboons were described regularly digging wells in the Namib Desert. Wells reached just over a meter in depth in the peak of the dry season. It appears that gemsbok initiated well digging, digging to 0.5 m in depth. While inefficient at digging through dry sand, baboons would then deepen the gemsbok-dug wells once they had hit wet sand (Hamilton et al. 1977).
Coyote (*Canis latrans*)	This study	~0.20 m	We observed a single shallow, 20 cm deep well in thick drying clay in the Sonoran Desert, USA. Not observed elsewhere. The coyote origin was verified with trail cameras.
Common wombat (*Vombatus ursinus*)	Millington 2020	2-4 m	In what appears to be a single case, a pair of wombats dug a 2-4 m deep well, which was used by other species during severe drought. This well was morphologically distinct from a burrow, as it descended vertically and was located at the base of a large gradual depression, described as a 'crater'. This behavior has not been observed elsewhere. Given widespread range contractions among wombats, particularly for dryland-inhabiting wombat species, wombat wells may have once been common on the landscape (IUCN Red List 2018).

Agile wallaby (*Macropus agilis*)	Doody et al. 2007	0.15 m	Agile wallabies dig clusters of 1-7 15 cm deep drinking ‘holes’. Doody et al. (2007) indicate that these holes were likely dug to avoid crocodile predation at the riverbank.
Common wallaroo (*Osphranter robustus*)	Wilson and Mittermeier 2015	Unknown, published image suggests ~0.2 m	Common wallaroos are reported digging wells in dry creek beds, despite the fact that they are mostly free-water independent, irregularly drinking water even when temperatures >43ºC. Photograph in Wilson and Mittermeier (2015) appears to be ~0.2 m in depth (Wilson and Mittermeier 2009-2019).

Table S2. Site and survey details for sites where water availability and camera trap analyses were conducted. Cane Springs was not surveyed for water availability and thus possesses NA values for survey length, distance to nearest water, and number of water availability surveys.

Lat	Long	Site, Desert, (elev. m)	Stream length (m)	Distance to nearest external water (m)	Number of water availability surveys (years)	Number of camera trap nights (years)
-113.3857	34.46983	Black Canyon, Sonoran Desert (813)	1,817	8,308	8 (2)	386 (2)
-113.5269	34.43563	Cattail Spring, Sonoran Desert (784)	318	1,904	7 (1)	1,234 (1)
-113.5151	34.49495	Greenwood Spring, Sonoran Desert (894)	400	1,368	7 (2)	1,021 (2)
-113.2009	34.35265	Hackberry Wash, Sonoran Desert (540)	1,680	1,628	10 (2)	482 (2)
-115.7977	35.23301	Cane Springs, Sonoran Desert (983)	NA	NA	NA	545 (1)

Table S3. Vertebrate species documented during trail camera monitoring. * denotes species definitively recorded drinking from equid wells. Column ‘H2O’ indicates species known to be free-water independent (‘I’) or dependent (‘D’), with reference. Species that are mostly free-water independent, but require it during periods of their life history (e.g. lactating), during extreme heat, or in the absence of succulent forage, are denoted with ‘I/D’. Given that most species have not been studied, presumed water-independent arid-adapted species, frequently observed in regions without surface water, are marked with ‘PI’ (presumed independent). Species that have been observed drinking regularly and are associated with more mesic habitats are marked as ‘PD’ (presumed dependent). The number of recorded visits are listed by resource type (‘D’ = Dry, ‘EW’ = Equid wells, ‘B’ = Background). Only species ≥100 g were included in statistical analyses to control for bias in detection probability. References: 1 = Switalski and Bateman 2017; 2 = Smyth and Bartholomew 1966; 3 = Moldenhauer and Wiens 1970; 4 = Golightly and Ohmart 1984; 5 = Lundgren et al. 2021b; 6 = Rosenstock et al. 1999; 7 = Lynn et al. 2006; 8 = Hyde 2011; 9 = Murphy and DeNardo 2019; 10 = MacMillen and Hinds 1983; 11 = Kiesow and Griffis-Kyle 2017; 12 = Nagy et al. 1976; 13 = Baldwin et al. 2004; 14 = Brown et al. 1972; 15 = Zervanos and Day 1977.

Species	**Common name**	**Class**	**Order**	**Mass (g)**	**H_2O**	**D**	**EW**	**B**
Accipiter cooperii *	Cooper's Hawk	Aves	Accipitriformes	526.64	PD	0	1	19
Ammospermophilus harrisii *	Ground Squirrel	Mammalia	Rodentia	126	I (1)	38	89	54
Amphispiza bilineata *	Black-throated Sparrow	Aves	Passeriformes	13.5	I/D (2)	1	9	60
Aphelocoma woodhouseii *	Woodhouse's Scrub-Jay	Aves	Passeriformes	90	PD	4	74	34
Artemisiospiza nevadensis	Sagebrush Sparrow	Aves	Passeriformes	18.5	D (3)	0	0	7
Baeolophus ridgwayi *	Juniper Titmouse	Aves	Passeriformes	16	PD	0	1	0
Bassariscus astutus *	Ringtail	Mammalia	Carnivora	1015	I (4)	2	3	3
Bos taurus *	Cattle	Mammalia	Cetartiodactyla	750000	D (5)	1976	905	1191
Bubo virginianus *	Great-horned Owl	Aves	Strigiformes	1191.2	PD	0	10	27
Buteo albonotatus	Zone-tailed Hawk	Aves	Accipitriformes	822.5	PD	0	0	18
Buteo jamaicensis *	Red-tailed Hawk	Aves	Accipitriformes	1362	PD	2	4	22
Callipepla gambelii *	Gambel's Quail	Aves	Galliformes	166	I/D (6)	213	268	326
Campylorhynchus brunneicapillus	Cactus Wren	Aves	Passeriformes	38.9	PI	1	0	2
Canis latrans *	Coyote	Mammalia	Carnivora	13250	I/D (4)	181	99	39
Caprimulgidae spp *	Nightjar Spp.	Aves	Caprimulgiformes	63	PI	5	29	26
Cardellina pusilla	Wilson's Warbler	Aves	Passeriformes	7	D (7)	0	0	3
Cardinalis cardinalis	Northern Cardinal	Aves	Passeriformes	42.6	PD	1	1	4

Cathartes aura *	Turkey Vulture	Aves	Cathartiformes	2200	PI	0	3	53
Catharus guttatus *	Hermit Thrush	Aves	Passeriformes	27.8	PD	0	2	12
Chamaea fasciata	Wrentit	Aves	Passeriformes	14.7	PI/D	0	0	1
Colaptes auratus	Northern Flicker	Aves	Piciformes	120	PD	0	2	0
Colaptes chrysoides *	Gilded Flicker	Aves	Piciformes	110.5	PI (8)	2	6	8
Corvus corax *	Common Raven	Aves	Passeriformes	1041.2	PI	4	116	304
Crotalus atrox	Western Diamond-backed Rattlesnake	Reptilia	Squamata	1965	D (9)	0	0	6
Dipodomys spp *	Kangaroo Rat	Mammalia	Rodentia	120	I (10)	2	1	2
Dryobates scalaris	Ladder-backed Woodpecker	Aves	Piciformes	34.5	PI (8)	5	0	1
Empidonax spp	Empidonax Flycatcher	Aves	Passeriformes	13.5	PD	0	0	2
Equus asinus *	Donkey	Mammalia	Perissodactyla	164998	D (5)	1104	969	956
Equus caballus *	Horse	Mammalia	Perissodactyla	3.00E+05	D (5)	527	220	358
Erethizon dorsatum	North American Porcupine	Mammalia	Rodentia	10750	PD	0	0	1
Geococcyx californianus *	Greater Roadrunner	Aves	Cuculiformes	376	PI	7	8	8
Geothlypis tolmiei	MacGillivray's Warbler	Aves	Passeriformes	10.4	PD	0	0	8
Geothlypis trichas	Common Yellowthroat	Aves	Passeriformes	9.5	PD	0	0	4
Haemorhous mexicanus *	House Finch	Aves	Passeriformes	21.4	D (7)	6	95	77
Icterus cucullatus *	Hooded Oriole	Aves	Passeriformes	24.3	PD	2	16	11
Icterus parisorum *	Scott's Oriole	Aves	Passeriformes	36.2	PI/D	0	10	4
Incilius alvarius *	Colorado River Toad	Amphibia	Anura	130	D (11)	4	93	7
Junco hyemalis	Dark-eyed Junco	Aves	Passeriformes	19	PD	0	0	20
Lanius ludovicianus	Loggerhead Shrike	Aves	Passeriformes	46	PI	0	0	2
Leiothlypis celata *	Orange-crowned Warbler	Aves	Passeriformes	9	PD	0	1	0
Lepus californicus	Black-tailed Jackrabbit	Mammalia	Lagomorpha	4175	I/D (12)	70	19	4
Lynx rufus *	Bobcat	Mammalia	Carnivora	8600	PD	21	28	26
Megascops kennicottii	Western Screech-Owl	Aves	Strigiformes	205	PD (8)	1	45	34
Melanerpes uropygialis *	Gila Woodpecker	Aves	Piciformes	65	I/D (8)	3	71	54
Melospiza lincolnii	Lincoln's Sparrow	Aves	Passeriformes	17.35	PD	0	0	4

Melospiza melodia	Song Sparrow	Aves	Passeriformes	22.7	PD	0	0	28
Melozone aberti	Abert's Towhee	Aves	Passeriformes	48.7	PD	0	3	8
Melozone fusca	Canyon Towhee	Aves	Passeriformes	44.4	PD	1	1	2
Mephitis mephitis *	Striped Skunk	Mammalia	Carnivora	3500	D (13)	18	6	2
Micrathene whitneyi *	Elf Owl	Aves	Strigiformes	41	PI (8)	1	6	1
Mimus polyglottos	Northern Mockingbird	Aves	Passeriformes	53	I/D (8)	1	2	104
Myadestes townsendi *	Townsend's Solitaire	Aves	Passeriformes	32.5	PD	0	7	13
Myiarchus spp *	Myiarchus Flycatcher	Aves	Passeriformes	29.5	PI/D	2	9	29
Neotoma spp *	Woodrat	Mammalia	Rodentia	236	I (14)	14	2	163
Odocoileus hemionus *	Mule Deer	Mammalia	Cetartiodactyla	57000	D (6)	268	136	267
Otospermophilus variegatus *	Rock Squirrel	Mammalia	Rodentia	663	PD	5	36	50
Ovis canadensis *	Bighorn Sheep	Mammalia	Cetartiodactyla	70275	I/D (6)	3	3	39
Pecari tajacu *	Javelina	Mammalia	Cetartiodactyla	20200	I/D (15)	155	137	100
Peromyscus spp *	Deer mouse	Mammalia	Rodentia	20.5	I (1)	0	1	79
Phainopepla nitens *	Phainopepla	Aves	Passeriformes	28	I/D (8)	1	1	1
Pheucticus melanocephalus *	Black-headed Grosbeak	Aves	Passeriformes	42	PD	0	4	1
Pipilo maculatus	Spotted Towhee	Aves	Passeriformes	40.4	PD	0	0	17
Piranga ludoviciana	Western Tanager	Aves	Passeriformes	30	PD	0	0	3
Pituophis catenifer	Gopher Snake	Reptilia	Squamata	1360.5	PI/D	0	0	1
Procyon lotor *	Northern Raccoon	Mammalia	Carnivora	6000	PD	2	1	0
Puma concolor *	Mountain Lion	Mammalia	Carnivora	63000	PI/D	37	9	37
Regulus calendula	Ruby-crowned Kinglet	Aves	Passeriformes	6.75	PD	1	2	16
Salpinctes obsoletus	Rock Wren	Aves	Passeriformes	16.5	I/D (2)	0	0	11
Sayornis saya	Say's Phoebe	Aves	Passeriformes	21.8	PD	2	0	2
Setophaga coronata	Yellow-rumped Warbler	Aves	Passeriformes	12	PD	0	1	9
Sialia mexicana	Western Bluebird	Aves	Passeriformes	26.5	PD	0	0	1
Sphyrapicus nuchalis	Red-naped Sapsucker	Aves	Piciformes	48.5	PD	0	0	1
Spilogale gracilis *	Spotted Skunk	Mammalia	Carnivora	600	PD	4	5	4
Spinus psaltria	Lesser Goldfinch	Aves	Passeriformes	9.23	D (8)	0	0	10

Sylvilagus audubonii *	Cottontail Rabbit	Mammalia	Lagomorpha	900	PD	122	31	9
Taxidea taxus *	American Badger	Mammalia	Carnivora	8000	PI/D	3	13	3
Toxostoma crissale	Crissal Thrasher	Aves	Passeriformes	62.7	PI	2	0	0
Toxostoma curvirostre *	Curve-billed Thrasher	Aves	Passeriformes	80.65	PI/D	10	19	14
Turdus migratorius	American Robin	Aves	Passeriformes	75.5	PD	0	0	7
Tyto alba	Barn Owl	Aves	Strigiformes	580	PI	0	0	1
Urocyon cinereoargenteus *	Gray Fox	Mammalia	Carnivora	4750	PD	227	186	191
Ursus americanus *	Black Bear	Mammalia	Carnivora	154250	PD	0	1	0
Zenaida asiatica *	White-winged Dove	Aves	Columbiformes	140	D (6)	19	127	133
Zenaida macroura *	Mourning Dove	Aves	Columbiformes	119	D (6)	18	65	205
Zonotrichia leucophrys *	White-crowned Sparrow	Aves	Passeriformes	25.82	PD	2	3	24

Table S4. Vertebrate use of water sources model results. The relationship between daily vertebrate activity patterns (measured as visit frequency and visit duration) and daily richness at equid wells, background waters and dry controls and as influenced by temperature and precipitation. Day was nested within site as a random effect. All analyses were conducted in R with the package 'glmmTMB' version 1.0.1 7 (Brooks et al. 2017). Omnibus test results were calculated using the function 'Anova' in the 'car' library (Fox and Weisberg 2019).

Response variable	**Final included variables**	**Test results**
Equids and cattle excluded, including only species ≥250 g.		
Visit frequency (*zero-inflated negative binomial distribution*)	Resource type	χ^2=411.5, $p < 0.0001$
	Avg. three-day maximum temperature	χ^2 =114.1, $p < 0.0001$
	Cumulative three-day precipitation	χ^2 = 0.06, $p = 0.80$
	Resource type * Avg. three-day maximum temperature	χ^2 = 98.5, $p < 0.0001$
	Resource type * Cumulative three-day precipitation	χ^2 = 3.1, $p = 0.21$
Species richness (*zero-inflated Poisson distribution*)	Resource type	χ^2 = 153.4, $p < 0.0001$
	Max daily temperature	χ^2 = 62.1, $p < 0.0001$
	Cumulative three-day precipitation	χ^2 = 0.13, $p = 0.71$
	Resource type * Max daily temperature	χ^2 = 40.9, $p < 0.0001$
	Resource type * Cumulative three-day precipitation	χ^2 = 2.7, $p = 0.25$
Visit duration (*zero-inflated negative binomial distribution*)	Resource type	χ^2 = 310.6, $p < 0.0001$
	Avg. three-day maximum temperature	χ^2 = 92.5, $p < 0.0001$
	Cumulative three-day precipitation	χ^2 = 0.3, $p = 0.56$
	Resource type * Avg. three-day maximum temperature	χ^2 = 8.03, $p = 0.02$
	Resource type * Cumulative three-day precipitation	χ^2 = 2.5, $p = 0.29$

Cattle only		
Visit frequency (*zero-inflated negative binomial distribution*)	Resource type	χ^2= 53.5, p < 0.0001
	Avg. three-day maximum temperature	χ^2 = 82.7, p < 0.0001
	Cumulative three-day precipitation	χ^2 = 0.0001, p = 0.99
	Resource type * Avg. three-day maximum temperature	χ^2 = 15.29, p = 0.0004
	Resource type * Cumulative three-day precipitation	χ^2 = 2.7, p = 0.25
Visit duration (*zero-inflated negative binomial distribution*)	Resource type	χ^2 = 210.1, p < 0.0001
	Avg. three-day maximum temperature	χ^2 = 21.4, p < 0.0001
	Cumulative three-day precipitation	χ^2 = 0.32, p = 0.57
	Resource type * Avg. three-day maximum temperature	χ^2 = 22.5, p < 0.0001
	Resource type * Cumulative three-day precipitation	χ^2 = 2.5, p = 0.29

Data S1. (Data_S1_Water_Pattern.gpkg)
Geospatial data of water feature locations per survey. Dataset thus contains site, date of survey, length of each water feature, and origin of each water feature (background water or equid well). See metadata description in Data S2's 'Metadata' tab. All relevant code is available on figshare and is described in metadata (figshare doi: 10.6084/m9.figshare.13668794).

Data S2. (Data_S2_Community_Responses.xlsx)
This excel workbook contains the data required to analyze vertebrate utilization of equid wells and vegetation responses to equid wells. The workbook contains four sheets, including a metadata sheet describing all columns in all datasets (including Data S1). All relevant code is available on figshare and is described in metadata (figshare doi: 10.6084/m9.figshare.13668794).

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Chapter 4: Echoes of the late Pleistocene in a novel trophic cascade between cougars and introduced donkeys

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Abstract

Introduced large herbivores have partly filled ecological gaps formed in the late Pleistocene, when many of the Earth's megafauna were driven extinct. However, surviving predators are widely considered unable to influence introduced megafauna, leading them to exert unusually strong herbivory and disturbance-related effects. We report on a behaviorally-mediated trophic cascade between cougars (*Puma concolor*) and feral donkeys (*Equus africanus asinus*) at desert wetlands in North America. In response to predation of juveniles, donkeys shifted from nocturnal to almost exclusively diurnal, thereby avoiding peaks in cougar activity. Furthermore, donkeys reduced the time they spent at desert wetlands by 87%: from 5.5 hours a day to 0.7 hours at sites with predation. These shifts in activity were associated with increased activity and richness of other mammal species and reduced disturbance and herbivory-related effects on these ecologically-distinct wetland ecosystems, including 49% fewer trails,

35% less trampled bare ground, and 227% more canopy cover. Cougar predation on introduced donkeys rewires an ancient food web, with diverse implications for modern ecosystems.

Introduction

Many of the world's largest herbivores and predators were lost in the late Pleistocene, most likely due to human hunting (Barnosky et al. 2004, Smith et al. 2018). A second wave of declines is ongoing, as the majority of surviving large herbivore species (henceforth megafauna) are now threatened with extinction (Ripple et al. 2015). Yet several megafauna species have also been introduced, thereby restoring lost species richness and potential ecological functions (Lundgren et al. 2018, Lundgren et al. 2020). However, it has long been assumed that surviving predators are incapable of exerting ecologically-significant predation pressure on introduced megafauna, leading to unusually strong herbivory and disturbance-related effects on modern ecosystems, relative to native megafauna (Fig. 1a-b).

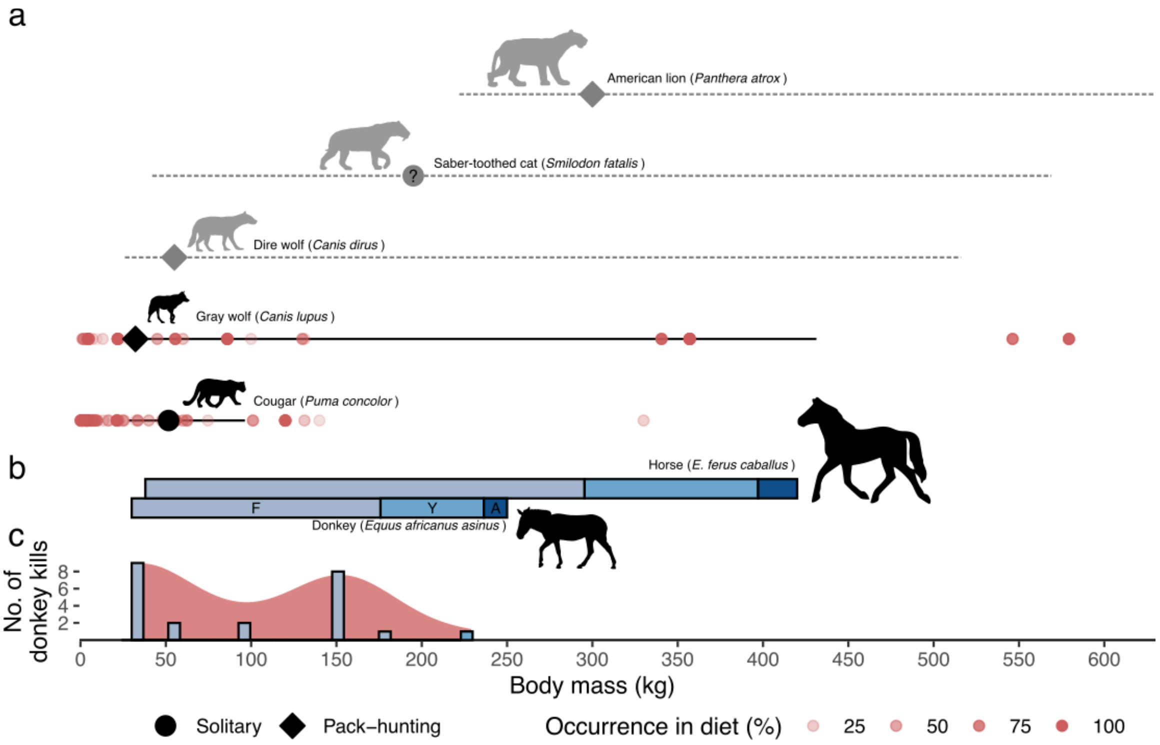


Figure 1. Body size and hunting style determine predator-prey interactions and may constrain the ability of extant predators to influence introduced megafauna. X-axis (body mass) is shared across all subplots. **a.** North American apex predators before and after the late Pleistocene extinctions. Horizontal lines indicate theoretical optimum prey body mass range of extant (black) and extinct (dashed) predators (from Van Valkenburgh et al. 2016). Points indicate average predator body mass and hunting style, which remains uncertain for *Smilodon fatalis* (denoted with question mark). Red points indicate published prey items by body mass, with transparency denoting the frequency of prey occurrence in diet (data from Middleton et al. 2021). Of extant predators, only the cougar (*Puma concolor*) substantially overlaps in geographic distribution with introduced equids in North America (IUCN Red List 2018, Wallach et al. 2019). **b.** Estimated body mass ranges for equid age classes (F=foal, Y=yearling, A=adult). **c.** Body mass density distribution (red fill) and frequency (overlaid bars) of cougar donkey kills from field surveys (this study).

We report on a novel trophic cascade (Wallach et al. 2015) between cougars (*Puma concolor*) and feral donkeys (*Equus africanus asinus*) in North America. Cougars co-occurred with a diversity of equid species for more than a million years until the North and South American late Pleistocene extinctions ~9-12,000 years ago (Williams et al. 2018). Paleoecological evidence, however, suggests that cougar-equid interactions may have been uncommon, with equids mainly preyed upon by larger or pack-hunting now-extinct predators (Fig. 1a-b, DeSantis and Haupt 2014). Cougars are likewise widely considered in research and policy as incapable of significantly influencing introduced equid populations or ecologies (National Research Council 2013). Despite this, we mapped widespread predation of juvenile donkeys across the Sonoran and Mojave Deserts of North America (Fig. 1c) and recorded the first documented predation of a yearling (Fig. 2a-b) and foal (Fig. 2c-d).

Figure 2. **First reported predation of feral donkeys by cougars, captured by trail camera. a-b.** Successful predation of a yearling donkey in the Sonoran Desert, Arizona. The cougar is looking up from the ground. Arrow in inset points to the cougar's left eye. **c-d.** Predation of a foal in Death Valley National Park, Mojave Desert, California.

Donkey ages were determined from tooth eruption sequences of carcasses. Images **a** and **c** were tonally adjusted for visibility (see Supplementary Figure 1 for original versions).

While predation influences populations through direct killing, it also drives predator-avoidance behaviors with cascading implications for the effects of herbivores on ecosystems (Laundré et al. 2010). However, it remains contested whether predation of juveniles can drive ecologically-relevant, behaviorally-mediated trophic cascades, as invulnerable adults may not respond to predation risk (Sinclair et al. 2003, Van Valkenburgh et al. 2016, Sandom et al. 2020). To answer this question, we investigated whether predation by cougars influenced donkey behavior and their associated effects on other vertebrates and vegetation at desert wetlands.

Results

To understand if donkeys altered their behavior to avoid cougar predation, we compiled trail camera images from 24 desert wetlands in the Sonoran and Mojave Deserts spanning 9,303 trap nights (Supplementary Figure 2, Supplementary Table 1). We compared donkey activity patterns between wetlands in regions with low densities of cougars and no evidence of predation (henceforth ‘low predation risk’) and regions with abundant cougars and widespread predation (‘high predation risk’). The high predation risk regions also included sites shielded by human recreational activity where cougars were locally absent, which were treated separately ('human shielding' Beschta et al. 2018).

Donkeys significantly changed their behavior in response to predation risk (Fig. 3a, Supplementary Figure 3). Donkeys were primarily nocturnal at low predation risk wetlands, but became almost exclusively diurnal at high predation risk wetlands, thereby avoiding the peak of cougar activity (Fig. 3a). Indeed, the nighttime attack captured on camera (Fig. 2c-d) was one of the few nighttime donkey visits to that wetland–with immediate consequences for the foal. Corroborating that these behavioral changes were a direct response to predation risk from cougars, donkeys were again nocturnal at human-shielded sites within this same high predation risk region (Fig. 3a).

Temperature drives water requirements, particularly in desert environments (Cain III et al. 2006). Desert wetlands can thus become foci of activity for water-dependent animals such as donkeys during the summer. To understand if cougars mediate this interaction, we calculated the daily activity of donkeys at each wetland (hours/day/site) from trail camera data and analyzed how it was shaped by maximum daily temperature and two indicators of predation risk: the presence of kills (cached carcasses) and the presence of cougars. We used multimodel inference (based on AICc) to choose the most parsimonious model.

Donkey activity was affected by the presence of kills (χ^2=300.4, p<0.001), maximum daily temperature (χ^2=55.4, p<0.001), and their interaction (χ^2=14.6, p=0.001). At wetlands without kills, activity reached an average of 5.5 hours/day on days ≥35ºC (SD=±4.4, max=16.5, Fig. 3b). However, at sites with kills, activity remained low and relatively stable regardless of temperature, averaging 0.7 hours/day on days ≥35ºC (±1.7, max=12.6, Fig. 3b). The presence of cougars (i.e., at sites with cougars but no kills) also affected activity, but to a lesser extent and was not included in the most parsimonious model (Supplementary Figure 4).

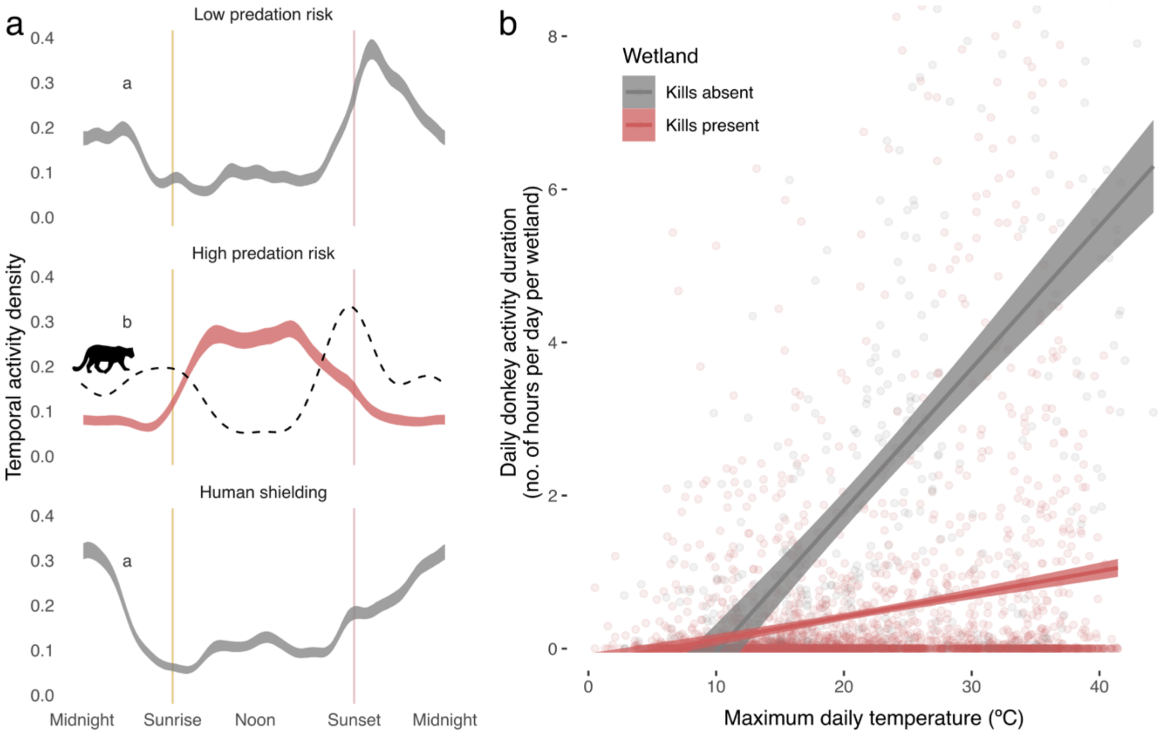


Figure 3. Cougars shape donkey behavior at desert wetlands. **a.** Donkey temporal activity under different levels of predation risk. X-axis indicates time of day. Ribbon indicates donkey activity 95% confidence intervals from bootstrapped detections, with letters indicating significance groupings based on non-overlap of confidence intervals (see Supplementary Figure 3). Dashed line indicates cougar activity pattern. 'Low predation risk' = sites in regions with low densities of cougars where predation was absent, 'high predation risk' = sites in regions with cougars and widespread predation, 'human shielding' = wetlands with recreational activity where cougars were absent, despite proximity to high predation risk wetlands. **b.** Relationship between maximum daily temperature and the activity of donkeys at wetlands (hours/day/site) for sites with and without predation.

Megafauna, including introduced equids, can competitively exclude smaller species from water points (Valeix et al. 2007, Hall et al. 2016). We thus identified all mammal species larger than a cottontail rabbit (*Sylvilagus audubonii*) from camera trap imagery and assessed whether cougar predation on donkeys, and corresponding changes in donkey behavior, was associated with increased use of wetlands by other species. As with donkeys, the activity duration of other mammals increased with maximum daily temperature (Fig. 4a, z=8.1, p<0.001). However, this was strongest at wetlands with cougar predation, where donkey activity was reduced (Fig. 4a, post hoc t-ratio=-6.46, p<0.001). Indeed, across all sites, the daily activity of other mammals was negatively related to the activity of donkeys on that same day (Fig. 4b z=4.5, p<0.001), which further supports that cougar predation on donkeys itself, not other factors, facilitates the activity of other mammal species at these wetlands. These increases in activity corresponded with higher mammal species richness at sites with active donkey predation (Fig. 4c, W=37.5, p=.045).

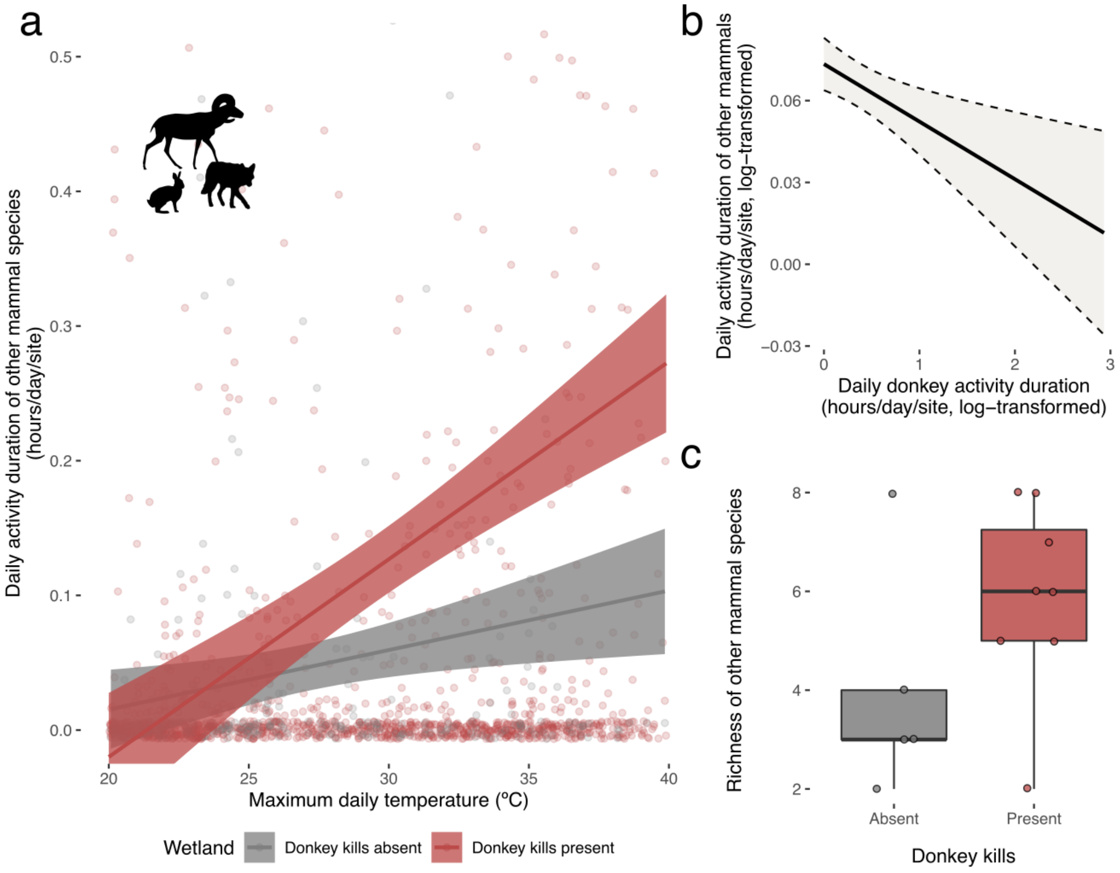


Fig. 4. Predation on feral donkeys was associated with increased utilization of wetlands by other mammal species. a. Duration of activity by other mammal species at wetlands increased with maximum daily temperature (χ^2=210.25, p<0.001), but to a greater extent at sites with active donkey predation (interaction term: t-ratio=-6.42, p<0.001). **b.** Daily activity duration of other mammals had a negative relationship to the activity of donkeys on that day, across all sites (z=4.5, p<0.001). Durations were log-transformed to reduce over dispersion. **c.** Richness of other mammal species at sites with and without donkey kills (W=37.5, p=.045). Given unequal trap nights, richness was interpolated following (Chao et al. 2014).

Cougar predation on donkeys was further associated with reduced herbivory and disturbance-related effects on these ecosystems. We collected data on nine soil and vegetation responses encompassing potential disturbance and herbivory-related effects of donkeys on desert wetlands (Supplementary Figure 6). We synthesized these data with a Principal Coordinates Analysis (PCoA) to find the primary axes by which wetlands differed from each other, revealing significant differences between sites with and without kills (PERMANOVA: R^2=0.20, F=3.54, p<0.001, Fig. 4a-c). Wetlands with kills had more vegetation, including 227% more canopy cover (from 12.7±16% to 42±34%, mean±SD, Supplementary Figure 5), and 183% more vegetation around water perimeter (from 21±21% to 60±18%, Supplementary Figure 5). Likewise, these sites had less disturbance, including ~49% fewer trails to water (from 3.2±2, to 1.6±0.7, Supplementary Figure 5) and 35% less trampled bare ground (from 77±20% to 50%±16%, Supplementary Figure 5).

The presence of cougars themselves (independent of kills), topographic complexity, and elevation did not explain dissimilarity in wetland structure (p=0.27-0.33, Supplementary Table 2). Likewise, geographic distances between sites did not influence wetland dissimilarity (multiple regression on distance matrices, R^2=0.007, F=0.82, p=0.58), indicating that the differences between wetlands were driven by predation upon donkeys and not by underlying spatial gradients.

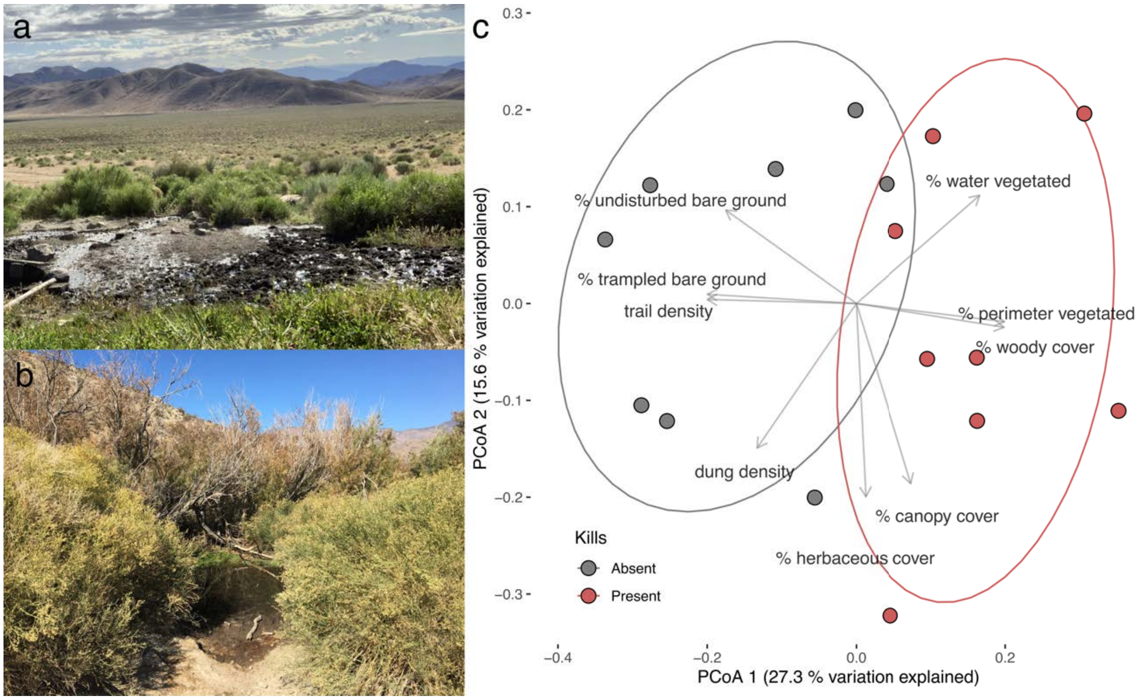


Fig. 5. Cougar predation is associated with reduced herbivory and disturbance-related influences on desert wetlands. **a.** A representative wetland lacking both cougars and kills compared to a nearby (~6km) wetland (**b**) where cougars and kills were present (site of the kill in Fig. 2C-D). Photos were taken at a similar distance from water's edge, by EJL (**a**) and OMM (**b**). **c.** Principal coordinates analysis (PCoA) showing significant differences in wetland structure with and without cougar predation on donkeys (PERMANOVA, F=3.5, $p<0.001$). Each point is a wetland. Relationship between response variables and PCoA axes are indicated by overlaid arrows and text. The presence of cougars themselves, elevation, and terrain complexity were not significant (PERMANOVA p=0.27-0.33), nor was the geographic distances between sites (F=0.82, p=0.58). See Supplementary Figure 5 for response of individual variables.

Discussion

For more than a million years, equids co-occurred with cougars and much larger predators, of which the latter were likely their primary predators (DeSantis and Haupt

2014). Cougar predation on juvenile donkeys nonetheless was strongly associated with altered donkey behavior, increased activity and richness of other mammals, and reduced effects on wetland vegetation and soil. While trophic cascades among native predators and herbivores are well-documented (e.g. Ripple and Beschta 2004), novel trophic cascades between predators and introduced herbivores, particularly when herbivores are much larger than native prey, remain widely ignored as a causative factor driving the effects of introduced herbivores in both research and policy.

Our results add to growing evidence that extant predators have a greater capacity to influence introduced equids than typically considered. This includes wolves (*Canis lupus*) and brown bears (*Ursus arctos*) in Eurasia and North America, jaguars (*Panthera onca*) in North and South America, and dingoes (*Canis dingo*) in Australia (Fig. 6, Supplementary Table 3). Cougars can be significant predators of introduced horses as well (Turner et al. 1992, Andreasen 2014), suggesting the possibility of behaviorally-mediated trophic cascades among these larger megafauna (Wallach et al. 2015) (Fig. 6). The return of equids after their ~12,000-year hiatus–and predation upon them by cougars–suggests a rewiring of food webs (Pires 2017), with diverse implications for modern ecosystems, the cougars and their prey, and for how these species are treated in policy.

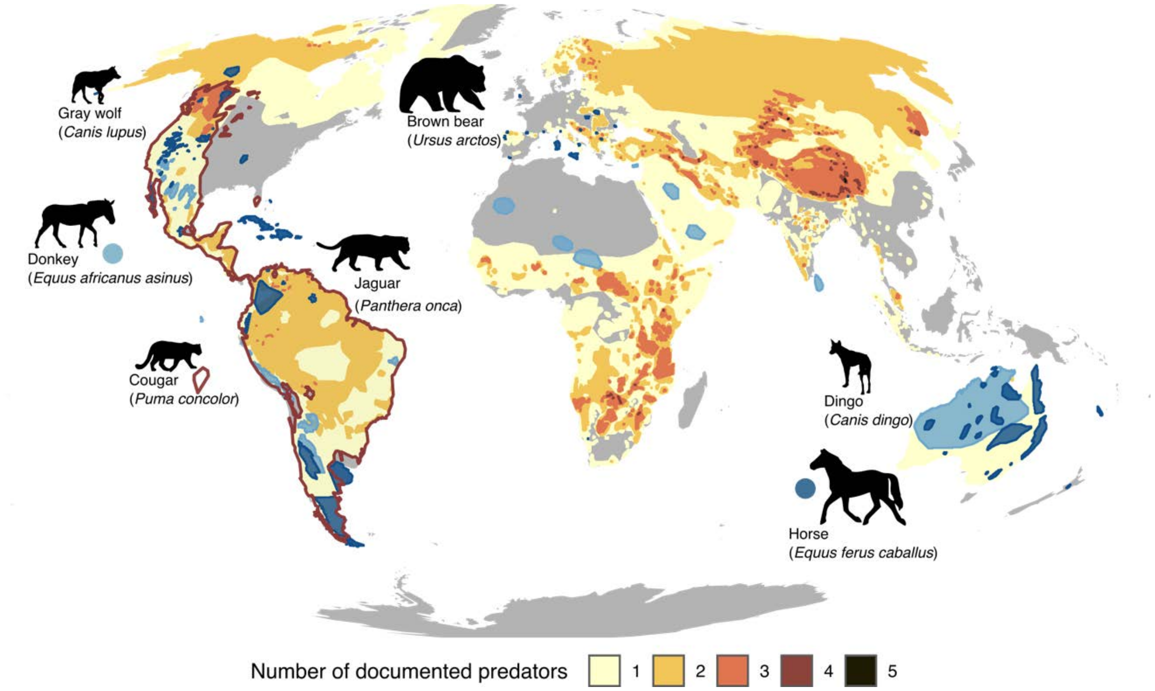


Fig. 6. Distribution of introduced equids and species richness of predators documented predating on equids. Introduced ranges of horses (dark blue) and donkeys (light blue) are overlaid on predator species richness (yellow-orange-black gradient). Cougar distribution is demarcated with red border overlay. The predators included have all been documented preying on equids. Those highlighted with icons (see Supplementary Table 3) have the potential to overlap in distribution with feral equids. Feral equids are among the most widespread and abundant introduced megafauna species (Lundgren et al. 2018, Wallach et al. 2019). Though rarely studied, the predators that survived the late Pleistocene extinctions have greater capacity to influence feral equids than usually considered. Predator range maps were drawn from the IUCN Redlist (IUCN Red List 2018), except for the dingo (Ripple et al. 2014). Introduced equid ranges are from (Wallach et al. 2019).

The influences of mammalian megafauna on wetlands, particularly in water-limited drylands, were likely ubiquitous from the early Cenozoic (30-40 million ybp) until the late Pleistocene extinctions (Smith et al. 2018, Lundgren et al. 2020). Megafauna well digging, disturbance, and herbivory can maintain wetland heterogeneity and water availability (Naiman and Rogers 1997, Kodric-Brown and Brown 2007). However, the effects of prehistoric megafauna, even those ≥1,000 kg, were likely mediated by predation, if only on juveniles (Van Valkenburgh et al. 2016)–potentially an ancient parallel to the behaviorally-mediated trophic cascade driven by cougar predation on juvenile donkeys.

Donkeys, cougars, and smaller-bodied prey of cougars, such as bighorn sheep (*Ovis canadensis*) and mule deer (*Odocoileus hemionus*), are entangled in an emerging ecological network. In addition to shaping donkey ecology, cougar predation on donkeys may thus engender novel evolutionary trajectories in cougars (Cattau et al. 2017) and reduce pressure on their other prey. These relationships may also yield overlooked consequences in response to ongoing donkey removals and near-ubiquitous cougar persecution. Donkeys were the primary recorded prey of cougars at our study sites (24 of 29 cached carcasses) and horses have been documented as primary prey elsewhere (Andreasen 2014): removing equids may thus lead to increased predation on smaller prey (Cliff et al. 2020).

Likewise, killing cougars in service of the livestock industry and to increase populations of deer and bighorn sheep for conservation and sport hunting (USDA APHIS Wildlife Services , Rominger 2018) may have consequences for feral equid populations and their ecological effects. As with many apex predators, persecution can reduce the ability of cougar populations to hunt larger, more challenging prey by removing older individuals from the population and by disrupting the transmission of hunting techniques from mother to young (Peebles et al. 2013). Even moderate persecution may thus reduce the potential for ecologically-significant trophic cascades between cougars and feral equids, despite their broad geographic overlap (Fig. 6).

Cougars avoided human recreation sites and were constrained by their need for topographic or vegetative ambush cover to hunt successfully (Supplementary Figure 7) (Dickson and Beier 2006). This created a mosaic of predation risk, which our study design utilized. However, without experimental manipulation of cougar presence, the stark differences observed between wetlands with and without predation remain correlative. Despite this, we argue that the proximity (e.g., ~2-6 km) of wetlands shielded by recreation, where vegetative cover was non-existent, to topographically similar wetlands with active predation and abundant vegetation, indicates that cougar predation was the primary driver of observed differences in mammal richness and activity and wetland structure.

Horses and donkeys, like the majority of extant megafauna, are threatened in their native ranges (Lundgren et al. 2018). This has led to calls for more inclusive conservation approaches (Wallach et al. 2019), which may find productive common ground with conservation efforts to increase protection and tolerance for cougars and other predators. Doing so may further influence the ecologies of feral donkeys. For instance, the effects of human shielding and the ambush cover requirements of cougars suggest that managing recreation and allowing for the reestablishment of pack-hunting wolves (*Canis lupus*) or larger-bodied jaguars (*Panthera onca*) would shift predation risk into places currently deemed safe, with broad implications for how feral equids influence ecosystems.

The effects of organisms emerge in relation to ecological contexts and are not essential to their dispersal histories, whether of unassisted colonization or human introduction (Simberloff 1980, Shafroth et al. 2002, Sagoff 2018). If we had conducted this research to enumerate the effects of feral donkeys on desert wetlands, without quantifying cougar predation, our data would contain a great degree of inexplicable noise. Instead we find echoes of the late Pleistocene in a novel trophic cascade between cougars and feral donkeys, with diverse ecological and evolutionary possibilities.

Methods

Theoretical predator prey ranges

We followed Van Valkenburgh et al. 2016's formulae to calculate theoretical optimal prey sizes based on allometric scaling relationships from observed diets in extant predators (Fig. 1). Pack-hunting and solitary hunting (e.g., cougars) species were treated with separate equations, given the ability of pack-hunting species to cooperatively kill larger prey (Van Valkenburgh et al. 2016).

Importance of observed prey items for cougars and gray wolves were derived from CarniDIET (Middleton et al. 2021). We only included studies that reported the frequency of a prey item across predator scats in a study. Predator and prey body masses were derived from Mass of Mammals (Smith et al. 2003). Donkey and horse body masses by age class were estimated from scaling formulae in (Knopff et al. 2010) and were calculated from adult body masses and birth weights reported in AnAge: The Animal Ageing and Longevity Database (2020).

Carcass and cougar surveys

We surveyed for cougar presence and donkey carcasses at 27 wetlands in Death Valley National Park. Surveys were conducted by walking the perimeter of wetlands and investigating every potential trail for cached carcasses (Beier et al. 1995). Carcasses and cougar sign were frequently encountered on tight <0.5 m tall trails through dense riparian vegetation. Cougar scats were identified visually by size and shape and their frequent association with very large scrapes. All surveys and scat identification were conducted by EJL, thus eliminating inter-observer variability.

We classified donkey remains as kills if they were located on cougar trails or if they were within 20 m of a cougar scat or scrape. Cougar trails usually terminated at the kill and were defined by their height (<1 m) and because they were unused by living donkeys–as determined by the lack of donkey track and sign and by camera traps. We estimated donkey ages by examining tooth wear and eruption sequences following resources for donkeys and horses (Martin 2002, The Donkey Sanctuary 2016). In some cases, where skulls could not be located, we estimated age by the fusion or lack thereof of appendicular bones. We estimated the ages of the two photographically captured kills (Fig. 2) by locating the carcasses and evaluating tooth eruption sequences as well.

Activity patterns of donkeys and cougars

We collected ca. 2.5 million trail camera images (Bushnell Trail Cam Pro) from over five years and 64 camera stations across 26 wetlands in the Sonoran and Mojave Deserts of North America (Fig S3, Supplementary Table 1). Sites averaged 388 trap nights per site, with a total of 9,303 trap nights across all sites and all seasons (Supplementary Table 1). Sites with less than 10 trap nights ($n = 2$) were excluded from analysis. All trail cameras were on water or on trails to water. Some sites contained multiple cameras, depending on the number of water-access points at each site, which were aggregated for analysis.

We evaluated the effect of cougars on the temporal patterns of feral donkeys with the overlap (v0.3.3) and circular packages (v0.4-93) in R (v4.0.0). To do so, we converted clock time to sun time, which is consistent relative to sunrise and sunset and is derived from the date and geographic coordinates of each trail camera (Nouvellet et al. 2012, Meredith and Ridout 2014). We compared donkey daily activity patterns between wetlands in regions with low densities of cougars and no evidence of predation (henceforth ‘low predation risk’) and regions with abundant cougars and widespread predation (‘high predation risk’). This latter region also included sites that were shielded by human activity, where cougars were locally absent ('human shielding', Beschta et al. 2018), despite proximity (e.g. <2 km) to wetlands with abundant cougars and predation.

Sampling effort (e.g., number of trap nights) and the number of donkey detections varied between sites and between predation risk categories, which would bias pooled estimates (Frey et al. 2017). We therefore resampled our data over 1,000 bootstraps, sampling equally between predation-risk categories and sites within each category. We selected 25% of the number of detections in the predation-risk category with the lowest number of detections, and then drew this quantity equally from each predation-risk category, divided equally from all sites within each category. From each subset we calculated donkey temporal activity using a circular von Mises density distribution kernel, as appropriate for time data (Meredith and Ridout 2014). From these resampled density distributions, we calculated 95% confidence intervals (CIs) to test if there was a significant difference between activity patterns under different levels of predation-risk, based on the visual overlap or non-overlap of CIs.

To understand how cougars influenced the extent to which donkeys utilized wetlands, we calculated the daily activity duration of donkeys at each wetland by assigning donkey detections into events, defined as any detection ≥30 minutes apart from any other. We then summarized the total event duration per day and site. Given that study sites ranged across several distinct populations, including low density ones, we focused on one large contiguous population in the Southern Panamint Mountains of Death Valley National Park (permit number DEVA-2018-SCI-0036). Unfortunately, density estimates were not available. This population consisted of 15 wetlands, (3,746 trap nights) and included sites with kills ($n = 9$) and without ($n = 6$) and sites with camera trap detections of cougars ($n = 9$) and without ($n = 6$). Note that the presence of cougars and kills did not perfectly correspond: one site had cougar detections but no kills, another had clear evidence of kills within the last year, but no detections were made during the study period (Supplementary Figure 2, Supplementary Table 1).

Given that surface-water dependency is driven by temperature we extracted daily maximum temperatures from a 4x4 km interpolated national dataset for each site (PRISM Climate Group 2020). We then analyzed the effect of local kills, cougar presence, daily maximum temperature, and their interactions on daily activity with a negative binomial mixed effect model in the R package ‘glmmTMB’ v1.0.2.1 (Brooks et al. 2017), nesting day within site as random effects. The presence of kills and cougars were based on study-wide presence or absence. We used multimodel inference (based on AICc) to remove spurious terms and selected the most parsimonious model, which included daily maximum temperature, local predation, and their interaction. Cougar presence itself was not included.

Vertebrate activity patterns

To understand how donkey activity patterns may in turn alter the activity of other vertebrate species, we further analyzed trail camera imagery, focusing again on the Southern Panamints Mountains of Death Valley to control for differences in donkey population sizes between study areas. Given the large number of images, we only identified mammals larger than a cottontail rabbit (*Sylvilagus audubonii*). As with the donkey images, images of the same species were grouped into ‘events’ based on a 30-minute window. We then analyzed how mammal activity (hours/day/site) varied by maximum daily temperature and the presence of kills, using a zero-inflated negative binomial model, nesting day within site. To better understand how this related to donkey activity, we analyzed how daily mammal activity related to the donkey activity of that same day, using a negative binomial distribution and nesting day within site as random effects. To assess if this further corresponded to differences in species richness, we used the R package ‘iNEXT’ v2.0.20, to interpolate richness (Hill order 0), accounting for differences in sampling effort at each site (Hsieh et al. 2016). We tested for differences in richness between sites with and without donkey predation with a Wilcoxon signed rank test for non-parametric data.

Effects of feral donkeys on wetlands

To understand if cougars influence the effects of donkeys on wetlands we collected data from 16 desert wetlands in Death Valley National Park in November of 2019. We focused on pools where donkeys accessed water, at which we measured the percent of surface water vegetated, the percent of water surface covered by canopy foliage, the number of access trails per pool, and the percent of the pool's perimeter with woody vegetation. To quantify the degree of disturbance extending upland from water access points we laid out 3 parallel 2 m wide and 30 m long belt transects 10 m apart, centered at spring access points. Sampling locations were not shielded from potential donkey herbivory and disturbance by geographic barriers (e.g. cliffs). Along the entirety of each belt transect we counted the number of dung piles, and every 10 m we estimated % trampled ground, % undisturbed bare ground, % herbaceous cover, and % woody cover in 1 m^2 quadrats (9 total per site). Although we collected data on plant cover by species, we did not include it in subsequent analyses because it was confounded by elevation and edaphic differences across sites, thus not directly capturing the effects of donkeys.

Instead of analyzing each of these response variables in sequential analyses, and because of their non-normality, we calculated Gower distance between sites based on all nine response variables and conducted a Principal Coordinates Analysis (PCoA), to identify the primary axes by which wetlands differed from each other. These first two axes (PCoA 1 and PcoA 2) explained 42.9% of total variation between sites (27.3 and 15.6% respectively). We then analyzed which factors explained differences between wetlands in this synthetic PCoA space using a PERMANOVA test in the R package 'vegan' v 2.5-6 (Oksanen et al. 2019) with 100,000 iterations. We included the presence of kills, the presence of cougars, elevation, and topographic complexity (Supplementary Figure 7) as independent variables.

To further test if these differences could be driven by underlying spatial gradients, we calculated a geographic distance matrix with the R package ‘geosphere’ v1.5-10(Hijmans 2019). We then conducted a Multiple Regression on Distances Matrices analysis with the function ‘MRM’ in the R package ‘ecodist’ v2.0.7 (Goslee and Urban 2007) with 1,000 iterations, which tested if the dissimilarity in wetland structure was explained by their distances from each other and thus underlying spatial gradients.

Constraints on cougar predation

To understand the factors that constrained interactions between donkeys and cougars, we evaluated how landscape contexts influenced the probability of cougar presence at sites with feral donkeys. As others have shown (Dickson and Beier 2006), cougars require ambush cover provided either by vegetation or topography. We thus calculated a synthetic terrain-complexity variable from a 1/3 arc-second digital elevation model (USGS National Geospatial Program 2019), which synthesized terrain roughness, terrain ruggedness, and slope with a Principal Components Analysis (PCA). PC1 explained 92.5% of total variation and was subsequently used as a terrain-complexity variable (Supplementary Figure 7).

To describe potential riparian ambush cover, we calculated total riparian area and the number of riparian patches by tracing the boundary of riparian vegetation in QGIS from satellite imagery (2016, Google), which was validated during field surveys.

To test if anthropogenic landscape factors affected cougar presence, we recorded if springs were in the vicinity (within 500 m) of campsites or high-use recreation areas.

We then employed logistic generalized linear mixed effect models to understand the relative importance of campsites, terrain-complexity, total riparian area (on a $\log_{10}$ scale), and the presence of alternative prey at each site (presence or absence of bighorn sheep or mule deer) in predicting the presence of cougars and the presence of kills, as determined by field survey data (scat and sign) and camera-trap detections. Given that no kills occurred at campsites we excluded this factor from that analysis to prevent singularity failures. The region of each wetland was treated as a random block to control for spatial autocorrelation (Fig S2, Supplementary Table 1). Alternative, more spatially explicit approaches, for instance using the R package '*spdep'* to create spatial neighborhood matrices and weights were not possible due to convergence failures in model. We excluded sites in two survey regions where cougar sign was absent across all sites, because the lack of sufficient sites within these block levels would weaken inferences (Harrison et al. 2018) and because absence may have been driven by regional historic or stochastic factors.

Using multimodel selection techniques, we selected a final, most parsimonious model (based on AICc), which retained total riparian area and the presence of campsites as predictors for cougar presence, both of which were significant (χ^2=6.5, p=0.01; χ^2=4.7, p=0.03, Supplementary Figure 6). The most parsimonious model to explain the presence of kills included only terrain complexity, which was significant (χ^2=5.0, p=0.03, Supplementary Figure 6).

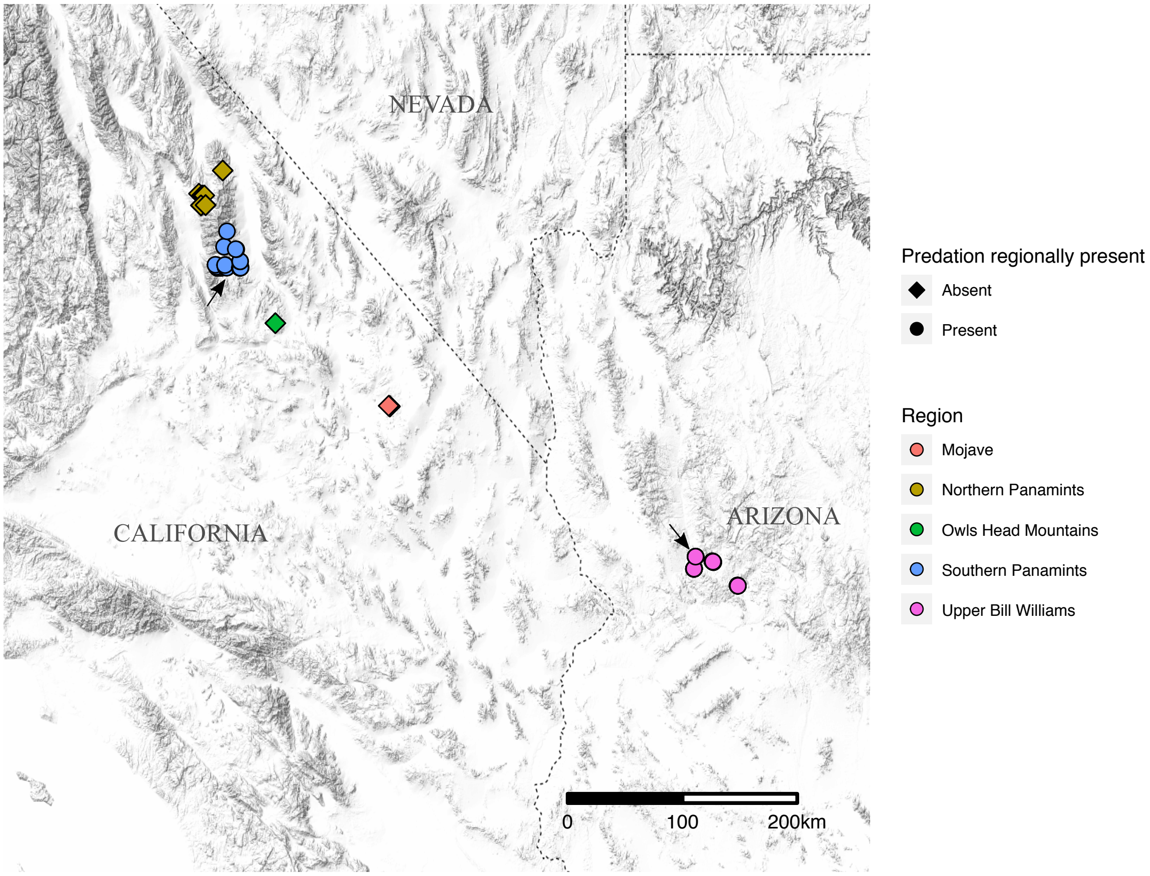
Supplementary Materials

Predator status in study areas

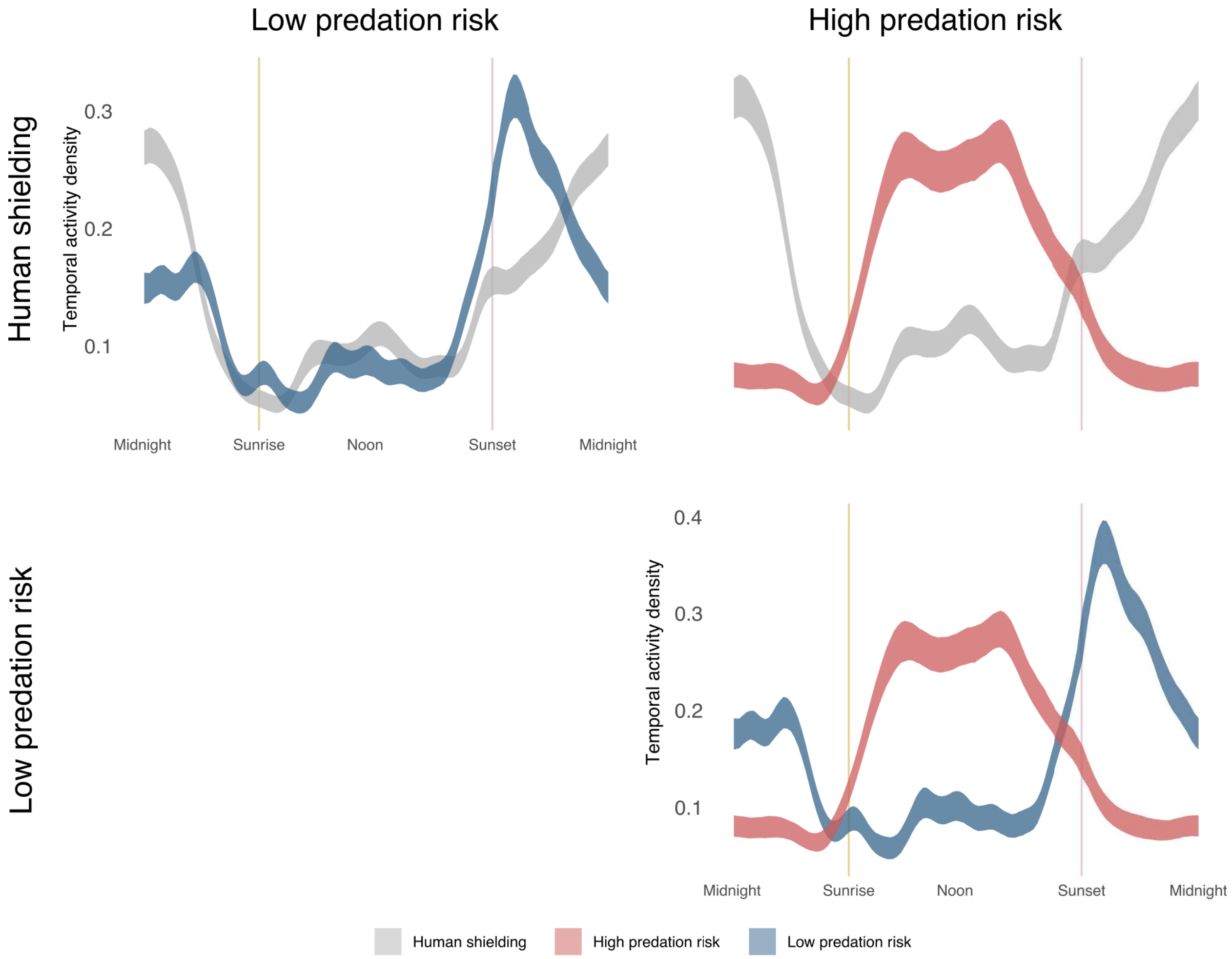
Trail camera imagery was compiled from wetlands in the Sonoran and Mojave Deserts (Supplementary Table 1, Supplementary Figure 2). The Sonoran Desert field sites occurred on Bureau of Land Management lands in central Arizona and data was collected from 2015-2018. Cougars are widely persecuted in this region, by recreational hunters and to protect livestock and to increase bighorn sheep production(Arizona Department of Game and Fish 2016).

The predation event captured at one wetland (Fig. 2a-b) was by a young cougar whom we suspect was observed two years prior with their mother. Both of these cougars were suspected of hunting wild donkeys and wild horses at the site, as many of the equids (including adults) had injuries suggesting feline attacks and because of the rapid disappearance of all horse foals. The mother, who wore a GPS collar, appears to have since been killed by the state wildlife agency, which removes cougars after killing two bighorn sheep (*Ovis canadensis*) within a 6-month period(Arizona Department of Game and Fish 2016). The majority of fieldwork in the Mojave Desert occurred in Death Valley, California. Cougars are protected from recreational hunting and from most types of lethal management in the state of California. As the largest contiguous protected area in the continental United States, Death Valley may thus have the strongest protected population of cougars in the world.

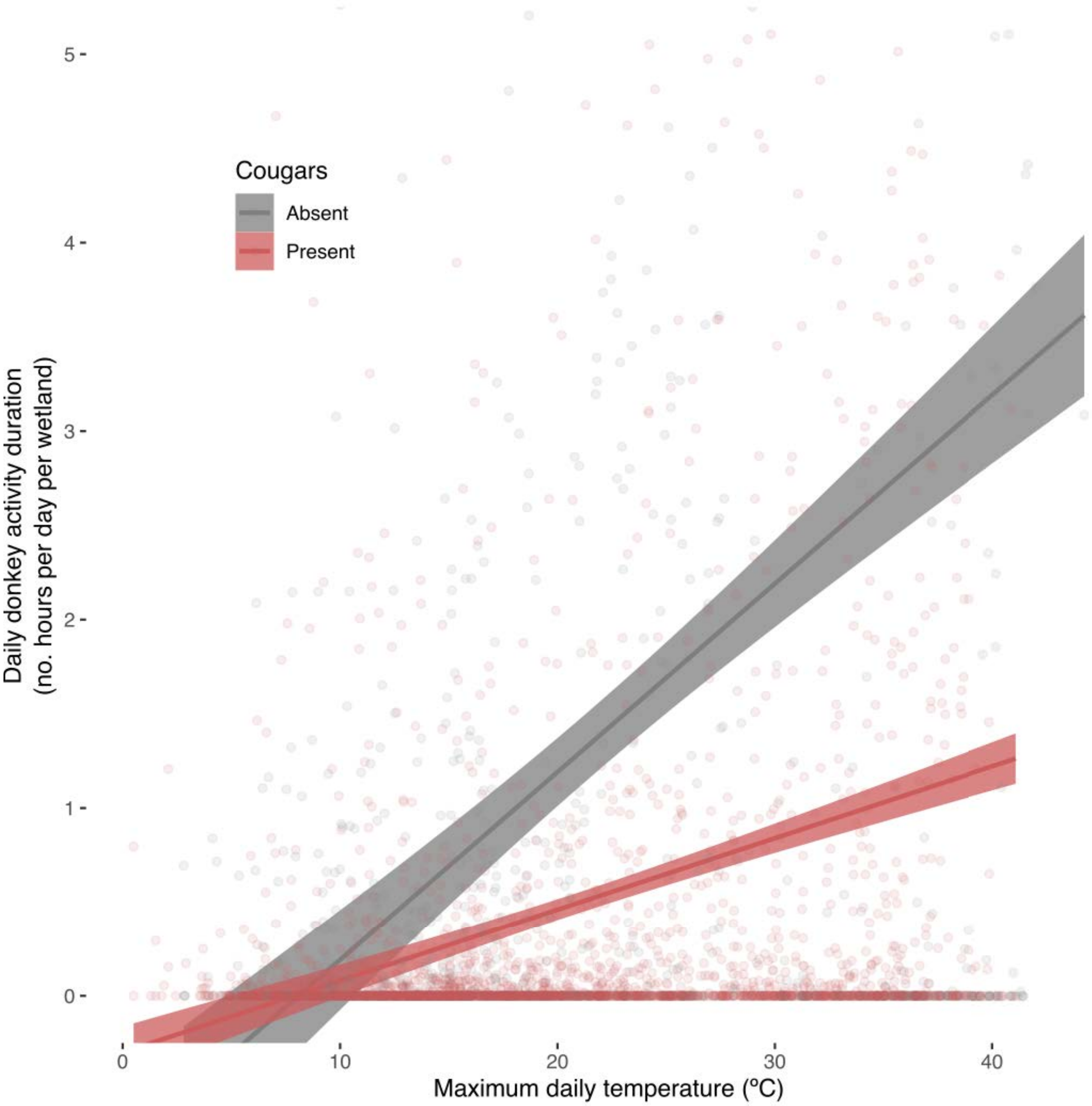
Supplementary Figure 1. Original images from Fig. 2a and Fig. 2c, prior to tonal correction for underexposure. Original files (.JPGs) are available upon request.



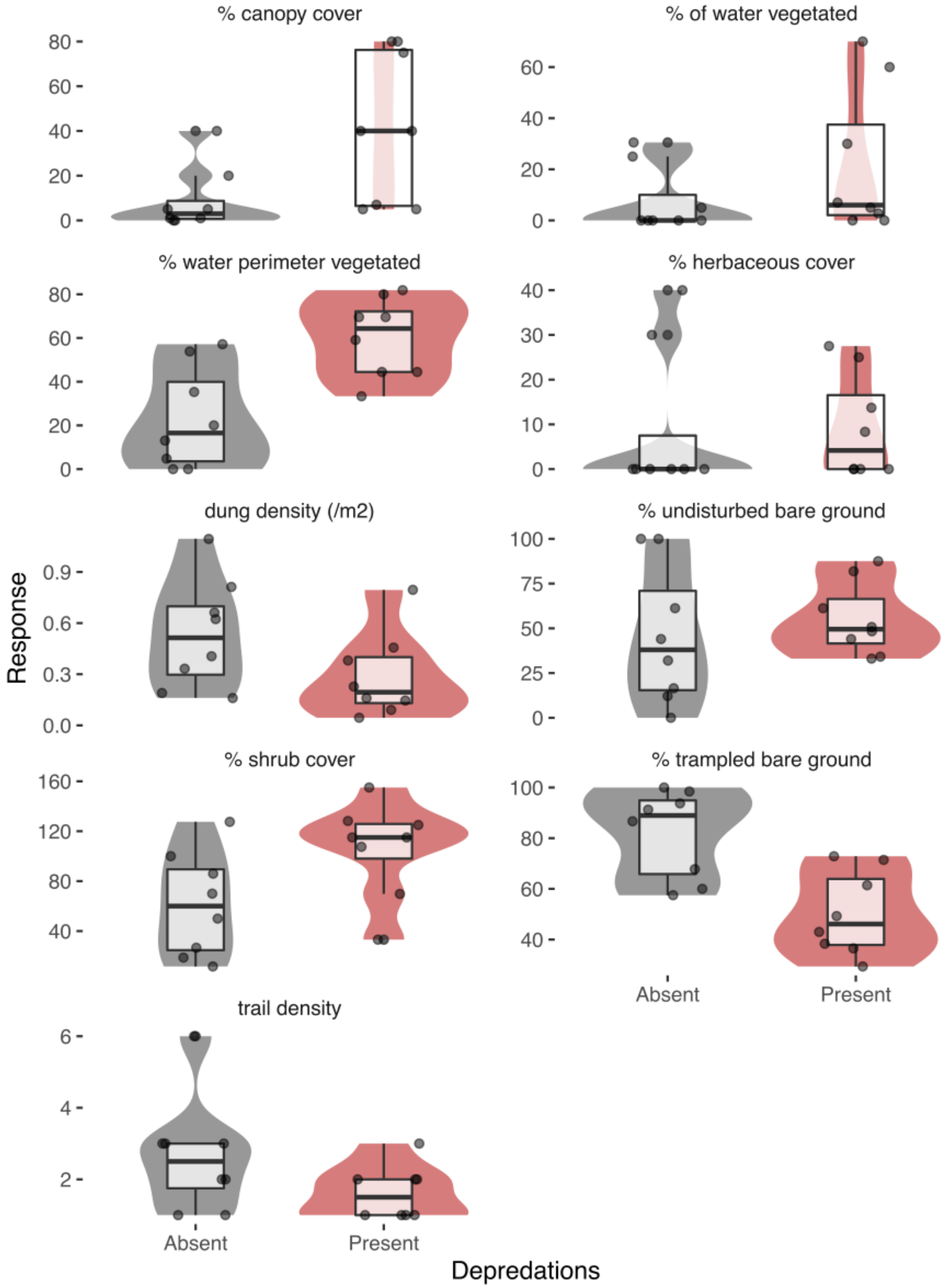
Supplementary Figure 2. Study regions across the Sonoran (‘Upper Bill Williams’) and Mojave Deserts (all other regions) of North America. Color indicates region, with shape indicating whether predation was documented within the region. Black arrows point to sites where kills (Fig. 2) were captured on camera traps. See Supplementary Table 1 for camera trap nights and details regarding which analyses included which sites.



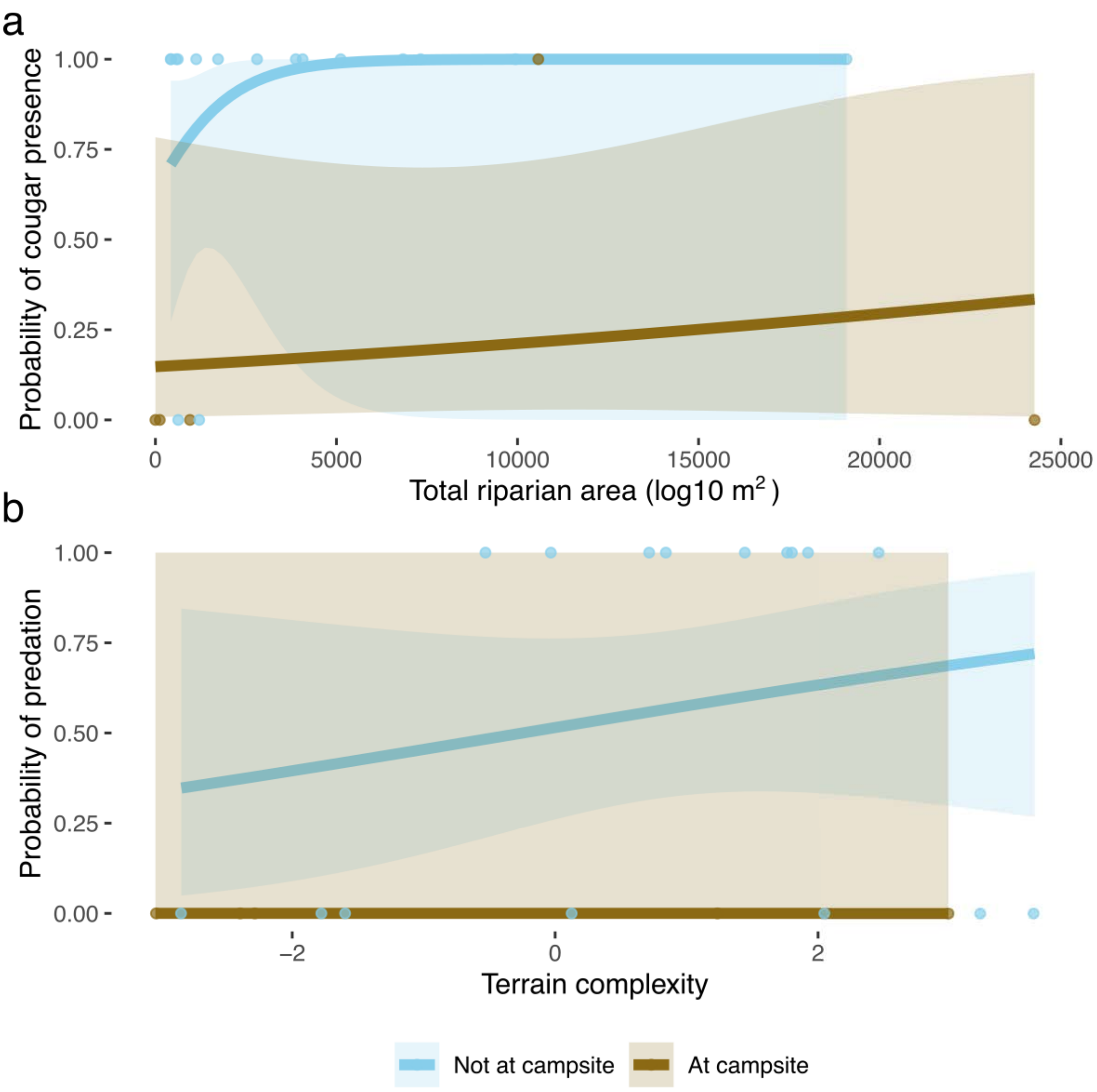
Supplementary Figure 3. Pairwise overlap in temporal activity patterns (y axis) of donkeys under different levels of predation risk. Ribbons indicate 95% confidence intervals across time (x-axis). Comparisons are as in a pairwise matrix, with rows and columns representing different predation risk categories.



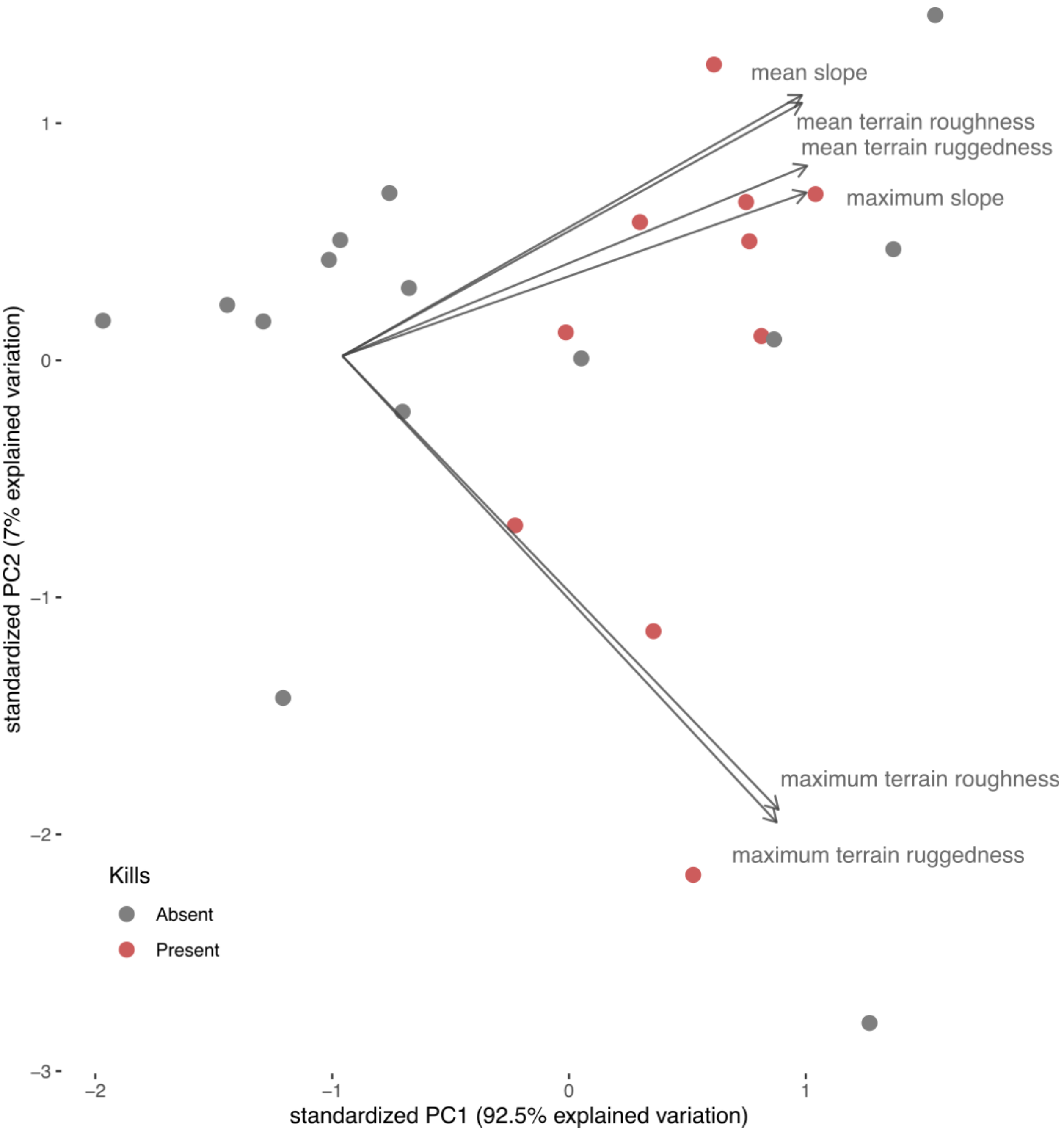
Supplementary Figure 4. The presence or absence of cougars themselves affected daily activity of donkeys (hours/day/site), but to a lesser extent than the presence of predation. Cougar presence was not included in the final most parsimonious model explaining daily occupancy. This suggests that behavioral responses are heightened at sites with high probability of successful ambush predation.



Supplementary Figure 5. Individual soil and vegetation responses at desert wetlands, in areas with and without kills. Fill indicates density distributions. Given their non-normality, these variables were analyzed synthetically with a PCoA and PERMANOVA test (Fig. 5).



Supplementary Figure 6. The most important factors influencing the presence of cougars and predation (e.g. kills) at desert wetlands in Death Valley National Park. A. Riparian area and campsites were significant in predicting cougar presence (riparian area: χ^2=6.5, p=0.01; campsites: χ^2=4.7, p=0.03). B. The presence of kills was predicted by terrain complexity (χ^2=5.0, p=0.03). Given that no kills occurred at human shielded campsite locations, that factor was excluded from analysis but is plotted here.



Supplementary Figure 7. Terrain complexity Principal Components Analysis synthesizing an ensemble of terrain complexity metrics, including terrain roughness, slope, and ruggedness. Terrain variables were calculated from a 1/3 arc-second digital elevation model (DEM) (USGS National Geospatial Program 2019) and extracted within a 100m buffer for each site. PC1 (92.5% of total variation) was used in subsequent analyses as a synthetic estimate of terrain complexity to reduce model overfitting.

Supplementary Table 1. Field site descriptions. Sites ranged across Sonoran and Mojave Deserts. Columns indicate region, corresponding to Supplementary Figure 1, and whether regional predation was documented. Local predation details (e.g. at the wetland) include whether cougars were detected (through scat and/or camera surveys) and whether kills were detected (number in parentheses indicates number of kills). Risk category, used in temporal analyses (Fig. 3A) is indicated as is camera trapping summary with details on number of camera stations (e.g. individual cameras at a site), total trap nights across camera stations, and number of years of monitoring. To control for different regional metapopulation sizes, only the Southern Panamints were included in wetland occupancy analysis (Fig. 3B). Final column indicates whether sites were surveyed for donkey-related effects on wetland vegetation and soils.

Wetland	Desert	Region	Regional predation	Local predation details	Risk category	Camera summary	Wetland effect survey
Anvil Spring	Mojave	Southern Panamints	yes	Cougars absent; kills absent	Human shielding	Cameras (1 station, 120 trap nights, 1 year)	surveyed
Arrastre Spring	Mojave	Southern Panamints	yes	Cougars present; kills present (1)	High predation risk	Cameras (2 stations, 86 trap nights, 2 years)	surveyed
Black Canyon	Sonoran	Upper Bill Williams	yes	Cougars present; Not surveyed	High predation risk	Cameras (4 stations, 432 trap nights, 2 years)	not surveyed
Blackwater Spring	Mojave	Northern Panamints	no	Cougars absent; kills absent	Low predation risk	No cameras	surveyed
Cane Springs	Mojave	Mojave	no	Cougars absent; kills absent	Low predation risk	Cameras (6 stations, 589 trap nights, 1 year)	not surveyed
Cattail Spring	Sonoran	Upper Bill Williams	yes	Cougars present; Not surveyed	High predation risk	Cameras (8 stations, 1088 trap nights, 1 year)	not surveyed
Five Mile Spring	Mojave	Southern Panamints	yes	Cougars present; kills present (2 + 1 kill captured on camera, Fig 2c-d)	High predation risk	Cameras (2 stations, 407 trap nights, 3 years)	surveyed
Greater View Spring	Mojave	Southern Panamints	yes	Cougars absent;	Human shielding	Cameras (1 station, 171 trap nights, 2 years)	surveyed

				kills absent			
Greenwood Spring	Sonoran	Upper Bill Williams	yes	Cougars present; kills present (Kill captured on camera Fig 2a-b)	High predation risk	Cameras (6 stations, 950 trap nights, 2 years)	not surveyed
Hackberry Wash	Sonoran	Upper Bill Williams	yes	Cougars absent; Not surveyed	High predation risk	Cameras (6 stations, 501 trap nights, 2 years)	not surveyed
Hatchet Spring	Mojave	Southern Panamints	yes	Cougars present; kills absent	High predation risk	No cameras	surveyed
Hidden Valley Spring	Mojave	Southern Panamints	yes	Cougars present; kills absent	High predation risk	Cameras (1 station, 57 trap nights, 2 years)	surveyed
Little Spring	Mojave	Southern Panamints	yes	Cougars present; kills absent	High predation risk	Cameras (2 stations, 533 trap nights, 3 years)	surveyed
Lost Spring	Mojave	Southern Panamints	yes	Cougars present; kills present (1)	High predation risk	Cameras (5 stations, 1108 trap nights, 2 years)	not surveyed
Lower Galena	Mojave	Southern Panamints	yes	Cougars present; kills present (3)	High predation risk	Cameras (1 station, 253 trap nights, 2 years)	surveyed
Lower Tuber Spring	Mojave	Northern Panamints	no	Cougars present; kills absent	Low predation risk	Cameras (3 stations, 318 trap nights, 2 years)	surveyed
Mesquite Spring	Mojave	Southern Panamints	yes	Cougars absent; kills present (1)	High predation risk	Cameras (3 stations, 430 trap nights, 2 years)	surveyed
Mud Spring	Mojave	Northern Panamints	no	Cougars absent; kills absent	Low predation risk	Cameras (1 station, 184 trap nights, 3 years)	surveyed
N Fork Johnson Canyon	Mojave	Southern Panamints	yes	Cougars present; kills present (1)	High predation risk	No cameras	surveyed
Owls Head Spring	Mojave	Owls Head Mountains	no	Cougars absent;	Human shielding	Cameras (2 stations, 199 trap nights, 2 years)	surveyed

				kills absent			
Powerful Women Spring	Mojave	Southern Panamints	yes	Cougars present; kills present (1)	High predation risk	Cameras (1 station, 444 trap nights, 2 years)	surveyed
Upper Galena	Mojave	Southern Panamints	yes	Cougars present; kills present (3)	High predation risk	Cameras (1 station, 266 trap nights, 2 years)	surveyed
Upper Tuber	Mojave	Northern Panamints	no	Cougars present; kills absent	Low predation risk	Cameras (3 stations, 318 trap nights, 1 year)	not surveyed
Warm Springs	Mojave	Southern Panamints	yes	Cougars present; kills present	High predation risk	No cameras	not surveyed
Wildrose	Mojave	Northern Panamints	no	Cougars absent; kills absent	Human shielding	Cameras (1 station, 251 trap nights, 2 years)	not surveyed
Willow Spring	Mojave	Southern Panamints	yes	Cougars present; kills present (10)	High predation risk	Cameras (4 stations, 1119 trap nights, 3 years)	surveyed

Supplementary Table 2. Full PERMANOVA model results. PERMANOVA was conducted with the function ‘adonis2’ in the R package ‘vegan’ v2.5-6 (Oksanen et al. 2019) with 100,000 iterations.

Variable	Degrees of freedom	Sum of squares	R^2	F	p-value
kills present	1	0.31	0.20	3.54	0.00014
cougars present	1	0.10	0.06	1.11	0.33
terrain complexity	1	0.10	0.06	1.13	0.31
elevation	1	0.10	0.07	1.19	0.27
Residual	11	0.95	0.61		
Total	15	1.56	1		

Supplementary Table 3. Evidence of predation on introduced wild equids by extant predators. The possibility that predators can influence introduced equids is frequently dismissed in policy and research. However, growing evidence suggests that extant predators have a greater capacity to influence equids than usually considered. In Africa and Asia, *Panthera uncia* (Wegge et al. 2012), *Panthera pardus* (Shehzad et al. 2015), *Panthera leo* (Fischhoff et al. 2007), and *Crocuta crocuta* (Grange et al. 2004) have been documented predating domestic or wild (non-introduced) equids and are displayed in Fig. 6, but are not included here as they do not overlap with introduced equid populations.

Predator	Description
Cougar (*Puma concolor*)	*Horses* Cougars have been documented preying on horses, though studies often have mixed results regarding the importance of horses in cougar diets (Berger 1986, Blake and Gese 2016). Predation on foals (Knopff et al. 2010) has been shown to have significant effects on population growth in some study areas (Turner et al. 1992, Greger and Romney 1999, Turner and Morrison 2001). However, a 25-year study on a heavily predated and unmanaged horse population found that horses began avoiding their historic summer rangelands (higher elevation with more vegetative cover), presumably to avoid cougar predation (Turner 2015). While predation on juveniles has been most commonly documented (Turner et al. 1992, Greger and Romney 1999, Turner and Morrison 2001, Turner 2015), Andreasen (Andreasen 2014) documented predation on adult horses as well (estimated ~420kg in her study area) by both male and (smaller-bodied) female cougars. In some study populations, horses were the primary prey item, particularly in mountain ranges with high densities of horses. Cougar influences on horse populations are likely sensitive to even low levels of persecution. For example, cougar predation appeared to drive population decline among horses in the Pryor Mountains of Montana and Wyoming until the removal of 3 cougars by humans. Following this, horse population growth rapidly increased (Ransom 2012). *Donkeys* Cougar predation on donkeys had not been documented in the literature until this study.
Gray wolf (*Canis lupus*)	*Horses* Horses can be a major component of wolf diets in some regions, including in Europe (Meriggi and Lovari 1996, Vos 2000, Lagos and Bárcena 2018) and in Canada, where wolves and horses overlap (Webb et al. 2009, National Research Council 2013). However, wolves do not currently overlap with most introduced horse populations in North America (Figure 6) given historic extirpation of wolf populations from much of the United States and Mexico. The cursorial and pack hunting strategy of wolves suggests that they would be able to hunt introduced horses and donkeys in areas without sufficient ambush cover for successful cougar predation. *Donkeys* Wolf predation has been documented on domestic donkeys in Iberia (Pimenta et al. 2018) and gray wolves have been observed chasing reintroduced Asiatic ass (*Equus hemionus*) in Israel (Gavin Bonsen *personal communication*).

	Wolves and donkeys do not currently overlap in North America (Figure 6). Whether gray wolves could reestablish in the desert environments occupied by donkeys remains unknown, yet is plausible given the presence of gray wolves in hot deserts in Eurasia (IUCN Red List 2018) and anecdotal records of gray wolves in hot, hyper-arid parts of the Sonoran Desert, such as the Pinacate Biosphere of Northern Mexico (Hayden 1998).
Jaguar (*Panthera onca*)	*Horses and donkeys* Jaguars can be major predators of domestic livestock, including horses and donkeys (Zimmermann et al. 2005, Jędrzejewski et al. 2017). To the best of our knowledge, no study has been conducted on how jaguars may influence feral equids in South America or Mexico, where they may overlap. Jaguars have experienced significant range contractions in North and South America (IUCN Red List 2018). Their reestablishment, particularly in the Southwestern United States, could lead to increased predation pressure on adult equids.
Dingo (*Canis dingo*)	*Horses* Horses are commonly recorded in dingo scats, albeit at low frequencies (Forsyth et al. 2019). Dingo predation on a feral horse foal was observed in the Painted Desert of Australia (ADW, *personal observation*) and dingo packs are known to kill feral horses in the Snowy Mountains, including foals at least as old as 6 months in age(Newsome et al. 1983). This has been thought to perhaps explain the larger size of dingo packs in that region (Newsome and Coman 1989). Experimental work found that dingo howls did not elicit maternal protectiveness responses among feral horse mares but that dominant stallions responded by spending more time in close proximity to foals, suggesting that dominant stallions may play an important role defending foals from dingo predation(Watts et al. 2020). *Donkeys* Donkeys have been recorded in dingo scats and dingo packs have been observed in pursuit of donkeys (Chris Henggeler *personal communication* Aug. 2019). Furthermore, the protection and stabilization of dingo populations has been strongly linked to reduced donkey abundance (Wallach et al. 2010). However, dingo predation on donkeys has not been directly recorded.
Brown bear (*Ursus arctos*)	*Horses* Brown bears have been documented predating domestic horses in Spain, including both yearlings and adults (Clevenger et al. 1994). In Alberta, Canada, grizzly bear (*Ursus arctos horriblis*) have been observed chasing horses and are suspected to be a major cause of mortality (Paul Boyce, *personal communication*). *Donkeys* Given widespread range contractions, brown bears and introduced wild donkeys do not currently co-occur (Figure 6**)**. Gobi Desert grizzly bears co-occur with Asiatic ass (*Equus hemionus*), but whether they predate these donkey-like equids is unknown (Tumendemberel et al. 2015). If grizzly bears were to reestablish in arid regions of North America (IUCN Red List 2018) then interactions with wild donkeys could be possible.

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Chapter 5: The inadvertent arks: the potential for introduced populations to alter conservation priorities

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Abstract

Conservation biology, like all applied scientific disciplines, is composed of both empirical facts and normative values. Normative values are essential to guide decision making, yet are rarely interrogated. We confront the conservation paradox of threatened introduced species by empirically interrogating how the normative value of *nativism*, a value that considers introduced biodiversity illegitimate and aspires to return ecological communities to historic configurations. To understand the extent to which different values might change global conservation priorities, we conducted spatial prioritization simulations for the optimal conservation of globally threatened mammal species under nativism, contrasting it with previously unarticulated alternative value scenarios. We find that valuing introduced populations can have diverse effects on conservation priorities. This includes potentially delisting as many as 20 threatened mammal species, which is more than have been saved from extinction through direct conservation intervention in the last 30 years. Other inclusive value scenarios increase the importance of currently overlooked landscapes, particularly in Australia, providing new opportunities to prevent species extinctions. We hope that our findings will inspire others to openly interrogate how nativism, and other normative values, influence conservation.

Introduction

The redistribution of organisms through introductions has led to the establishment of numerous introduced populations that are simultaneously threatened in their native ranges (Lees and Bell 2008, Marchetti and Engstrom 2015, Lundgren et al. 2018). Despite their global threat status, these introduced populations remain targets of conservation eradication and control programs. This presents a conservation paradox, as preventing global extinctions is one of conservation's primary aims (Convention on Biological Diversity 2011-2020).

This paradox raises important questions about how conservation biology should respond to the redistribution of life. This is particularly relevant as many species may not be able to live in their historic native ranges due to climate change and other anthropogenic pressures. For example, the Javan rusa deer (*Rusa timorensis*) is Critically Endangered from poaching and habitat loss in its native range of Indonesia (IUCN Red List 2018). The Javan rusa has also been introduced to continental Australia, where it is considered a pest and is the subject of culling and eradication efforts (PestSmart Connect). If the Javan rusa becomes extinct in its native range, should the International Union for the Conservation of Nature (IUCN) list the species as extinct? Or should conservation policy value the Australian populations, either by accepting their presence in their new home, or as a source population for future repatriation to Java?

This question has no simple answer because it is determined not by science and empirical knowledge, but by the normative values that guide decision-making. One normative value of particular relevance to how we understand introduced populations is *nativism*. Nativism is a belief that species belong in the place in which they evolved or immigrated to on their own (i.e. without human interference) (Pollan 1994, Gould 1998, Peretti 1998, Hettinger 2001). Nativism denies value to those organisms whose dispersal histories are intertwined with our own and aspires to recreate historic species configurations–reflective of how places *ought* to be in the absence of human influence. Thus, many introduced species are described as harmful, not because of measurable effects on other species, but because they do not belong (Chew and Hamilton 2011). It is in this way that introduced taxa are ignored from biodiversity datasets and threat assessments as they are not seen as legitimate forms of biodiversity (Schlaepfer 2018a, Schlaepfer 2018b, Wallach et al. 2019).

Despite increasing skepticism about the utility and appropriateness of nativism (Davis 2009, Mascaro et al. 2012, Chew 2015, Sagoff 2018, Schlaepfer 2018a, Schlaepfer 2018b, Díaz et al. 2019), this value remains important to many in the field of conservation biology and thus should be evaluated upon its own merits in shaping conservation discourse and policy. Likewise, previous calls for conservation to embrace more expansive and inclusive value systems have not clarified how these values would be implemented nor how they would negotiate concern for both native and introduced populations (Schlaepfer et al. 2011, Lundgren et al. 2018, Wallach et al. 2018, Wallach et al. 2019).

We therefore quantified the scale and pattern of the conservation paradox of introduced species for global mammals. We then proposed three alternative ways to value introduced biodiversity with the aim of preventing global extinctions. These included proactively protecting introduced populations of threatened species as refuges; accepting introduced populations as having conservation value and thus delisting globally threatened species based on the extent of their introduced range; and recognizing the independent value of both native and introduced populations as independent collective entities with their own evolutionary trajectories. To understand how nativism and these alternatives could influence conservation policy, we tested the relative effect of these various formulations of possible conservation values with quantitative spatial prioritization simulations to identify landscapes where conservation resources would be best spent.

Methods

We focused on threatened terrestrial mammals (*n*=1,225) as their threat statuses are well known and their native distributions have been thoroughly mapped by the IUCN Red List (2018). These ranges were compiled with introduced ranges digitized from the peer-reviewed literature and a variety of databases (PestSmart Connect , Long 2003, DAISIE European Invasive Alien Species 2017). To describe the overall pattern of modern biotic redistribution we analyzed which biogeographic realms (Olson et al. 2001) have donated versus received introduced mammals and the degree to which introduced mammals represent global mammalian diversity.

Value scenarios

We formulated four value scenarios. In the *nativist* scenario–the *status quo*–we prioritized the conservation of only the native ranges of threatened species (Near Threatened species were considered threatened), as nativism considers only native populations as legitimate biodiversity. Following IUCN Red List guidelines (section 2.1.3), populations introduced with the intent to reduce extinction risk (e.g. conservation translocations) were treated as native populations, as were introductions geographically adjacent to native populations (IUCN Red List 2018). In the *additive* scenario, we prioritized the conservation of the entire range of threatened species, including introduced populations, even if the introduced population was larger than the native population. This was under the rationale that introduced populations are unstable and may collapse (Simberloff and Gibbons 2004) and that global stochasticity in climate and human pressures may warrant the most conservative approach to prevent global extinctions.

In the *globalist* scenario the primary goal was to reduce global extinctions, wherever possible. Thus, we reevaluated species threat statuses globally, based on the size of the combined introduced and native ranges. In this way, some species were de-listed globally–deprioritizing both the native and introduced ranges of these now cosmopolitan species. This scenario assumes that introduced populations are legitimate components of biodiversity and are thus monitored with equal care as native populations and are no longer targeted for eradication. To reassess threat statuses, we used IUCN listing criteria and assumed a linear relationship between range size and population size (following Mogg et al. 2020). We considered a 20% change in total range size relative to native-only range size as criteria for the change in threat between one level to another (e.g. from Critically Endangered to Endangered). We decided to use relative range size, instead of absolute range sizes, given that some native populations are endangered because of rapid population declines, though retain large geographic ranges (e.g. Sambar deer, *Rusa unicolor*).

Finally, the *relativist* scenario independently considered the value of both introduced and native populations as collectives with their own evolutionary trajectories. We therefore assessed the threat status of native and introduced populations separately. All native threatened populations were included (as their threat statuses did not change) but introduced populations were only included if they qualified as threatened themselves, based on their range size relative to the species' native range size (**Table 1**).

Table 1. Value scenarios. Alternative ways to imagine the exclusion or inclusion of introduced organisms under the umbrella of conservation concern. Table lists the value scenarios analyzed, their rationale, and changes (if any) to threat statuses. Changes in threat status (in globalist and relativist scenario) affected prioritization simulations both by removing species (if delisted) and by changing priority weighting (see text).

Scenario	**Rationale**	**Threat status**
Nativist	Only native populations have value.	Same as IUCN
Additive	The entire range, native and introduced, of a species has value. Species threat status is not affected by introduced populations because the stability of the introduced populations is unknown.	Same as IUCN
Globalist	There is no inherent value to native populations relative to introduced ones. The goal is simply to reduce global extinctions wherever possible.	Threat reevaluated globally at a species-level based on introduced range size. If a species' introduced range is large enough, the entire species becomes de-listed in threat and thus removed from simulation.
Relativist	Both introduced and native populations are valued as collectives with independent evolutionary trajectories.	Native ranges have same threat status as IUCN. Introduced ranges are independently

		assessed, relative to the size of the native range.

Spatial prioritization

Species ranges were rasterized to produce feature layers for the prioritization analysis using the R package '*exactextractr'* v0.4.0 (Baston 2020) and a Mollweide projection at a 30x30km resolution. Introduced ranges that were only reported at the scale of country or provincial boundaries were omitted from spatial prioritization analyses, as the large sizes of these political entities (e.g. all of Russia) would lead to global delisting, even if the overall population was likely small. However, to account for these populations, 1% of that total area was used in re-assessing species threat statuses for the *globalist* value scenario. This cutoff is arbitrary yet conservative for the purposes of this simulation.

We conducted spatial prioritization analyses using the R package '*prioritizr'* v5.0.1 (Hanson et al. 2020), which uses integer linear programming techniques to find optimal solutions for spatial conservation planning problems. We used a 'maximum utility' objective to find the 'biggest bang for the buck' solution that most efficiently conserved as many species as possible per a specified conservation budget, in this case the number of land units (e.g. pixels). Alternative approaches (e.g. to find the minimum cost solution to meet conservation goals per species) were not mathematically solvable.

Species were assigned weights based on their threat status. We weighted Near Threatened species with a weight of 1, Vulnerable species with a weight of 3, Endangered species with a weight of 5, and Critically Endangered, Extinct in the Wild, and Extinct species with a weight of 7. Thus, the prioritization algorithm gave extra importance to protecting the most endangered taxa. In doing so, changes in threat status in the *globalist* and *relativist* value scenarios altered the importance of those populations in each prioritization simulation.

We iteratively calculated prioritization solutions for each value scenario, increasing the total number of land units in the conservation budget from 1% of the Earth's surface to 30%. The resulting solutions were summed to provide a continuous ranking of relative priority per land unit. We then summarized how different value scenarios affected conservation planning by evaluating how they shifted priorities between biogeographic realms (Olson et al. 2001).

Species endangerment, and thus conservation priorities, are driven by a variety of anthropogenic pressures, including habitat modification, species exploitation, and chemical pollution (Díaz et al. 2019). Many of these drivers are linked to poverty, urbanization, and human density, data which are readily available on a global scale. We thus analyzed how different value scenarios interact with these factors in predicting whether a land unit would be prioritized (as a binary response). We did this with binomial generalized linear models in the R package 'glm'. For independent variables, we included human population density, the Human Development Index, and the Human Footprint Index. Human population density per km^2 were drawn from IMAGE (2019).

The Human Development Index synthesizes education, income, and life expectancy on the country-scale thus presenting a multivariate estimate of poverty and quality of life (data from 2013, United Nations Development Programme 2020). he

Human Footprint Index (data from 2009, Venter et al. 2016) was used as a general indicator of human land use intensity. Thus, these latter two variables capture interrelated but distinct aspects of human occupancy patterns, with the Human Development Index describing overall poverty and quality of life and the Human Footprint Index indicating overall landscape modification. These thus likely reflect different dimensions of anthropogenic pressures (e.g. poaching and direct exploitation versus landscape modification).

Results

Overall, we identified 265 introduced mammal taxa. Introduced taxa come from all realms bar Antarctica and Oceania, but primarily from the Palearctic and Indomalaya (26% each), followed by the Afrotropics (15%), Australasia (12%), and the Neotropics (10%) and Nearctic (9%) (**Fig. 1A).** Overall, most realms received similar numbers of species (**Fig. 1A),** with Australasia and the Neotropics receiving the most (**Fig. 1A).** Introduced mammals represent 52 of 115 terrestrial mammal families, including up to 100% of the species in some families (**Fig. 1B).**

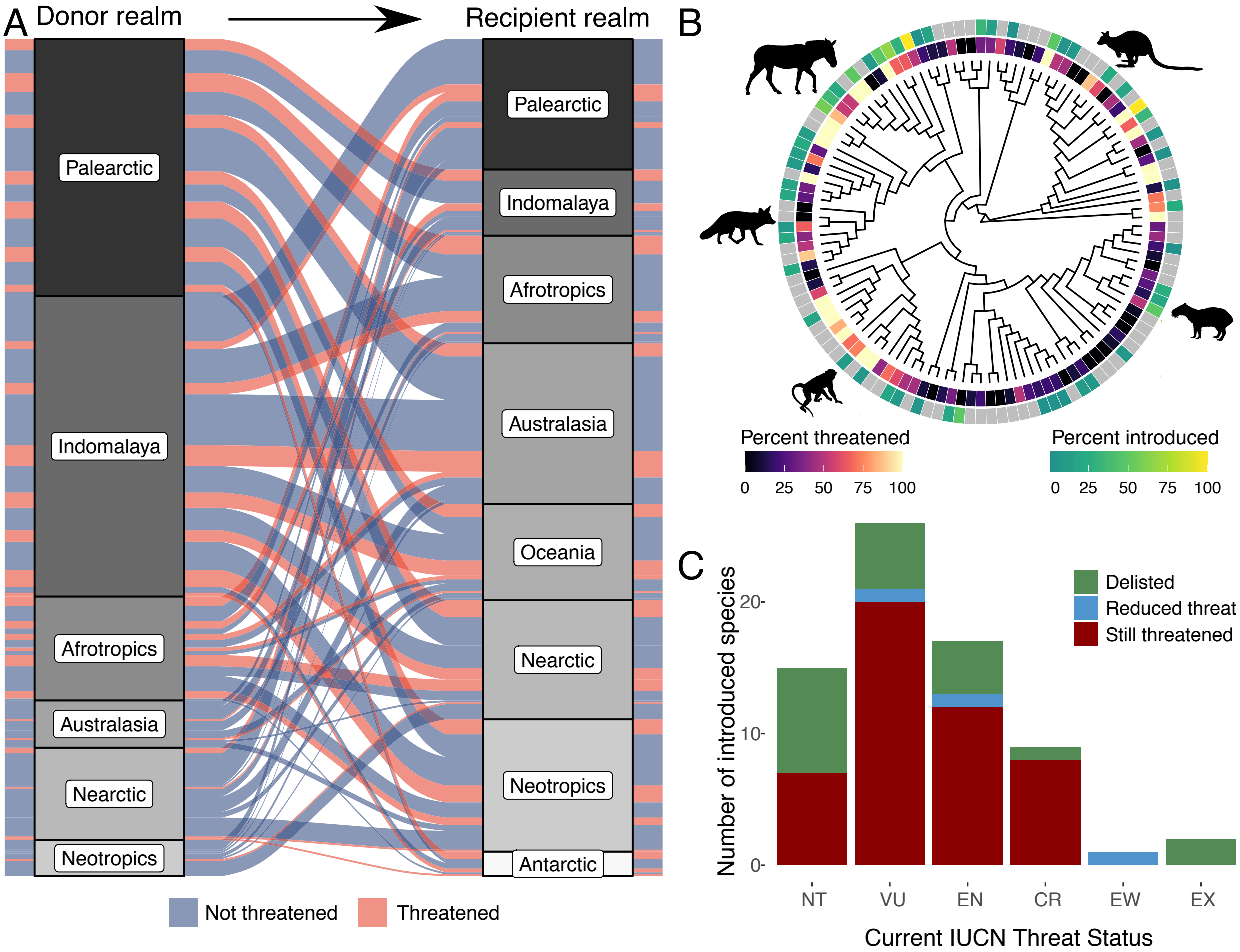

Figure 1. The redistribution of mammals. A. Height of boxes and colored bands indicate the number of species introduced from donor realms (left-hand boxes) to recipient realms (right-hand). Blue indicates non-threatened species and red indicates threatened (including Near Threatened species). Only interchanges (introductions between realms) are plotted. **B.** Phylogenetic distribution of threatened and introduced species by family. Inner colored band indicates percent of family threatened and outer band indicates percent of family introduced. Phylogeny from PHYLACINE (Faurby et al. 2018) **C**. Including introduced populations in global threat assessments delists 20 species and reduces threat levels for an additional 3, of 70 threatened introduced mammals. NT=Near Threatened, VU=Vulnerable, EN=Endangered, CR=Critically Endangered, EW=Extinct in the Wild, EX=Extinct.

Seventy species, or 22% of the 265 introduced species, are threatened in their native ranges, similar to the 25% of all terrestrial mammal species that are threatened. Overall, introductions have provided new populations for 3% of all threatened mammal species. If global threat statuses are re-assessed with introduced ranges included (e.g. the *globalist* value-scenario) 23 threatened species have their threat status reduced, 20 of which become completely delisted (**Fig 1C**).

Changing if and how we value these threatened introduced species has effects on how we should prioritize conservation efforts. Under the value scenario of *nativism*–business as usual–the global tropics are the highest priority landscapes to most effectively protect the maximum number of species per land unit (**Fig. 2A, Fig. 3A**). However, if introduced populations are valued with the same threat status as their native populations (*additive* value scenario), then Australia–home to 16 threatened introduced mammals–and parts of the southwestern United States and the Caribbean become almost equally important for global conservation goals (**Fig. 2A-B, Fig. 3A-B**).

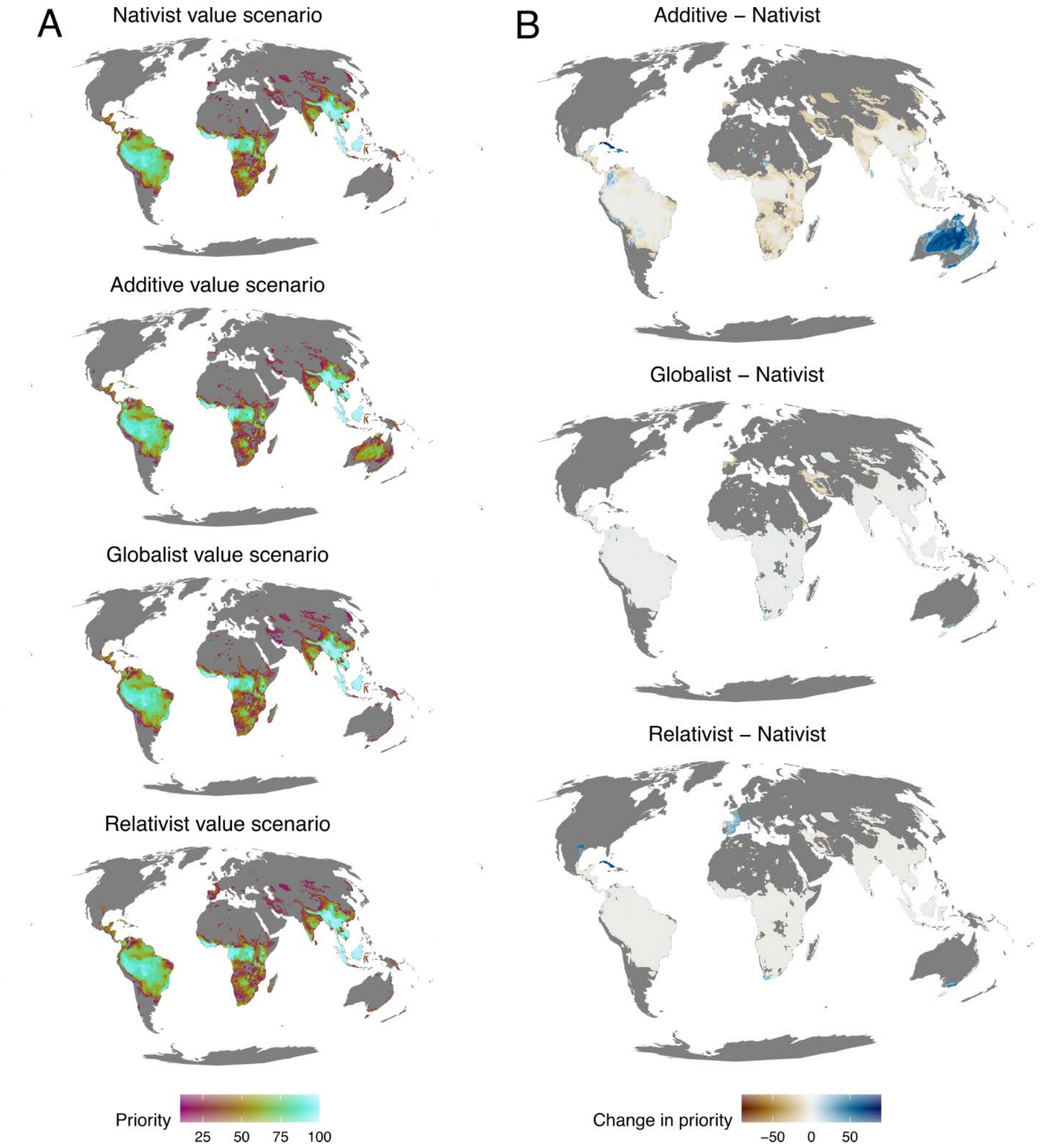

Figure 2. Manipulating value systems changes conservation priorities. A. Priority conservation areas to maximize the number of threatened species protected per land unit under different value scenarios (Table 1). Priority rankings (colored fill) were calculated by increasing the total conservation budget (e.g. number of land units to be prioritized) from 1% of the Earth's surface to 30%. **B.** Difference between the three alternative conservation value scenarios and nativism. White indicates no change, while brown indicates de-prioritization and blue indicates increased prioritization.

In the *globalist* scenario, where 20 species were delisted and 3 more reduced in threat-status, prioritization solutions show little difference from *nativism*, except that some small areas, mostly in Europe and central Asia become slightly deprioritized (**Fig. 2A-B, Fig. 3A-B**). Finally, in the *relativist* scenario, where native populations retain their original IUCN status but introduced populations are assessed independently, small introduced populations became threatened, thus increasing the importance of landscapes in parts of the Nearctic (Texas and the Caribbean), the Neotropics, Southeastern Australia, and Europe where a diversity of introduced species with small ranges dwell (**Fig. 2A-B, Fig. 3A-B**).

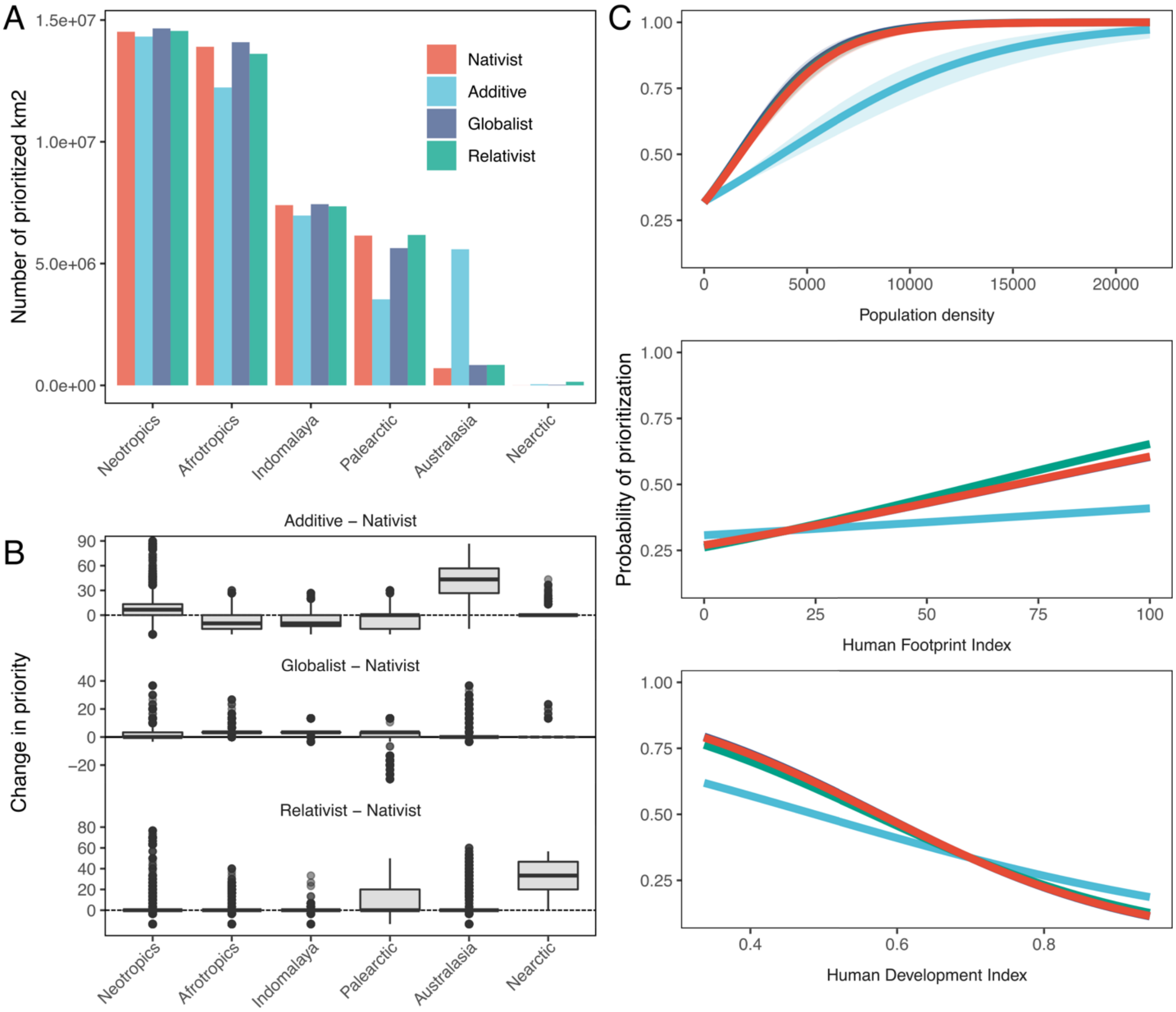

Figure 3. Change in conservation priorities under different value scenarios summarized by biogeographic realm A. Total prioritized land area (km^2) per biogeographic realm under different value scenarios. **B.** Change in land unit (pixel) priority per realm under different value scenarios relative to *nativism*, calculated from the ranked priority value (0-100). Only land units that were prioritized in at least one scenario are included. **C.** Endangerment, and thus conservation priorities, are driven by broad scale patterns of human influence, including human population density, landscape modification (Human Footprint Index), and poverty and quality of life (measured with the Human Development Index). However, these relationships are modified by different value systems. Legend shared with panel A. Note that some value scenario results are covered by the nativist scenario.

Conservation priorities were significantly driven by the anthropogenic factors influencing the endangerment of mammalian species, including the Human Footprint

Index ($\chi^2 = 454$, $p < 0.0001$), and the Human Development Index ($\chi^2 = 1{,}978$, $p < 0.0001$) (**Fig. 3C,** for model results). However, different value scenarios modified these relationships in significant ways. The negative relationship between landscape modification (Human Footprint Index) and conservation prioritization was reduced for the relativist scenario (interaction term: $\chi^2 = 454$, $p < 0.0001$), as many introduced species with small ranges exist in modified, agricultural or semi-urban landscapes. On the other hand, the additive value scenario weakened the relationship between conservation prioritization and both the Human Development Index (which synthesizes poverty and education and longevity, $\chi^2 = 1{,}978$, $p < 0.0001$) and population density ($\chi^2 = 12$, $p = 0.006$). This was driven by the shift in importance from developing nations in the global tropics to central Australia–shifting the onus of conservation work to the developed world.

Discussion

As an applied scientific discipline, conservation biology, like medicine, operates in the interplay of empirical facts and normative values. Values are how we make decisions to act and are how we compose ethical arguments to, for instance, not cut down rainforests or kill rhinos for their horns or blow off mountain tops for coal. However, it is essential that applied scientific disciplines interrogate their values, with as much rigor as they interrogate their empirical understandings of the world (Yanco et al. 2019).

Many introduced mammals are threatened in their native ranges but are omitted from conservation because of *nativism*. If we tweak this value, our conservation priorities change. For the most part, these changes were modest (Fig. 2)–as the scale of endangerment of terrestrial mammals–driven primarily by habitat loss and exploitation (Díaz et al. 2019)–is more profound than the scale of introductions. However, new opportunities do emerge, depending on different visions of an inclusive conservation ethic.

If introduced populations are considered as important as native populations (*additive* scenario), then central Australia with its rich, introduced large-herbivore community could be considered a biodiversity hotspot to reduce the risk of extinction of these ecologically important species and their globally endangered functional group (Werner et al. 2006, Ripple et al. 2015, Doughty et al. 2016, Lundgren et al. 2018, Wallach et al. 2018, Lundgren et al. 2020).

For example, the final surviving native population of the African wild ass (*Equus africanus*) is Critically Endangered, with an estimated population of 150-200 (**Fig. 4A**). Active conservation efforts are challenging as their habitat is remote and occupied by warring tribes. However, wild, free-roaming populations of donkeys, feral descendants of wild asses*,* thrive in the deserts of Australia and North and South America where they have restored lost ecological roles (Kodric-Brown and Brown 2007, Lundgren et al. 2020). Meanwhile, domestic and some wild introduced donkey populations have experienced steep declines in recent years, driven by Chinese demand for *ejiao,* a beauty product made from their skins–a process converging with broader wildlife exploitation in the trade of rhino, pangolin, and other animal body parts (Wallach et al.

2018). While still prioritizing conservation efforts in their native range, should introduced donkeys–in central Australia and elsewhere–be proactively conserved?

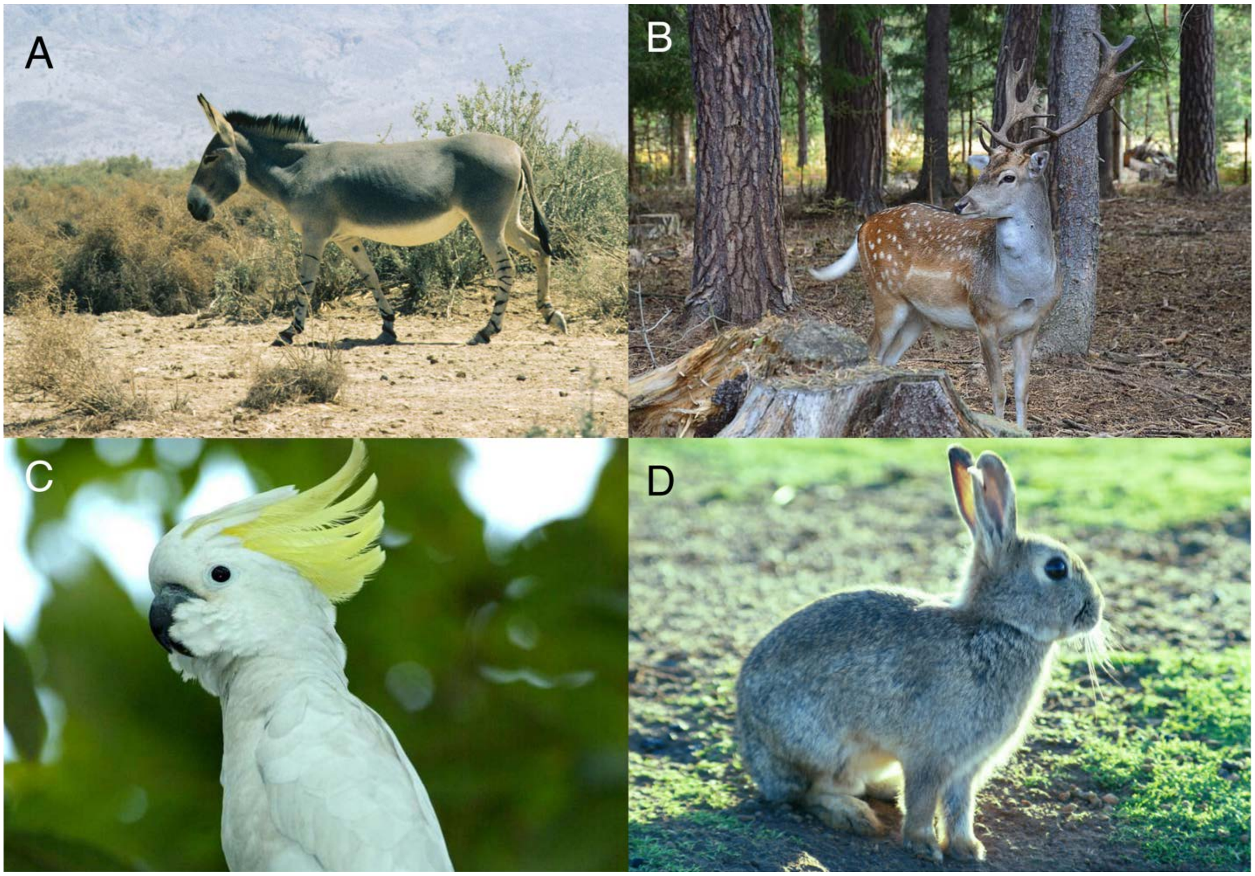

Figure 4. Threatened species whose conservation may benefit from inclusivity towards introduced populations. A. The African wild ass (*Equus africanus*) is Critically Endangered with a population of 150-200 individuals in remote, war-torn areas of Northeast Africa. Yet their introduced post-domestic relatives have populations in North and South America and Australia. **B.** The fallow deer (*Dama dama*) is Least Concern according to the IUCN–yet only several hundred individuals live in this species' native range, because Roman-era introductions across Europe and Great Britain have been culturally adopted as native. **C.** The yellow-crested cockatoo (*Cacatua sulphurea*) is Critically Endangered in Indonesia, where its populations have collapsed from the pet trade. Yet, in one pet-trade hub, Hong Kong, they now have a thriving and genetically-diverse population. **D.** Approximately 200 populations of European rabbit (*Oryctolagus cuniculus*), Endangered in their native range, have been introduced around the world.

Valuing introduced populations as legitimate wildlife and including them in global threat assessments (e.g. the *globalist* scenario) immediately delists 20 species, and reduces threat levels for 3 others. This is greater than the estimated 7-16 mammal extinctions prevented by active conservation intervention since 1993 (Bolam et al. 2020), yet bears no financial cost. After all, including introduced populations in global threat assessments is not unheard of–if the introduction is old enough and has become culturally adopted as native. For example, despite having a native population of <200 individuals, the fallow deer (*Dama dama*) is listed as Least Concern by the IUCN (**Fig 4B)** because of ancient introductions across Europe where they were introduced by Phoenicians, Romans, and Normans (IUCN Red List 2018). Note that this contradicts IUCN Red List guidelines for treating an introduced population as native: there is a lack of 'conservation intent' in those introductions and the introduced range exceeds the 'reasonable' geographic proximity specified (guidelines section 2.1.3, IUCN Red List 2018).

Alternatively, independently assessing the threat status of introduced populations, thereby conserving small populations of threatened species (*relativist* scenario) increases concern for often-overlooked, modified and urbanized landscapes–conservation frontiers outside the traditional wilderness model. In addition to mammals, numerous (~40) threatened birds have been introduced around the world, with many introduced into urban environments (**Fig. 4C**). In many cases, the very same process endangering their native populations–the wildlife trade–is the source of these new populations (Gibson and Yong 2017). Relaxing nativism and expanding conservation efforts into urban environments provides novel opportunities to protect species without land acquisition, can find common ground with environmental justice efforts in urban areas, and can connect the populace–for whom nativism may not be a core value–with caring for the organisms with whom their lives intersect (Shaffer 2018).

The human-mediated dispersal of organisms has implications for the future of biodiversity. Rapid evolution within introduced populations–and interacting native ones–conceives new evolutionary trajectories and interdependencies (Carroll et al. 2005, Schlaepfer et al. 2005, Herrel et al. 2008, Cattau et al. 2017, Vizentin-Bugoni et al. 2019). After all, dispersal, including large-scale interchanges from the geologic collisions of continental and oceanic biotas, is a progenitor of biodiversity and potentially ecological resilience (Vermeij 1991). Nativism, however, sees these processes today as 'unnatural'. The European rabbit (*Oryctolagus cuniculus*) (**Fig 4D**), Endangered in its native range (IUCN Red List 2018), has established at least 187 distinct populations, ranging from the subarctic to the tropics and across all 16 of the world's biomes (as defined by Olson et al. 2001). Charles Darwin believed one island population of European rabbit to be a new species, due to their remarkably divergent morphology (Darwin 1868). It thus may be worth asking whether consideration should be made for the current and future biodiversity of *Oryctolagus*, particularly given the threat status of European rabbits in their native range.

Devaluing introduced biodiversity reduces our ability to respond creatively to global change and insists on rigid adherence to a normative value–not an empirical fact. We do not endorse any of these scenarios, either nativism or its alternatives as proposed in these simulations. We conducted the simulations described in this study to investigate how valuing introduced species in different ways can influence global conservation priorities . We found that stewarding introduced biodiversity, with consideration for potential conflicts with other resident taxa, may contribute to preventing global extinctions. We hope that our findings will inspire others to openly consider how nativism and other normative values influence conservation goals.

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