

PERSPECTIVE

Exploring the potential for ‘Gene Conservation Units’ to conserve genetic diversity in wild populations

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Abstract

1. Genetic diversity is important for species persistence and Gene Conservation Units (GCUs) have been implemented for forest trees to protect genetic diversity and evolutionary processes in situ. The Convention on Biological Diversity stipulates the protection of genetic diversity as an Aichi target, and so we explore the potential for GCUs to be implemented more widely.

2. Our global systematic review showed that GCUs are currently implemented primarily for plant species of economic importance (109/158 species studied), but a questionnaire sent to land managers and conservationists (60 U.K. participants) revealed strong support for fully integrating genetic information into conservation management (90% agree), and for creating GCUs for other plant and animal taxa.

3. Using four case studies of U.K. species of conservation importance which vary in genetic threat and population dynamics (two insect species, a fungus and a plant), we highlight that GCU implementation criteria need to be flexible to account for variation in effective breeding population size and geographic extent of target species. The wider uptake of GCUs would ensure that threatened genetic diversity is protected and support evolutionary processes that aid adaptation to changing environments.

KEYWORDS

conservation, gene conservation unit, genetic diversity, in situ

1 | INTRODUCTION

Intra-specific genetic diversity is key in providing populations with the capacity to adapt to changing environmental conditions and to challenges from novel pests and diseases (Barrett & Schluter, 2008; Hoffmann & Sgro, 2011). Genetic diversity may be neutral (no effect on fitness) or adaptive (Holderegger et al., 2006), and loss of genetic diversity can lead to lower fitness (Reed & Frankham, 2003), changes to physiology (Roelke et al., 1993) and higher loads of pathogens and infectious diseases (Cunningham et al., 2008). Therefore, conserving

genetic diversity is important for mitigating biodiversity loss (Reed & Frankham, 2003) and enabling species to respond to changing environments (Wernberg et al., 2018). Despite its importance, conservation of genetic diversity, and hence local adaptation, is rarely included in policy and conservation management (Laikre, 2010). However, under the Convention of Biological Diversity (CBD), maintenance of genetic variation is an Aichi target (target 13) (CBD, 2011). A recent analysis showed that although many CBD country reports mentioned maintaining genetic variation, this mainly focused on agricultural or forestry species, and used primarily ex situ approaches to genetic conservation

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(Hoban et al., unpubl. ms.), such as captive breeding and seed banks. Ex situ approaches are usually implemented as a last resort, and only contain a 'snapshot' of a species' genetic diversity (Koskela et al., 2013). Thus, more attention to genetic conservation in wild species is needed, especially given proposed targets for CBD's post-2020 biodiversity framework to maintain genetic diversity within wild species (Hoban et al., 2020).

To meet these CBD targets, in situ conservation approaches must be designed to maintain genetic variation. For example, conserving populations deemed to be Evolutionary Significant Units (ESUs) (de Guia & Saitoh, 2007), for example Coho salmon *Oncorhynchus kisutch* (National Marine Fisheries Service, 2012), implementing genetic rescue and translocations to increase genetic diversity in populations (Fredrickson et al., 2007; Johnson et al., 2010; Whiteley et al., 2015) or improving connectivity (i.e. dispersal and gene flow) between populations (Jangjoo et al., 2016). These methods aim to conserve distinct populations in situ (ESU) or to increase genetic diversity in small wild populations. There are also methods that specifically use genetic data to prioritize objectives for conservation management such as to prioritize connectivity or evolutionary potential (Nielsen et al., 2020). In situ conservation through Gene Conservation Units (GCU) focuses on managing for genetic diversity in wild populations within defined areas (Maxted et al., 2000). 'Dynamic gene conservation' is promoted in these areas by maintaining and managing populations in their natural habitats to allow adaptation to environmental changes through natural selection. By designating GCUs across the ecological range of a species, and managing these sites to allow reproduction and dynamic evolution, the GCUs conserve the adaptive genetic variation within species, and allow ongoing evolution and change. GCUs are novel in their emphasis on encouraging natural genetic adaptation, allowing populations in the wild to persist and adapt to future change, this dynamic process is particularly important in environments that are undergoing change. For current GCUs for trees, specific criteria are given including the population size and geographic size, to allow for dynamic gene conservation through natural regeneration (Koskela et al., 2013). However, this operationalization may not be applicable to other taxa and in different habitats.

In this policy perspective paper, we discuss current global application of in situ genetic conservation management techniques, considering whether the GCU approach could be effective for conserving evolutionary potential in a wide range of other taxa. We review current implementation of GCUs and use a structured questionnaire to canvass conservationists' and land managers' opinions concerning adopting a system of GCUs to protect biodiversity. We then test whether existing methods for voluntary accreditation of GCUs for trees (Koskela et al., 2013) are appropriate for application to other taxa, and recommend alterations to these methods, illustrating these recommendations for four case study species (*Erebia ephron* (butterfly), *Bombus distinguendus* (bee), *Campanula rotundifolia* (plant) and *Hypocrepopsis rhododendri* (fungus)). Our paper focuses on the United Kingdom, but the policy recommendations we develop are relevant for creating GCU networks across Europe and beyond.

2 | CURRENT IMPLEMENTATION OF GCUs AND OTHER IN SITU GENETIC CONSERVATION TECHNIQUES

Firstly, we aimed to gain a better understanding of the taxa that are currently the focus of GCUs globally (we refer to any areas managed for genetic conservation as GCUs) and other in situ conservation programmes including types of species and their socio-economic importance. Our literature review included published papers and 'grey literature' such as government/NGO reports. We extracted information on the focal species, the in situ genetic conservation method applied, and the reason for conservation action (economic or conservation importance) (see more information in Methods S1). We found genetic conservation implemented in 158 species, mostly trees and other plants (Figure S2). The most common programme was establishment of a GCU (72.8%), followed by assigning an ESU (without official ratification; 15.8%), and genetic rescue by translocation (8.9%), captive breeding (1.9%) or habitat connectivity (0.6%) (Figure S2). GCUs were selected to protect genetic resources of economically important plant species including about 100 tree species, and 10 species of crop wild relatives (Figure S2), such as citrus, wheat, maize and chilli. The European Forest Genetic Resources Programme (EUFORGEN) (www.euforgen.org) promotes conservation of genetic resources through a pan-European strategy for the establishment of GCUs (Koskela et al., 2013), resulting in over 3200 GCUs harbouring more than 4000 populations of about 100 tree species. A subsample of these forms a core network which aims to capture current genetic diversity across Europe for a number of forest tree species by representing populations from different local climate and environmental conditions (de Vries et al., 2015). Therefore, GCUs have been successfully used to protect genetic diversity in mainly economically important plant species in the wild. The proposed future CBD targets focus on protecting genetic diversity within all wild species (Hoban et al., 2020), making it vital to explore the potential to extend the GCU approach to other plant and animal taxa.

3 | EXPLORING THE SCOPE FOR IMPLEMENTING GCUs MORE WIDELY AS A TECHNIQUE TO CONSERVE GENETIC DIVERSITY

We used a structured questionnaire to canvass conservationists' and land managers' opinions concerning adopting a system of GCUs to protect biodiversity. We want this GCU method to be something that is co-developed with stakeholders so that it is something that practitioners and land managers are willing to sign up for, and therefore any concerns and benefits were important for us to understand. Our experience suggests that a co-development approach is likely to appeal to land managers as it gives them greater ownership of the process (O'Brien et al., 2021). We received responses from 60 U.K. participants including researchers (26%), non-governmental organisations (33%), private land managers (7%), government/non-departmental public bodies (24%) and others (4%) (Figure S3). Responses provided information on

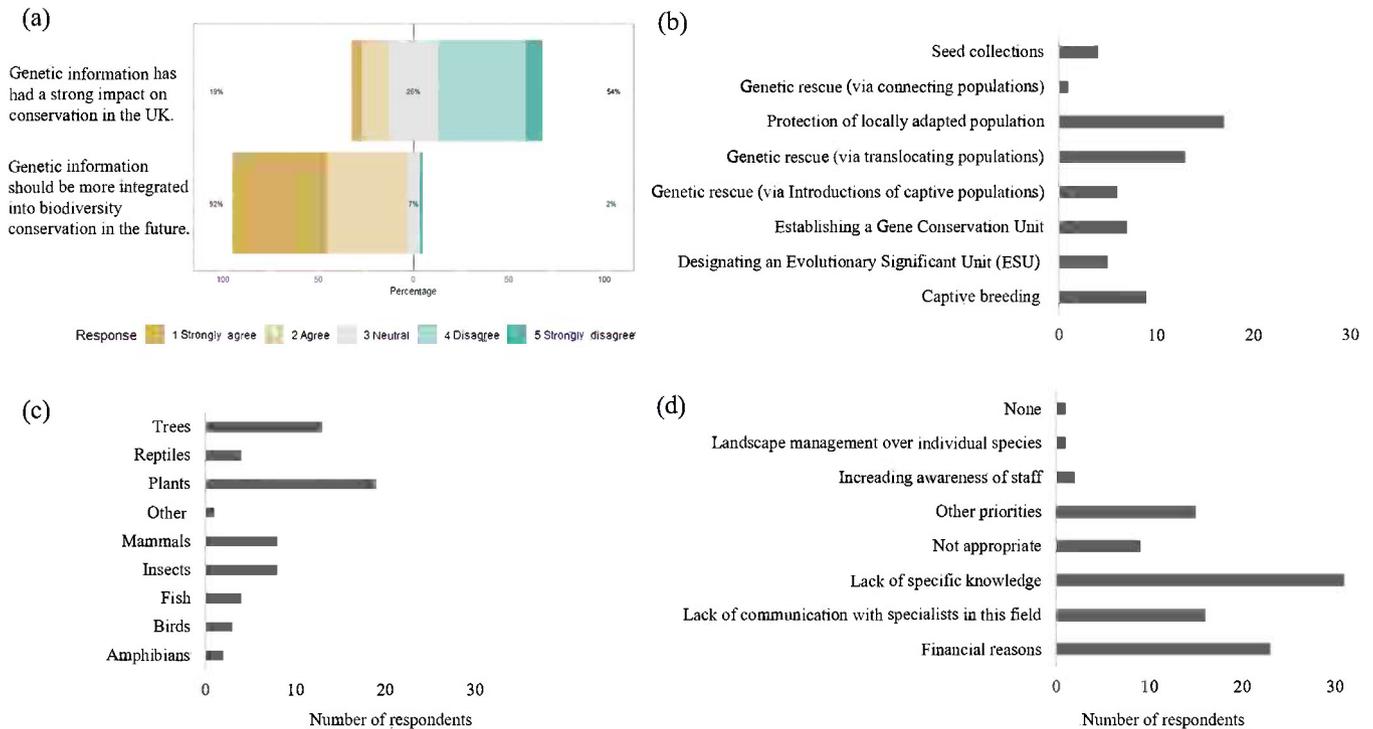


FIGURE 1 Current in situ genetic conservation implemented by conservationists and land managers. (a) Opinions of current and future implementation of genetic conservation; responses to statements were collected in a Likert scale. (b) Types and frequency of genetic conservation management currently implemented. (c) Type and frequency of taxa included in genetic conservation management. (d) Perceived barriers to implementing genetic conservation management

current genetic practises and support for developing GCUs for species conservation, including opinions on perceived risks, benefits and feasibility of GCUs (see Methods S1). This information provided insight into the scope for GCU implementation, and whether existing methods could be applied to other species. Genetic conservation is valued in the United Kingdom (Figure S4–S6) and in situ genetic conservation management has focused on plant species (Figures 1b and 1c), confirming the findings from our literature review. Most organisations surveyed do not have a genetic conservation policy (Figure S5c), although many participants considered that genetic information should be more integrated into conservation in the future (Figure 1a). The main perceived barriers to implementing genetic conservation management are lack of specific knowledge and financial constraints (Figure 1d). These hamper progress, despite support for integrating genetic information into conservation management in the United Kingdom. Therefore, there is merit in exploring the feasibility of extending GCU policy to include all species so that, when accompanied by simple guidelines, GCUs may serve as a genetic conservation technique which could be implemented by land managers.

Conservationists and landowners listed several perceived benefits of GCUs (Figures 2a and 1b). The most frequently mentioned was maintaining genetic diversity and adaptability of populations, allowing them to persist and continue to adapt in response to environmental changes and other challenges. The most frequently cited benefits for landowners related to financial gains (e.g. benefits to economically exploited species, attracting public funding), prestige and pride

that land managers experienced when conserving their land for species resilience, and wider conservation benefits (e.g. increasing connectivity, GCUs acting as gene banks). The role of GCUs in raising awareness of the importance of species conservation was often mentioned as a general benefit or a benefit to landowners, with a recognition that more awareness and engagement on the importance of genetic diversity and adaptability could promote genetic conservation activities in the future. Respondents also suggested several potential risks of designating populations as GCUs (Figure 2c), including neglecting non-target species, overlooking populations outside of the GCU and negative genetic consequences, including inbreeding. There were mainly positive responses regarding the potential to recognize GCUs for more mobile target species such as large mammals, insects and birds (Figure 2d). Respondents considered that to make them applicable to more mobile species, GCU boundaries should be flexible, accounting for dispersal distances, with adaptable criteria to suit species' characteristics such as population size and geographical scale. Another concern was that future climate change may displace populations uphill or to more northern latitudes (i.e. poleward), and that GCUs may need to move with them.

There were mixed responses regarding the potential for GCU management to conflict with current management actions (Figure 2e). While some stated that the GCU would enhance the existing management plans, others stated that there could be conflicts if the area was not already managed for the conservation of the focal species. Other conflicts raised included concerns that current management plans

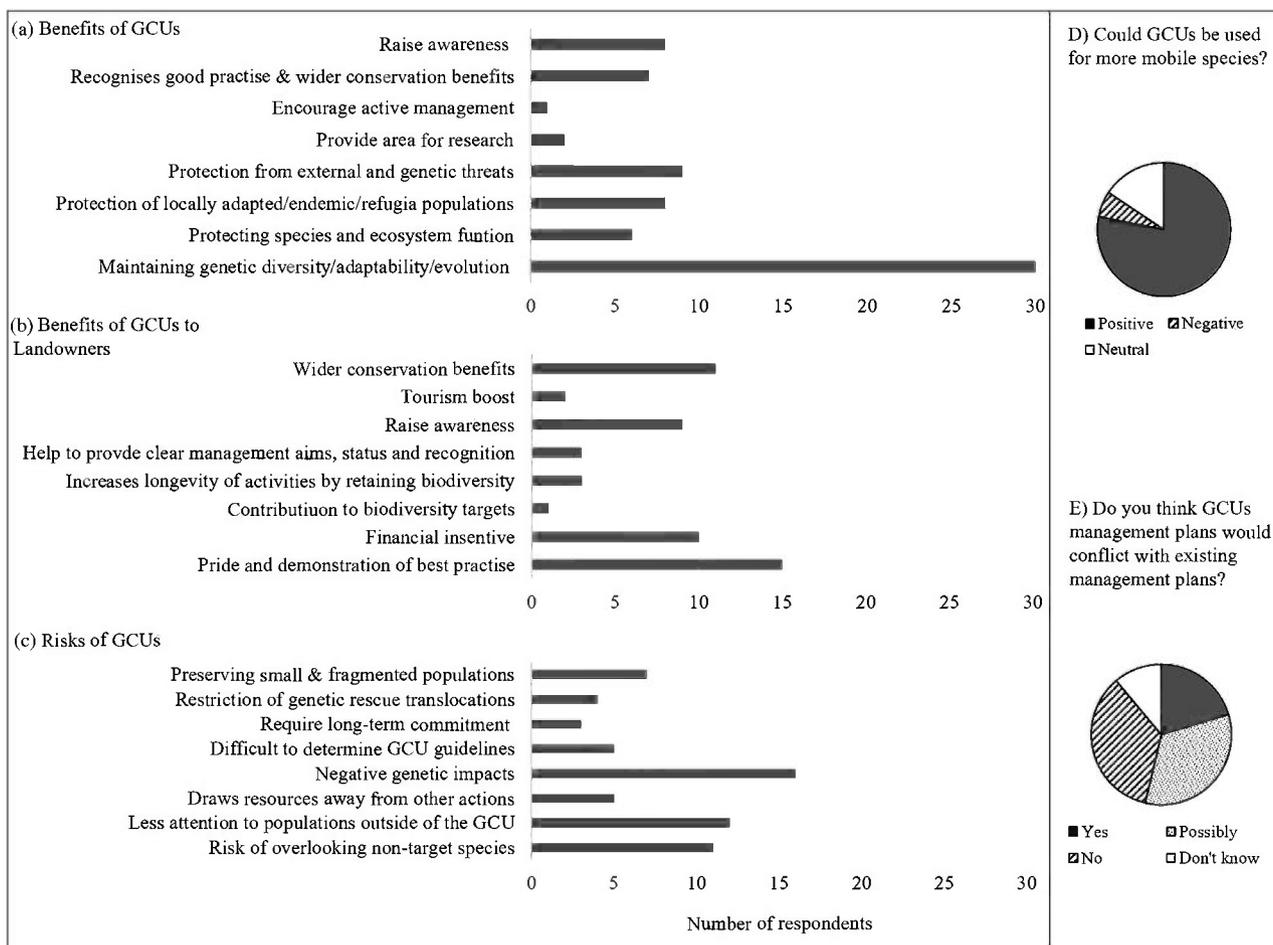


FIGURE 2 Questionnaire responses of 60 conservationists and land managers to test the feasibility, risks and benefits of extending the GCU concept to other species (open-ended answers grouped into broad categories). (a) Perceived benefits of GCUs. (b) Perceived benefits of GCUs specifically to land managers. (c) Perceived risks of GCUs. (d) Perceived feasibility of extending GCUs to include more mobile species. (e) Perceived conflicts of GCU management plans with existing management plans

might fail to recognize genetic diversity and evolutionary processes, for example if 'pure bred' conservation measures are in force, for example deliberately removing hybrids. Similarly, some responses expressed concern for 'keeping things apart' rather than allowing mixing and gene flow in the area. Although one objective of GCUs for trees is to protect adaptive traits, other objectives are to encourage dynamic gene conservation, through natural processes which may involve mixing and connecting-up habitats. Similarly, a new objective for GCUs for other taxa may be to increase genetic diversity, thereby introducing new genes through captive breeding or translocations from elsewhere. Most respondents whose answers were grouped into 'yes' or 'possibly' gave some advice to reduce these potential conflicts, including having flexible criteria, and working alongside land managers to fully integrate the GCU management plan into existing plans. Some respondents also expressed concern for yet another system of registering sites of high conservation interest, and suggested that instead of a standalone scheme, GCUs could be integrated with current practises.

Therefore, responses indicate general support from conservationists and land managers for the GCU approach for other taxa, as well as

raising some concerns. To address these concerns, we propose a flexible approach, including voluntary certification (not statutory designation) with simple standardized selection criteria that can be adapted for each target species or group of target species. This would allow GCU boundaries to move, for example if populations are displaced uphill or northwards under future climate change. To explore how GCU criteria may need to be tailored to suit particular species, we consider four exemplar case study species.

4 | DEVELOPING GCU GUIDANCE TO PROTECT A WIDE RANGE OF SPECIES: FOUR CASE STUDY SPECIES

EUFORGEN has developed minimum criteria for registering populations as GCUs on the publicly available EUFGIS database (Koskela et al., 2013). GCUs for forest tree species must have a management plan, at least one target species, with a breeding population of at least 50 (marginal or scattered tree populations) or 500 (stand-forming conifer or broadleaf species) individuals. To explore the feasibility of

TABLE 1 Case study species of U.K. conservation importance used to create selection criteria for GCU

| Species and genetic risk | U.K. population threats | Contribution of U.K. population to species diversity | Genetic risks | GCU selection criteria |
|---------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Mountain ringlet <i>Erebia epiphron</i> : Moderate  | <ul style="list-style-type: none"> Climate change | <ul style="list-style-type: none"> High unique genetic diversity in England Low elevation range edge | <ul style="list-style-type: none"> Risk of loss of English genetic diversity | <ul style="list-style-type: none"> Area to include metapopulation GcUs to capture unique genetic diversity in England/allowing natural adaptation to climate change |
| Hazel gloves <i>Hypocrepis Rhododendri</i> : Negligible  | <ul style="list-style-type: none"> Heavy grazing Habitat change Invasive spp. | <ul style="list-style-type: none"> Bottleneck in Scottish populations Source populations in North America with higher genetic diversity | <ul style="list-style-type: none"> No evidence of adaptive variation Little risk as Scottish genetic diversity is a subset found elsewhere | <ul style="list-style-type: none"> Area = could not be determined More data required |
| Great yellow bumblebee <i>Bombus distinguendus</i> : Serious  | <ul style="list-style-type: none"> Habitat loss Climate change | <ul style="list-style-type: none"> Scotland holds last remaining genetic diversity from United Kingdom | <ul style="list-style-type: none"> Genetic diversity already lost due to declines Low genetic diversity | <ul style="list-style-type: none"> Area to include total area of suitable habitat GcUs in within each island group and mainland |
| Harebell or Scottish bluebell <i>Campanula rotundifolia</i> : Moderate  | <ul style="list-style-type: none"> Habitat loss (through agricultural intensification and woodland regeneration) | <ul style="list-style-type: none"> The United Kingdom contains three cytotypes: tetraploid, pentaploid and hexaploid | <ul style="list-style-type: none"> Potential hybridisation with non-native genotypes Declines in Scotland would impact hexaploid cytotype | <ul style="list-style-type: none"> Area to include the entire grassland habitat GcUs across the different cytotypes |

Note: The four case study species vary in genetic risk, population dynamics and taxa to understand whether criteria can be designed for different species of varying genetic importance. GCU criteria is suggested for all species, with Hazelgloves requiring more demographic data to determine GCU criteria. References: Mountain ringlet, Franco et al. (2006) and Minter et al. (2020); Hazelgloves, Grundy et al. (2012); Great yellow bumblebee, Charman et al. (2010); Harebell, Stevens et al. (2012) and Wilson et al. (2020). Genetic risk derived from Hollingsworth et al. (2020).

developing GCUs for species other than forest trees, we selected four species to act as test cases and developed criteria specific to each. These case study species differ in their level of genetic risk and population dynamics, but are all of conservation importance in the United Kingdom (Table 1). These differences between species highlighted the need to retain certain criteria and to revise or introduce others.

4.1 | Deciding on the effective population size for GCU

The minimum size of a genetically viable population (or breeding population) is defined as $N_e = 500$ where the goal is to maintain long-term evolutionary potential in a population (Franklin, 1980), and this is incorporated into the GCU forest guidelines to protect genetic

diversity and ensure continued evolutionary processes (Koskela et al., 2013). An N_e of 500 is also suggested for any initiative for the conservation of genetic diversity in wild populations (Hoban et al., 2020). N_e can be inferred from N_c which represents a population census, and a N_e of 500 roughly equates to an N_c of 5000; however, there is variation in this ratio among taxa (Hoban et al., 2020). A universal 'rule of thumb' N_e or N_c for inclusion in a GCU would be difficult to put into practice as these numbers will vary considerably among taxa. For example breeding populations may represent individuals; however, in eusocial species such as bumblebees, each nest represents one breeding unit. In practice, identifying 5000 individuals in an area would be unrealistic for many species. Thus, rather than providing a set N_e or N_c value, we suggest that the population size threshold for inclusion in a GCU needs to be taxon specific and calculated using information on the species biology.

4.2 | Recommended GCU criteria appropriate for each case study species

4.2.1 | *Bombus distinguendus*

The number of great yellow bumblebee *Bombus distinguendus* breeding colonies among different sites across its distribution range from 12 to 63, with a mean of 25 (Charman et al., 2010). The population density of the great yellow bumblebee is 19.3 nests/km² of suitable habitat (Charman et al., 2010). Gene flow occurs within Scottish island groups (Figure S7a), but little occurs between them (Charman et al., 2010), therefore it would be appropriate to designate a GCU for each island group (Orkney, Outer Hebrides, Inner Hebrides) and the mainland population. Therefore, GCUs could be designated to incorporate the total area of occupied suitable habitat (>2 km²) in the islands and mainland group, with conservation management to increase gene flow within each group.

4.2.2 | *Erebia epiphron*

The mountain ringlet butterfly, *Erebia epiphron* (U.K. distribution: Figure S7b), occurs in discrete colonies where they are locally abundant, but with little dispersal between populations (Czech populations; Kuras et al., 2003). Designated GCUs should include the entire metapopulation (e.g. Eastern Lake District, England or Ben Lawers, Scotland) and should contain suitable upland habitat, with appropriate grazing regimes (Ewing et al., 2020).

4.2.3 | *Hypocreopsis rhododendri*

Hazelgloves, *Hypocreopsis rhododendri* (U.K. distribution: Figure S7c), is a parasitic ascomycete fungus which requires abundant host populations, the wood decaying 'glue fungus' *Pseudochaete corrugata* (Grundy et al., 2012). The number of breeding individuals is unknown but the presence of the host fungus may be used as an effective proxy to indicate the population number for the parasite. Further understanding of this species' biology, along with demographic and genetic data for the host fungus, is required before GCU design can be considered. This case study species highlights the importance of information on species' biology to design GCUs.

4.2.4 | *Campanula rotundifolia*

Harebells *Campanula rotundifolia* are widespread but declining (U.K. distribution: Figure S7d) and form four cytotypes (differences in the number of sets of chromosomes), three of which occur in the United Kingdom: tetraploid, pentaploid and hexaploid (Wilson et al., 2020). GCUs could be created in different areas of the range to incorporate different cytotypes. *Campanula rotundifolia* is locally common in tall-

herb grassland habitats (Stevens et al., 2012), so we suggest a GCU area which incorporates the entire occupied grassland in a particular site.

5 | MANAGEMENT RECOMMENDATIONS

Considerable time and thought have been invested in developing the concept of GCUs for in situ conservation of forest tree species and here we explore the support for, and the feasibility of, using this approach across a wider range of species as a means of achieving the CBD Aichi target of maintaining genetic variation. Our study suggests that GCUs could conserve genetic diversity in a wide range of target species and we present guidelines for the minimum qualification criteria that must be met for GCU certification (Box 1). As such GCUs could be classed as 'other effective area-based conservation measures' (OECMs): areas that are achieving effective in situ conservation of biodiversity outside of protected areas (CBD, 2018).

Some GCU criteria used for forest trees remain appropriate for GCUs for other taxa (Box 1, Criterion A, B, F and G) (Koskela et al., 2013). However, other criteria must be tailored to particular species (Box 1, Criterion C, D and E). Firstly, the breeding population size (N_e) of the target species must be calculated species specifically, and it is not appropriate to apply a single 'rule of thumb' N_e for multiple taxa (Box 1, Criterion C). Secondly, the land area of a GCU should be inferred by the space required to support a minimum breeding population, and will differ depending on the target species' mobility and dispersal characteristics (Box 1, Criterion E). The distribution of the breeding population for inclusion in the GCUs will depend on the species distribution type (distinct or local, metapopulation or continuously distributed) (Box 1, Criterion D), which can be identified on the basis of genetic, demographic or ecoregion data. GCUs for species with continuous populations can be identified using ecoregions (different climatic zones). Genetic data could be used to identify genetic diversity 'hotspots', or to select populations based on the objective to prioritize connectivity or evolutionary potential (see Nielsen et al., 2020). As with GCUs for forest trees, those for other taxa will not be statutory designations and therefore there will be flexibility as long as the minimum viable population is maintained.

The operationalization of a GCU for trees is to encourage dynamic gene conservation by recognising appropriate breeding populations in a geographic area to manage these populations to promote regular cycles of natural regeneration to occur. For other taxa, the operationalization of GCUs must similarly promote the occurrence of natural regeneration or reproduction. This will be achieved through conservation management actions listed in the management plan that promote persistence of the focal species, and mitigate genetic threats. Depending on the conservation objective of the GCU (Box 1, Criterion B), this may for example involve connecting up habitats to increase gene flow, or translocating individuals (genetic rescue) into the GCU to increase genetic diversity. Genetic and population monitoring of focal populations would also be appropriate to ensure sufficient population sizes for reproduction and healthy genetic diversity.

Box 1. Gene Conservation Unit criteria for terrestrial species

Criterion A: At least one target species must be included in the GCU

Multiple target species can be included if they meet species criteria

Criterion B: Conservation objective

(Bi) To maintain genetic diversity

(Bii) To conserve adaptive or other traits in distinct population

(Biii) To increase genetic diversity (with additional methods e.g. captive breeding or translocation)

Criterion C: Population size

Breeding population should be tailored to species specific requirements and depending on distribution (Criterion D) and biological characteristics

Criterion D: Distribution

(Di) Distinct or local

(Dii) Metapopulation

(Diii) Continuous distribution

Criterion E: Land area

Land area must contain the appropriate breeding populations of target species and appropriate habitat cover

Criterion F: Management objectives

(Fi) Maintaining genetic diversity must be key management goal

(Fii) Ensure continued existence of target species

(Fiii) Create favourable conditions and actions to mitigate genetic threats for target species through habitat management

Criterion G: Monitoring

(Gi) Field surveys are undertaken to monitor population size of target species

(Gii) Field visits to ensure favourable conditions for target species are maintained

Criterion H: Database

GCU must be listed on a publicly accessible database which has clear definitions of the data to ensure consistency.

Although we have described some enthusiasm for the efficacy and feasibility of the GCU system for multiple taxa, alternatives to this method were suggested by some respondents to our questionnaire. Some individuals stated that rather than a stand-alone scheme, the GCU objectives could instead be integrated into existing land protection methods. However, a caveat to this suggestion is that GCUs would be a voluntary certification, allowing more land owners and conservation bodies to register their land if it meets the GCU general criteria.

We have highlighted how existing methods for GCU designation could be altered for other taxa; however, deciding which taxa should be the focus of a GCU is something which needs to be further explored, and is beyond the scope of this paper. Whether GCUs could be used for multiple taxa or may be more species specific, along with the types of species to include, are all issues which need to be further discussed with stakeholders. Species prioritisation tools could be used, such as selecting species based on their socio-economic and/or cultural value (Hollingsworth et al., 2020) or combining criteria based on species value, management costs and threat status (Joseph et al., 2009).

6 | CONCLUSIONS AND NEXT STEPS

There is a need to develop a system for in situ genetic conservation. By building on the GCU approach successfully applied to trees in Europe, it will be possible to develop a system that is of low cost to participants and that can coexist with current management practices, and one that aligns with proposed expansion of OECMs (CBD, 2018). For land managers to register sites as GCUs, funds are required to establish and maintain an international database, such as EUFGIS for tree species, where common criteria are applied for the listing of GCUs of a given species and the same descriptors are used to characterize the selected populations. These data could then be used to select populations to establish a core network of GCUs for each species that would capture the diversity across its distribution range. Additionally, further investigation into the application of GCUs for other taxa requires additional discussion about how to prioritize species for GCUs, for which we have set up a Gene Conservation Unit working group, to facilitate discussion and make key decisions on taking this approach forward to implement the first non-tree GCU.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

M.M., D.O. and J.H. conceived the ideas. M.M. collected the data. M.M. analyzed the data. M.M. drafted the manuscript. All authors contributed to the final manuscript.

DATA AVAILABILITY STATEMENT

Ethical approval for this project states that questionnaire responses must remain anonymous and therefore these data cannot be shared. Literature review data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.3j9kd51hm> (Minter et al., 2021).

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SUPPORTING INFORMATION

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