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Site selection for European native oyster (Ostrea edulis) habitat restoration projects: An expert-derived consensus

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Abstract

- 1. The European native oyster (*Ostrea edulis*) is a threatened keystone species which historically created extensive, physically complex, biogenic habitats throughout European seas.
- Overfishing and direct habitat destruction, subsequently compounded by pollution, invasive species, disease, predation and climate change have resulted in the functional extinction of native oyster habitat across much of its former range.
- 3. Although oyster reef habitat remains imperilled, active restoration efforts are rapidly gaining momentum. Identifying appropriate sites for habitat restoration is an essential first step in long-term project success.
- In this study, a three-round Delphi process was conducted to determine the most important factors to consider in site selection for European native oyster habitat restoration projects.
- 5. Consensus was reached on a total of 65 factors as being important to consider in site selection for European native oyster habitat restoration projects. In addition to the abiotic factors typically included in habitat suitability models, socio-economic and logistical factors were found to be important. Determining the temporal and spatial variability of threats to native oyster habitat restoration and understanding the biotic factors present at a proposed restoration site also influence the potential for project scale-up and longevity.
- 6. This list guides site selection by identifying: a shortlist of measurable factors which should be considered; the relevant data to collect; topics for discussion in

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INTRODUCTION

1 1

participatory mapping processes; information of interest from the existing body of local ecological knowledge; and factors underpinning supportive and facilitating biotic factor, decision making, Delphi, ecological restoration, project logistics, socio-economic have documented their site selection process, either as part of a sitespecific feasibility study (e.g. Laing, Walker & Areal, 2006; Shelmerdine & Leslie, 2009; De Mesel et al., 2018; Fariñas-Franco et al., 2018; Pouvreau et al., 2021), or as part of large-scale habitat suitability assessments across a broad area such as the North Sea (Smaal et al., 2017; Kamermans et al., 2018; Pogoda et al., 2020b). The focus of these studies has largely been the abiotic and/or biotic factors defining habitat suitability (Laing, Walker & Areal, 2006; Shelmerdine & Leslie, 2009; Smaal et al., 2017; Kamermans et al., 2018; Pouvreau et al., 2021), with some also addressing

have historically received some of the lowest levels of legislative and practical protection and have suffered global declines (Airoldi & Beck, 2007; Kasoar et al., 2015). In Europe, drastic declines of the native oyster, Ostrea edulis, and its fisheries have been documented since the industrial revolution, with overfishing being the main driver of population collapse (Thurstan et al., 2013; Fariñas-Franco et al., 2018). Other human-induced stressors, such as sedimentation, pollution, disease, invasive species, predation and climatic events have compounded already depleted native oyster populations and contributed to the near extirpation of this habitat (Gercken & Schmidt, 2014; Halpern et al., 2015; Pogoda et al., 2019).

Bivalve reefs are a productive and biodiverse coastal habitat. They

regulatory frameworks.

KEYWORDS

factors, threats

Healthy native oyster habitat can support enhanced biodiversity and provide a range of ecosystem services (Pogoda et al., 2020a; zu Ermgassen et al., 2020a). Consequently, there are growing efforts to restore native oyster populations and the complex biogenic habitat they create. Marine ecosystem restoration has historically been viewed as costly and prone to failure, leading to low rates of implementation compared with terrestrial restoration (Saunders et al., 2020). While native oyster restoration in the USA is well established, restoration efforts across Europe are largely in the pilot stages. The number of new projects and locations is increasing rapidly, however, and lessons are fast being learnt (Preston et al., 2021). Europe has amongst the most fragmented biodiversity globally, and a high proportion of marine habitats remain in 'unfavourable conservation status' (Brondízio et al., 2019). Therefore, a core element of the EU Biodiversity Strategy for 2030 is the long-awaited EU Nature Restoration Regulation. The adoption of this ambitious proposal could mark a turning point for the restoration and recovery of EU habitats and species (European Environment Agency, 2020; European Commission, 2022). Against this backdrop of increased uptake and interest in oyster restoration globally (Duarte et al., 2020), the United Nations (UN) Decade on Ecosystem Restoration and the UN Oceans Decade are further highlighting the urgent need for marine restoration efforts (United Nations General Assembly, 2020a; United Nations General Assembly 2020b). This focused attention on marine restoration is helping to build confidence and broaden the scope of restoration efforts in terms of species, geography and scale.

Site selection is widely recognized as being a crucial element in determining long-term project success (Bayraktarov et al., 2016). Several previous European native oyster habitat restoration projects

with regard to other protected species such as seagrasses. In order to fulfil restoration objectives, it is important that selected sites support long-term survival, fitness and reproduction of the native oyster, in addition to initial settlement and growth (Kamermans et al., 2018; Pogoda et al., 2019; Pogoda et al., 2020a). Furthermore, given current projections of global climate change, it is important to consider both present and future site suitability in relation to ecological and socio-economic restoration goals (Howie & Bishop, 2021). In Europe, site connectivity has been taken into account in site selection for the translocation of northern horse mussels (Modiolus modiolus) in Strangford Lough, Northern Ireland, using a series of coupled hydrodynamic and particle dispersal models (Elsäßer et al., 2013). Similar methods were later utilized to assess abiotic factors and connectivity relating to the native oyster in Strangford Lough, which can be used to inform strategic site selection for future restoration efforts in this region (Smyth et al., 2016).

logistical and regulatory concerns (De Mesel et al., 2018; Fariñas-

Franco et al., 2018; Pogoda et al., 2020b). Similarly, oyster restoration

site selection studies in the USA have primarily focused on habitat

suitability, as well as the condition of and connectivity with remaining

oyster populations (e.g. Mann & Evans, 2004; Starke, Levinton &

Doall, 2011; Beseres Pollack et al., 2012). In rare cases, for example

work done by Puckett et al. (2018) in North Carolina, site selection

has gone so far as to consider permitting and logistical considerations

While the more mature field of native oyster habitat restoration in the USA has been critically important in guiding restoration efforts in Europe, there are notable biological differences between the dominant oyster species of the USA Atlantic coast and in the Gulf of Mexico, Crassostrea virginica, and the European species, O. edulis, which have some bearing on habitat suitability and site selection criteria. For example, C. virginica is predominantly an estuarine species, with well described interactions between salinity, fecundity, growth rate and disease prevalence (e.g. Paynter & Burreson, 1991;

Baillie & Grabowski, 2018). In contrast, *O. edulis* has a stronger affinity for high salinities and the interactions between disease prevalence and abiotic factors are less well described (see Sas et al. (2020) for a summary of current knowledge). Additionally, female *O. edulis* brood their young, potentially leaving them more prone to Allee effects at low density compared with their broadcast spawning *Crassostrea* spp. relatives. Most native oyster restoration efforts in Europe are taking place in locations where native oysters are not currently habitat forming (as defined by the OSPAR Commission, 2009), or the species is locally extinct (Pogoda et al., 2020b), therefore vital knowledge pertaining to the role of environmental setting and intraspecies interactions within native oyster habitats is lacking in the European context.

Prior to considering abiotic habitat suitability, restoration practitioners must assess and mitigate potential threats to the oysters themselves or the associated biogenic reef habitat at a proposed restoration site (Preston et al., 2021). Understanding the relative severity of threats, their interactions and their spatial and temporal distribution informs management and resulting site selection (zu Ermgassen et al., 2020a). Moreover, restoration efforts often exist within dynamic, crowded seascapes, so stakeholder engagement, sitespecific logistics and local feasibility are also key in determining the suitability of a site for native oyster restoration. Although such factors have typically been tackled within ongoing project management (Schuster & Doerr, 2015; Fitzsimons et al., 2019), gauging stakeholder opinion and logistical challenges are critical from early on in site selection. Indeed, recent site selection activities in western Australia also include such factors in their site selection processes (Cook et al., 2022).

Site selection for native oyster habitat restoration projects has been identified as a priority research area (Pogoda et al., 2020a; zu Ermgassen et al., 2020a). While there are many examples of site selection for native oyster habitat restoration across a range of spatial scales, and existing guidelines provide broad themes for consideration (Fitzsimons et al., 2019; Preston et al., 2020a), a comprehensive overview of the many considerations which should be accounted for in site selection is currently lacking. To support more efficient and successful restoration practices, this study uses the Delphi process to draw upon pan-European expertise to identify the most important factors in site selection for European native oyster habitat restoration projects. The resulting list of factors can be used as a comprehensive starting point for site selection in new restoration efforts (see also Hughes & zu Ermgassen, 2021), and provides a robust baseline for future site selection work to build upon.

2 | METHODS

Important factors for site selection in European native oyster habitat restoration projects were identified using a three-round Delphi process (Dalkey, 1969). The Delphi process is an anonymous, iterative and systematic questionnaire process which is well suited to addressing complex data gaps and has been shown to result in less bias than traditional round-table approaches (Grisham, 2009; Mukherjee et al., 2015). The Delphi process has been used in upwards of 40 ecology and conservation studies, including several previous uses in ecosystem restoration or restoration ecology (e.g. Orsi, Geneletti & Newton, 2011; Fisher et al., 2019; Cortina-Segarra et al., 2021). A common aim of Delphi studies is to generate consensus regarding conflicting or intertwined topics that cross disciplinary boundaries (Grisham, 2009). Since native oyster habitat restoration in Europe transcends a range of habitats, scales and motivations, the Delphi process is suitable for distilling expert knowledge into site selection guidelines.

2.1 | Expert participant recruitment

The Native Oyster Restoration Alliance (NORA) is a European network including representatives from governmental agencies, science and non-governmental organizations, as well as oyster growers, fisheries co-ops and other private enterprises, who share a common interest in furthering native oyster habitat restoration in Europe (Pogoda et al., 2019). Expert participants were invited to participate in this study through an open call on the NORA website on the 2nd of November 2020 and an announcement at the NORA3 conference on the 4–5 November 2020. Additionally, project leads from all projects listed on the NORA and Native Oyster Network (UK and Ireland) websites at the time were contacted directly to invite them to participate in the project.

2.2 | The Delphi process

The Delphi process was conducted between December 2020 and May 2021. The questionnaire was hosted online, and all communications between researchers were conducted via email. Round one consisted of several short-answer questions to collect information on expert participants' background and expertise, followed by an open-ended questionnaire, where each expert participant was asked to provide an exhaustive and confidential list of factors that they regarded as important to consider in native oyster habitat restoration site selection under three predefined categories: (1) abiotic factors; (2) biotic factors; and (3) socio-economic factors (Figure 1; Table 1; Table S1, Supporting Information). Expert participants were also asked to provide numerical parameters or thresholds alongside their suggested factors, where appropriate, or to indicate methods of measurement or inference where applying thresholds was not suitable. Questionnaire responses were collated, and duplicated suggestions grouped to avoid repetition. Suggested factors that related to project management more broadly, rather than site selection specifically, were removed following consultation with the relevant expert participants. Clarification of concepts and wording was also obtained where necessary. The list of factors was then grouped into five site selection categories: (1) threats to native oyster habitat restoration; (2) project logistics; (3) abiotic factors; (4) biotic

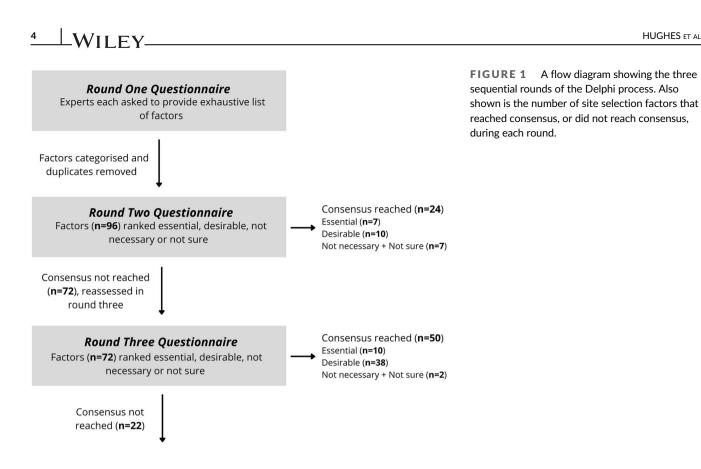


TABLE 1 The number of factors identified by the expert participants in Round One of the Delphi process as being important to consider in site selection for European native oyster habitat restoration projects, separated by category

Category	Number of factors
Threats to native oyster habitat restoration	14
Project logistics	11
Abiotic factors	23
Biotic factors	29
Socio-economic factors	19
Total	96

factors; and (5) socio-economic factors. The resulting factors were communicated to the expert participants as a Round One summary, and expert participants were offered the opportunity to comment or request clarification regarding the proposed list. Unanimous approval of all changes and the resulting list was obtained before proceeding to Round Two.

In Round Two of the Delphi process, expert participants were asked to indicate whether each factor was 'Essential', 'Desirable' or 'Not necessary' to consider during site selection, or whether they were 'Not sure'. 'Essential' factors may directly compromise native oyster survival, growth or reproduction, or may prevent project establishment outright, so must be considered in all site selection efforts. 'Desirable' factors may be important in increasing the probability of successful restoration, or encouraging long-term and large-scale restoration benefits, but may not be critical to consider at all potential sites. Within each section, a short answer comments box was included to gather supporting references and clarifying or qualifying comments to provide wider context to the responses.

Where >70% of expert participants classified a factor as 'Essential' or 'Desirable', the factor was deemed to have reached consensus (Figure 1). Factors classified 'Not Necessary' or 'Not sure' by >60% of experts were discarded and not taken forward to the third round, given the strong indication that such factors were not important for site selection. These thresholds were identified based upon recommendations from Mukherjee et al. (2015) and existing collaborators' experience using the Delphi process. The expert participants were asked to individually review the Round Two summary and were given the opportunity to comment on the findings and to 'rescue' discarded factors. Factors which did not reach consensus in Round Two were revisited in the third and final round (Figure 1).

In Round Three, in addition to revisiting the factors for which no consensus was reached in Round Two, expert participants were asked to provide information regarding the disease and invasive species status of their project site. This was to allow assessment of whether disease and invasive species status impacted the responses to some factors. In Round Three, a number of factors failed to exceed the 70% threshold as either 'Essential' or 'Desirable' independently, but were identified as being either 'Essential' or 'Desirable' by the vast majority of experts (i.e. 'Essential' and 'Desirable' combined >70%). It was agreed that these factors were important in native oyster habitat restoration site selection and should be included in the final list of factors. In these cases, the percentage scores for 'Essential' or 'Desirable' were compared and a simple majority used to determine the outcome. Factors which failed to reach consensus (i.e. not

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exceeding the combined 70% threshold) were discarded and not carried through to the final list (Figure 1). Expert participants were provided with the Round Three summary and asked to identify any concerns or approve the final classification of all factors. The final list was unanimously approved.

3 | RESULTS

3.1 | Summary of expert participant experience

Twenty-five Delphi questionnaires were completed. Between the expert participants, active restoration projects from 20 different locations were represented, primarily in the UK and North Sea regions. Some expert participants had worked together on these projects. One expert participant had experience of a natural recovery arising from aquaculture, and one represented a sea-based oyster production facility (Figure 2). The two remaining expert participants had worked on native oyster habitat restoration in the past but did not represent projects currently ongoing. Of the expert participants, 13 had worked on native oyster projects in the UK, five in the Netherlands, four in Ireland, and one in each of Sweden, Germany, Belgium, Spain, Greece, Croatia and France. Some had worked in multiple countries.

All participants were experts in native oyster habitat restoration, with the majority of expert participants having a background in conservation (n = 18) and/or ecology (n = 16). Expertise in project management (n = 10) or public engagement and communications (n = 5) was also common among the expert participants. Smaller numbers of the expert participants identified expertise in oyster

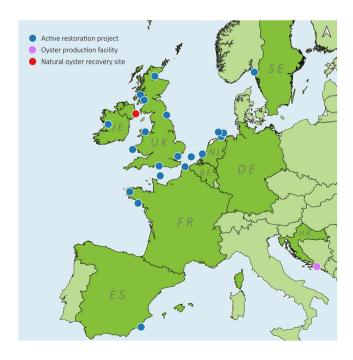


FIGURE 2 A map showing the primary project sites represented by all expert participants involved in this study.

growing (n = 4), fisheries management (n = 3), and other sectors such as hydrodynamic research (n = 1), hatchery culture research (n = 1), economics (n = 1) and scientific diving (n = 1). Of the expert participants, most represented two, three or four employment sectors (n = 9, 10, 3 respectively), indicating high levels of multidisciplinary expertise in oyster restoration.

Between the expert participants, the level and longevity of experience differed. Seven experts had over 20 years of experience in marine conservation, whereas eight had fewer than 5 years of experience. Native oyster habitat restoration is a relatively new area of marine conservation, so the majority (72%) of expert participants had between 1 and 6 years of experience, with only 16% having worked in native oyster habitat restoration for more than 10 years. The number of native oyster habitat restoration projects that expert participants had been involved in from the site selection stage ranged from zero to more than five, and generally corresponded with the length of time working in native oyster habitat restoration.

Disease and invasive species status differed across the project sites represented. Fourteen expert participants reported presence of diseases [specifically those listed by the World Organisation for Animal Health (OIE) and/or the European Commission (EC)] at their restoration site. High-impact invasive non-native species [INNS, namely the carpet sea squirt (*Didemnum vexillum*) and/or the American slipper limpet (*Crepidula fornicata*)] were also reported as being present by 12 expert participants, with five experts reporting the presence of both these INNS. The invasive Pacific oyster (*Crassostrea gigas*) was identified as present by 15 expert participants. Nine expert participants reported the presence of at least one INNS plus an OIE/EC listed disease at their site.

3.2 | Factors identified through the Delphi process

A total of 96 factors were identified, after duplicates had been removed, through Round One of the Delphi process (Table 1; Table S1, Supporting Information).

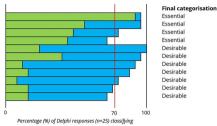
After three rounds, the Delphi questionnaires led to consensus on 65 (68%) of the original 96 factors that are important to consider in site selection for European native oyster habitat restoration projects. Of those that reached consensus, 17 were classified as 'Essential' and 48 as 'Desirable' (Figure 3). These 'Essential' and 'Desirable' factors can be used as a checklist by restoration practitioners in the early stages of site selection. The complete list of essential and desirable factors provided in Figure 3 aims to be all-encompassing, and should be used selectively depending on context, location, scale and project goals.

3.2.1 | Threats to native oyster habitat restoration

Eleven threats to native oyster habitat restoration reached consensus through the Delphi process (Figure 3a). Threats that were considered 'Essential' (n = 4) in site selection directly compromise

(a)

- Factor Protection from destructive fishing methods Absence of dredging in the area where restoration is being performed Minimum dissolved oxygen concentration Absence of extractive practices Low sedimentation rate Absence of unregulated harvesting or poaching Absence of high impact invasive non-native species Low pollution levels (e.g. TBY, PAHs, other hydrocarbons and heavy metals) Minimal sewage outflow within close proximity to the site Inorganic nutrient concentrations are below harmful threshold
- THREATS Absence of OIE/EC listed diseases

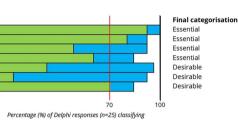


each factor as "Essential" and "Desirable

Desirable Desirable Desirable Desirable Desirable

(b)

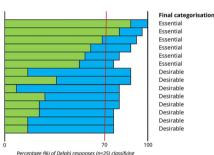
- Factor Agreements that the area can be used for restoration
- LOGISTICS Licencing and regulation
- Availability of source oysters
- Site safety concerns Area of site
- PROJECT Low intensity of anchoring or mooring
- Site accessibility



each factor as "Essential" and "Desirable"

(c)

- Factor Substrate suitability for settlement (type, stability, quality and quantity) Summer water temperature conditions provide potential for reproduction Salinity minimum Low seabed mobility
- Salinity range Water temperature maximum in summer
- Turbidity (low)
- Variant (low) Wave exposure (low to moderate) Concentration of inorganic nutrients (nitrates and phosphates) Water temperature minimum in winter
- ACTORS
- Volume of freshwater inputs from rivers and streams Current velocity (low to moderate) Existence, strength and flushing of tides (low to moderate) ABIOTIC
- Water pH (pH range, maximum and minimum)



Percentage (%) of Delphi responses (n=25) classifying each factor as "Essential" and "Desirable"

(d)

(e) Factor

SOCIO-1

- Factor Evidence of historical distribution of <u>O. edulis</u> at site Low predator abundance Site lies within historical range of O. edulis Connectivity with naturally occurring larval broodstock Potential for biodiversity enhancement of the site Prevalence of OIE/EC diseases Phytoplankton abundance (measured using chlorophyll a) Low levels of harmful algae Balanced food web with predators of predators
- Prevalence of high impact invasive non-native species Existing non-vyster habitats not negatively impacted by restoration activities Low abundance of species that compete for settlement area

Factor Enggement with policy makers and environmental regulators Stakeholder interest and support Local ecological knowledge Potential for ecosystem service enhancement Potential for ecosystem service enhancement with relevance to stakeholders

Potential for Sutentific research Cooperation with (non-oyster) fisheries Cooperation and potential co-location with local oyster fisheries or aquaculture Area not essential for livelihoods (e.g. through fishing)

Absence of key benthic fisheries target species at the site Site requires environmental goals and targets to be met through restoration activity

- FACTOR
- Prevalence of non-native species
- BIOTIC

Potential to develop local partnerships

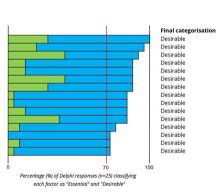
Potential for scientific research

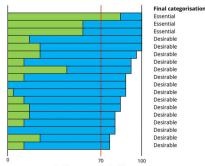
Potential for citizen science research

Education value

Returning heritage value to the area Protected area status Coastal community development and well-being Boosting local economy and providing job opportunities

Absence of biotoxins Prevalence, density and distribution of the Pacific Oyster





Percentage (%) of Delphi responses (n=25) classifying each factor as "Essential" and "Desirable

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FIGURE 3 The percentage of Delphi responses (n = 25) classifying each factor as 'Essential' or 'Desirable'. For each factor, green indicates the 'Essential' percentage, and blue indicates the 'Desirable' percentage. A final categorization is also provided. The vertical red line represents the 70% consensus threshold, which must be surpassed, either individually or when combined, for a factor to be considered either 'Essential' or 'Desirable' in site selection. Parts (a)–(e) show each of the five categories: (a) threats; (b) logistics; (c) abiotic factors; (d) biotic factors; and (e) socio-economic factors respectively.



FIGURE 4 'Essential' factors to consider in site selection for native oyster habitat restoration, separated into four categories: threats, logistics, abiotic factors, and socio-economic factors. *Note*: No biotic factors reached consensus as 'Essential' (Hughes & zu Ermgassen, 2021).

native oyster survival and reproduction. These mainly included activities which physically damage the sea bed (Figure 4), such as destructive fishing, dredging (relating to maintenance or capital dredging as opposed to fishing using dredges) and extractive practices (sand and gravel extraction). In addition, there was consensus that a low dissolved oxygen concentration (<0.5 mg/L; Davis, 1975) compromises biological function and survival of oysters and is therefore 'Essential' to consider in site selection. An exact threshold was, however, not agreed, as co-variance with other abiotic factors means that *O. edulis*'s tolerance to low dissolved oxygen differs not only depending on duration, but also on location and context.

The list of factors considered 'Desirable' (n = 7) was dominated by water quality concerns, with experts reaching consensus on the inclusion of low sedimentation rate, low pollution levels, minimal sewage outflow and inorganic nutrient concentrations (nitrates and phosphates). There was also consensus that understanding the prevalence of high impact INNS and OIE/EC listed diseases (*Bonamia ostreae*, *B. exitiosa*, *Marteilia refringens*, *Mikrocytos mackini* and Herpes virus OsHV-1-µVar) is 'Desirable' in site selection. The final 'Desirable' factor in this section was the absence of unregulated harvesting or poaching of oysters.

3.2.2 | Logistics

Seven logistical factors regarding native oyster habitat restoration reached consensus through the Delphi process (Figure 3b). Factors considered 'Essential' (n = 4) were diversely related to permissions (agreements with landowners, marinas, wind farms or government, favourable licensing and regulation), site safety and availability of source oysters (Figure 4).

Logistical factors considered 'Desirable' (n = 3) were site area, which determines the potential for project scale-up and population expansion, and site accessibility (regarding wave height, distance from shore and depth). Also included was low intensity of anchoring and mooring. It was noted that mooring intensity is inherently high in marina sites, which for other reasons, such as their accessibility for public outreach, may be considered beneficial when selecting a site.

3.2.3 | Abiotic factors

Fourteen abiotic factors reached consensus through the Delphi process (Figure 3c). Abiotic factors encompassed characteristics of the underlying substrate, water temperature, salinity, and hydrodynamic

features of the site. Several of these factors were considered 'Essential' (n = 6) as they underpin the biological niche in which oyster growth and reproduction can occur (temperature and salinity in particular, Figure 4). Water temperature was considered 'Essential' as it provides the cue for oyster reproduction in summer (Chapman et al., 2021). The maximum temperature threshold (28-30°C; Bayne, 2017) was also considered 'Essential' in light of anthropogenic climate change. Both the minimum salinity threshold (>20 PSU; Davis & Ansell, 1962) and optimum salinity range (25-35 PSU; Davis & Ansell, 1962) were considered 'Essential' as they impact the survival and growth of O. edulis.

Factors determining substrate suitability (type, stability, quality, quantity and seabed mobility) were also considered 'Essential' because young oysters require appropriate substrate to settle on (Figure 4). Sites with high seabed mobility or unconsolidated sediment, for example in the form of mobile sand waves, are likely to experience high shear stress, which can cause oysters to become smothered, dislodged or damaged. Seabed mobility of less than 0.8 cm per day (Grant, Enright & Griswold, 1990) is therefore generally required.

Of the abiotic factors considered 'Desirable' (n = 8), some have influence over the value of factors considered to be 'Essential'. For example, the volume of freshwater inputs from rivers and streams can affect minimum salinity and salinity range, while wave exposure and current velocity can affect seabed mobility. Water guality indicators, such as turbidity and inorganic nutrients, were also identified as 'Desirable' to consider. The impact of water quality on oyster habitat can vary, for example, with the existence, strength and flushing of tides, which was considered a 'Desirable' factor to consider for this reason. Similarly, water temperature minimum in winter (of <5°C: Bayne, 2017), is also 'Desirable' to consider as it causes strong reductions in oyster metabolism and functioning. Extreme low temperatures can also result in mortalities owing to freezing in intertidal or very shallow sites. Finally, water pH (minimum, maximum and range) also reached consensus as 'Desirable' to consider. The critical pH level for significant mortality in O. edulis sits at approximately pH 6.9 (Bamber, 1990). There is limited evidence that pH in European estuaries and seas currently varies to the degree that it has negative impacts on bivalve growth or survival. Under future global change scenarios, further evidence may be required to determine the impact of pH on native oysters (Howie & Bishop, 2021).

3.2.4 **Biotic factors**

No biotic factors were considered 'Essential', but 15 biotic factors reached consensus as 'Desirable' (Figure 3d). These included selecting sites within the known historical range of O. edulis, and sites with evidence of historical O. edulis distribution (e.g. through fishery records, middens, shells, fossils or historical ecology studies), as well as present day connectivity with naturally occurring larval broodstock. Additionally, factors related to ecological interactions with other predatory or competitive species, such as low predation, a balanced predatory food web and a low abundance of species that compete for settlement area, were considered 'Desirable'. Considering whether the abundance of phytoplankton was sufficient, but not excessive, was also identified as 'Desirable'. Since restoration often takes place with the primary aim of restoring biodiversity, it may also be appropriate to consider whether some locations are more likely to support a higher diversity of species post restoration than others.

The prevalence, density and distribution of INNS, including the invasive Pacific oyster (C. gigas), as well as the prevalence of OIE/EC diseases (B. ostreae, B. exitiosa, M. refringens, M. mackini and Herpes virus OsHV-1-µVar) is 'Desirable' to consider alongside relevant biosecurity procedures. Ecosystem health indicators, such as low levels of harmful algae and the presence/absence of biotoxins may also indicate the suitability of a site and are therefore 'Desirable' to consider. While each of these factors presents a potential risk to O. edulis restoration, they are now widely distributed throughout Europe and it is increasingly accepted that restoration efforts must work with their presence (Shumway, 1990; Laing, Walker & Areal, 2006; Christianen et al., 2018; Sas et al., 2020). Nevertheless, restoration projects should consider the degree to which their presence or abundance presents a risk, and some projects may opt to avoid the risk altogether.

Lastly, consideration of the presence, abundance and relative location of existing non-oyster habitats, both to ensure they are not negatively impacted by restoration activities and to capitalize on the potential benefits of integrated restoration of the seascape, was considered 'Desirable'.

3.2.5 Socio-economic factors

Eighteen socio-economic factors reached consensus through the Delphi process (Figure 3e). 'Essential' socio-economic factors (n = 3) included engagement with policy makers and environmental regulators, and stakeholder interest and support, as well as the utilization of local ecological knowledge (LEK; Figure 4). Local ecological knowledge, which integrates traditional ways of knowing into scientific frameworks (Gann et al., 2019), is widely seen as an important element in environmental decision making and conservation activities on the ground (Berkström et al., 2019; Theodorou et al., 2022).

The remaining socio-economic factors were 'Desirable' (n = 15) to consider. These included selecting sites where cooperation with other industries, including oyster and non-oyster fisheries, is possible, as well as seeking restoration sites where key benthic fisheries target species are absent, and the proposed area is not essential for livelihoods. Such factors increase the potential for restoration projects to collaborate constructively with key stakeholders such as fishers. Considering the location of restoration within already protected areas (e.g. no-take zones and gear restrictions) was also deemed 'Desirable', because this increases the likelihood of protection being afforded to the restored oysters. Furthermore, the

legal designation or status of a site may provide further impetus or support for restoration activities, in order to achieve existing environmental goals and targets, and may therefore be worthwhile to consider during site selection.

Funders increasingly consider a wider suite of social and ecological benefits when assessing projects (Laing, Walker & Areal, 2006). It is therefore desirable to consider the potential for a project site to develop local partnerships and benefit the local community, for example through education, returning heritage value, boosting local economies and providing job opportunities. Additionally, the potential for a site to support scientific research, be that through formal science or citizen science, may be looked upon positively by funders, as well as yielding benefits to the wider restoration community in terms of knowledge gain.

Finally, many expert participants highlighted that it is 'Desirable' to consider ecosystem service enhancement within their project goals. While the scientific evidence of ecosystem service delivery by *O. edulis* is not yet well defined (zu Ermgassen et al., 2020b), consideration of where the potential for ecosystem service delivery may be maximized should still be considered where ecosystem service delivery is a project goal (Theuerkauf, Eggleston & Puckett, 2019).

4 | DISCUSSION

This expert-derived list of 65 factors to consider in site selection for native oyster habitat restoration in Europe provides an overview for all emerging restoration efforts, upon which to develop their restoration planning. The list serves several aspects of site selection: (1) it may be used to guide habitat suitability models by providing a short list of measurable factors which should be included; (2) it provides new projects with an overview of the relevant data to collect when undertaking the site selection process; (3) it provides an overview of factors that should be discussed during participatory mapping processes, and guidance as to which information may be of interest from the existing body of LEK; and (4) it highlights that early establishment of whether the site is located within a supportive or facilitating regulatory framework can be helpful when engaging both with funders and regulators, which may be important for scaling up the spatial and temporal scale of restoration efforts.

Abiotic factors (Figure 3c) remain crucial in site selection as they bound the ecological suitability of the site. For *O. edulis*, these factors are well documented in habitat suitability models that have been developed for offshore areas in Europe (Smaal et al., 2017; Kamermans et al., 2018; Pogoda et al., 2020b). The expert-derived lists of abiotic factors and measurable threats support this process, by providing a starting point for scoping out which datasets should be sought when undertaking habitat suitability modelling and mapping. The list stops short of providing thresholds for abiotic factors related to the growth and survival of oysters, as it was clear from participating experts that there is little agreement on threshold values. Possible values associated with many factors were deemed to be context specific, or synergistic, such that a single value could not be

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agreed upon. Some threshold values have been provided in the Results section where there was reasonable agreement between the expert participants and published literature. Additionally, published studies provide summaries of abiotic thresholds under differing situations, which can be used in tandem with this list (see De Mesel et al., 2018; Pogoda et al., 2020b; Hughes, 2021; Hughes & zu Ermgassen, 2021). An illustration of the potential utility of this list is provided by its recent inclusion in an effort to map the theoretical niche of O. edulis across Europe, both to guide the abiotic parameters used in the initial niche model and to unpick the nuance surrounding the model which cannot be explained by abiotic parameters alone (Stechele et al., 2022a). There is still much potential for future development of habitat suitability modelling, with models specific to inshore locations in Europe yet to be developed beyond a few broadscale efforts (e.g. UK Environment Agency, 2020; Stechele et al., 2022a). The consensus drawn through the Delphi process across a diversity of restoration sites and ecological systems suggests that these 'Essential' factors are common to inshore and offshore habitats alike, and hence that the factors listed should be considered in both inshore and offshore habitat suitability modelling.

The list of factors may also help to guide participatory mapping processes to capture the relevant LEK from existing stakeholders. Stakeholders often have a deep understanding of their local ecosystems based upon years of insight and non-scientific ecological observation (Berkström et al., 2019; Theodorou et al., 2022). Local ecological knowledge can be effectively integrated into the site selection process through early and open consultation, and by ensuring that community members have a seat at the decision-making table. Incorporating this information into site selection helps empower local communities and gives recognition to their understanding. improving the social licence of the restoration project, while also addressing the frequent absence of biotic and abiotic data at the scale relevant to site selection. Local communities can also provide day-today observation of a restoration site, which is valuable in the early detection of issues such as poaching or mass mortalities. Indeed, it is recognized by the Society of Ecological Restoration that restoration strategies which incorporate LEK alongside formal science can be particularly effective in achieving restoration goals (Gann et al., 2019). Given the widespread extirpation of O. edulis habitat in Europe, LEK often provides the most detailed information relating to the historical distribution and management of oysters.

The listed factors were proposed based not only on the experts' experience with site selection processes to date, but also incorporating their experience of managing projects, and their understanding of facilitating factors in project success. The resulting list of factors therefore provides a comprehensive overview of not only the key abiotic factors which may be included in habitat suitability modelling, but also factors relating to project logistics (Figure 3b), biotic (Figure 3d) and socio-economic factors (Figure 3e), which are critical in project planning and execution (Fitzsimons et al., 2019; Preston et al., 2020a). The listed 'Essential' socio-economic factors, such as stakeholder interest and support (Figure 4), underpin project acceptance and can be pivotal in acquiring funding,

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project approval and/or social licence to operate (Imeson & van den Bergh, 2006; Deitch et al., 2021; Lupp et al., 2021). By considering such a range of factors at the site selection stage, the potential success – biologically, socially and logistically – as well as the potential benefits of the restoration activities can be maximized. Such holistic consideration of a range of factors at the site selection stage may prove increasingly important to ensure that native oyster habitat restoration keeps pace with the ambitious plans to restore marine habitats in Europe (European Commission, 2022), given the evidence from the USA that social and practical elements of restoration are critical in achieving scale-up and project longevity (DeAngelis et al., 2020).

Site selection can take place at a range of scales. Initially a broader 'search area' might be considered. For example, in offshore areas in Belgium and the Netherlands, habitat suitability surveys were conducted over up to 100 km², in order to narrow down potential areas suitable for O. edulis habitat restoration within windfarms. In nearshore areas, initial site selection within a broader geography, such as a country or region, may take place over a similar scale, to identify individual estuaries or stretches of coastline most amenable to restoration efforts. In these cases, the 'Essential' factors shown in Figures 3a-e should be assessed. It is also recommended that all 'Desirable' factors be considered at both the large and the small scale, although a critical eve should be cast over the factors to determine which are relevant to the aims of the restoration project, and which data are accessible at the scale relevant to support the process. For example, at the broader spatial scale in Europe, salinity will play a role only in some limited geographies, such as the western Baltic. In most regions, it is only once a more restricted location is selected, such as an estuary, that the role of salinity may come into play. In nearshore areas, it is relatively typical for the site selection process to begin at a smaller spatial scale, often because certain site selection criteria are intrinsically met, such as returning the cultural heritage relating to O. edulis, as is the case with projects such as ENORI, Cuan Beo and the Solent Oyster Restoration project (see https://essexnativeoyster. com/, https://noraeurope.eu/ireland-galway-bay-oyster-restorationprojecta/, https://www.bluemarinefoundation.com/projects/solent/). In these cases, the site de facto encompasses some of the factors listed, such as evidence of historical O. edulis distribution at the site (Figure 3d), coastal community development and wellbeing, and boosting local economies through providing job opportunities (Figure 3e).

In order to increase the utility of this list, factors were identified as either 'Essential' or 'Desirable' to be considered in site selection. Factors deemed 'Essential' to consider should be included in all site selection processes. These include ensuring that the site is protected from destructive practices such as extraction (Figure 3a), that it is possible to obtain permissions to work at the site (Figure 3b), that the site is suitable for the survival and reproduction of *O. edulis* [i.e. that a minimum dissolved oxygen level of 0.5 mg/L (Davis, 1975) is not crossed, and that summer temperatures are conducive to reproduction], and that the site is logistically safe to work in (Figure 3b). While some of these 'Essential' factors, such as engagement with stakeholders and regulatory authorities (Figure 3e) are more typically addressed in project management, the expert participants agreed that their consideration at the early stages of broader site selection is warranted, given the critical role that these parties play in ensuring the success of restoration efforts and the variable levels of engagement that may be found spatially.

In the global context, it may seem surprising that the 'availability of source oysters' (Figure 3b) was considered an 'Essential' factor; however, unlike in the USA, restoration practitioners in Europe frequently experience widespread shortages of genetically suitable and biosecure source oysters, which presents significant challenges to project management (zu Ermgassen et al., 2021). The location of the restoration site can strongly influence the availability of ovsters through its proximity to commercial growers, hatcheries or spatting ponds, with similar disease and INNS status. Consideration of the genetic population structure and diversity of the source oysters is also important to avoid genetic population bottlenecks or low effective population sizes, particularly at sites with extant populations of O. edulis, where there is often a need to maintain local genetic adaptations or disease resistance (Pogoda et al., 2019). The disease and INNS status of both the stock and the restoration site is critically important in the European context, where biosecurity concerns, relating to high-impact INNS and OIE/EC diseases are subject to a strong regulatory framework [including, but not limited to, The Council Directive 2006/88/EC (European Union, 2006) and Regulation (EU) 2016/429, 'The Animal Health Law' (European Union. 2016)].

Given the concerns regarding INNS and OIC/EC diseases, it may seem curious that the absence of INNS and OIC/EC diseases, in particular *B. ostreae*, was deemed 'Not Necessary' to consider in site selection. In addition, knowledge of their prevalence at a site was classified as 'Desirable' as opposed to 'Essential'. This is largely because these OIE/EC diseases are already present at a vast number of restoration sites, with 14 of the expert participants reporting presence of OIC/EC diseases at their primary restoration site. This exemplifies that many projects are opting to 'live with disease', relying on the potential of disease tolerant or resistant oysters as an alternative to avoiding impacted sites (Fitzsimons et al., 2019; Sas et al., 2020). OIE/EC listed diseases must, however, be considered by all projects within robust biosecurity plans, developed in conjunction with the relevant regulatory authorities, even when they are not considered as a factor in site selection (zu Ermgassen et al., 2020).

Similarly, expert participants classified understanding the prevalence and spatial distribution of INNS as 'Desirable'. As with disease, many potential restoration sites already have high prevalence of INNS, with 12 of the expert participants reporting presence of high-impact INNS at their current project sites. Some INNS, such as the carpet sea squirt (*D. vexillum*), American oyster drill (*Urosalpinx cinerea*) and American slipper limpet (*C. fornicata*), can be particularly damaging to native oyster populations through spat predation and competition for settlement area leading to eventual competitive exclusion (Hancock, 1954; Laing, Walker & Areal, 2006; Helmer et al., 2019; Preston et al., 2020b; zu Ermgassen et al., 2020c). The

restoration community has, however, largely accepted the presence of these species as an underlying attribute of some potential restoration sites. Where they occur, it may be desirable to consider their prevalence to avoid potential negative interactions on a smaller spatial scale, for example, by avoiding restoration in areas with the highest densities of *C. fornicata* (Helmer et al., 2019; Preston et al., 2020b; zu Ermgassen, 2022), or in order to maximize the potential biodiversity gains resulting from restoration activity (Lown et al., 2021).

Understanding the prevalence of the invasive Pacific oyster (*C. gigas*), was also considered 'Desirable'. This INNS also now co-occurs with the native oyster in many locations, where it can form mixed-species reefs with *O. edulis* (e.g. Zwerschke et al., 2018). Currently, the full extent of potential competitive interactions and habitat alteration is still the subject of ongoing research, with recent work suggesting that the Pacific oyster may in fact be beneficial in enhancing recruitment of the native oyster, consolidating sediments and providing shell material for settlement (Christianen et al., 2018; Stechele et al., 2022b). Many sites, however, are still at the early stage of *C. gigas* invasion and *O. edulis* recovery; therefore these observations should be interpreted with caution until interspecies interactions at higher densities are fully understood.

Ecological restoration is defined by the Society of Ecological Restoration as 'the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed', and reintroduction as 'returning biota to an area where it previously occurred' (Gann et al., 2019). Evidence that the species being restored was historically distributed at potential restoration sites is therefore usually considered a critical factor in site selection. It was therefore surprising that the expert participants identified selecting sites within the known historical range of O. edulis and sites with evidence of historical O. edulis distribution as 'Desirable' as opposed to 'Essential'. In the European context, however, O. edulis habitats have all but disappeared and evidence of the historical distribution of O. edulis, in particular in offshore sites, is extremely challenging to obtain (Bennema, Engelhard & Lindeboom, 2020). Even inshore, determining the exact age of extinction of historical native oyster beds can present a significant challenge, as shell material can persist for millennia, and written records from locations distant to key trading ports is often scant (Fariñas-Franco et al., 2018; Bergström, Thorngren & Lindegarth, 2022). Nevertheless, there is significant evidence that oyster beds were extremely widely distributed throughout the North Sea (Gercken & Schmidt, 2014; Bennema, Engelhard & Lindeboom, 2020; Sander et al., 2021), and in many coastal estuaries where they are no longer in evidence (Beck et al., 2011). Given the strong evidence for the widespread distribution of the habitat historically, and the connectivity at the seascape scale that this implies, the expert participants articulated that it was appropriate not to insist on physical evidence of the historical presence of oyster beds in all cases. Furthermore, when considering the potential impacts of anthropogenic climate change, expert participants recognized that, while all current restoration efforts are taking place within the historical range of O. edulis, constraining future restoration efforts in

this regard may not always be appropriate (Howie & Bishop, 2021). Any future restoration effort taking place outside of the currently understood historical range must, however, be planned with the explicit consent of environmental regulators and with due consideration to the connectivity of proposed sites with the current distribution of the habitat (National Species Reintroduction Forum, 2014).

All other biotic factors in this study were also classified as 'Desirable' to consider in native oyster habitat restoration site selection (Figure 3d). This arises both from differing biotic baseline conditions between locations (e.g. disease status) as discussed earlier, and from the temporal and spatial variability inherent in both predator-prey interactions and phytoplankton growth (Figure 3d). For example, native oysters are preyed upon by the common starfish, *Asterias rubens* (Perry & Jackson, 2017), which commonly displays 'boom and bust' population dynamics, resulting in unpredictable inter-annual variability in their impact on oyster populations (Uthicke, Schaffelke & Byrne, 2009). Given their potential impact, however, expert participants identified an awareness of these threats as 'Desirable' to consider in site selection.

Interestingly, a number of factors identified as 'Threats' were not classified 'Essential' (Figure 3a). These are primarily related to water quality indicators. In the case of water quality, a paradox exists whereby threats may be considered opportunities in native oyster habitat restoration projects. Inorganic nutrient concentrations, pollution levels, sewage outflows, low dissolved oxygen and sedimentation can have significant negative impacts on native oyster growth and survival but can also be remediated through the filtering services provided by oysters (Newell, 2004; Kellogg et al., 2013; zu Ermgassen et al., 2020b). Ovster habitat restoration activities may be undertaken to remediate intermediate levels of eutrophication, which means that avoiding such areas in site selection cannot be considered 'Essential'. For eastern oysters in the USA, a Habitat Suitability Index (HSI) model has been developed which identifies locations where the oyster reef-related ecosystem service of water filtration can be maximized (Theuerkauf, Eggleston & Puckett, 2019). European projects are also harnessing this service, for example, the Dornoch Environmental Enhancement Project in Scotland, has the explicit aim of enhancing biodiversity and improving water quality (Native Oyster Restoration Alliance, 2022), while in the highly eutrophic Mar Menor lagoon (Spain), the RemediOS project is investigating the viability of producing native oyster seed using local broodstock for future oyster restoration, with bioremediation as one of its main objectives (Native Oyster Restoration Alliance, 2022).

Finally, the participating experts strongly emphasized the benefits of considering the potential for a site to support ecosystem service enhancement in terms of engaging both with stakeholders and funders (Laing, Walker & Areal, 2006). While the recovery of ecosystem services is a commonly cited reason for undertaking restoration, both according to the expert participants and the published literature (e.g. Pogoda et al., 2019; zu Ermgassen et al., 2020a), the science underpinning the quantification of services associated with *O. edulis* is far from complete (Lee et al., 2020; zu

Ermgassen et al., 2020b). The near extirpation of oyster habitat makes it challenging to assess the potential ecosystem service delivery. Restoration efforts must therefore play a critical role in developing this understanding. Once the interaction between abiotic and biotic variables and ecosystem service delivery is better understood, models can be developed which can inform site selection on the basis of stakeholder interests (e.g. Gray et al., 2019) and can account for other habitats in the seascape (e.g. Gilby et al., 2020). Given the increasing interest in seascape-scale restoration, both in policy and practice (DeAngelis et al., 2020; Clover, 2022), the potential for new restoration sites to contribute towards building this evidence base should, at least in this early stage of native oyster restoration science, be given some weighting when determining where to restore.

5 | CONCLUSIONS

The current expansion of native oyster habitat restoration in Europe looks set to continue, with an increasing number of international agreements committing governments to improving and restoring their degraded seascapes (e.g. the European Green Deal and the EU Biodiversity Strategy for 2030 (European Environment Agency, 2020; European Commission, 2021)). Many European countries are also enacting additional domestic legislation which encourages enhanced biodiversity restoration, such as the UK Environment Act (UK Parliament, 2021). Political pressure on marine industry can also hold influence, for example with Nature Inclusive Design, and oyster restoration efforts specifically, being part of the new tenders for offshore wind farms in the Netherlands. This highlights the enormous significance of the political setting, both nationally and regionally, on site selection.

This study provides much needed guidance for expanding native oyster habitat restoration efforts by identifying the key factors which should be considered in site selection. By bringing together experts from across Europe, with experience from projects spanning a wide range of contexts and locations, this Delphi study represents the best current understanding of factors that are both 'Essential' and 'Desirable' to consider in site selection for European native oyster habitat restoration. Despite the European focus of this effort, many of the factors identified, particularly those relating to logistical and socio-economic elements of restoration, are applicable to habitat building shellfish and other coastal marine habitats both within and outside of Europe. Critically, this study highlights that the suitability of a restoration site cannot be determined by considering abiotic factors and habitat suitability alone, but rather that logistical and socio-economic considerations are crucial to long-term and largescale restoration success.

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CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

AUTHOR CONTRIBUTIONS

Anna Hughes: Data curation; project administration; writing - original draft; writing - review and editing. Kruno Bonacic: Validation; writing - review and editing. Thomas C Cameron: Validation; writing - review and editing. Ken Collins: Validation; writing - review and editing. Fiz da Costa: Validation; writing - original draft. Alison Debney: Validation; writing - review and editing. Luca Ancel van Duren: Validation; writing - review and editing. Jesper Elzinga: Validation; writing - review and editing. José Fariñas-Franco: Validation; writing review and editing. Celine Gamble: Validation: writing - review and editing. Luke Helmer: Validation; writing - review and editing. Zoë Holbrook: Validation; writing - review and editing. Eric Holden: Validation; writing - review and editing. Katherine Knight: Validation; writing - review and editing. James Murphy: Validation; writing review and editing. Bernadette Pogoda: Validation: writing - review and editing; funding acquisition. Stephane Pouvreau: Validation; writing - review and editing. Joanne Preston: Validation; writing review and editing. Alec Reid: Validation; writing - review and editing. Emilie Reuchlin-Hugenholtz: Validation; writing - review and editing. William Guy Sanderson: Validation; writing - review and editing. David Smyth: Validation; writing - review and editing. Brecht Stechele: Validation; writing - review and editing. Åsa Strand: Validation; writing - review and editing. John Theodorou: Validation; writing - review and editing. Matt Uttley: Validation; writing - review and editing. Ben Wray: Validation; writing - review and editing. Philine zu Ermgassen: Conceptualization; funding acquisition; methodology; supervision; writing - original draft; writing - review and editing.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

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