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Rewilding through inappropriate species introduction: The case of European bison in Spain

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Abstract

Most European rewilding initiatives are based on the recovery of large herbivores, particularly European bison *Bison bonasus*, aiming at restoring ecosystem processes and increase trophic complexity. The growing support for the release of bison as a wild species, and change its legal status, in Spain, as an ecological analogue of the extinct steppe bison *Bison priscus*, makes it an excellent example to reflect the limits of a rewilding biogeographically advisable. We discuss if this initiative could be justified from ecological, biogeographical, ethical, and legal reasons. Besides remarkable taxonomic and functional differences between both bison species, the Mediterranean environment, under the present and future climatic scenarios, does not suit the European bison. Furthermore, there is no evidence to support the presumption that the European bison was ever present in the Iberian Peninsula, with legal implications. We expect that our approach will be inspirational for similar assessments on rewilding initiatives globally.

For affiliations refer to page 6

KEYWORDS
Bison, ecological restoration, Mediterranean, Rewilding, species introduction

1 | INTRODUCTION

Since the first proposals for restoring large carnivore populations (Soulé & Noss, 1998; Soulé & Terborgh, 1999), the concept of rewilding has been used for different purposes, even introducing confusion and contradictory viewpoints (Hayward et al., 2019; Nogués-Bravo et al., 2016). The different rewilding proposals (Gordon, Manning, et al., 2021; Gordon, Pérez-Barbería, et al., 2021; Oliveira-Santos & Fernández, 2010; Rubenstein & Rubenstein, 2016; Rubenstein et al., 2006; Smith, 2005; Svenning, Pedersen, Donlan, Ejrnæs, et al., 2016a; Svenning, Pedersen, Donlan, Ejrnæs, et al., 2016b) have been the subject of intense debate, where essays, conceptual and opinion articles outnumber empirical studies (Pettorelli et al., 2018). In practice, demonstrations of effective rewilding have been very scarce to date (Theunissen, 2019; Zimov, 2005). The objectives pursued by these initiatives have been difficult to achieve because they often lack a scientifically sound justification for their local implementation (Pettorelli et al., 2018).

Most rewilding initiatives are based on the recovery of large herbivores, aiming to restore ecosystem functioning and increase trophic complexity (Gordon, Manning, et al., 2021; Gordon, Pérez-Barbería, et al., 2021; Perino et al., 2019), either in its purest "*rewilding Max*" form or in more practical ways, named "*rewilding lite*." Among them, "*livestock rewilding*" (a form of rewilding lite) proposes the use of autochthonous breeds as ecological analogue of extinct wild herbivores in places where both wild and domestic herbivores are missing (Gordon, Manning, et al., 2021; Gordon, Pérez-Barbería, et al., 2021); although livestock rewilding is not exempt from controversy (Gordon, Manning, et al., 2021). In the European Union (EU), most rewilding projects are based on the recovery of megaherbivores and, in particular, the European bison *Bison bonasus* (Pettorelli et al., 2018; Rewilding Europe, 2023), the largest European extant herbivore, of which only a dozen specimens survived at the beginning of the twentieth century (Kowalczyk & Plumb 2022; Tokarska et al., 2011). Since then, European bison have been translocated across several countries, to reduce the danger of their random extinction in a single location. Currently, the European bison numbers approximately 9500 individuals of which 7300 are distributed in free-ranging populations across 11 countries (EBPB, 2021; Plumb et al., 2020). Consequently, European bison have been moved from Vulnerable to Near Threatened by the IUCN (Plumb et al., 2020).

The interest in recovering this iconic species has crossed the borders of its natural range. In Spain, the proposal to introduce this species started in 2010 (sensu IUCN/SSC, 2013). The main justifications relied on the recovery of the bison depicted in Paleolithic art, reconstructing the fauna of the Pleistocene, and fighting forest fires and Global Warming. In other countries, the European bison was incorporated "*as wildlife in Zoological nucleus, a special category between a stockbreeding site and a Zoo Park*" and, thus, bison are considered "*as cattle in all respects*" (Björk et al., 2022), being subordinated to livestock regulations (Pérez-Barbería et al., 2022). In 2020, however, there was a qualitative leap, as a request by an NGO was submitted to the Spanish Government with the aim of including the European bison in the Spanish List of Wild Species in Special Protection Regime (Royal Decree 139/2011). Such a request was rejected since its approval would imply that of a non-native species would be released into the wild in Spain under the framework of conservation laws. While it is true that the European bison is listed in Annexes II and IV of the EU 92/43/EEC Habitats Directive, as a priority species, the commitment to its protection befits biogeographical regions that are very different from those found in the Iberian Peninsula.

The growing interest, for example by some NGOs, in introducing European bison in the Iberian Peninsula requires us to critically analyze whether its introduction could be justified in terms of conservation from ecological, biogeographical, ethical, and legal points of view. Furthermore, these initiatives must consider social, economic, or political impacts that it may generate (IUCN/SSC, 2013), although this issue goes beyond the scope of this piece.

2 | THE PRESENCE OF STEPPE BISON IN THE IBERIAN PENINSULA

In the Late Pleistocene fossil record, from the Iberian Peninsula there is only evidence of the presence of steppe bison *Bison priscus* (Figure 1; the third most represented species in Cantabrian Upper Paleolithic art, e.g., Altamira cave; Gálvez, 2016). Steppe bison were larger than

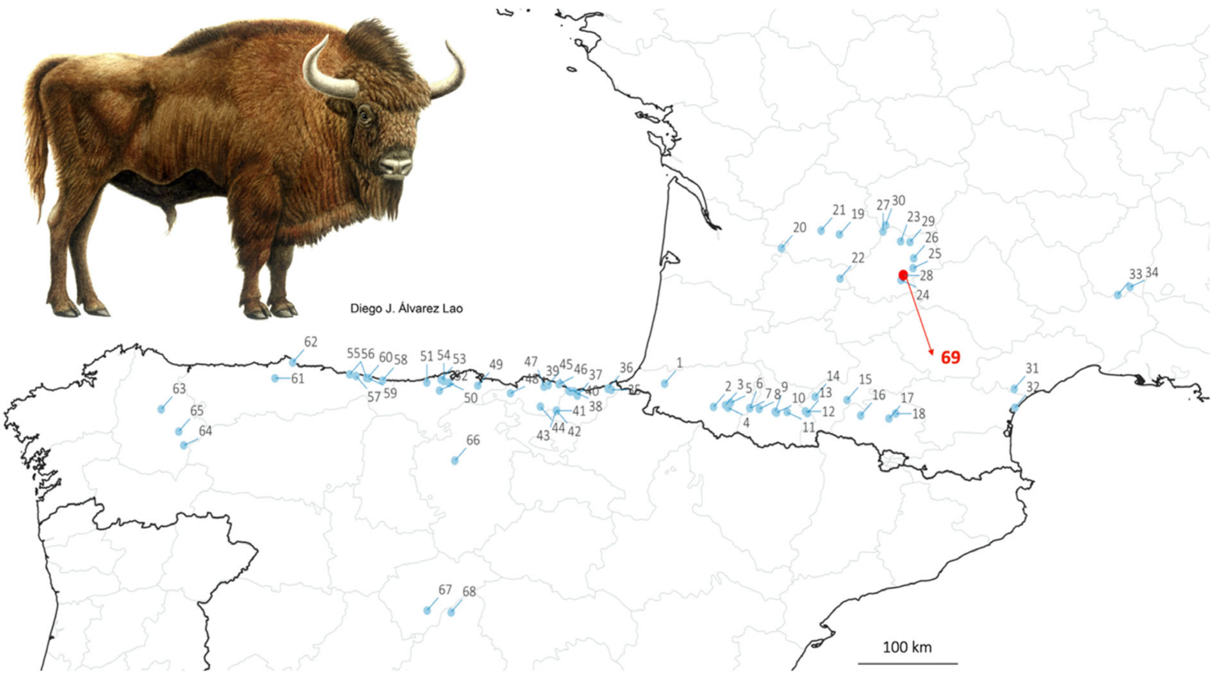

FIGURE 1 Reconstruction of the appearance of a steppe bison *Bison priscus* (drawing by Diego Álvarez-Laó). Sites where *Bison* spp. fossil remains have been found in the SW Europe. Blue dots represent the locations of confirmed fossil remains from steppe bison *B. priscus*; whereas the red dot (number 69) shows the only site where confirmed fossil remains from *B. bonasus* have been in SW Europe (numbers represent palaeontological sites; see Appendix A in Data S1 for details).

FIGURE 2 Adult male skulls of an Iberian steppe bison (left) and a present-day European bison (right) represented at the same scale (images by Pedro M. Castaños and David Nogués-Bravo).

European and American bison, with clear morphological differences, such as a large hump on the shoulder and larger size of the horns (Boeskorov et al., 2016; Guthrie, 1990; Stuart, 2021; Figure 2). Cave paintings also suggest that it possibly had an abundant mane. Its fossils are frequently found in northern Iberia (Figure 1) associated with other species inhabiting the cold and arid "Mammoth Steppe" (e.g., mammoth *Mammuthus primigenius*, woolly rhino *Coelodonta antiquitatis*; Álvarez-Laó & García, 2011). Along the Cantabrian Mountains, the steppe bison fossil remains are very abundant in the Late Pleistocene (45–19 ky BP; Álvarez-Laó et al., 2015; Castaños et al., 2012). Further south in Iberia, the steppe bison have been found only in some isolated sites, dated between 42 and 32 ky BP (Figure 1; Galindo-Pellicena et al., 2019; Sala et al., 2010).

The "Mammoth Steppe," representative habitat of the steppe bison, was an open environment corresponding to a cold and very arid climate dominated by graminoids (Guthrie, 2001) and forbs, consumed mostly by megaherbivores (Willerslev et al., 2014). This steppe-tundra merged biome went from being one of the most abundant ecosystems during the Late Pleistocene, in the middle and upper latitudes of the Holarctic realm (from NE Spain to Alaska), to disappearing completely in recent times, without analogous ecosystem occurring nowadays (Drucker, 2022; Guthrie, 2001; Zimov et al., 2012). Megafauna was essential for this ecosystem, recycling nutrients through herbivory, trampling and fertilizing by dung, urine, and carcasses (Drucker, 2022; Zimov, 2005; Zimov et al., 2012). Driven by climate change and megafauna extinctions, at the end of the Late Pleistocene the "Mammoth Steppe" was mainly replaced by the tundra and taiga.

The steppe bison inhabited southern Europe when temperature and rainfall were much lower than today (Bernard et al., 2009; Rousseau et al., 1994). Their most recent Iberian remains are dated between 13,424 and 13,766 years cal BP (Castaños, 2017). After retreating north and east, the last known steppe bison survived in the Yukon, Canada, and becoming definitively extinct there about 6400–5400 years ago (Wang et al., 2021; Zazula et al., 2017).

3 | THE ABSENCE OF EUROPEAN BISON IN THE IBERIAN PENINSULA

The European bison is a species of unclear and debated origin (Grange et al., 2018; Massilani et al., 2016; Palacio et al., 2017; Soubrier et al., 2016; Spassov, 2016) with a complex history of local extirpations and expansions during the Late Pleistocene (Kowalczyk & Plumb, 2022). The timing of population replacements between steppe and European bison was correlated with major paleoenvironmental shifts (Soubrier et al., 2016). Paleogenetic analysis of bison remains from the last 50,000 years reveals the influence of climate changes on the dynamics of both bison in Europe (Massilani et al., 2016). But European bison have never been found in traditional southern glacial refugia (Figure 1; Sommer & Nadachowski, 2006), and the Iberian Peninsula is not considered as a suitable area for European bison under different modeling scenarios (Pilowsky et al., 2023).

During the Holocene, the European bison expanded westwards, reaching southwestern France (Figure 1), but not the Mediterranean peninsulas (Benecke, 2005; Kowalczyk & Plumb, 2022; Massilani et al., 2016). Its fossils are abundant in the plains southeast of the Baltic Sea, representing >20% of wild ungulates in faunal assemblages. This proportion gradually decreases toward the south and west, where only isolated specimens testify to its presence (Benecke, 2005; Hoffman-Kamińska et al., 2019). Alternatively, the PHYLACINE database (Faurby et al., 2018) proposes that European bison reached the Mediterranean peninsulas. However, the geographical distribution of fossil bones matches with the modeling of its potential habitat, according to which its optimum would also lie in Central and Eastern Europe (Cromsigt et al., 2012; Kuemmerle et al., 2012a, 2012b; Pilowsky et al., 2023). The cryophilic nature of the European bison supports the observed geographical pattern. Average winter temperature <−5°C is the most important climatic factor shaping its habitat use today (Kuemmerle et al., 2012a). This is also supported by genomic analysis, showing genetic adaptations to colder temperatures (e.g., genes responsible for hair development; Gautier et al., 2016). This factor contrasts with the average winter temperature in mainland Spain, 6.4°C (Anonymous, 2021), reaching 0°C in the coldest month only on the highest peaks of the mountain systems, and a mean temperature of 22.7°C in August. Climatic scenarios for the Iberian Peninsula predict significantly warmer and more arid conditions (Araújo, 2011; Carvalho et al., 2020), compromising the viability of introduced bison populations. The climate of the Iberian Peninsula is, therefore, not suitable to support the species today, and even less so in the light of future climate forecasts (IUCN/SSC, 2013; Paniagua et al., 2019).

The analysis of parietal art has been considered as evidence for the presence of the European bison in different parts of Europe (Soubrier et al., 2016). However, in this case, cave paintings are not sufficient to determine the presence of the European bison in the Iberian Peninsula, because it lacks the power which bone morphology and molecular tests have due to the subjective interpretation of the artist/observer. The closest undisputable presence of fossil European bison to the Iberian Peninsula is that of L'Igue du Gral (Lot, Occitanie, SW of France; Figure 1) constituted by two specimens dated 10,260 ± 50 and 10,180 ± 40 years BP (Massilani et al., 2016). Climatically, these correspond to a period of transition to the Holocene, when the climate was somewhat colder than today. This locality may lie close to the limit of the natural range of the species (Massilani et al., 2016). Moreover, the rise of the sea level after the glacial maximum may limited the colonization of the Iberian Peninsula through the narrow corridor lying to the west of the Pyrenees (Álvarez-Laó & García, 2011). This inability to overcome the Pyrenean barrier has been recorded for species such as moose *Alces alces* (Breda & Marchetti, 2005; Schmölcke & Zachos, 2005) and saiga antelope *Saiga tatarica* (Altuna & Marizkurrena, 1996). A potential reason for a species' presence in a region despite an absence from the fossil record could be insufficient archaeological and paleontological excavations. This scenario does not apply to the Iberian Peninsula, which boasts a rich fossil record for megafauna species, including mammoths, reindeer, and even musk oxen which vanished during the climatic warming from the Pleistocene to the Holocene (Álvarez-Laó et al., 2020; Álvarez-Laó & García, 2011).

It has been also suggested that the presence of the European bison may have passed unnoticed in the Iberian Peninsula because of the difficulty of differentiating the bones of bovines (Jirku, 2022; van Vuure, 2005). The main diagnostic characters to distinguish both genera are found in the metacarpals and in the skull, mainly the horn cores, the frontal, the parietal, the occipital, and the petrous bone (Figure 2; Galindo-Pellicena et al., 2019; Gee, 1993; Guadelli, 1999; Stampfli, 1963). These possible misidentifications would hardly alter the overall picture of the ancient distribution of Europe bison at large (Benecke, 2005), since this same issue should apply throughout its geographical range. Since the last record of Iberian steppe bison (>10,000 years ago), out of 110 Iberian sites with remains of Holocene bovines (Arribas, 2004), all the morphologically identified remains were either aurochs or domestic cattle, and none were bison. This contrast with Central and Eastern Europe where bison remains are systematically present. In the Iberian Pleistocene, out of 139 sites, steppe bison were identified in 43, aurochs in 81, and in 15 were the elements attributed to a large, undetermined, bovid (Arribas, 2004).

While paleontological and biogeographic evidence do not support the idea that the European bison reached the Iberian Peninsula, there is evidence that the aurochs coexisted with the steppe bison there and survived up to historical times (Jánossy, 1986). The most recent archaeological data of aurochs in Iberia is from the Late Roman period, from the cave of Amalda (Gipuzkoa, Spain), dated to the 4th–5th century AD (Mariezkurrena, 1990). These dates are contemporary with the last historical reference, that of Maurus Servius Honoratus, a Latin grammarian of the 4th century, who mentions the presence of aurochs in the Pyrenees (Gesneri, 1551). There is no written evidence of European bison occurring in the Iberian Peninsula. The closest historical data, which is its westernmost documentary record, is that of Venantius Fortunatus in the 6th century AD who, referring to the game species in the Vosges region (France) he mentions the *bufali* (buffaloes) and the *uri* (aurochs) as living together (Nisard, 1887). This locality coincides with the geographical limit of the available palaeontological and archaeological information (Benecke, 2005).

In the Iberian Pleistocene, there are frequent skeletal remains of steppe bison and aurochs, but in the Holocene, there is objective evidence, not only archaeological, but also historical (documentary), of the aurochs, but there are no vestiges of the European bison.

4 | STEPPE BISON FUNCTIONAL ANALOGUES?

There are several differences in terms of anatomical, functional, and environmental requirements between steppe and European bison (Figure 2). The steppe bison was mainly a powerful grazer, a specialist of the cold herbaceous steppe (Guthrie, 2001; Saarinen et al., 2016), whereas the European bison, according to its craniodental anatomy, is a mixed feeding herbivore that evolved in grasslands or mixed habitats, including forests (Mendoza & Palmqvist, 2008), with intermediate digestive capacity (Hofmann, 1989) and its preference for grazing depends on the available environment (Bocherens et al., 2015; Kerley et al., 2012). The European bison is therefore generalist species, better adapted to the diversified habitats that emerged in the Holocene (Gautier et al., 2016; Hoffman-Kamińska et al., 2019), even having overestimated their adaptation to forest habitats (Bocherens et al., 2015; Kerley et al., 2012). Therefore, considering the functional role played by steppe bison (specialist grazer) and its habitat (the "Mammoth Steppe"), the introduction of European bison would not restore any ecological function lost recently within the Iberian Peninsula, because the Mammoth Steppe has no chance of restoration nor analogous nowadays in these latitudes. The European bison seems to have avoided the sclerophyllous evergreen Mediterranean vegetation altogether (Drucker, 2022; Jirku, 2022) so would likely require supplementary feeding and water. Previous attempts to maintain European bison in Mediterranean Spain failed, with the death of several individuals by starvation, even at moderate densities (Appendix B in Data S1).

Beyond the consideration of whether extant wild herbivores in Spain may or may not fulfill similar ecological functions as those of the steppe bison, and given that the habitat of the steppe bison no longer occurs in the Iberian Peninsula, hundreds of thousands of livestock heads from cattle and horse breeds (including autochthonous ones) in Spain are currently being handled in extensive and semi-extensive regimes (Urivelarrea & Linares, 2020; Zabalza et al., 2021). Under those regimes, extensive livestock contribute to reducing the risk of wildfires and the survival of moors, subalpine meadows and ensure the persistence of wolves *Canis lupus* in some areas, while attenuating wolf–human conflicts (e.g., López-Bao et al., 2013; Velado-Alonso et al., 2021). It could be also argued that the extensive livestock that already exists there would presumably fulfill an equivalent function to extant bison (Velado-Alonso et al., 2020). Evidence suggests a similar functional effect of cattle and bison grazing (both American and European bison), whether compared with European or American bison (Ratajczak et al., 2022; Towne et al., 2005; Valdés-Correcher et al., 2018).

On the other hand, in Mediterranean environments, red deer (*Cervus elaphus*) browse woody plants with more intensity than European bison, with subsequent impacts on reducing the risk of wildfires (Bartolome Filella et al., 2024).

Furthermore, the predators of steppe and European bison would not be comparable either, since the main predators of steppe bison were the now extinct cave hyena *Crocuta crocuta spelaea* (Utge et al., 2020) and the cave lion *Panthera leo spalaea* (Guthrie, 1990), whereas the European bison is marginally hunted by wolves and brown bears *Ursus arctos* (Jankowski et al., 2019; Jędrzejewski et al., 2000).

5 | LEGAL AND NORMATIVE ASPECTS RELEVANT FOR INTRODUCING BISON

Article 10 of the EU Habitats Directive promotes (not binding) the reintroduction of native species listed in the Annex IV of the directive, which limits them to their natural range. In Spain, Law 42/2007 advocates for the reintroduction of native wild species that have historically gone extinct, provided there is credible written evidence of their historical presence. Given the existing evidence, European bison does not meet this criterion.

Presumed benefits of introducing the European bison include the production of complementary income to livestock, tourism, and hunting activities to avoid the abandonment of rural areas and reduce the risk of wildfires (Morán, 2016). The IUCN considers the introduction of an organism outside of its natural range only if this is a close species that could perform the lost ecological function of the extinct taxon (IUCN/SSC, 2013). It is not possible to introduce the European bison in Spain as an ecological replacement of the extinct steppe bison because neither its habitat ("Mammoth Steppe") nor the bison that occurred there persist in recent times. It is also not possible that the introduction of a single species can restore the trophic complexity of this disappeared cold habitat. Nor can the introduction of the European bison be an assisted colonization, because of the lack of future suitable climatic conditions for the species, as discussed above, may well pose a bioethical problem, requiring intense human action. Indeed: "*If released into an area that is definitively not* [suitable] *habitat, it is an irresponsible release with no conservation benefit*" (IUCN/SSC, 2013).

Furthermore, any proposed release must consider, under the responsibility of the administrative authority, the legal requirement of a favorable risk analysis required by Royal Decree 630/2013, of the Spanish Catalogue of Invasive Species. Risk analysis not only refers to the environmental, ecological, or asset damage of their release, but must also determine whether the species can survive on its own in nature (Appendix B in Data S1). In addition to current regulations, one must consider the ethical and side effects of such an introduction, for example, the moral commitment represented by the IUCN/SSC guidelines (2013) for translocations outside native ranges. Finally, beyond legal and normative aspects, these initiatives must consider social, economic, or political impacts (IUCN/SSC, 2013), which would include understanding the acceptability, or lack thereof, for the introduction of European bison.

By that logic, if the replacement of the steppe bison by the European bison would be accepted, there is no reason to oppose the reintroduction of other species that became extinct in the Iberian Peninsula during the same period, or later. This would be the case, for example, of hyenas, dholes *Cuon alpinus*, and lions or leopards *Panthera pardus* (Altuna, 1972; Álvarez-Laó, 2003; Álvarez-Laó et al., 2020; Arribas, 2004). In all these cases, in contrast to the steppe bison, these species still exist outside of the Iberian Peninsula.

6 | CONCLUSIONS

Based on the evidence summarized here, we advocate for not introducing the European bison in the Iberian Peninsula (a non-native species). Although the legal impediment for the introduction of unequivocally a non-native species is clear, social pressures must abide by the law, and it is necessary to consider the need to have an objective scientific basis to fulfill conservation laws (Cusack et al., 2020). Conceptually, we argue that introducing European bison in the Iberian Peninsula would not even qualify as rewilding (sensu Carver et al., 2021; Perino et al., 2019; Svenning, Pedersen, Donlan, Ejrnæs, et al., 2016a; Svenning, Pedersen, Donlan, Ejrnæs, et al., 2016b). The introduction of European bison would not restore any ecological function lost recently within the Iberian Peninsula, and the Mediterranean environment, under the present climatic regime, and its projections into the future, does not suit the European bison. The recovery of European bison can be considered a responsibility for those countries that overlap with its former natural range, which is not the case of any country featuring a Mediterranean environment.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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