Integrating environmental archives into conservation: Using historical data to evaluate species suitability for reintroduction

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Abstract. Evidence-based conservation planning is typically informed by recent data, but anthropogenic activities have shaped biodiversity throughout history and recent prehistory, and long-term environmental archives can provide unique information on past ecological states and change. Environmental archives can be particularly important for informing conservation actions that address disrupted or lost biodiversity, such as species reintroductions, where species selection often fails to consider the full information-content or quality of past data. Here, we explore the potential to incorporate past evidence into reintroduction planning in a more systematic and comparative manner, by developing a framework of biological and ecological criteria for evaluating different aspects of the former status of lost species. These criteria help to define whether a species can be interpreted as native under modern environmental conditions, and whether its former population status, ecology or extinction are adequately understood. This framework clarifies evidence, assumptions and uncertainty around past species status, providing insights unavailable from a modern ecological perspective, and should be considered at the outset of planning to assess whether some species represent better contenders for reintroduction than others.

Keywords: conservation palaeobiology, data quality, environmental archives, historical baselines, historical ecology, Holocene, long-term data, translocation

1. Conservation evidence from environmental archives

Limited resources are available to combat the global biodiversity crisis, meaning that difficult conservation decisions need to be made. Different candidate conservation strategies must therefore be compared and evaluated [1,2]. To enable identification of appropriate activities for protecting and restoring biodiversity, an evidence-based approach is required, where robust data are used to guide management and policy decisions [3,4]. Evidence-based conservation is informed by a range of data types, including data on both the ecological and human dimensions of biocultural systems [5,6]. However, if available data are incomplete or biased, then conservation interventions may be based upon erroneous assumptions and have inappropriate targets [7].

Conservation planning is almost exclusively informed by modern data. Natural biodiversity states and human-caused depletion are primarily defined by recent historical baselines (e.g. [8]), and even 'long-term' ecological datasets typically represent only multi-decadal durations [9-11]. Even within this timeframe, loss of knowledge of older biodiversity states and persistent downgrading of perceived 'normal' environmental conditions, known as 'shifting baseline syndrome', is recognised as a pervasive problem in conservation associated with widespread conservatism in setting management and recovery targets [12]. However, environmental archives reveal that anthropogenic activities have shaped biodiversity for much longer than the recent past, with evidence of substantial worldwide human impacts at multi-century and multi-millennial scales [13-15]. Failure to incorporate evidence of past impacts can have negative real-world consequences for conservation planning [16-18]. For example, current-day systems have typically experienced 'extinction filters' (species losses, shifts in ecosystem structure and function) caused by ancient human activities, meaning that ecological, biogeographic and conservation inferences based upon modern baselines can be biased and misleading [19].

Information on past biodiversity states and change can be obtained from specimen- or object-based archives (e.g. zooarchaeological and fossil records, sediment cores) and document-based archives and other past human-produced media (e.g. written historical records). These records can provide unique information on past biodiversity patterns and processes, biotic responses to past change and ecological tipping points, extinction dynamics and selectivity, system recovery after extreme events, and the effects of different past human activities [20,21]. Several academic disciplines, including conservation palaeobiology, historical ecology, landscape ecology, applied zooarchaeology and restoration ecology, have developed to incorporate information from environmental archives into conservation [22-24].

However, this goal is hindered by both conceptual and logistical barriers. Long-term records reveal a complex picture of constant biodiversity change in response to both natural and human-caused changes [25], challenging identification of specific static baselines that can be used to set wildlife management and ecosystem restoration goals [26], and the magnitude and temporal scale of past change can be hard for conservationists to appreciate [27]. Reconstructing this dynamic biodiversity history is hindered by the varying quantity, quality, completeness and bias shown by different archives, and locating, extracting and interpreting archival information requires specialist investigative and analytical frameworks associated with multiple academic disciplines [28,29]. These archives also differ from modern ecological datasets in fundamental parameters such as taxonomic, geographic and temporal representation and resolution, meaning that past and present data are not directly comparable (the 'epistemological gap'), and available archives may be insufficient to reconstruct many aspects of past biodiversity ('epistemological pessimism') [30]. Practical incorporation of environmental archives in conservation is also hindered by inadequate communication and collaboration between palaeontologists, archaeologists, historians and conservationists, with a widespread lack of recognition of archival information-content, value and utility by many conservationists perpetuating a research-implementation (or 'knowing-doing') gap [29,31]. It is therefore essential to develop new approaches that integrate environmental archives into conservation thinking, planning and strategy, and explore how these data can inform decision-making between candidate management actions.

2. Evaluating historical data to guide species reintroductions

Evidence from environmental archives is particularly important for conservation actions that address disrupted or lost biodiversity, including species reintroductions, habitat or landscape restoration, and restoration of ecosystem functionality and services through rewilding initiatives. These activities have diverse goals that can differ from a desire to simply return ecosystems to past states, such as strengthening system resilience to future change, or providing human benefits such as improving connectivity with nature [32]. However, they are all underpinned by the need to understand past environmental conditions, as they are inherently motivated by the fact that biodiversity and ecological processes have been altered in some way since some past timepoint (typically through past human activities) and need rectifying through some type of intervention. It is thus crucial to evaluate what past environmental data are available to guide planning in these fields.

Established guidelines and modelling approaches are available to inform species reintroductions once candidate species are identified, including selection of source populations, reintroduction sites, optimal demographic parameters for founder populations, and translocation methods [33]. However, whereas comparative species prioritization frameworks are available to guide many other areas of conservation planning [34-36], species selection for reintroductions can be potentially arbitrary or subjective, and is influenced by contingent non-ecological factors (e.g. human and organizational factors) such as species charisma and subjective local interest or preference [37-39]. Species' eligibility for reintroduction is typically supported by basic evidence that it was formerly native to the target region, or that the reintroduction site constitutes suitable habitat within ecologically appropriate proximity to its known past range, but often with little consideration of other information available in environmental archives [33]. However, the quality and quantity of available information about past species status varies hugely across species and systems, with complex natural and human-mediated changes in biotic distributions across recent millennia, making it challenging to define what 'native' even means in a modern biodiversity context [40,41]. Failing to acknowledge this knowledge about past biodiversity risks excluding key insights, nuance and context around the feasibility and suitability of potential reintroductions.

Here, we consider whether information from environmental archives can be used in a more rigorous, systematic and comparative manner, to develop strategic guidelines on species suitability for reintroduction and biodiversity restoration efforts. We present a framework for evaluating available historical data across a series of biological and ecological criteria that are relevant to reintroduction decision-making, acknowledging both the information-content and complexity of these data, and the incompleteness, gaps and barriers in our knowledge of past biodiversity. This critical assessment aims to define and weight our current knowledge about the regional history of different species, to establish an objective set of criteria that can help to assess whether these species should be viewed as appropriate contenders for reintroduction.

To explore how environmental archives can provide new perspectives for conservation decision-making, we use examples from the vertebrate faunal record of Britain, a region with rich environmental archives, a long legacy of human and non-human impacts on biodiversity, and a depleted current-day biota containing numerous potential reintroduction candidates (figure 1). We define a series of criteria representing information on different aspects of the former status of lost species, which are uniquely informed by environmental archives, and are integral to interpreting whether a species can be considered native and could constitute an appropriate contender for reintroduction. These criteria highlight the unique and nuanced insights on species status provided by past archives, and the varying information quality that might make past baselines challenging or impossible to establish. Some criteria are illustrated with examples of both novel data insights and data quality issues, whereas others are framed around whether data uncertainty exists for a particular ecological parameter. We group these criteria into two broader themes: (*1*) Was the species native under modern environmental conditions; (*2*) Do we have a good understanding of its former population status, ecology and extinction? It is important to note that the criteria are not strictly ordered or ranked, especially within the second theme. They can be interpreted additively or cumulatively to assess overall strength, direction, and confidence of evidence for reintroduction suitability of different species (figure 2), to evaluate whether some species represent better overall contenders for reintroduction than others. They can also be used to downlist or exclude species if they do not meet defined thresholds or if existing information is insufficient to evaluate key parameters.

3. Reintroduction criteria informed by past archives

Theme A: Did a native population exist under modern environmental conditions?

(1) ***Was the species ever regionally present?***

Eligibility for reintroduction is typically dependent upon evidence that an extirpated species was formerly native [33]. However, species might have been interpreted as native based upon inference or misinterpretation of past data, but might not actually be represented in regional environmental archives. If records exist, their quality and resolution might be insufficient to confirm definite species identification, with possible past occurrence based only upon provisional identifications from poorly-preserved remains or vague historical accounts that do not necessarily refer to local populations.

Example 1 (*evidence of past status*): Bison were present in Britain across several warm interglacial periods during previous Ice Age cycles over the past 400,000 years, but Britain's former mammalian megafauna contained only the now-extinct species *Bison priscus* and *B. schoetensacki* rather than the extant European bison *B. bonasus* [42,43]. These species were associated with different environments and niches (*B. priscus* was a grazer adapted to herbaceous steppe habitat, whereas *B. bonasus* is a more generalist mixed feeder also adapted to forest environments), and are thus associated with different functional roles and environmental impacts [44]. While the recent fossil and zooarchaeological records provide extensive evidence of other large mammal species present in Britain during recent millennia (e.g. aurochs *Bos primigenius*, European elk *Alces alces*, red deer *Cervus elaphus*), there is no evidence that *B. bonasus* ever colonised Britain during the current interglacial period [45,46].

Example 2 (*data uncertainty*): Bones from two British fossil sites have been provisionally identified as black stork (*Ciconia nigra*). However, species-level identification is difficult and they cannot be definitely distinguished from white stork (*C. ciconia*), which is also recorded in British fossil and archaeological sites and historical accounts [47].

(2) *Was the species present during the Holocene?*

The Holocene Epoch, the current interglacial period dating from the end of the last Ice Age glaciation (11,700 years ago) to the present, has experienced relatively stable 'modern' bioclimatic conditions similar to current-day states, with species and population losses during this period almost entirely associated with human activities [48,49]. In contrast, the preceding Pleistocene Epoch experienced marked climatic and environmental fluctuations between cold glacial and warm interglacial states, with biotic communities and ecosystems often having no direct analogues to modern states, and Pleistocene faunal turnover was associated with natural as well as anthropogenic change [50]. Given these major environmental differences between time periods, it is important to distinguish whether a species was regionally present during the Holocene or only during the Late Pleistocene. Although the concept of rewilding was initially proposed to restore Pleistocene megafaunal diversity and ecological function [51], regionally extirpated species that disappeared before the Holocene may have been adapted to environmental conditions that are very different from modern states, and may have disappeared naturally in response to changing conditions. The quality of past records, in terms of species identification or a lack of dates or dated contexts for fossil material, might also be insufficient to confirm definite persistence or natural recolonisation of Pleistocene species in the Holocene.

Example 1 (*evidence of past status*): Aesculapian snakes (*Zamenis longissimus*) are recorded from several late Middle Pleistocene sites in southeast England, under environmental conditions that were climatically different from today [52]. Although the species is recorded as having occurred as far north as Denmark during the warmest phase of the Holocene [53], unlike several other reptile species there is no evidence that it naturally recolonised Britain at the start of the Holocene.

Example 2 (*data uncertainty*): The European tree frog (*Hyla arborea*) was present in Britain during warm periods of the Pleistocene [54]. However, the only putative evidence for postglacial presence is based upon brief sixteenth and seventeenth century written accounts, which either do not definitely refer to the British fauna, simply mention the presence of 'Green Tree Frog' alongside other amphibians in Britain with no additional details, or discuss the species' contemporary medicinal use and suggest the trade of animals into Britain [55,56]. There is no physical evidence for the former presence of tree frogs in Britain during the Holocene, unlike other regionally extinct amphibians that are present in zooarchaeological and fossil deposits [57].

(3) ***Do past records reflect introductions of non-native species or knowledge from other regions?***

Species have been deliberately or accidentally transported by past human activities for thousands of years, both as living wild or captive individuals and as body parts for purposes such as trade, and have often established persistent populations outside their native ranges [58]. Written historical accounts and knowledge of animals or plants could also potentially represent transferred knowledge of biodiversity from other regions rather than local environmental conditions.

Example 1 (*evidence of past status*): The great bustard (*Otis tarda*) is known in Britain from a single sixteenth-century zooarchaeological specimen from a royal palace in London, and a historical breeding population that was hunted for food and became extinct in the nineteenth century [47]. Although bones of large-bodied birds are much more likely to be preserved and identified in the recent fossil and zooarchaeological records due to well-known taphonomic biases [59], the species is otherwise only recorded in Britain from the Late Glacial period of the Late Pleistocene and the immediate postglacial period when landscapes were still open [47], and a suggested Roman-era record was a misidentification [60]. Its absence from the Holocene record suggests it probably disappeared naturally following climatic warming and the associated shift from open grassland to closed forest habitats in Britain at the Pleistocene–Holocene transition, and its historical-era reappearance is associated with the expansion of deforested agricultural landscapes and probably represents human introduction for hunting and consumption.

Example 2 (*data uncertainty*): The pygmy cormorant (*Microcarbo pygmaeus*) occurs in southeast Europe and southwest Asia, but is also represented by two bones from a late medieval British well that also contained historical kitchen waste, suggesting the bird had been eaten [61]. These bones may have originated from a bird from an otherwise unrecorded local wild population, or from historical trade in exotic birds for food or pets [47].

Theme B: If the species was definitely present, what was its status?

(4) ***Is the lost population distinct from surviving populations?***

Extirpated populations can show local morphological and genetic differentiation from surviving populations, and are sometimes considered taxonomically distinct. Related living populations may therefore not represent straightforward surrogates for potential reintroduction on the basis of taxonomic congruence. Although most lost populations can be assigned to well-defined species, their taxonomy can also be unclear, making it difficult to establish whether they are really regionally extinct and/or whether conspecific populations still exist elsewhere.

Example 1 (*evidence of past status*): Gadfly petrels (*Pterodroma* sp.) are recorded from coastal Iron Age sites in Scotland, but these seabirds are now extinct in Britain. Ancient DNA analysis reveals that the Scottish *Pterodroma* is a phylogenetically distinct lineage closely related to living populations in Madeira and Cape Verde. Together, these populations form part of a young evolutionary radiation and have not undergone sufficient divergence to unambiguously represent distinct species [62], making it unclear whether living populations can be interpreted as conspecific.

Example 2 (*data uncertainty*): Coregonid whitefish exhibit complex variation and taxonomy. Houting (*Coregonus oxyrinchus*), a long-snouted whitefish, formerly bred in rivers in southeast England but became extinct in the nineteenth century. All long-snouted migratory whitefish from the North Sea Basin were formerly regarded as houting, but morphological and genetic studies of historical specimens have provided varying conclusions over whether the houting was conspecific with another species still present in Britain (*C. lavaretus*), or instead represented an extant evolutionarily significant conservation unit showing local genetic adaptations, or a morphologically distinct, now-extinct species [63-65].

(5) ***Do we understand the species' past regional distribution and ecology?***

Records of former species occurrence may be limited due to sampling biases, hindering our ability to reconstruct their past distribution or landscape use. Reconstructing key ecological parameters of lost populations, such as their trophic or movement ecology (e.g. past migration), can be complex and typically requires specialist approaches such as stable isotope analysis [66,67]. These populations may also have occurred under distinct bioclimatic or environmental conditions and differed in their local ecology from extant populations surviving elsewhere, such that the species now exhibits niche truncation across its remaining range, complicating the possibility of ecological inference from modern populations [68].

Example: The moor frog (*Rana arvalis*) is known from a single definite Holocene record and a second possible record from adjacent sites in southeast England [57], with its wider possible British distribution remaining unknown due to a lack of assessment of Holocene amphibian bone assemblages. These records represent the westernmost European Holocene localities for this species [69], and it is therefore possible that the lost British population was locally adapted to unique range-edge ecological conditions [70], challenging our ability to understand its specific environmental tolerances and habitat requirements.

(6) ***Was the species formerly widespread or rare?***

Multiple definitions of 'common' and 'rare', based on different ecological parameters, are available to guide conservation planning [71,72]. There is extensive debate around the ecological roles of common and rare species, and keystone species such as top predators can be uncommon within ecosystems [73,74], but locally rare populations may be less likely to contribute to ecological functioning or to constitute a significant component of species' global populations [75]. Several key ecological parameters for past biotic communities, such as population abundance, are difficult or impossible to reconstruct due to taphonomic and sampling biases such as time-averaging, preferential preservation of larger skeletal elements, and postmortem transport [28,59], and accumulation in the zooarchaeological record is influenced by past human-wildlife interactions such as preferential hunting of certain species that are also challenging to understand. However, presence or absence across multiple sites can be used as a proxy for relative abundance in well-sampled taxonomic groups or systems, especially if ecologically similar species are recorded in the same contexts and thus indicate higher preservation and detection potential.

Example: Waterfowl bones are relatively abundant in freshwater wetland sites in the British Holocene zooarchaeological and fossil records, due to extensive past human hunting of waterfowl species and favourable preservational conditions [47]. All extant British freshwater duck species are recorded from many Holocene sites, but the only extirpated Holocene British duck, the red-crested pochard (*Netta rufina*), is reported from a single postglacial site in Somerset [47], suggesting it had a much more restricted distribution and abundance across British landscapes compared to other species.

(7) *Were populations continuously present before extinction?*

Populations of some species have continuously occupied landscapes that were environmentally stable through the Holocene, but the past regional status of other species has undergone considerable natural spatiotemporal variation. A lack of past long-term population continuity may have been driven by dynamic natural landscape-level change, or wider-scale bioclimatic shifts that altered regional environmental suitability. Complex patterns of population shifts in response to past change may be evidenced by species with strong dispersal ability, and such species may have only been present irregularly in some landscapes as intermittent populations.

Example 1 (*evidence of past status*): Sturgeon that formerly occurred in British coastal and inland waters have traditionally been interpreted as European sturgeon (*Acipenser sturio*). However, genetic analysis and examination of sturgeon scutes from archaeological sites reveal that European sturgeon populations in northern Europe were naturally replaced during the early medieval period by Atlantic sturgeon (*A. oxyrinchus*) from North America. This species may have colonised in response to climate change during the medieval 'Little Ice Age', when lower water temperatures shifted the species-specific suitability of local spawning conditions [76].

Example 2 (*data uncertainty*): Dalmatian pelicans (*Pelecanus crispus*) are recorded from several British wetland sites from the Bronze Age onward. However, southern Britain represents the northwestern limit of this species' climatic tolerance, and pelicans may have only colonised when winter temperatures became higher in the mid or late Holocene. Wetland landscapes in southern England also experienced successive marine inundations throughout the Holocene, making them periodically unsuitable for pelicans, suggesting the species may have experienced a series of regional extirpations and recolonisations [77] (figure 2).

(8) *Was the species dependent upon local habitats for key life-history stages?*

Individuals in now-lost populations may have remained present within a specific local landscape or ecosystem for their entire life-cycle, or may have undergone predictable or irregular geographic movements of varying magnitude, potentially in response to short-term environmental change. Importantly, species may not have used target regions for key life-history stages (e.g. regular breeding, staging or wintering areas) and may instead have only been present as vagrant or transient individuals rather than as permanent native populations. Identification of juvenile or immature remains may be necessary to determine presence of former breeding populations.

Example 1 (*evidence of past status*): Little auks (*Alle alle*) breed in the high Arctic but are recorded from a surprising number of Holocene land-based fossil sites across Britain, including sites far inland in southern Britain [47]. The species is prone to 'wrecking', where large numbers of birds are blown inland by storms, and it is assumed that British records represent 'wreck' events rather than a wider regular breeding or wintering distribution [78].

Example 2 (*data uncertainty*): European and Atlantic sturgeons are both historically recorded from British inland waters, but northwest European populations became severely depleted during the medieval period through overfishing [79], and sturgeon have only occurred as rare vagrants in Britain during recent centuries. Importantly, there is no known evidence that sturgeon definitely bred in Britain, and it cannot be ruled out that past British records may merely represent non-breeding individuals that dispersed from continental European spawning rivers for temporary foraging [80].

(9) *Do we understand when and why the species disappeared?*

Varying information is available on the extinction chronologies and drivers of lost species known from Holocene contexts. Many faunal records from archaeological or fossil sites are undated or only have associated dates (indirect or inferred dates) instead of direct radiometric dates, and possible historical accounts of species otherwise only known from older sites may not be reliably identified. Importantly, dates for the last known occurrence of now-extinct populations do not necessarily correspond with true extinction dates, and probabilistic analysis of multiple available dates (incorporating scoring criteria for non-definite or poorly constrained records) is necessary to estimate potential extinction timings [81-83]. In the absence of a robust understanding of extinction dates or historical accounts of human-wildlife interactions, it is not possible to correlate population losses with potential causative drivers within chronological frameworks, or to confirm that these threats are now mitigated and modern landscapes are suitable to support the species.

Example: Lynx (*Lynx lynx*) were initially thought to have disappeared from Britain during the early or mid Holocene, in response to natural environmental change or low-intensity deforestation in the Mesolithic [84]. Radiocarbon dating instead indicates lynx survival until c. 1500 years ago, suggesting that human pressures such as higher-intensity deforestation, declining deer populations and/or persecution may instead have been key extinction drivers [46]. Historical accounts from the seventh to sixteenth centuries contain accounts or depictions of animals that may represent lynx, but the identity of these animals (e.g. sixteenth century wild 'lions' in Scotland) is uncertain [46]. The potential 'extinction window' for lynx thus spans more than a millennium, and regional disappearance cannot be correlated easily with specific co-occurring extinction drivers.

4. Discussion

Our critical evaluation of biodiversity archive information-content and quality establishes a framework for evaluating our knowledge of multiple parameters of past species status. Determining the quantity and certainty of information associated with each parameter can define the strength of support for reintroduction across sets of potential candidate species. This framework highlights how reintroduction assessment requires a more nuanced consideration of past evidence beyond a straightforward binary classification of former species presence or absence, and our exploration of the variability and complexity of past evidence challenges easy categorisation of now-lost species as being 'native' or not to a particular region [40].

4.1. Using a historically-informed suitability framework to guide reintroduction planning

If a species is well-identified in environmental archives, was definitely native during the Holocene, relied on local landscapes for key life-history stages, and had well-understood extinction drivers that are now mitigated, we propose that it represents a better reintroduction candidate compared to species with more poorly understood past status or threats. Preferential reintroduction of species in these latter criteria can instead risk promoting restoration targets that do not represent past biodiversity states. Evaluating past population continuity, distribution, and abundance or rarity is also necessary, to understand whether species were integral components of past ecosystems and/or had very specific environmental requirements, providing further important baselines to consider when selecting potential reintroduction candidates. In particular, it is very hard to justify the introduction of species that cannot be confirmed as formerly native under Holocene environmental conditions (i.e. do not meet criteria in Theme A of our framework) under the definition of species reintroduction. We recommend that our criteria are used as a set of objective open standards to assess species suitability for reintroduction based upon current historical knowledge and data quality, for example by defining high, medium and low-priority species groupings. They can also define evidence and assumptions and help to articulate our uncertainty about available evidence, and thus support formal approaches for setting reintroduction objectives and priorities such as structured decision-making [85].

Our framework is intended to be scalable and flexible, to align with the focus and scope of conservation efforts. We illustrate it using examples of lost species at a national level, but it can also be used to evaluate past status of populations within particular landscapes or systems of interest across different taxonomic and spatial scales (e.g. past status of subspecies or ecomorphs; local-scale evidence for species known to have occurred across wider regions). For example, European elk definitely occurred in Britain during the Holocene [45], but its past presence in specific landscapes is less certain (e.g. inferred presence in the East Anglian Fens is based upon dubiously identified droppings that are probably referable to red deer [86]). This approach can also assess evidence on past landscape or habitat states or ecosystem functions and services, to guide regional restoration or restocking. Additional criteria can also potentially be defined and evaluated, and the evidentiary thresholds we propose can be modified depending upon biodiversity restoration goals. Further parameters could include species' past resilience and ability to withstand anthropogenic pressures and environmental change, or evidence that the ecology of reintroduced populations might differ from that of historically lost populations in distinct ways (e.g. differing migratory patterns, as shown by reintroduced white storks in Britain [87]). We define evidence for presence or absence during the Holocene as an important and defensible threshold for evaluating 'native' status, but we acknowledge that bioclimatic and environmental states have not remained stable across the Holocene [49,50]. Other temporal thresholds can thus potentially be used (e.g. more recent historical baselines) if these are environmentally appropriate within the context of a particular project. However, temporal thresholds for defining native status must be clearly defined and justified based upon knowledge of past environmental change and how this relates to modern restoration goals, otherwise a misunderstanding of past states and change could lead to inappropriate restoration targets.

This systematic framework also identifies knowledge-gaps, and can thus be used to guide targeted future research to improve our understanding of the past status of poorly-known species. Such research can include further field excavations, assessment of existing archival collections (e.g. ancient biomolecular or stable isotope analyses), and evaluation of whether comparative inferences can be made from surviving populations that exist elsewhere under potentially different ecological conditions and contexts. Importantly, in contrast to many other actions that are impacted by uncertainty in the urgent 'crisis discipline' of conservation [88], we often still have the luxury of time to maximise information on past populations through further research, and establish optimal evidentiary baselines to guide reintroduction planning before practical activities need to commence.

4.2. Incorporating historical evidence into wider reintroduction planning

Our suitability framework should not be used in isolation to make decisions around species selection for reintroduction, but must form part of a wider evaluative context that also draws upon knowledge beyond environmental archives. Additional ecological criteria must also be considered [33,89], including: are current-day habitats appropriate and are threats mitigated, versus how much management is required to establish suitable conditions and/or are novel threats now present; could the species recolonise naturally or is human intervention essential; would reintroduction provide a substantial benefit to the species' global status (e.g. is it globally threatened); and would reintroduction provide wider benefits to other species or ecosystem interactions, functions or services? Evaluation of ecological feasibility must include rigorous population-level and landscape-level assessments (e.g. population viability analysis, species distribution modelling, habitat connectivity analysis) to evaluate whether candidate species could establish viable self-sustaining populations in current environments and remain resilient to predicted future change [90-92]. As reintroductions typically take place within human-occupied 'social-ecological' landscapes and are dependent upon finite conservation resources, evaluation of the socio-cultural, logistical and economic contexts, feasibility, suitability, value, competing interests, and associated trade-offs is also essential. Such factors include local community support or conflict, cost-benefit analysis, the potential for net future cultural or economic benefits, and whether candidate species align with national-level or other biodiversity targets [93,94].

Past evidence should be integrated alongside these other metrics within combined evaluation frameworks, which could be developed for strategizing species reintroduction priorities at regional or national levels. These different ways of assessing reintroduction suitability are not additive, but must be considered carefully and weighed up on a case-by-case basis. It is also important to distinguish clearly between evidence and subjective value; both constitute valid components of reintroduction decision-making, but it is crucial to recognise their different identities and roles [85]. For example, it may be preferable to prioritise species that provide keystone functions and regulate ecosystem services, or those with minimal wider impacts on ecosystems; or species that disappeared more recently [95]. Differing targets or 'types of species' may be appropriate depending upon project context and goals, but it is essential to recognise that this preference is subjective, and takes place within socio-cultural landscapes of changing opportunity and interest.

Despite the importance of considering other eligibility criteria in addition to past data, our framework demonstrates the critical need to evaluate environmental archives at the outset of reintroduction planning. Importantly, whereas some species will be identified as appropriate reintroduction candidates using past data, others will be downweighted by knowledge about their former status, or because of poor, contradictory or absent information that challenges the possibility of understanding their former status. It is clearly crucial to understand whether some species were never actually native, were naturally rare or intermittently present, or never used target landscapes for major life-history stages, and the selection of such species for introduction may not be justifiable if past evidence also identifies higher-priority candidates. Similarly, why would a species be promoted for reintroduction if little is known about its past occurrence, status, or reasons for previous disappearance in contrast to other candidates? Whilst it can be argued that absence of evidence does not in itself indicate evidence of former absence, this argument cannot justify or promote the introduction of species for which information on past presence is lacking. Valid reasons may exist for selecting such species on the basis of other environmental or social-ecological benefits (e.g. ecosystem service restoration; as surrogates to maintain ecosystem functionality) [96]. More radical conservation approaches are also increasingly being explored, including conservation translocation outside species' historical ranges or assisted colonisation in response to climate change [97]. However, these actions cannot be prioritised on the basis of past data or even potentially justified as reintroductions, and must be backed by strong evidence that they will support functionality or other introduction goals without adverse effects on native biodiversity caused by species that are not locally adapted to postglacial ecosystems.

In this light, it is important to recognise that several species that we highlight as low-priority or inappropriate candidates on the basis of past data (European bison, Aesculapian snake, European tree frog, great bustard) are the focus of current translocation efforts or discussions in Britain. These species do not meet confirmed native status under the criteria in Theme A: there is no evidence for native British populations during the Holocene, and no evidence that European bison was ever regionally present at all. However, they have either already been translocated in projects framed at least partly as reintroduction programmes (European bison, great bustard [91,98]), are now present in Britain as invasive populations that are discussed in terms of their perceived former native status (Aesculapian snake [99]), or are proposed as reintroduction candidates in the near future (European tree frog [100]). Whilst these projects may provide other tangible environmental benefits such as restoration of ecosystem processes, it is essential that such actions are explicit about their objectives and evidence, and specifically the extent to which they have evaluated information from environmental archives about past species status. Without such clarity, they risk criticism as potentially unjustifiable from ecological, legislative and ethical perspectives [44]. These activities thus highlight the need for wider adoption of a comparative multi-species framework that ensures past data are critically evaluated at the beginning of reintroduction project selection and development, to make conservationists aware of the complex nature of past biodiversity change and the differing ways that species might be regarded as native or non-native.

Our approach is not intended to be restrictive. Whilst we highlight species that fail to meet our criteria or that illustrate complexities in aspects of their past status that must be considered by decision-makers, historical evidence can also promote other species as strong candidates for reintroduction (e.g. beaver *Castor fiber* in Britain [101]) (figure 1). Instead, our framework provides guidelines to alert decision-makers to different criteria associated with past states and change that must be considered when thinking about possible reintroductions, but are often not appreciated from a modern ecological standpoint. We hope this framework can provide new perspectives that inform strategic policy-making, such as planning by the England Species Reintroductions Taskforce (www.gov.uk/government/groups/england-species-reintroductions-taskforce), the Scottish Code for Reintroduction Translocations [102], or the US National Park Service's Resist-Accept-Direct Framework (www.nps.gov/subjects/climatechange/resistacceptdirect.htm). Data from environmental archives can be used to guide reintroduction planning by thinking in terms of "should we" as well as "can we", with our framework enabling assessment of the relative suitability of different proposed actions across sets of candidate species within a world of limited resources.

Our criteria highlight the importance of evaluating the confidence we have in our understanding of key information necessary to restore past biodiversity. We recommend thinking about historical ecology in terms of what we do know, what we might know following further research, and what we potentially cannot ever know (and whether the existence of knowledge in this final category might exclude some reintroduction choices). Environmental archives vary hugely in the information they provide about different species and systems [24,103], and different archives (e.g. with different temporal resolutions) can provide varying, sometimes contradictory signals about past species status, requiring expert assessment of their sources and biases. For example, different taxonomic groups vary considerably in the ease with which species can be reliably identified from ancient skeletal remains, and in availability of modern comparative material to aid identification, with complex associated taxonomic biases in the likelihood of accurate determination, misidentification, or under-reporting of past species from zooarchaeological and fossil collections. These problems are compounded by a lack of adequate published information about many collections, with species inventories from many sites lacking diagnostic information or illustration of relevant specimens, meaning that many past identifications remain unverified. For example, diving duck bones are challenging to identify accurately to species level [104], and although red-crested pochard (see criterion 6) was originally reported as definitely identified from an Iron Age site in Somerset, it was included in a brief faunal list with no accompanying information, with subsequent authors highlighting the difficulty of diagnosing other diving duck bones from this site [105]. Synthesis and review of available evidence is thus essential, taking into account issues around past data quality and uncertainty [77,106].

It is also important to remember that whilst we must work with the knowledge available today, our understanding of past biodiversity is constantly improving. For example, some British animal and plant species traditionally regarded as introductions are now recognised as threatened or extirpated natives (e.g. pool frog *Pelophylax lessonae*), whereas other species formerly considered native and designated as national conservation priorities are now interpreted as probable or definite historical introductions (e.g. white-clawed crayfish *Austropotamobius pallipes*) [107,108]. Rigorous morphometric and biomolecular identification methods for archival specimens are increasingly accessible, and initiatives such as the Category F extension to the British List of birds aim to make ecologists more familiar with past biodiversity baselines [109]. We highlight the importance of re-evaluating historically archived zooarchaeological and fossil collections that have not been investigated using modern taxonomic approaches, especially for smaller vertebrates. However, although ongoing investigation of old and new collections is essential to improve our knowledge of past biodiversity, such activities are threatened by dwindling taxonomic expertise and specimen-based identification skills amongst the current generation of researchers, and insufficient recognition of the potential environmental relevance of many existing collections [110,111]. Developing approaches that encourage greater engagement and training in the use of specimen-based archives will be a key challenge facing biodiversity practitioners in the twenty-first century.

Species reintroductions, ecological restoration and rewilding can be promoted and initiated for many reasons, and it is crucial to understand the original motivations underpinning such projects to evaluate how best to use past data as evidence in project planning. Although these initiatives are all ultimately forward-looking [112,113], without a good understanding of the past we risk misunderstanding fundamental conservation parameters and making inappropriate or ineffective decisions. Indeed, reintroductions often fail [114], highlighting the importance of drawing upon all available knowledge baselines to make the best management and planning choices, from candidate species selection onward. Environmental archives have been specifically employed to inform and guide some proposed reintroductions [115,116], and the importance of incorporating historical perspectives into interdisciplinary reintroduction planning is promoted by some practitioners [117]. However, there remains a major shortfall in extending conservation evidence to include lessons from the past, by integrating data from environmental archives into environmental thinking through a variety of potential approaches [29,118,119].

We encourage biologists, managers, decision-makers and policy planners to avoid the pitfalls posed by shifting baselines, and to better align reintroduction, restoration and rewilding programmes with the evidence-based conservation framework by working more closely with researchers trained in historical disciplines. Evidence from the past can inform decision-making and help to prioritize species reintroductions and other environmental management actions, and a collaborative and interdisciplinary approach is needed to maximise the effective interpretation and incorporation of this crucial evidence within conservation. A new level of critical engagement with environmental archives is essential to guide optimal restoration of lost biodiversity in a changing world.

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Authors' contributions. STT: Conceptualization, investigation, methodology, project administration, resources, validation, visualization, writing–original draft, writing–review & editing. JJC: Conceptualization, investigation, methodology, validation, writing–review & editing. AMM: Investigation, validation, writing–review & editing. RJK: Validation, writing–review & editing. MAH: Methodology, validation. RPY: Methodology, validation, writing–review & editing.

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Figure 1. Framework of biological and ecological criteria relevant to decision-making on species reintroductions that can be uniquely informed by past data, grouped under two themes and illustrated using examples of species from the British vertebrate record. Beaver (*Castor fiber*) used as a comparison, as the past status and history of this species in Britain is well-understood compared to other examples [101].

Figure 2. Evaluation of reintroduction criteria for extirpated British population of Dalmatian pelican (*Pelecanus crispus*), demonstrating information-content and quality of past evidence that can inform potential reintroduction suitability under current level of knowledge.