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# Everything Is Connected: Ecosystem Functioning as a Rationale for Conservation Translocations

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## Simple Summary

Conservation translocations are a well-established intervention to enable the restoration of populations of threatened species and aid their recovery. Increasingly, translocations are being considered as a way of restoring ecosystem function but often through the planting or release of species considered to be important to the functioning of the ecological community at the release site. This research aims to show that considering ecosystem function in conservation translocation projects is a valuable approach regardless of whether the translocation involves a keystone species or ecosystem engineer. To do this, I selected a pair of woodland plant species that might generally be overlooked in their native habitat due to short stature and annual life cycle. I undertook vegetation surveys at sites hosting these species and characterized the functional diversity and composition of plant communities identified. From this analysis, I can demonstrate that even rare species that contribute very little to the biomass of a community can deliver distinctive and important functional roles, and this supports the case to reintroduce these species to woodlands from which they have been lost. I recommend this approach in a wider range of translocation projects to enable the ongoing resilience of ecosystems and recovery of threatened species.

## Abstract

Conservation translocations have become a mainstream tool for species recovery but their capacity for delivering enhanced ecological function has been broadly overlooked despite the potential for increasing functional diversity and consequent ecosystem resilience. I argue that concepts such as functional rarity and functional distinctiveness are valuable for prioritizing species for conservation translocation and present a case study that demonstrates the ecological value of two species of annual hemiparasite from the genus *Melampyrum*. The data consist of species presence across 17 sites combined with trait data for each of the 82 species identified. I apply various methods to calculate functional distinctiveness and identify which traits deliver significant ecological benefit to the surrounding communities. In doing so, I aim to show that obscure and overlooked species might be more substantive in their functional role than their biomass and appearance might otherwise imply. Finally, I acknowledge caveats in this approach and suggest a way forward that navigates any limitations to effectively use ecological role and functional distinctiveness to prioritize species for conservation translocation and incur benefits to species and ecosystems in need of restoration and rehabilitation.

**Keywords:** conservation translocation; ecosystem function; reintroduction; ecological replacement; functional rarity; *Melampyrum pratense*; *Melampyrum sylvaticum*



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## 1. Introduction

The concept of 'conservation benefit' is implicit in the actions of the global conservation community whose efforts aim to address and reverse the biodiversity crisis. Achieving the balance of net benefit is, however, sometimes challenging, particularly when undertaking interventions such as conservation translocations which are associated with higher risks than many other management approaches. Nevertheless, conservation translocations have become an important tool in species recovery and now number into the many thousands of projects encompassing fungi, plants and animals [1–3]. The IUCN definition of conservation translocations specifies that achieving conservation benefit must be part of the rationale for, and an outcome of, wildlife releases but is clear in stating that the conservation benefit may be accrued by species and ecosystems [4]. The motivation for undertaking a conservation translocation could therefore constitute the restoration of a lost ecological function that plays a role in ecosystem dynamics [5]. But whilst species and ecosystems *can* be the beneficiaries, most CTs are undertaken to address species declines and not ecosystem outcomes—in a recent review of plant conservation translocations <14% of the 1440 reasons given for undertaking conservation translocations were to replace a lost ecological function [1].

There is a growing body of literature that calls for translocations to address ecosystem degradation through the reinstatement of lost ecological functions [6] but relatively few examples. Interventions such as these are sometimes defined as ecological replacement, and generally involve the movements of species known to be keystone species or ecosystem engineers [7,8]. These are species whose role in an ecosystem is crucial to the ecosystem's health and ongoing resilience. In many cases, an ecosystem would shift to an alternative state were it not for the presence of such species, and ecosystem restoration cannot happen satisfactorily without them. However, there must be very many species who deliver valuable ecosystem roles that are not recognized as being keystone species or ecosystem engineers but whose translocation to degraded ecosystems would be an important step in repairing ecological integrity.

The impetus to consider the functional role of a species undergoing conservation management is further supported by the development of the IUCN Green Status of Species assessment [9]. Functional viability is recognized as a key metric of conservation success and as such, has been integrated into the Green Status of Species assessment to demonstrate the magnitude of positive impacts resulting from conservation management [10]. However, functional roles are properties of a species that are relational in their nature; because ecological function results in impacts on the surrounding biotic and abiotic environments, we can think of functional roles as being implicitly associated with ecological interactions such as competition, predation, food provision, nutrient cycling and carbon fixation. The extent to which a species can offer distinct and useful ecological function can only be evaluated at community scale and is relative to the functions provided by other species in that location.

Adopting measures of functional diversity has been promoted as a way of strengthening decision-making in conservation and increasing the likelihood that conservation benefits are achieved [11]. Further to this, functional rarity has been suggested as a key property in community dynamics [12] and in the context of conservation translocations, could help to identify priorities for action that are more ecologically meaningful than measures of rarity or extinction risk. For species that have been lost from an ecosystem, it is useful to determine their functional role so that assessments can be made of the value and/or importance of restoring that role through translocation [13]. By incorporating assessments of functional distinctiveness, conservation translocations of functionally im-

portant species would be promoted thereby maximizing the potential for translocations to deliver ecologically meaningful benefits to the recipient community.

This paper aims to provide a way of recognizing valuable qualities in species that are not necessarily thought to be ecosystem engineers in the conventional understanding of the term. I explore an approach that attempts to quantify functional distinctiveness of all the species in a taxonomically defined assemblage, so that translocations can be prioritized for species that have unique roles to play in ecosystem interactions and processes. The study objectives are to demonstrate how there might be utility in adopting a quantitative approach using statistical analyses to define functionally distinct species. I also aim to use this analysis to articulate caveats to the approach to enable its responsible and effective use in the conservation of species and ecosystems alike.

## 2. Materials and Methods

### *2.1. Study Species*

The focal species in this study were *Melampyrum sylvaticum* L. and *M. pratense* L., two annual species from the family Orobanchaceae and endemic to Europe. Both species have disjunct distributions occupying areas in boreal regions of Scandinavia, Britain, Ireland and Iceland, and montane regions in southern and central Europe. They are associated with a range of habitats but predominantly found in birch woodlands and heath with a cool-temperate to sub-Arctic climate [14]. Both species have been Red Listed in parts of their ranges (*M. sylvaticum* in the UK [15], *M. pratense* in Iceland [16]) and both are thought to be in decline elsewhere [17,18]. The species have been subject to reintroductions to address population loss and fulfil an ecological role [19,20].

The genus *Melampyrum* has some distinctive ecological features [21] that commend it as a good candidate for this study. The plants of this genus are facultative root hemiparasites that appear to require hosts from a relatively restricted range of species—notably not grasses as the close relatives in genus *Rhinanthus* are known to parasitize—including ericoid shrubs such as *Vaccinium myrtillus* and trees such as *Betula pubescens* [14]. They also have unusually large seeds, especially for annuals and relative to the typical size of the plants, that carry an appendage known as an elaiosome. As a result, wood ants such as members of the genus *Formica* have been recorded as seed dispersers [22]. Finally, this genus does not conform to the typical understanding of being a keystone species or ecosystem engineer and as such, the articulation of its functional distinctiveness is a useful demonstration of the importance of looking beyond the labels to objectively identify functional distinction within a conservation context.

### *2.2. Data Collection*

The dataset utilized in this study comprises plant community data derived from surveys conducted in the field between 2003 and 2018 in combination with trait data derived from online sources for each species present.

Vascular plant species presence was recorded at 17 sites in Scotland, England and Wales (Table S1), 11 at which one or both *Melampyrum pratense* and *M. sylvaticum* occur. A further six are sites to which *M. sylvaticum* was translocated to achieve the aims of the Species Recovery project. The sites are all on acidic soils in the English uplands, Yr Wyddfa National Park, Wales, and the Scottish Highlands. They consist of a mixture of old growth birch or birch–oak woodland and heath communities, sometimes existing as a heath–woodland mosaic. As is typical of the British uplands, the climate is cool-temperate at all sites.

Data from 14 sites were originally collected for other studies but have not been published until now. These studies consisted of surveys to describe sites which support

*Melampyrum*, including the abiotic environment and species presence and absence used to report vegetation classifications according to the British National Vegetation Classification https://jncc.gov.uk/our-work/nvc/ (accessed on 12 September 2025). The sampling regime varied but according to the requirements of the statistical approach (Section 2.3), issues arising from sampling variation were overcome by using a community-level species list that takes only presence–absence of the respective species at sites, and avoids the need for consistent abundance measures. Eighty-two vascular plant taxa were identified, all but two to species level, the remaining species being identified to species aggregate, namely *Euphrasia officinalis* agg. and *Taraxacum officinale* agg. (Table S1).

Trait data were taken from PLANTATT [23] and Ecoflora [24] databases, all traits were downloaded for the full set of species. Where traits could not be defined for all species, they were removed from the dataset. The resulting list of traits was then checked for redundancy of information which arose where different sources referred to the same traits by different names and these variables were merged when necessary. The final list of twenty-six traits covers environmental tolerance, growth form, reproductive traits, and provisioning traits. A full list is provided in Supplementary Materials Table S2.

### *2.3. Statistical Analysis*

Community data and trait data were used in combination to calculate functional distinctiveness using the R [25] package FUNRAR [26] in RStudio version 3.5.1 [27]. The distinctiveness index is a distance metric that indicates the multivariate similarity of species based on their traits relative to their associates in any given site. To determine which traits were important in conferring distinctiveness, factor analysis of mixed data (FAMD) was applied to the trait dataset using the multivariate analysis package FactoMineR version 2.15 [28].

## 3. Results

### *3.1. Functional Distinctiveness*

In comparison to the species in their surrounding communities in this dataset, *Melampyrum sylvaticum* and *M. pratense* achieved much higher distinctiveness index scores than the community mean (Figure 1; means for *M. sylvaticum* = 0.463 ± 0.021 (SD) and *M. pratense* = 0.478 ± 0.022 (SD)). This indicates that these species have a combination of traits and ecological tolerances that are highly distinct from their associates.

### *3.2. Identifying Traits That Confer Distinctiveness*

Whilst the distinctiveness index can quantify the level of functional differentiation at species level, it cannot reveal the traits that confer uniqueness in an ecological context. To address this, Figure 2 displays the FAMD ordination of species (factors) in this dataset (for full species names see Supplementary Materials Tables S1 and S2 and for FAMD outputs see Table S3) along the first and second principal components or dimensions. Dimension 1 represents a spread of species of which *Larix decidua* (lar.dec) is the outlier in the upper end of the x axis scale with a score of 10.164. The other end of the scale is occupied by a number of species that spread across dimension 2. These consist of two ferns in the lower left quadrant—*Pteridium aquilinum* (pte.aqu) and *Gymnocarpon dryopteris* (gym.dry) whose dimension 1 scores are −2.437 and −2.373, respectively, and also received the lowest scores on dimension 2 −3.945 and −3.439, respectively. The species receiving the lowest scores on dimension 1 and occupying the extreme position at the opposite end of dimension 2 are *Melampyrum pratense* (mel.pra) and *M. sylvaticum* (mel.syl): dimension 1 scores are −3.162 and −2.829, respectively, and dimension 2 scores are 9.414 and 9.152, respectively.

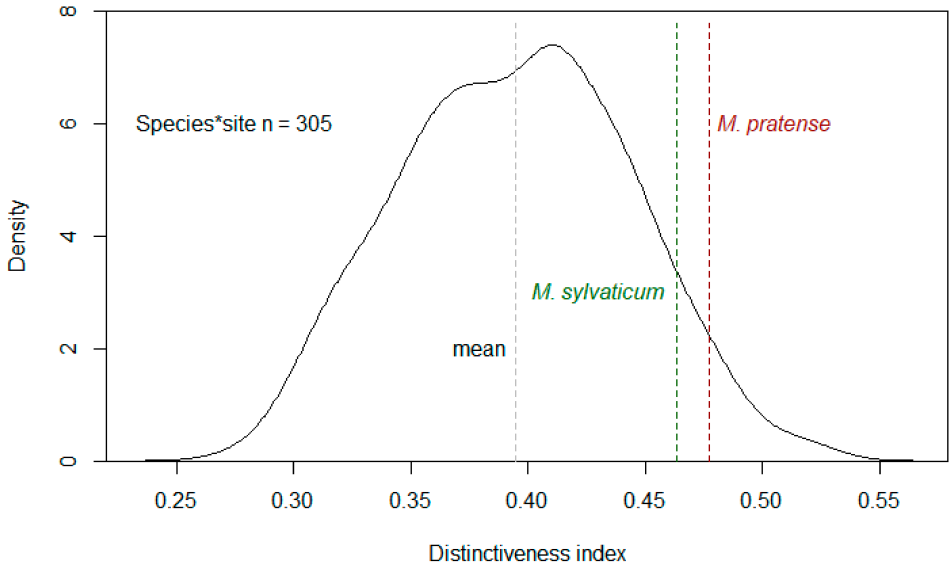


**Figure 1.** Kernal density plot displaying distribution of 305 distinctiveness scores calculated for each species relative to the other species at each site at which it occurs. The distinctiveness index is a distance metric that indicates the multivariate similarity of species based on their traits relative to their associates in any given site. Lower scores indicate species with higher functional redundancy, high distinctiveness index indicates species with relatively unique trait sets. Mean distinctiveness index is indicated by the grey dashed line with *Melampyrum* species depicted in green and red dashed lines.

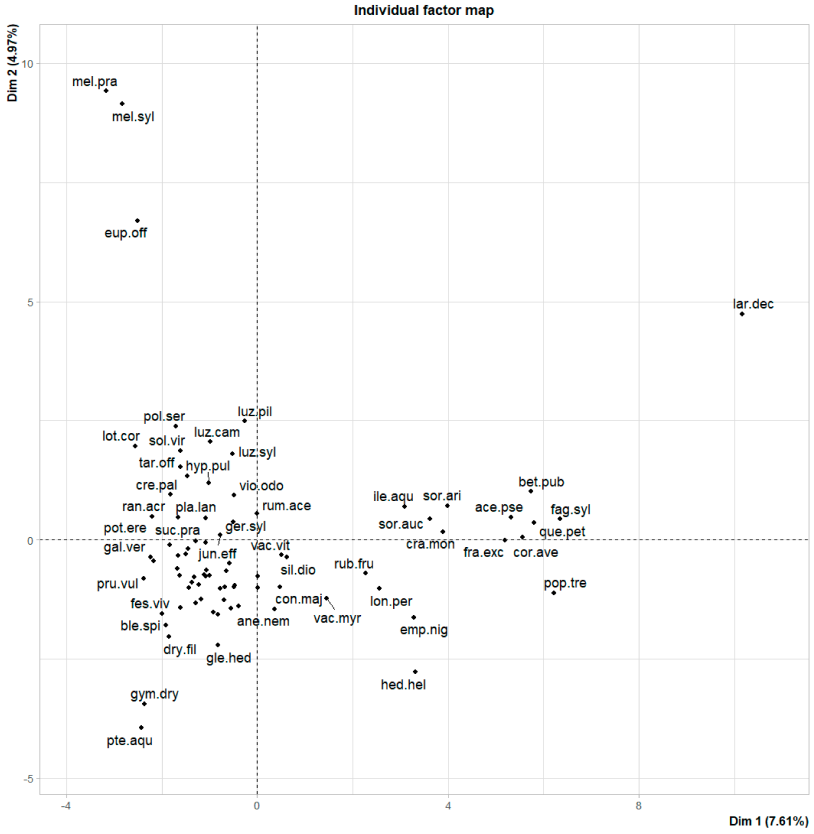


**Figure 2.** Factor map generated using factor analysis for mixed data (FAMD). Factors = species, labels are abbreviations of species name, see Supplementary Information for full names (Tables S1 and S2). For clarity, the following species labels have been omitted in the lower left quadrant: agr.can, agr.cap, agr.sto, ant.odo, car.nig, cir.het, dac.glo, des.ces, des.fle, dry.fil, fes.ovi, fes.rub, fra.ves, gal.sax, ger.rob, hol.lan, hol.mol, jun.squ, lat.lin, lat.pra, lys.nem, nar.str, oxa.ace, per.viv, poa.pra, ran.rep, sed.alb, teu.sco, tri.rep, ver.cha, vic.sep, vio.riv.

The second output of FAMD is presented in Figure 3 where the species traits (variables) that were used to ascribe species to ordinated scores in Figure 2 have themselves been ordinated. Although the dimensions are truncated compared to the factor map (Figure 2), the orientation of the variables can be used to infer what traits explained the major variation in species distinctiveness as identified in Figure 1. The position of lifeform, inflorescence type, height, woodiness and stem woodiness in the right-hand portion of dimension 1 explains why *Larix decidua* occupies its outlier position—tree species have clustered in the upper right quadrant of the ordination (Figure 2) but *L. decidua* is distinct in being a cone-bearing tree where the others are angiosperms. Similarly, the traits including seed dispersal (the dispersal agent and appendages on the dispersal unit) and particularly, nutrition and perennation occupy the upper range of scores represented by variables on dimension 2. This corresponds to the spread of points representing the hemiparasitic Orobanchaceae, *Euphrasia officinalis*, *Melampyrum sylvaticum* and *M. pratense* (Figure 2).

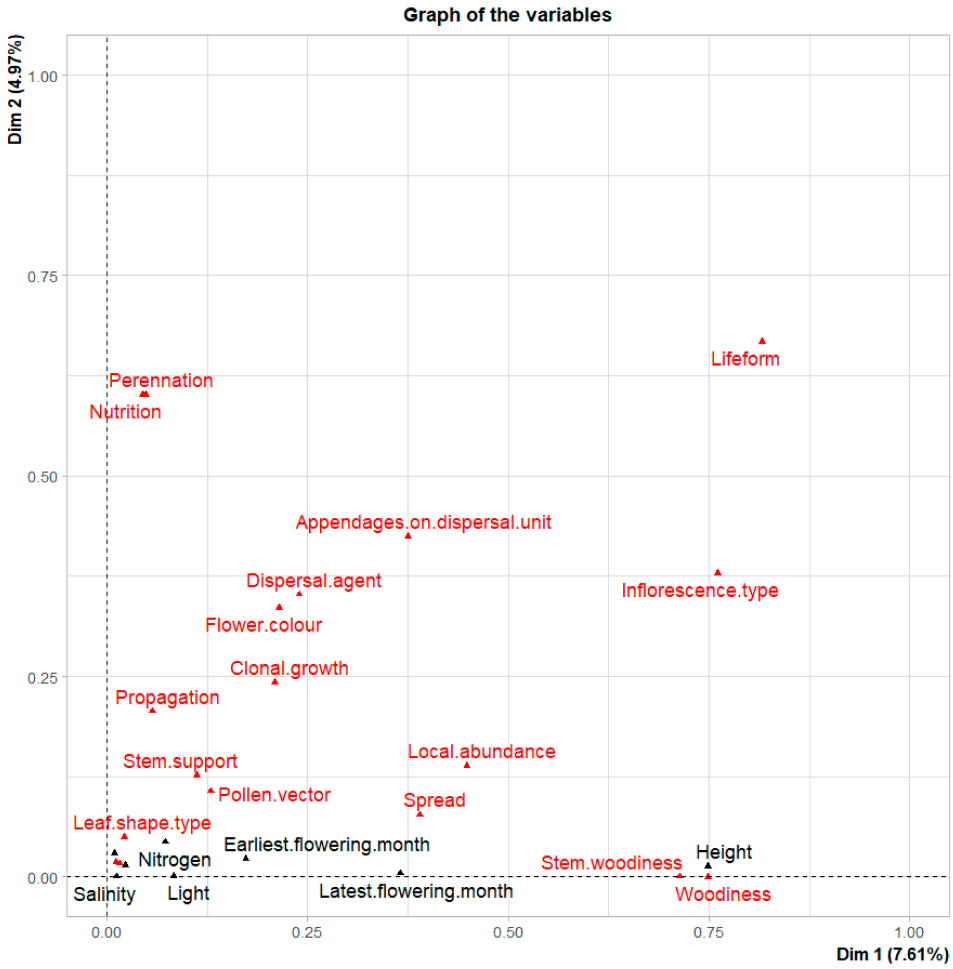


**Figure 3.** Variable ordination generated using factor analysis for mixed data (FAMD). Variables = trait types, for full list of trait categories making up trait types, see Supplementary Information (Table S2). Red labels and symbols denote categorical variables, black labels and symbols denote continuous variables. For clarity, the following variable labels have been removed from around the point at which the zero lines on dimension 1 and 2 intersect: moisture, reaction, more.than.1clonal.growth.form, heterophylly.

Table 1 provides the $\cos^2$ and v test breakdown against dimension 1 for each of the categorical variables in the FAMD and highlights the specific traits (and not just the variable or trait type as seen in Figure 3) that are associated with distinctiveness in these communities. As inferred from Figure 2, the dominant explanator of variation in dimension 1 is the difference between traits associated with trees vs. all other plant groups.

These were lifeform (phanerophyte referring to trees), woody vs. herbaceous growth, winged seeds as opposed to all other types of seed appendage, bird-dispersed seeds vs. abiotic seed dispersal, height exceeding width when describing spread and stem woodiness.

**Table 1.** Selected FAMD output statistics highlight traits that are most significantly associated with dimension 1 and most relevant to demonstrating functional distinctiveness of the genus *Melampyrum* at 17 sites in England, Wales and Scotland. Eighty-two species were included in the dataset with number of observations per trait category denoted by 'n'. Trait categories with which *Melampyrum* conforms are underlined. Significance uses a threshold of v test > 2 = significant (*), and >3 = highly significant (**) with significant v test statistics indicated in bold font. Full FAMD outputs are provided in Table S3.

| Trait Type | Trait Category | n | $cos^2$ | v Test | Significance |
|---|---|---|---|---|---|
| Lifeform | chamaephyte | 11 | 0 | −0.062 | |
| | geophyte | 5 | 0.016 | −0.695 | |
| | helophyte | 2 | 0.021 | −0.752 | |
| | hemicryptophyte | 46 | 0.478 | **−4.843** | ** |
| | phanerophyte | 15 | 0.911 | **7.924** | ** |
| | therophyte | 3 | 0.076 | −1.9 | |
| Woodiness | herbaceous | 63 | 0.883 | **−7.787** | ** |
| | woody | 19 | 0.883 | **7.787** | ** |
| Appendage on dispersal unit | elaiosome | 7 | 0.059 | −1.495 | |
| | hooks | 1 | 0.026 | −0.695 | |
| | mucilage | 7 | 0.063 | −1.339 | |
| | none | 60 | 0 | −0.097 | |
| | pappus | 3 | 0.037 | −1.05 | |
| | wings | 4 | 0.628 | **5.144** | ** |
| Dispersal vector | abiotic | 52 | 0.139 | **−2.155** | * |
| | ants | 8 | 0.082 | −1.768 | |
| | carried.birds | 3 | 0.224 | **2.537** | * |
| | carried.mammals | 3 | 0.019 | −0.728 | |
| | eaten.birds | 15 | 0.283 | **3.164** | ** |
| | man | 1 | 0 | −0.003 | |
| Spread | height < width | 10 | 0.013 | −0.69 | |
| | height = width | 46 | 0.388 | **−3.866** | ** |
| | height >> width | 1 | 0.321 | **3.884** | ** |
| | height > width | 25 | 0.36 | **3.732** | ** |
| Stem woodiness | non-woody | 62 | 0.865 | **−7.604** | ** |
| | woody | 20 | 0.865 | **7.604** | ** |

Table 2 provides the $cos^2$ and v test breakdown against dimension 2 for each of the categorical variables in the FAMD. Again, it highlights the specific traits that are associated with distinctiveness in these communities (and not just the variable or trait type as is seen in Figure 3). In this case, the variation in species can be seen to be linked to the traits conferring distinctiveness to the two species of *Melampyrum* and the closely related *Euphrasia officinalis*. These trait categories are annual perennation as opposed to perennial, seeds bearing elaiosomes, yellow flowers, ant-dispersed seeds and hemiparasitic nutritional strategy.

**Table 2.** Selected FAMD output statistics highlighting traits that are most significantly associated with dimension 2 and most relevant to demonstrating functional distinctiveness of the genus *Melampyrum* at 17 sites in England, Wales and Scotland. Eighty-two species were included in the dataset with number of observations per trait category denoted by 'n'. Trait categories with which *Melampyrum* conforms are underlined. Significance uses a threshold of v test > 2 = significant (*), and >3 = highly significant (**) with significant v test statistics indicated in bold font. Full FAMD outputs are provided in Table S3.

| Trait Type | Trait Category | n | $cos^2$ | v Test | Significance |
|---|---|---|---|---|---|
| Perennation | annual | 3 | 0.674 | **6.981** | ** |
| | biennial | 1 | 0.000 | −0.087 | |
| | perennial | 78 | 0.588 | **−6.040** | ** |
| Appendage on dispersal unit | elaiosome | 7 | 0.473 | **5.24** | ** |
| | hooks | 1 | 0.007 | 0.446 | |
| | mucilage | 7 | 0.01 | −0.661 | |
| | none | 60 | 0.38 | **−4.277** | ** |
| | pappus | 3 | 0.037 | 1.306 | |
| | wings | 4 | 0.035 | 1.493 | |
| Flower color | blue | 4 | 0.003 | −0.379 | |
| | blue-violet | 2 | 0 | 0.027 | |
| | brown | 8 | 0.094 | **2.203** | * |
| | cream | 2 | 0.009 | −0.612 | |
| | green | 21 | 0.078 | **−2.15** | * |
| | mauve | 1 | 0.002 | 0.222 | |
| | none | 4 | 0.106 | −2.7 | |
| | pink | 6 | 0.021 | −0.945 | |
| | purple | 4 | 0.008 | −0.521 | |
| | red-purple | 1 | 0 | −0.054 | |
| | violet | 2 | 0 | 0.041 | |
| | white | 14 | 0.001 | 0.172 | |
| | yellow | 13 | 0.252 | **3.577** | ** |
| Dispersal vector | abiotic | 52 | 0.14 | **−2.678** | * |
| | ants | 8 | 0.479 | **5.278** | ** |
| | carried.birds | 3 | 0.001 | 0.245 | |
| | carried.mammals | 3 | 0 | −0.001 | |
| | eaten.birds | 15 | 0.015 | −0.906 | |
| | man | 1 | 0.002 | 0.257 | |
| Nutrition | autotrophic | 79 | 0.674 | **−6.981** | ** |
| | hemiparasitic | 3 | 0.674 | **6.981** | ** |

For quantitative variables, only height achieved a notable $cos^2$ value of 0.749 (on a scale of 0 to 1) in the FAMD dimension 1. This exceeded all other quantitative variables by some margin and as a data exploration tool, the $cos^2$ value can be used to infer that other variables are much more poorly represented by that dimension. Dimension 2 scores for all variables fell below 0.044 and it can be confidently assumed that quantitative variables were negligible in explaining variation in the dataset along this dimension.

## 4. Discussion

### *4.1. Everything Is Connected, or How Traits Become Functionally Significant*

The analysis presented here, combining trait data with site-based surveys of species presence, demonstrates that functional diversity can be used to build a picture of an ecosystem which is more insightful than lists of species names alone. Organisms are not just passive receptors of their surroundings but functional in their ecosystems forming inter-

actions that can facilitate resilience and maintain biodiversity. In turn, this approach to defining functional role could be used in selecting species to be restored through conservation translocation. The utility of this approach is that the emergent functional profile of species is based on multiple variables that are relative to the functional profile of the community as a whole. As a result, the articulation of functional distinctiveness integrates multiple aspects of the community that contribute to ecosystem processes and does not arbitrarily isolate certain traits over others. In this study system, the species from the genus *Melampyrum* are particularly notable for their unique set of traits but it is important to articulate how these traits impact upon other species to demonstrate the distinctiveness of the interactions between this genus and others in the community in which they occur.

The color of flowers is ecologically significant because they affect the visibility and desirability of the flowers to different pollinators. Yellow flowers are attractive to bees and some other insect groups and are relatively infrequent in the birch woodlands and heathlands of temperate and boreo-montane regions upon which this study is based (16% of species, see Table S2). Given this, the flower color and tendency to form dense patches under open canopies means that the *Melampyrum* plants are likely to constitute an important pollen and nectar resource for animals that rely on such food sources. Ant dispersal of *Melampyrum* seeds is another route to providing food availability for woodland species—ants (and other animals) are attracted by the oily appendage to the seed known as an elaiosome [29]. Wood ants often build large, mounded nests and as such are ecosystem engineers in their own right, moving leaf litter and contributing to decomposition and detrivorous trophic levels.

*Melampyrum* species are hemiparasitic (as is a third Orobanchaceae species present, *Euphrasia officinalis*) forming haustorial connections with woody shrubs and tree species such as *Vaccinium myrtillus*. This strategy is significant—particularly in forested systems—because it allows the plants to accumulate more carbon than would be possible to support the annual perennation and seed set that this species exhibits [30]. This essentially means that the hemiparasites redistribute carbon from hosts into resources that are more accessible to ground-dwelling flora and fauna. Nitrogen is also redistributed when hemiparasites syphon nutrients from hosts resulting in leaf tissue having a higher N concentration than most other herbaceous species and mimicking the role of legumes in providing N-rich leaf litter when plants senesce [31]. The annual lifecycle means that these inputs occur as a pulse of nutrient-rich materials in a system that is flooded with low quality litter from trees and in patches that enhance diversity at small scales.

The final ecosystem function provided by *Melampyrum sylvaticum* and *M. pratense* of note is that of provision of resources to its own parasites, namely rust fungi which find suitable habitat on the underside of leaves, and which can be themselves threatened species [32]. However, this trait is not captured in the existing dataset or analysis and therefore raises pertinent questions regarding the legitimacy of an approach which is so heavily data-reliant. These questions are addressed in the following section.

### *4.2. Caveats and Limitations in Using Ecosystem Functioning*

Some caveats exist with regards to using functional rarity as a method of prioritizing species for translocation. These caveats are not insurmountable problems but may affect how the concepts are applied to aid conservation decision-making.

#### 4.2.1. Function Is Relational and Therefore Context Dependent

Functional rarity is only relative to the other species in each site/assemblage included in the analysis, so species distinctiveness indices may change according to how many communities are analyzed and how unique they are in each of those communities. For this

reason, species under consideration for translocations into a site must be considered on a case-by-case basis so that the relative functional distinctiveness is calculated appropriately. This might incur more field surveys and become a barrier to proper consideration of functional distinctiveness in translocation projects.

An alternative to generating species lists through site-based surveys is to use published lists of species assemblages appropriate to the ecosystem or location forming the focus of the conservation intervention. These might constitute phytosociological community lists if working with plant communities, or other published information relevant to assemblages in other taxonomic groups. If such information has not been published, online resources such as the Global Biodiversity Information Facility (https://www.gbif.org/) can be used to generate location-specific species lists which can be tailored to address particular taxonomic groups or functional types. These bespoke lists can also be defined by time period to incorporate the species that were once resident but no longer found in a given ecosystem or location. The advantage of this for reintroduction is being able to objectively evaluate the relative contribution that a species might have made in the past, and decide whether the loss of that ecological role warrants a higher prioritization for translocation into the site in question.

#### 4.2.2. Functional Descriptions Are Only as Good as the Data They Are Based on

In Section 2.2, I flagged the issue of deleting traits from the dataset where they were not available for a substantive proportion of the species included. This approach has been shown to be methodologically robust across a range of taxonomic groups when studying functional diversity [33]. However, the omission of traits obviously has implications for the evaluation of functional distinctiveness as it may result in omitted traits being overlooked and species erroneously being thought of as ecologically redundant within a set of sites and communities included in a study.

The analysis presented above highlights how closely overlapping the niches were of the two *Melampyrum* species and indeed, there may be cases when *Melampyrum pratense* might naturally replace *M. sylvaticum* and vice versa due to subtle advantages conferred by local habitat conditions. However, in Section 4.1, I highlight the capacity of *Melampyrum* species to host fungi, and it is important to acknowledge that this property was not identified using the trait-based analysis. Instead, it was identified from a review of peer-reviewed literature and might have been overlooked if the evaluation of functional role was limited to trait databases. Furthermore, different assemblages of fungal infection have been identified on the two species and this can be attributed to slightly different phenolic profiles that could only be discerned through biochemical investigations [34]. This demonstrates that functional distinctiveness may only emerge if we look closely enough and at the prescient features which are often unknown without extensive exploratory research.

#### 4.2.3. Functional Distinctiveness Might Not Be the Most Important Aspect of Ecological Function

In some circumstances, such as severely degraded habitats, the pursuit of distinct functional roles may not be the most important aspect of ecosystem dynamics to focus on. It is well known that species diversity is desirable in part because it brings ecological redundancy which in turn results in ecological resilience to ecosystem disruption from climate shocks, disease and erosion of ecosystem processes linked to global change [35]. For example, the ability of plants to disperse to suitable habitats is severely limited as a result of defaunation and the loss of dispersing animals [36] but the greatest impacts on plant dispersal result from the losses of large mammals that were generalist seed consumers and dispersers. In this study, functional redundancy resulting from having many species with very overlapping seed consumption preferences would have maintained a level of seed

dispersal even assuming numerous species extinctions. Consequently, the reinstatement of large mammals as seed dispersers will arguably have a much greater impact than focusing on the restoration of distinctive species that are probably more specialist in their feeding. A similar message can be drawn from a study on plant communities in Australia that indicated species loss did not necessarily translate into losses of function under future climate change scenarios [37]. However, the perception of functional redundancy is likely to be inflated given that only five traits were included in the study and many functions will have been overlooked by concentrating on traits such as growth form and specific leaf area [37]. Furthermore, other studies point to the importance of including specialist species in a variety of systems in order to improve the diversity of response to ecosystem disruption and maintain ecological processes [38]. Overall, it is true to say that ecological redundancy is protective of ecosystems to species loss when the functions are common to many species, but this fails to recognise the importance of many less obvious functions and the maintenance of these distinct functions is crucial to enhancing ecological functioning and community resilience.

### *4.3. Functional Prioritization Within the Wider Context of Conservation Translocations*

The distinctive ecological function of *Melampyrum pratense* and *M. sylvaticum* has been demonstrated here within a very narrow set of ecosystems in upland Britain but for this approach to be widely adopted, the key learnings need to be stated to allow for extrapolation to other scenarios. This section aims to outline a set of steps which will allow the assessment of functional distinctiveness to inform conservation translocations.

#### 4.3.1. Identify Degraded Ecosystems Suitable for Supporting Translocation

In most conservation translocations, the recipient site (i.e., the site at which translocated individuals will be released, planted or introduced as inoculated) constitutes an area where the focal species is thought to be able to survive to achieve improvement in the species' status. However, in the proposed approach, it is recognized that most ecosystems are degraded in some way, and the translocation of species might be prioritized where the species can address some of the losses of structure or function to benefit the recipient ecosystem, and not just the focal species itself. To this end, it makes sense to identify degradation that can be addressed through species restoration, rather than those that require abiotic manipulation, as candidate sites in which to use function-driven conservation translocations as a tool for ecosystem repair.

#### 4.3.2. Evaluate the Level of Species Loss

Although this approach places more importance on function than taxonomic identity, it is valuable to be able to evaluate the level of species loss against historic baselines which are recorded as species presence by site. The word 'evaluate' has been deliberately used here—in some cases, it might be as simple as comparing published species lists for a given ecosystem—however, in other cases where published lists do not exist, multiple sources of evidence should be consulted to assess the extent to which species that are currently missing might have ordinarily occurred there.

#### 4.3.3. Determine Functional Profile of the Community of Interest

Once an ecosystem has been identified and the expected or observed species presence has been defined, the approach outlined above using FUNRAR and FAMD packages could be employed to quantitatively describe the functional profile of that community and a set of reference communities reflecting similar climatic, edaphic and management histories. Other methods might be employed to similar effect by using checklists of traits that confer ecosystem function and comparing these across key functional roles as assessed

across a number of similar sites. However, less sophisticated techniques may fail to convey the interactions between traits, and species that might deliver combinations of traits might not be so effectively identified as can be achieved using the multivariate techniques applied here.

#### 4.3.4. Identify Key Functional Roles for That Community

Upon considering the functional profile of the recipient ecosystem with reference to other similar systems, it should be possible to infer which ecological processes are important to ecosystem function and resilience. In doing so, it will also be possible to identify those functional roles that have been lost from the system, and the traits that deliver those functions. A clear articulation of which ecosystem processes might need restoring or strengthening can then be made.

#### 4.3.5. Identify Species That Might Deliver Such Processes

Through quantitative analysis such as using FUNRAR and FAMD, or using qualitative methods of scrutinizing trait profiles of species from the same taxonomic grouping, species can be identified that might deliver the ecological functions with which the focal ecosystem(s) are thought to be deficient. The most obvious candidates are the species that have been lost from that site but the value of using a quantitative or structured approach to profiling the functional contribution of a species is that other species could be considered as ecological proxies and translocated under the term known as ecological replacement.

#### 4.3.6. Test the Hypothesis That Translocation Will Deliver Functional Enhancement

There is potential for conservation translocations to contribute to understanding niche limits of focal species [39] and this is also the case for understanding the functional role—the act of describing the functional distinctiveness and translocating a species into a community is essentially the process of hypothesis generation and testing. Exploratory methods such as those employed in this study—multivariate ordination—facilitate the generation of hypotheses as to what functional roles and ecosystem processes are missing. Monitoring can test the hypothesis that the functional role is being delivered although this is not necessarily as straightforward as assessing the success of the translocation in terms of survival, reproduction and recruitment. The monitoring of population dynamics of the translocated species must be accompanied by monitoring the impacts of the translocated species to gauge the nature and magnitude of ecological function. This might demand a wider range of skills and monitoring that would normally be associated with a conservation translocation as multiple trophic guilds and a range of environmental factors are potentially affected components.

The testing of hypotheses through conservation interventions such as translocation invites the exploration of scenarios which can help in planning and evaluating the success of a conservation translocation program. There are three likely outcomes: the first is that the translocation fails and the functions are not delivered; the second is that the translocation is successful in terms of establishing the population, but the predicted functional role is not fulfilled; the third scenario is where the translocation successfully establishes the founder individuals and they are functionally viable delivering the anticipated ecosystem processes and ecological interactions. To diagnose these scenarios, the monitoring scheme should be able to judge translocation success using success measures such as survival, reproduction and recruitment of offspring, but also assess functional impacts on other species and the abiotic environment.

### *4.4. Shifts in Functional Distinctiveness Under a Changing Climate*

As discussed above, functional role is a relational concept that relies on understanding the relative contribution of a given species within the context of the communities it occupies or those communities we might translocate them to. However, the nature of interactions is also influenced by the abiotic environment changing the extent to which species might have an advantage over others, or the extent to which a species can successfully deliver particular functional roles. The impact of global environmental change, including climate change on functional dynamics has been demonstrated in various groups of organisms including estuarine invertebrates and fish [40], bats [41] and birds [42], and over geologic timescales that reveal multi-trophic impacts of climatic fluctuations [43]. This dynamic environment and its potential to affect the relative distinctiveness of a focal species promotes the comparison of functional profile across sites that represent comparable but differing environments [44] as I recommend in the above approach, but also that the different environments are further scrutinized to explore the potential for shifts of functional distinctiveness vs. functional redundancy that a changing environment will incur.

## 5. Conclusions

Our success in slowing the global decline of biodiversity will, in part, depend on maintaining abiotic and biotic interactions that deliver the niche requirements of threatened species. Being able to accurately describe the dimensions of an ecological niche is key to the effectiveness of interventions such as conservation translocations and every attempt to create a population of an endangered fungi, plant or animal is essentially a test of our understanding of the species' niche. However, organisms are not passive receptors of whatever their surroundings throw at them, and they in turn impact upon the environment and other organisms around them. This leads to the key message of this paper: while ecosystem-level processes are essential to maintain survival of the species we prioritize and conserve, they also form part of the rationale for undertaking a translocation, and as conservation scientists, we have a responsibility to understand and facilitate these community-level roles. Growing evidence suggests that rare species deliver distinctive functions that can sustain biogeochemical processes and maintain ecosystem resilience to external perturbations. In a world where we cannot save everything, species that are functionally distinct should be prioritized more highly than those that might be equally rare, but functionally redundant. The evaluation of species contributions to ecosystem function in the context of past or proposed conservation translocations is likely to improve our understanding of the threatened systems we are trying to protect, the success of conservation translocations, and ultimately, will help maintain resilience in systems facing multiple threats and their cumulative impacts.

**Supplementary Materials:** The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/wild3030030/s1, Table S1: DalrympleSE_Wild_SuppMat1_SpeciesPresenceBySite.xlxs; Table S2: DalrympleSE_Wild_SuppMat2_Mel_comm_traits.xlxs, Table S3: DalrympleSE_Wild_SuppMat3_FAMDoutputs.xlxs.

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**Graphical Abstract Explanation:** Organisms are not just passive receptors of their surroundings but functional in their systems forming interactions that can facilitate resilience and maintain biodiversity promoting them as species to be restored through conservation translocation. The genus *Melampyrum* L. has a unique set of ecological attributes that combine to fulfill a distinct functional role in the woodland and heath systems included in this study. Green arrows represent requirements for suitable climate, pollination, hosts and dispersal vectors that maintain the species in situ. Red arrows convey potential for negative or stabilizing processes such as fungal infection, competition and adverse weather. Yellow arrows represent functions that benefit the wider ecosystem through water and nutrient cycling, host and competitor suppression, and provision of nectar, pollen, seeds, elaiosomes and habitat.

## Abbreviations

The following abbreviations are used in this manuscript:

| | |
|---|---|
| FAMD | Factor analysis of mixed data |
| FUNRAR | Functional rarity |

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