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Restoring genetic diversity to facilitate the implementation of the EU Nature Restoration Law

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ABSTRACT

Governments and economic blocs are recognising that the world faces a biodiversity crisis. The restoration of biodiversity to the levels prior to widespread human induced damage has been incorporated as a crucial component of conservation in the Global Biodiversity Framework of the Convention of Biological Diversity. The Nature Restoration Law (NRL) forms part of the European Union's response and after its adoption by the European Parliament and the Council of the European Union, it has formally become the Nature Restoration Regulation (NRR). The NRL aims to play a role in restoring ecosystems, habitats and species but does not expressly include genetic diversity, the third biodiversity component. Considering genetic diversity in strategic biodiversity planning is important to help nature adapt to rapid anthropogenic change. We have reviewed the text of the NRL and note opportunities to incorporate genetic diversity in National Restoration Plans to augment its implementation. In particular, genetic diversity assessments are well aligned with the NRL's aspiration to enhance connectivity, and genetic indicators can assess the effectiveness of its implementation. Here we give

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examples where restoration has incorporated genetic diversity to ensure long term wide-reaching success. This is of relevance beyond the NRL and applies generally to policy for nature restoration efforts globally, especially those related to the Global Biodiversity Framework.

1. Background

In June 2022, the European Commission (EC) proposed a new law "to restore ecosystems for people, the climate and the planet", referred to as the Nature Restoration Law (EC, 2022, hereafter "NRL"). After two years of trilogues between the European Union (EU) institutions, the European Parliament and the EC a revised version of the NRL proposal was adopted in June 2024 which subsequently became the Nature Restoration Regulation. This represents a significant step in EU environmental policy. Whilst this is an EU initiative, the global commitment to biodiversity restoration enshrined in Global Biodiversity Framework Target 2 means that approaches developed in Europe can be applied in any continent, nation or region.

The EC proposes establishing an EU-wide methodology for assessing ecosystem condition, which would allow specific restoration targets and the development of national restoration plans (European Parliament, 2024). These will need to be documented, assessed, and to have a unified monitoring approach. The NRL (and its Annexes) focuses primarily on ecosystems and species, and only one mention of "genetic exchange" is present (Annex VII) with no text on "genetic diversity" or its synonyms ("within species diversity" or "intraspecific diversity", European Parliament, 2024). Both ecosystems and species, however, depend on genetic diversity for resilience to natural biotic and abiotic change as well as to anthropogenic threats, including the five direct drivers of biodiversity loss identified by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES): climate change, pollution, direct exploitation, changing land and sea use, and invasive species (Díaz et al., 2019). Recognising that there are several definitions for 'ecological resilience' (see review by Van Meerbeek et al., 2021), we use it here to mean the ability of populations to return to their reference conditions following a perturbation (Pimm, 1984), and to absorb change and maintain ecological function (Holling, 1973). By extension, resilient populations underpin resilient ecosystems. Maintaining and restoring genetic diversity is needed for long-term successful species and ecosystem restoration. Thus, the effectiveness of the implementation of the NRL would be further enhanced by incorporating within-species genetic diversity restoration actions. Further, genetic diversity should in fact be a key component of any restoration strategy globally. The examples in this paper are focussed on the ecosystems detailed in the NRL. However, these ecosystems are found globally and include those facing the greatest threat (Díaz et al., 2019) including forests, rivers and wetlands and agricultural systems, as well as urban land. The examples also cover all three realms: marine, freshwater and terrestrial.

2. Why restoring genetic diversity can improve the implementation of the NRL

Halting and reversing biodiversity loss can only be accomplished by a shift to humanity working more extensively with nature, allowing nature's own tools to be a key part of the restoration process. Genetic diversity is the variation at the DNA level, including differences among individuals and populations Table 1. It gives species the potential and flexibility to respond to pressures through adaptation, while also underpinning fitness of individuals and their populations. Genetic diversity is integral for establishing and maintaining healthy self-sustaining populations. These populations in turn support ecosystem function and resilience to regulation of the environment (*e.g.* soil fertility, biological control, pollination). Thus, within-species genetic diversity also increases overall ecosystems resilience (Prunier et al., 2023). Maintaining and restoring genetic diversity is therefore crucial for the implementation of the NRL. Importantly, this can be linked to global efforts to monitor and maintain genetic diversity required by the Kunming-Montreal Global Biodiversity Framework (KM-GBF) of the Convention on Biological Diversity (CBD, 2022a, 2022b; Robuchon et al., 2023). Genetic diversity is fundamentally composed of alleles, heterozygosity and variation in their distribution across individuals or populations. It is important to note that restoration of alleles may not be possible if they have gone globally extinct. However, increasing size and connectivity among populations can help reduce genetic diversity loss, as well as inbreeding, and bolster heterozygosity.

To maximise success, a biodiversity restoration strategy must encompass ecosystems, species and genetic diversity. Restoration may use materials sourced *in situ* (in natural populations) or *ex situ* (in collections). *Ex situ* conservation is particularly useful for restoration action if the whole species has suffered extreme loss of genetic diversity. Further, zoos, botanical gardens and seed banks can preserve genetic diversity *ex situ* and provide insurance against catastrophic events (O'Brien et al., 2022). *Ex situ* populations have played a central role in many restoration projects, conserving unique genetic diversity and preventing extinctions, but they do not necessarily facilitate the same multi-pressured adaptive processes as natural settings (Schoen and Brown, 2001; Smith et al., 2023). By contrast, *in situ* conservation facilitates natural adaptation, if populations are sufficiently large (crucially with effective population size $Ne > 500$; Hoban et al., 2021), thus supporting the long-term success of restoration, can maintain different genetic lineages compared to *ex situ* populations, and can benefit other organisms in their habitat. Given their complementary strengths, restoration actions should seek to combine both approaches, where relevant. The CBD now calls on Parties, including the EU, to restore genetic diversity within and between populations of native, wild and domesticated species to maintain their adaptive potential (Target 4; CBD, 2022a). Another global commitment of the KM-GBF is to "*ensure that by 2030 at least 30% of areas of degraded terrestrial, inland water, and marine and coastal ecosystems are under effective restoration [...]*" (Target 2; CBD, 2022a). Integrating genetic diversity conservation, monitoring and management in the implementation of the NRL (Fig. 1) *via* National Restoration Plans would thus contribute to efforts for reaching KM-GBF targets (Goal A, Target 4; CBD, 2022a) and National Biodiversity Strategy and Action Plans (Hoban, 2024) as well as targets 2.5 and 15.5 of the Sustainable Development Goals (UN, 2015). It would also align with the Habitats Directive in which populations must achieve Favourable Conservation Status, which is sometimes interpreted to include maintaining genetic diversity (Laikre et al., 2009).

Genetic diversity has already been lost in many European species, in part due to pressures from a long history of human settlement combined with species' post-glacial colonisation histories (Hewitt, 2000; Leigh et al., 2019; Pearman et al., 2024). Such a loss of genetic diversity makes European species and populations particularly vulnerable in the face of change. Genetic diversity is not always spatially correlated with species diversity (Schmidt et al., 2022; Marta et al., 2023) and it is unclear how it relates to ecosystems diversity, as a result, it needs specific conservation and policy attention. Nevertheless, specific genetic diversity targets would likely incentivise policy makers and land managers in nature restoration actions. Crucially, *in situ* conservation of genetic diversity in wild species has been shown to be compatible with economic land uses such as farming and forestry, and to be supported by land managers (Minter et al., 2021). As shown in case study 1, land managers can be vital allies when they participate in the co-development of genetic diversity-based restoration (O'Brien et al., 2021). Incorporating

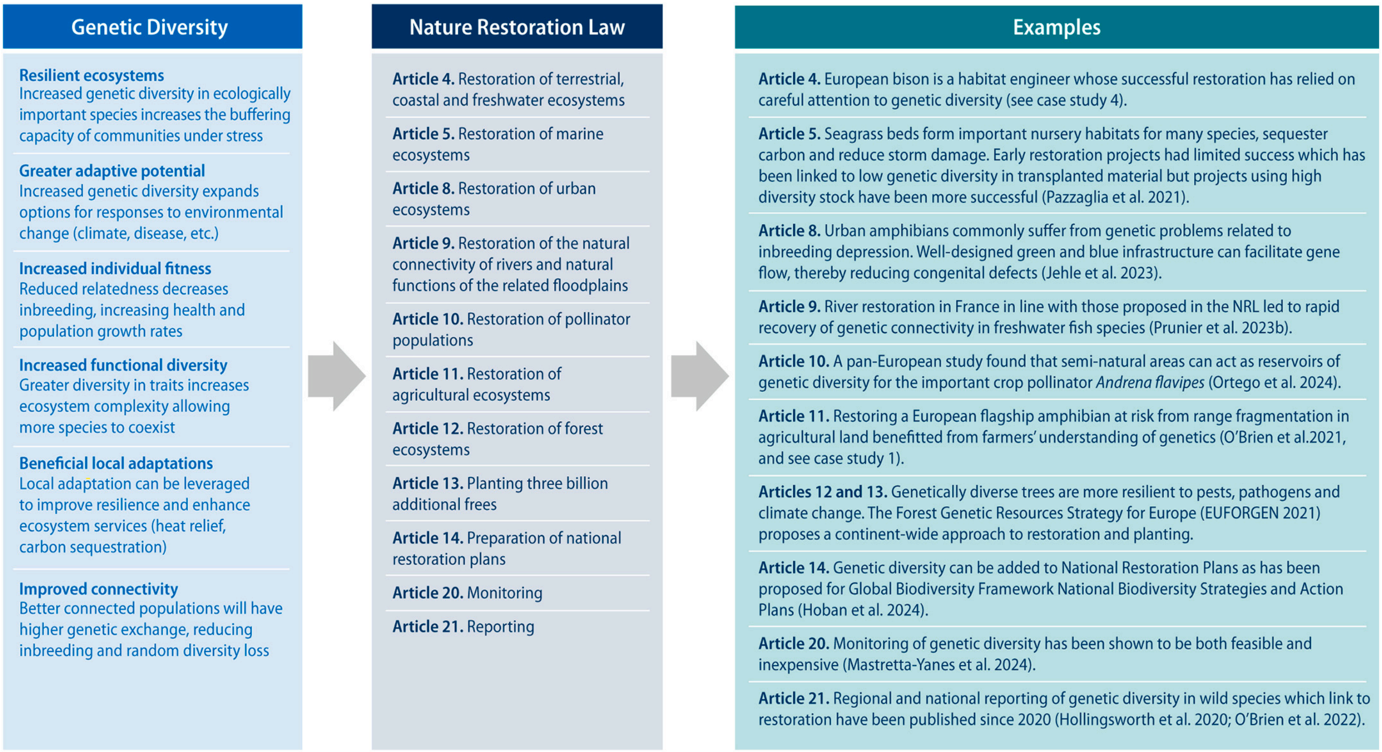
Table 1
Glossary of terms and abbreviations used in this paper.

Term	Explanation	Webpage/reference
CBD	The UN Convention on Biological Diversity; international policy instrument ratified by 196 nations.	http://www.cbd.int/.cbd.int
Complementary indicator	A voluntary CBD GBF indicator. For genetic diversity these indicators are "“the proportion of population maintained within species” abbreviated PM indicator and the Scorecard of Genetic Diversity.	CBD, 2022b; https://www.cbd.int/doc/decisions/cop-15/cop-15-dec-05-en.pdf https://www.nature.scot/doc/scotlands-biodiversity-progress-2020-aichi-targets-conserving-genetic-diversity-development-national
COP15	The 15th Conference of the Parties to the Convention on Biological Diversity. COP15 was held in Montreal in December 2022 hosted by China (the meeting should have been held in Kunming, China, but was changed due to the pandemic).	www.cbd.int/meetings/COP-15
DNA-based indicators	Indicators based on assessment of variation in the DNA collected from temporally separated samples of individuals of a species to monitor trends in genetic diversity. EBVs for genetic composition are used for DNA-based indicators Note: this is NOT eDNA which only measures occurrence of species, not the essential variation within species which the present DNA-based indicators focus on.	O’Brien et al., 2022; Andersson et al., 2022; Dussex et al., 2023; Kurland et al., 2023; Saha et al., 2024
EBV	Essential Biodiversity Variable – fundamental metric used to assess and monitor biodiversity over space and time. Different EBVs are applied to ecosystems, communities, species, and genetic composition.	https://geobon.org/ebvs/what-are-ebvs
EBVs for genetic composition	Essential Biodiversity Variables for assessing and monitoring genetic diversity. These parameters include measures of genetic diversity within populations, between populations and includes estimating *Ne*. EBVs for genetic diversity are used for DNA-based indicators.	Hoban et al., 2022
Ecosystem resilience	The ability of an ecosystem to withstand and recover from different types of environmental disturbance.	https://www.stockholmresilience.org/
Ex situ conservation	Conservation of species/populations outside their native environment in a human-controlled environment (*e.g.* zoos, botanical gardens, *etc.*)	
GBF	The Kunming-Montreal Global Biodiversity Framework adopted by the CBD COP15. Includes Goals to 2050 and Targets to 2030. Goal for genetic diversity: “The genetic diversity within populations of wild and domesticated species, is maintained, safeguarding their adaptive potential”. Target for genetic diversity: “to maintain and restore the genetic diversity within and between populations of native, wild and domesticated species to maintain their adaptive potential”.	CBD, 2022a https://www.cbd.int/gbf
GBF Monitoring framework	Strategy adopted by CBD COP15 to monitor trends in genetic diversity to support implementation of the GBF. Includes Headline indicators that parties need to report on and Complementary Indicators that are voluntarily.	CBD, 2022b https://www.cbd.int/gbf/related/monitoring
GCU	Genetic Conservation Unit - concept used by the European Forest Genetic Resources Programme to describe a forest area aimed to protect forest genetic resources of one or more forest tree species.	https://www.euforgen.org/forest-genetic-resources/conservation/gcu
Genetic diversity	Variation at the DNA-level. Also known as intraspecific diversity. Occurs below the species level as variation within and between separate populations.	Allendorf et al., 2023
Goal A	Goal of the GBF that focuses on the 2050 vision for biodiversity. Goal A for genetic diversity is: “The genetic diversity within populations of wild and domesticated species, is maintained, safeguarding their adaptive potential.”	CBD, 2022a
Headline indicator A.4	A mandatory indicator of the CBD GBF monitoring framework which tracks “the proportion of populations within species with an effective population size (*Ne*) > 500”. Implementation can use DNA–techniques, but to allow large scale, global implementation, non-DNA proxies for genetic measurements are needed (proxy-based indicators)	CBD, 2022b
In situ conservation	On-site conservation, conserving biodiversity in the natural site of occurrence	
IPBES	The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. An independent body establishes strengthen science-policy in the area	https://www.ipbes.net/
KM-GBF	Same as GBF (above). KM abbreviates Kunming-Montreal since the CBD COP15 meeting was supposed to be held in Kunming, but was finally held in Montreal (see COP15)	CBD, 2022a https://www.cbd.int/gbf
Ne	Effective population size. A standard population genetic parameter that describes the rate of loss of genetic diversity of a population and its adaptive potential. An *Ne* above 500 is considered to maintain adaptive capacity. *Ne* is an EBV for genetic composition and can be used in restoration to assure adaptive capacity of key animal and plant populations.	Allendorf and Ryman, 2002
Ne indicator	Indicator based on assessment of the effective population size of populations and for detecting changes of *Ne* over contemporary time frames. DNA- or proxy-based methods can be applied. In the CBD GBF monitoring framework *Ne* > 500 is Headline indicator A.4.	CBD, 2022b; Andersson et al., 2022; Mastretta-Yanes and da Silva et al., 2024
NRL	The Nature Restoration Law adopted by the European Parliament and the Council of the European Union in June 2024.	https://environment.ec.europa.eu/topics/nature-and-biodiversity/nature-restoration-law_en
NRP	National Restoration Plan to be prepared by all EU member states and cover the period up to 2050 with intermediate deadlines *e.g.*, 2030. Should include restoration measures necessary to meet the restoration targets and fulfilment of Articles 4-13.	Chapter III, Article 14 of the NRL https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX%3A32024R1991&qid=1722240349976
NRR	The Nature Restoration Regulation through which the NRL comes into effect.	https://environment.ec.europa.eu/news/nature-restoration-law-enters-force-2024-08-15_en
Population	A biological entity below the species level. Species consists of multiple populations that *e.g.* occur in different regions of the distribution range. Populations can be identified with DNA-techniques as genetically distinct clusters that can reflect genetic adaptation to local conditions. In the absence of DNA-data populations can be identified by demographic, geographic or other information.	Waples and Gaggiotti, 2006 https://onlinelibrary.wiley.com/doi/10.1111/j.1365-294X.2006.02890.x

(*continued on next page*)

Table 1 (*continued*)

Term	Explanation	Webpage/reference
Proxy-based genetic indicators	Indicators aimed at tracking genetic diversity over time but which do not rely on direct measures of genetic diversity but use substitutes (proxies) for DNA-data such as demographic measures of census size, population occurrence and distribution.	Mastretta-Yanes and da Silva et al., 2024
Restoration	The act of reversing human induced biodiversity degradation and returning ecosystems, species and genetic diversity back to a good state. Includes the recovery of evolutionary processes and diverse and resilient populations, species and ecosystems.	Hoban et al., 2020; https://environment.ec.europa.eu/topics/nature-and-biodiversity/nature-restoration-law_en



Genetic Diversity

Resilient ecosystems
Increased genetic diversity in ecologically important species increases the buffering capacity of communities under stress

Greater adaptive potential
Increased genetic diversity expands options for responses to environmental change (climate, disease, etc.)

Increased individual fitness
Reduced relatedness decreases inbreeding, increasing health and population growth rates

Increased functional diversity
Greater diversity in traits increases ecosystem complexity allowing more species to coexist

Beneficial local adaptations
Local adaptation can be leveraged to improve resilience and enhance ecosystem services (heat relief, carbon sequestration)

Improved connectivity
Better connected populations will have higher genetic exchange, reducing inbreeding and random diversity loss

Nature Restoration Law

Article 4. Restoration of terrestrial, coastal and freshwater ecosystems

Article 5. Restoration of marine ecosystems

Article 8. Restoration of urban ecosystems

Article 9. Restoration of the natural connectivity of rivers and natural functions of the related floodplains

Article 10. Restoration of pollinator populations

Article 11. Restoration of agricultural ecosystems

Article 12. Restoration of forest ecosystems

Article 13. Planting three billion additional trees

Article 14. Preparation of national restoration plans

Article 20. Monitoring

Article 21. Reporting

Examples

Article 4. European bison is a habitat engineer whose successful restoration has relied on careful attention to genetic diversity (see case study 4).

Article 5. Seagrass beds form important nursery habitats for many species, sequester carbon and reduce storm damage. Early restoration projects had limited success which has been linked to low genetic diversity in transplanted material but projects using high diversity stock have been more successful (Pazzaglia et al. 2021).

Article 8. Urban amphibians commonly suffer from genetic problems related to inbreeding depression. Well-designed green and blue infrastructure can facilitate gene flow, thereby reducing congenital defects (Jehle et al. 2023).

Article 9. River restoration in France in line with those proposed in the NRL led to rapid recovery of genetic connectivity in freshwater fish species (Prunier et al. 2023b).

Article 10. A pan-European study found that semi-natural areas can act as reservoirs of genetic diversity for the important crop pollinator *Andrena flavipes* (Ortego et al. 2024).

Article 11. Restoring a European flagship amphibian at risk from range fragmentation in agricultural land benefitted from farmers' understanding of genetics (O'Brien et al.2021, and see case study 1).

Articles 12 and 13. Genetically diverse trees are more resilient to pests, pathogens and climate change. The Forest Genetic Resources Strategy for Europe (EUFORGEN 2021) proposes a continent-wide approach to restoration and planting.

Article 14. Genetic diversity can be added to National Restoration Plans as has been proposed for Global Biodiversity Framework National Biodiversity Strategies and Action Plans (Hoban et al. 2024).

Article 20. Monitoring of genetic diversity has been shown to be both feasible and inexpensive (Mastretta-Yanes et al. 2024).

Article 21. Regional and national reporting of genetic diversity in wild species which link to restoration have been published since 2020 (Hollingsworth et al. 2020; O'Brien et al. 2022).

Fig. 1. The beneficial role genetic diversity can play in facilitating restoration success (left), the key Articles of the European Nature Restoration Law it will aid (centre) and practical examples (right).

genetic diversity in the implementation of the NRL would thus recognise the vital role of land managers and those who rely on marine resources in safeguarding biodiversity, as has been demonstrated by tree Gene Conservation Units (discussed below, Minter et al., 2021).

3. Genetic diversity is key to achieving the NRL's ambitions for restoration targets

To maximise future ecosystem resilience, genetic diversity would enhance the proposed EU wide standards for national restoration plans (Articles 14 and 15 of the NRL). NRL Article 14 states that restoration measures should take "into account the latest scientific evidence" (European Parliament, 2024), an evidence need that conservation genetics and genomics can readily fill (Fig. 1). Going through the NRL, Article by Article, genetic diversity has a key role to play.

4. Genetic diversity should be an inherent criterion in restoring connectivity under the NRL

Land use change, including habitat fragmentation, is one of the five main pressures on biodiversity noted by IPBES (Díaz et al., 2019). Enhancing ecosystem connectivity is part of the KM-GBF Goal A (CBD, 2022b) and the Convention on Migratory Species (CMS, 2019), and the NRL notes the importance of restoring genetic exchange to improve connectivity across habitats (European Parliament, 2024). Enhancing connectivity has also been a core target of EU funding through the Common Agricultural Policy (EU CAP Network, 2023). Habitat fragmentation interrupts or limits gene-flow in many species, which can lead to measurable genetic diversity and fitness loss over time. Monitoring change in genetic diversity can therefore assess habitat fragmentation and connectivity restoration success (*e.g.* Jehle et al., 2023). Genetic data are already being used to monitor population connectivity in dozens of species across the EU, including trees (Fady et al., 2016), freshwater fish (Andersson et al., 2022) and marine species (Assis et al., 2021). A shared approach to monitoring connectivity through genetic means across such projects and directives could support and accelerate the attainment of multiple EU policy goals. It can also provide valuable information to help land managers plan restoration.

5. Genetic diversity can be monitored and reported on using direct genetic methods or by using simple non-DNA proxies

Chapter IV of the NRL discusses monitoring (Article 20) and reporting (Article 21). Developments in DNA sequencing technologies are driving down costs and increasing the accessibility of DNA-based monitoring of biodiversity. However, there are still resource and capacity barriers to truly widespread and universal monitoring of genetic diversity through DNA-sequencing and it is still often reserved for selected species or populations. Recognising this, simpler non-DNA based proxies have now been developed (Hoban et al., 2020; O'Brien et al., 2022; Mastretta-Yanes and da Silva et al., 2024). A key non_DNA based proxy, effective population size (*Ne*), helps conserve genetic diversity (typically when above 500) and can be inferred from census counts improving accessibility for many animals and vascular plants (Hoban et al., 2020). Consequently, $Ne > 500$ has been accepted as CBD (2022b) Headline Indicator A.4 for Goal A and Target 4. Importantly for restoration, $Ne > 500$ can be applied at regional and local levels to assure adaptive capacity is reached for local populations of key species (Andersson et al., 2022; Kurland et al., 2023) following restoration events. *Ne*, genetic diversity and connectivity have also been considered in other European policies including in setting favourable population conditions for Habitats Directive species (Mehtälä and Vuorisalo, 2007; Wójkiewicz et al., 2021). The Genetic Diversity Scorecard (Hollingsworth et al., 2020; O'Brien et al., 2022) is a related approach made up of six indicators, each of which can be assessed using either direct or proxy-based measures of genetic diversity, and is a CBD (2022b) Complementary Indicator. Genetic diversity monitoring based on different proxies are now already being applied at a national or subnational level within four European countries: Belgium, France, Sweden and the UK (Hollingsworth et al., 2020; Andersson et al., 2022; O'Brien et al., 2022; Hoban et al., 2023; Kurland et al., 2023; Mastretta-Yanes and da Silva et al., 2024). Additionally, DNA-based monitoring is now in the pilot phase in Germany (BIGFOOT), Sweden (SWAM), and Switzerland (GenDiv). Guidelines produced by the International Union for Conservation of Nature (IUCN) on selecting species and population for genetic diversity monitoring (Hvilsom et al., 2022) are already available. Thus, there are practical monitoring methods in place, and there is an opportunity to set simple transparent restoration targets that are meaningful at multiple geographic scales and aligned with the EU's role within the High Ambition Coalition for Nature and People. By setting SMART – Specific, Measurable, Achievable, Relevant and Time-bound – targets for genetic diversity, policy makers and practitioners can measure restoration progress and ensure management interventions are effective.

6. Reporting for the NRL can use existing tools

Existing programmes, such as the European Forest Genetic Resources Programme EUFORGEN's network of Genetic Conservation Units (GCU), show that safeguarding genetic diversity at a European scale is practical. The GCU network covers the whole continent, as well as Turkey, and is built around the concept of dynamic gene conservation, maintaining evolutionary processes within tree populations. The genetic resources within GCUs can be a key asset in restoration programmes (EUFORGEN, 2021). The GCU concept could be applied to other habitats and species (Minter et al., 2021). Many marine species have been subject to genetic assessments (Wennerström et al., 2017) and there is an opportunity to develop a systematic programme of monitoring and reporting of diversity (Thomson et al., 2021). This would support the attainment of NRL Article 5 (Restoration of marine ecosystems). Crucially, the GCU approach is also compatible with management of the land for economic gain (Minter et al., 2021). Article 12 of the NRL focuses on forest restoration, and adding consideration of genetic diversity will strengthen the NRL for biodiversity and recognise existing good management.

7. Restoration built upon genetic diversity

Since genetic diversity underpins species and ecosystem resilience (Sgrò et al., 2011; Mason et al., 2022), including genetic diversity in restoration plans seems relevant both for biodiversity conservation and securing long-term success for publicly and privately funded projects, thus justifying financial outlay. There are examples within Europe and elsewhere which highlight the effectiveness of projects that explicitly build genetic diversity into their restoration plans.

Case study 1. Habitat restoration leads to recovery of European Protected Species

The great crested newt (*Triturus cristatus*) is a European Protected Species. A disjunct range edge population in the Scottish Highlands had been steadily declining until a restoration project that combined knowledge about the species' local habitat requirements and genetic structure. The Highland population is genetically distinct and its extirpation would therefore represent the irreversible loss of a unique genetic lineage (O'Brien et al., 2021). Once the status of the lineage had been discovered, a species recovery plan was devised and implemented through collaboration between scientists, local volunteers, farmers, foresters and other land managers. The plan used genetic data to identify priority locations for habitat restoration. The need to safeguard genetic diversity was also a key tool in engaging farmers and foresters, as they are familiar with the importance of genetics in their working lives. An evaluation after six years found a 26 % increase in breeding ponds with enhanced connectivity between them (O'Brien et al., 2021). This case study exemplifies NRL implementation of Articles 4 (terrestrial, coastal and freshwater ecosystems), 9 (rivers and floodplains), 11 (agricultural), 12 (forest).

Case study 2. Post-restoration population growth is enhanced by genetic diversity

European grasslands are highly threatened and have been the focus of many restoration programmes. Success has varied, leading to evaluations of the importance of different methods and factors (Resch et al., 2022). A study examining the restoration success of the grassland plant devil's-bit scabious (*Succisa pratensis*) in Flanders (Belgium), a key species for pollinators, found faster growing populations had higher genetic diversity, linking genetic diversity with population fitness (Van Geel et al., 2021). Furthermore, devil's-bit scabious genetic diversity also had a small but important impact on below-ground restoration of arbuscular mycorrhizal increasing community diversity (Van Geel et al., 2021). The project relied on stock already *in situ* without taking into account genetic diversity at the beginning of the project. This example shows genetic diversity can impact the speed and overall success of a restoration, as well as the complexity of the community restored, and suggests that greater success could have been achieved if enhancing local genetic diversity had been part of the original project plan. It highlights implementation of NRL Articles 4, (terrestrial, coastal and freshwater ecosystems), 8 (urban), 10 (pollinators), 11 (agricultural).

Case study 3. Restoring connectivity of fragmented populations

The Arctic fox (*Vulpes lagopus*) in Scandinavia was severely overhunted for fur from the early 1900s to the early 20th century. Even after legal protection entered into force, the population failed to recover (Keeling Hemphill et al., 2020). A genetic study found that the Scandinavian population is fragmented into three subpopulations with limited genetic exchange (Keeling Hemphill et al., 2020). Monitoring of the southernmost sub-population since 2000 showed this had led to inbreeding depression expressed as reduced juvenile survival been included throughout the species management and restoration programme. A series of measures have been taken to support the fragmented populations including supplementary feeding, culling of competitive red foxes and an *ex-situ* breeding programme. The *ex-situ* breeding programme was established with wild caught cubs from the nearby region and releases of these captive-bred Arctic foxes introduced locally-new genetic variation and acted as gene flow among sub-populations. These efforts led to a doubling in the population size in the south, the re-establishment of many populations and increased connectivity between them (Keeling Hemphill et al., 2020). This case links to NRL Articles 4 (terrestrial, coastal and freshwater ecosystems), 12 (forest).

Case study 4: Restoration of a species formerly extinct in the wild

European Bison (*Bison bonasus*) once inhabited much of Europe and northern Asia, but was extirpated over most of its range due to habitat loss and overhunting, with the last three wild populations hunted to extinction in the 19th and early 20th centuries. However, 54 captive individuals remained (Bołbot and Raczyński, 2013). From the 1920s onward, bison were the subject of an *ex situ* breeding programme which sought to avoid inbreeding depression as well as ensuring that the managed population did not include hybrids with American bison or cattle (Bołbot and Raczyński, 2013). Only 12 of the 54 animals were found to be of pure European Bison origin, leading to a reduced founder base for the breeding programme (Olech, 2023). Reintroduction of captive stock began in the Białowieża Forest, Poland in 1929 and has continued there and in other European countries. Though historical levels of genetic diversity can never be restored, due to reintroductions, habitat management and the removal of hunting pressure, there are now over 7000 free-living bison across Eastern Europe (Olech, 2023). Despite genetic depletion, the self-sustaining bison populations have had subsequent positive impacts on habitat-level restoration goals, as European bison act as important long-distance seed dispersers (Jaroszewicz et al., 2008), enhance beetle community composition (Schwerk et al., 2021), and preliminary evidence suggests they improve grassland carbon sequestration (Kaštovská et al., 2024). There has been consistent emphasis on the management of the remaining European bison genetic diversity throughout, which, combined with natural purging of deleterious genes has minimised the impacts of inbreeding following the population bottleneck (Olech, 2023). This example links to NRL Articles 4 (terrestrial, coastal and freshwater ecosystems), 12 (forest).

8. Conclusion

- Including genetic diversity in national restoration plans is well-aligned with the aims of the NRL and could further enhance its implementation. We have presented examples of how each NRL Article is linked to genetic diversity.
- Our case studies (1–4 above and Fig. 1) show how genetic diversity has been used in practice in Europe in the recent past and these examples can be used as models for future interventions.
- Within the NRL, including genetic diversity in the national assessment of each habitat would be beneficial to ensure adaptability of populations of species, improve resilience of ecosystems and for monitoring success of restoration actions.
- Genetic diversity is a key criterion in restoring connectivity, a central tenet of the NRL.
- Genetic monitoring and target setting are practical and ready to use and can form part of the NRL's contribution to the CBD KM-GBF - at European, national and subnational levels.
- Rapid implementation of genetic diversity monitoring in the NRL using existing DNA-based studies and simpler proxy indicators can help to safeguard Europe's genetic diversity.

CRediT authorship contribution statement

David O'Brien: Writing – review & editing, Writing – original draft, Project administration, Methodology, Investigation, Conceptualization. **Tsipe Aavik:** Writing – review & editing, Writing – original draft, Investigation. **Ancuta Fedorca:** Writing – review & editing. **Martin C. Fischer:** Writing – review & editing, Writing – original draft, Investigation. **Robin Goffaux:** Writing – review & editing, Writing – original draft, Investigation. **Sean Hoban:** Writing – review & editing, Writing – original draft, Investigation. **Peter Hollingsworth:** Writing – review & editing, Writing – original draft, Investigation. **Christina Hvilsom:** Writing – review & editing, Writing – original draft, Investigation. **Robert Jehle:** Writing – original draft, Investigation. **Belma Kalamujić Stroil:** Writing – review & editing, Writing – original draft, Investigation. **Francine Kershaw:** Writing – review & editing, Writing – original draft, Investigation. **Peter Klinga:** Writing – review & editing, Writing – original draft, Investigation. **Alexander Kopatz:** Writing – review & editing, Writing – original draft, Investigation. **Deborah M. Leigh:** Writing – review & editing, Writing – original draft, Visualization, Conceptualization. **Ivan Paz-Vinas:** Writing – review & editing, Writing – original draft, Investigation. **Marine Robuchon:** Writing – review & editing, Writing – original draft, Investigation. **Gernot Segelbacher:** Writing – review & editing, Writing – original draft, Investigation. **Viktoria Takacs:** Writing – review & editing, Writing – original draft, Investigation. **Cristiano Vernesi:** Writing – review & editing, Writing – original draft, Investigation. **Linda Laikre:** Writing – review & editing, Writing – original draft, Project administration, Investigation, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

No data was used for the research described in the article.

References

Allendorf, F.W., Ryman, N., 2002. The role of genetics in population viability analysis. In: Beissinger, S.R., McCullough, D.R. (Eds.), Population Viability Analysis. University of Chicago Press, pp. 50–85.

Allendorf, et al., 2023. Conservation and the Genomics of Populations, 3rd ed. John Wiley & Sons, Hoboken.

Andersson, et al., 2022. Monitoring genetic diversity with new indicators applied to an alpine freshwater top predator. Mol. Ecol. 31, 6422–6439. https://doi.org/10.1111/mec.16710.

Assis, et al., 2021. Weak biodiversity connectivity in the European network of no-take marine protected areas. Sci.Total Environ. 773, 145664. https://doi.org/10.1016/j.scitotenv.2021.145664.

Bołbot, M., Raczyński, J., 2013. Rejestracja rodowodowa żubrów jako narzędzie restytucji gatunku. European Bison Conservation Newsletter 6, 5–20.

CBD, 2022a. Kunming-Montreal Global Biodiversity Framework. Decision adopted by the COP15, Montreal, Canada, December 2022. Available at https://www.cbd.int/doc/decisions/cop-15/cop-15-dec-04-en.pdf.

CBD, 2022b. Monitoring framework for the Kunming-Montreal Global Biodiversity Framework. Decision adopted by the COP15, Montreal, Canada, December 2022. Available at: https://www.cbd.int/doc/decisions/cop-15/cop-15-dec-05-en.pdf.

CMS, 2019. Improving ways of addressing connectivity in the conservation of migratory species. Resolution 12.26. https://www.cms.int/sites/default/files/document/cms_cop13_res.12.26_rev.cop13_e.pdf.

Díaz, et al., 2019. The Global Assessment Report on Biodiversity and Ecosystem Services: Summary for Policymakers. IPBES. https://doi.org/10.5281/zenodo.3553579.

Dussex, et al., 2023. Range-wide and temporal genomic analyses reveal the consequences of near extinction in Swedish moose. Commun. Biol. 6, 1035. https://doi.org/10.1038/s42003-023-05385-x.

EC, 2022. Proposal for a Nature Restoration Law, Directorate-General for the Environment. https://environment.ec.europa.eu/publications/nature-restoration-law_en.

EU CAP Network 2023. Habitat connectivity: good for the environment and good for business. https://eu-cap-network.ec.europa.eu/publications/habitat-connectivity-good-environment-and-good-business_en.

EUFORGEN, 2021. Forest Genetic Resources Strategy for Europe. European Forest Institute.

European Parliament, 2024. https://www.euforgen.org/fileadmin/templates/euforgen.org/upload/Publications/Thematic_publications/FGR_Strategy4Europe.pdf.

Fady, et al., 2016. Forests and global change: what can genetics contribute to the major forest management and policy challenges of the twenty-first century? Reg. Environ. Chang. 16, 927–939. https://doi.org/10.1007/s10113-015-0843-9.

Hewitt, G., 2000. The genetic legacy of the Quaternary ice ages. Nature 405, 907–913.

Hoban, et al., 2020. Genetic diversity targets and indicators in the CBD post-2020 global biodiversity framework must be improved. Biol. Conserv. 248, 108654. https://doi.org/10.1016/j.biocon.2020.108654.

Hoban, et al., 2021. Effective population size remains a suitable, pragmatic indicator of genetic diversity for all species, including forest trees. Biol. Conserv. 253, 108906. https://doi.org/10.1016/j.biocon.2020.108906.

Hoban, et al., 2022. Global genetic diversity status and trends: towards a suite of Essential Biodiversity Variables (EBVs) for genetic composition. Biol. Rev. 97, 1511–1538. https://doi.org/10.1111/brv.12852.

Hoban, et al., 2023. Monitoring status and trends in genetic diversity for the Convention on Biological Diversity: an ongoing assessment of genetic indicators in nine countries. Conserv. Lett. 16, e12953. https://doi.org/10.1111/conl.12953.

Hoban, et al., 2024. How can biodiversity strategy and action plans incorporate genetic diversity and align with global commitments? BioScience 106. https://doi.org/10.1093/biosci/biae106.

Holling, C.S., 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics 4 (1), 1–23. https://doi.org/10.1146/annurev.es.04.110173.000245.

Hollingsworth et al., 2020. Scotland's Biodiversity Progress to 2020 Aichi Targets: Conserving Genetic Diversity-development of a National Approach for Addressing Aichi Biodiversity Target 13 that Includes Wild Species. Inverness, Scottish Natural Heritage.

Hvilsom, et al., 2022. Selecting Species and Populations for Monitoring of Genetic Diversity. IUCN. https://doi.org/10.2305/IUCN.CH.2022.07.en.

Jaroszewicz, et al., 2008. The European bison as seed dispersers: the effect on the species composition of a disturbed pine forest community. Botany 86 (5), 475–484. https://doi.org/10.1139/B08-012.

Jehle, et al., 2023. High evolutionary potential maintained in common frog (*Rana temporaria*) populations inhabiting urban drainage ponds. Diversity 15, 738. https://doi.org/10.3390/d15060738.

Kaštovská, et al., 2024. Rewilding by large ungulates contributes to organic carbon storage in soils. J. Environ. Manag., 120430 https://doi.org/10.1016/j.jenvman.2024.120430.

Keeling Hemphill, et al., 2020. Genetic consequences of conservation action: restoring the arctic fox (*Vulpes lagopus*) population in Scandinavia. Biol. Conserv. 248, 108534. https://doi.org/10.1016/j.biocon.2020.108534.

Kurland, et al., 2023. New indicators for monitoring genetic diversity applied to alpine brown trout populations using whole genome sequence data. Mol. Ecol. 33, e17213. https://doi.org/10.1111/mec.17213.

Laikre, et al., 2009. Importance of genetics in the interpretation of favourable conservation status. Conserv. Biol. 23, 1378–1381. https://doi.org/10.1111/j.1523-1739.2009.01360.x.

Leigh, et al., 2019. Estimated six per cent loss of genetic variation in wild populations since the industrial revolution. Evol. Appl. 12, 1505–1512. https://doi.org/10.1111/eva.12810.

Marta, et al., 2023. Spatial prioritization of amphibian intraspecific genetic diversity: the need of accounting for palaeoenvironmental legacies. Biol. Conserv. 284, 110179. https://doi.org/10.1016/j.biocon.2023.110179.

Mason, et al., 2022. Attributes of climate resilience in fisheries: from theory to practice. Fish Fish. 23, 522–544. https://doi.org/10.1111/faf.12630.

Mastretta-Yanes, A., da Silva, J., et al., 2024. Multinational evaluation of genetic diversity indicators for the Kunming-Montreal Global Biodiversity Monitoring framework. Ecol. Lett. 27, e14461. https://doi.org/10.1111/ele.14461.

Mehtälä and Vuorisalo, T., 2007. Conservation policy and the EU Habitats Directive: favourable conservation status as a measure of conservation success. Eur. Environ. 17, 363–375.

Minter, et al., 2021. Exploring the potential for 'Gene Conservation Units' to conserve genetic diversity in wild populations. Ecol. Sol. Evidence 2, e12061. https://doi.org/10.1002/2688-8319.12061.

O'Brien, et al., 2021. Reversing a downward trend in threatened peripheral amphibian (*Triturus cristatus*) populations through interventions combining species, habitat and genetic information. J. Nat. Conserv. 64, 126077. https://doi.org/10.1016/j.jnc.2021.126077.

O'Brien, et al., 2022. Bringing together approaches to reporting on within species genetic diversity. J. Appl. Ecol. 59, 2227–2233. https://doi.org/10.1111/1365-2664.14225.

Olech, W., 2023. The relationship between inbreeding and fitness is different between two genetic lines of European bison. Diversity 15, 368. https://doi.org/10.3390/d15030368.

Pearman, et al., 2024. Monitoring species genetic diversity in Europe varies greatly and overlooks potential climate change impacts. Nat. Ecol. Evol. 8, 267–281. https://doi.org/10.1038/s41559-023-02260-0.

Pimm, S.L., 1984. The complexity and stability of ecosystems. Nature 307 (5949), 321. https://doi.org/10.1038/307321a0.

Prunier, et al., 2023. Genetic erosion reduces biomass temporal stability in wild fish populations. Nat. Commun. 14, 4362. https://doi.org/10.1038/s41467-023-40104-4.

Resch, et al., 2022. Long-term recovery of above- and below-ground interactions in restored grasslands after topsoil removal and seed addition. J. Appl. Ecol. 59, 2299–2308. https://doi.org/10.1111/1365-2664.14145.

Robuchon, et al., 2023. Conserving species' evolutionary potential and history: opportunities under the Kunming–Montreal Global Biodiversity Framework. Conserv. Sci. Pract. 5, e12929. https://doi.org/10.1111/csp2.12929.

Saha, A., Kurland, S., et al., 2024. Monitoring genome-wide diversity over contemporary time with new indicators applied to Arctic charr populations. Conserv. Genet. 25, 513–531. https://doi.org/10.1007/s10592-023-01586-3.

Schmidt, et al., 2022. Genetic and species-level biodiversity patterns are linked by demography and ecological opportunity. Evolution 76, 86–100. https://doi.org/10.1111/evo.14407.

Schoen, D.J., Brown, A.H.D., 2001. The conservation of wild plant species in seed banks: attention to both taxonomic coverage and population biology will improve the role of seed banks as conservation tools. BioScience 51, 960–966. https://doi.org/10.1641/0006-3568(2001)051[0960:TCOWPS]2.0.CO;2.

Schwerk, et al., 2021. Impact of European bison grazing (Bison bonasus (L.)) on species and functional traits of carabid beetle assemblages in selected habitats in Poland. Biology 10 (2), 123. https://doi.org/10.3390/biology10020123.

Sgrò, et al., 2011. Building evolutionary resilience for conserving biodiversity under climate change. Evol. Appl. 4, 326–337. https://doi.org/10.1111/j.1752-4571.2010.00157.x.

Smith, et al., 2023. Extinct in the wild: the precarious state of Earth's most threatened group of species. Science 379 (6634), add2889. https://doi.org/10.1126/science.add2889.

Thomson, et al., 2021. Charting a course for genetic diversity in the UN Decade of Ocean Science. Evol. Appl. 14, 1497–1518. https://doi.org/10.1111/eva.13224.

UN, 2015. Transforming our world: the 2030 agenda for sustainable development, UN. https://sdgs.un.org/publications/transforming-our-world-2030-agenda-sustainable%20development-17981.

Van Geel, et al., 2021. The role of genetic diversity and arbuscular mycorrhizal fungal diversity in population recovery of the semi-natural grassland plant species *Succisa pratensis*. BMC Ecol. Evol. 21, 200. https://doi.org/10.1186/s12862-021-01928-0.

Van Meerbeek, K., Jucker, T., Svenning, J.C., 2021. Unifying the concepts of stability and resilience in ecology. Journal of Ecology 109 (9), 3114–3132. https://doi.org/10.1111/1365-2745.13651.

Waples, R.S., Gaggiotti, O., 2006. What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. Mol. Ecol. 15 (6), 1419–1439. https://doi.org/10.1111/j.1365-294X.2006.02890.x.

Wennerström, et al., 2017. Baltic Sea genetic biodiversity: current knowledge relating to conservation management. Aquat. Conserv. Mar. Freshwat. Ecosyst. 27, 1069–1090. https://doi.org/10.1002/aqc.2771.

Wójkiewicz, et al., 2021. Low effective population size and high spatial genetic structure of black poplar populations from the Oder valley in Poland. Ann. Forest Sci. 78, 37. https://doi.org/10.1007/s13595-021-01055-2.