RESEARCH ARTICLE

UN Decade on Ecosystem Restoration

An objective-based prioritization approach to support trophic complexity through ecological restoration species mixes

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Abstract

1. Reassembling ecological communities and rebuilding habitats through active restoration treatments require curating the selection of plant species to use in seeding and planting mixes. Ideally, these mixes should be assembled based on attributes that support ecosystem function and services, promote plant and animal species interactions and ecological networks in restoration while balancing project constraints. Despite these critical considerations, it is common for species mixes to be selected opportunistically. Reframing the selection of seed mixes for restoration around ecological objectives is essential for success but accessible methods and tools are needed to support this effort.

2. We developed a framework to optimize species seed mixes based on prioritizing plant species attributes to best support different objectives for ecosystem functions, services and trophic relationships such as pollination, seed dispersal and herbivory. We compared results to approaches where plant species are selected to represent plant taxonomic richness, dominant species and at random. We tested our framework in European alpine grasslands by identifying 176 plant species characteristic of the species pool, and identified 163 associated attributes affiliated to trophic relationships, ecosystem functions and services.

3. In all cases, trophic relationships, ecosystem functions and services can be captured more efficiently through objective-based prioritization using the functional identity of plant species. Solutions (plant species lists) can be compared quantitatively, in terms of costs, species or objectives. We confirm that a random draw of

plant species from the regional plant species pool cannot be assumed to support other trophic groups and ecosystem functions and services.

4. *Synthesis and Applications*. Our framework is presented as a proof-of-concept to help restoration practitioners better apply quantitative decision support to plant species selection to efficiently meet ecological restoration outcomes. Our approach may be tailored to any restoration initiative, habitat or restoration targets where seeding or planting mixes will be applied in active treatments. As global priority and resources are increasingly placed into restoration, this approach could be advanced to help make efficient decisions for many stages of the restoration process.

KEYWORDS

decision support, functional traits, optimization, plant traits, seed mixes, species selection, trophic networks

1 | INTRODUCTION

The specific objectives of terrestrial ecological restoration will vary, but generally aim to return a habitat to a naturally functioning and stable state. Restoration is often operationalized through the planting or seeding of mixtures of plant species as an active treatment meant to re-establish plant communities in degraded sites, usually informed by the plant species composition at reference sites (Brudvig & Mabry, 2008; Zobel et al., 1998). This begins by defining a species pool for the ecosystem of interest (the regional species pool, Zobel et al., 1998), and by taking stock of what species can be sourced from the wild or from commercial native seed producers (the restoration species pool; Ladouceur et al., 2018; Zobel et al., 1998). However, seed and planting mixes used for restoration are often a low-diversity subset of the relevant species pool and are composed opportunistically (Barr et al., 2016). Species selection must be balanced within project constraints (e.g. budgets, labour, time) and within other project targets (e.g. increase plant cover, prevent erosion). These species mixes have a major impact on restoration success and have implications for the multi-taxa functionality of the restored ecosystems (Guiden et al., 2021). How species mixes can be optimized to maximize restoration goals efficiently within project constraints remains an open question and an urgent task for implementing the United Nations Decade on Ecosystem Restoration.

It is widely recognized that rebuilding habitats requires the consideration of ecosystem services and functions, fauna and plant–animal relationships (Kollmann et al., 2016; McAlpine et al., 2016). Integrating these relationships in ecological restoration is a complex task that remains largely unaddressed despite increased calls for consideration (Cross et al., 2020; Dixon, 2009; Lindell, 2008; Majer, 1989, 2009; Menz et al., 2011). Plant functional traits can help identify ecosystem services or functions facilitated by plant species, and optimizing functional diversity or particular trait convergence in restoration species selections has been shown to lead to favourable outcomes

(Brudvig & Mabry, 2008; Laughlin et al., 2018; Wang et al., 2020). Fauna also contribute crucial ecosystem functions to plants, such as seed dispersal (regeneration), pollination (seed production), herbivory (reduction of competitive dynamics) and patchy nutrient return (Olff & Ritchie, 1998). Optimizing plant species mixes to facilitate multiple ecosystem services and functions, including those facilitated through trophic relationships, could thus enhance restoration success. This has been demonstrated in the establishment of fruit-bearing trees to facilitate dispersal from other diverse patches by frugivores in tropical rainforests (Heelemann et al., 2012; Lamb et al., 1997), but relationships like these are important in other habitat types as well, and remain underexplored in restoration ecology.

However, the restoration of ecosystem services, functions and animal communities simultaneously is challenging due to complex processes, life cycles and dependence on plants as well as other trophic levels (Chan et al., 2006; Guiden et al., 2021). Plant–animal interaction networks, both mutualistic (pollination and frugivory) and antagonistic (herbivory), are highly non-random (Bascompte & Jordano, 2007; Lewinsohn et al., 2006; Rezende et al., 2007), and a disruption in these interactions can lead to trophic cascades across and within systems (Knight et al., 2005; Valiente-Banuet et al., 2015). Plant–animal interaction networks are often nested, that is, some species have many interactions in their networks, and many species have few (Bascompte et al., 2003). When considering balancing project constraints and restoration targets in a relatively low-diversity species mix for restoration, it is unlikely that a random draw from the regional plant species pool will provide resources to optimize trophic networks and other ecosystems services and functions. Systematic decision-making can quantitatively support complex multivariate decision-making problems such as this (Chan et al., 2006; Hill et al., 2014; M'Gonigle et al., 2016), with extremely flexible and diverse potential applications.

Here, we present a proof-of-concept for the optimization of active restoration species mixtures (for seeding or planting treatments) for supporting different objectives. We used species-rich European

subalpine and alpine calcareous grasslands as a case study. These habitats are sensitive to disturbance, and impacted by ski resorts and other tourism activities, making them a target system for ecological restoration across European Natura 2000 sites (Garcia-Gonzalez, 2008). We identified 176 plant species that frequently occur in the target ecosystem on a biogeographical scale as the potential regional and restoration species pool of interest (Ladouceur et al., 2018; Zobel et al., 1998). We used trait databases and literature to compile traits related to regeneration and relationships between the 176 plant species in our species pool and the insects, birds and mammals that are typical of these habitats and depend on particular plant species for various life stages. Hereafter, we refer to the traits and aspects of plant species that represent these relationships and characteristics of interest, as plant attributes.

Our primary aim is to develop and evaluate a quantitative decision-making framework to assist in species selection for seeding and planting mixes for restoration projects. To do so, we designed five objectives for prioritizing plant attributes that support ecosystem functions, services and trophic dependencies. We optimized for these objectives by finding the smallest number of plant species needed to deliver all of the attribute targets set within each objective (Possingham et al., 2000). We then developed four plausible species selections to compare with prioritized selections including a focus on dominant species, random draws from the plant species pool to represent different taxonomic resolutions, and completely random draws from the plant species pool. We used our study system to investigate whether optimized species pools deliver objectives for ecosystem functions or services more efficiently than selecting dominant plant species, for taxonomic richness, or randomly.

2 | MATERIALS AND METHODS

We designed and tested an optimization approach to prioritize species mixes for planting or seeding in restoration projects based on ecological objectives. Below, we describe how we (a) selected plant species that represent a defined regional species pool; (b) identified plant attributes that contribute to different restoration outcomes; (c) constructed objectives and optimized attributes and (d) evaluated across optimized plant species mixes based on objectives.

2.1 | Species selection

We compiled a list of the most frequent native species occurring in alpine calcareous grassland habitat types on a continental scale, using a synthesis of >1 million field surveys (Schaminée et al., 2016), reporting species frequencies in the habitat types of the European habitat classification system (EUNIS, https://www.eea.europa.eu/data-and-maps/data/eunis-habitat-classification), directly assigned to habitat types of conservation concern (see Table S1). We identified native plant species that occur above a particular frequency (>5% of total occurrences) in calcareous alpine grassland habitat types on a European-wide scale. Expert opinion suggests that

species below this frequency were found to be more typical of other habitat types. This resulted in a list of 176 native plant species that occur frequently in the calcareous alpine grasslands of continental Europe. We considered this to be the species pool of this habitat and we assumed all species can co-occur or can coexist. Furthermore, we consider all plant species in the pool as equal candidates for inclusion in seed mixes to meet prioritization objective targets.

2.2 | Attribute selection

For the 176 plant species that were of interest for our goals, we collated traits related to dispersal, phenology and nitrogen fixation available from the TRY plant trait database (Kattge et al., 2011), as well as associations with mammals, birds, and herbivorous and pollinating insects from additional sources (see Table 1). The list of associated faunal species was refined to keep only species that occur in this habitat. Plant species frequency of occurrence values was used to rank plant species' relative abundance within the habitat type on a biogeographical scale, which we used to classify plant species dominance for a fixed species list for comparison with prioritized objectives (Table 1, see Table S1).

We then grouped the 163 plant attributes into nine broad categories based on the ability to support specific ecosystem functions or services (Table 1): bird trophic diet, bird herbivory, bird shelter, seed dispersal syndrome, Lepidoptera relationships (species specific-pollination, herbivory), pollination syndrome, mammal herbivory, nitrogen fixation and flowering month. The range of attributes supported by plant species varied greatly, with some highly specialized plant species supporting only one attribute (e.g. *Galium estebanii*) while others support many attributes (e.g. *Poa alpina*, alpine meadow grass (56 attributes) and *Sedum album*, white stonecrop (58 attributes)) (see Table S1).

To assign attributes to species we used a binary classification scheme, where a value of 1 was used when an attribute was present in a given plant species, resulting in a plant species-attribute matrix. In some instances, the presence of an attribute is dependent on the connection between the plant species and a species of other trophic groups, such as birds or butterflies (Lepidoptera). Some Lepidoptera species depend on different plant species at different life stages (larval herbivory vs. adult pollination/visitation), which we accounted for (Table 1). For birds, we connected trophic dependencies between attributes. For example, the plant species *Aster alpinus* (alpine aster) has a beetle pollination syndrome, and the bird *Turdus torquatus* (ring ouzel) feeds on beetles as part of its diet, so alpine aster is potentially an important habitat component for beetles, and the ring ouzel (see Table S1). Because we used categorical trait/attribute values here, we did not average traits across species when multiple values were found. If a plant species was represented in the data as having multiple dispersal syndromes, for example, we recorded them all. Additionally, we recognize not all plant species provide equal quantities of resources for other trophic levels and that our binary classification scheme currently does not reflect that. This approach is adaptable to represent different types of relationships flexibly;

TABLE 1 Plant species attributes, ecological role and data source of each attribute used, grouped by broad ecosystem function or service category. Complete list in Table S1

Broad attribute category (# of attributes)	Plant attributes	Ecological significance and explanation of objective approach	Source
Attributes related to trophic, dependencies, ecosystem functions and services			
Bird shelter (1)	Shrub plant growth form	Seed dispersal services	(Cramp, 1978; del Hoyo et al., 2016)
Herbivorous Bird Diet (20)	20 species of alpine bird that occur in these habitats (by expert opinion and available data). The herbivorous diet of each bird was identified, and connected with the plant species pool, each bird species is treated as an attribute		
Insectivorous Bird Diet (28)	28 species of alpine bird that occur in these habitats (by expert opinion and available data). The insectivorous diet of each bird was identified, and connected with the insectivorous pollination syndrome attribute of the plant species pool, each bird species is treated as an attribute		
Dispersal syndrome (8)	Wind, endozoochory, exozoochory, humans, insects, water, explosive, unassisted	Natural dispersal mode related to self-regeneration	From (Kattge et al., 2011) via (Diaz et al., 2004; Fitter & Peat, 1994; Gachet, n.d.; Kleyer et al., 2008, n.d.; Moretti & Legg, 2009; Paula et al., 2009; Poschlod et al., 2003; Royal Botanic Gardens Kew, 2008)
Lepidoptera Pollinator (18)	18 species of European butterflies and moths (Lepidoptera) that are recorded as being a pollinator of a plant species in the plant species pool of this habitat	Specific Lepidoptera species–plant relationships, representing the use of different plants throughout life cycles (larval and adult)	(German Federal Office for Nature Conservation, n.d.; Leraut, 2016; Paolucci, 2013; Steiner et al., 2014; Willner, 2016, 2017; Ziegler, 2019)
Lepidoptera Herbivory (64)	64 species of European butterflies and moths (Lepidoptera) that have been recorded as feeding directly on a plant species at the larval stage in the plant species pool of this habitat		
Pollination syndrome (11)	Main mode of pollination of each plant species, and the insect taxon considered to be most important for pollination: Ants, bees, beetles, bumblebees, flies, Hymenoptera, self, Syrphidae, Thysanoptera, wasps, Orthoptera, wind	Pollination syndrome including broad insect taxons, representing general plant–pollinator relationships	From (Kattge et al., 2011) via (Diaz et al., 2004; Fitter & Peat, 1994; Gachet, n.d.; Moretti & Legg, 2009; Poschlod et al., 2003)
Mammal Herbivory (4)	Ingested by mammals generally, and specifically herbivory by marmots, ibex, and chamois, key herbivores of this system	Seed dispersal and grazing services	(Andreoli et al., 2016; Bassano et al., 1996; Parrini et al., 2009)
Nitrogen Fixation (1)	Leguminous plant species	Soil quality improvement	(Schaminée et al., 2016)
Flowering month (9)	Represents every month February–October	Provision of seasonal resources for pollinators	(Aeschinmann, 2004; Plantarum, n.d.)
Attributes used for comparison objectives			
Taxonomic Diversity/ Biodiversity by Genus (115)	One plant species is selected from each taxonomic genera (115 genera total) within the defined regional species pool	For this objective, a species from each taxonomic genus is selected randomly to represent a null representation of taxonomic richness	(The Plant List, 2013)

(Continues)

TABLE 1 (Continued)

| Broad attribute category (# of attributes)	Plant attributes	Ecological significance and explanation of objective approach	Source
Taxonomic Diversity/ Biodiversity by Family (34)	One plant species is selected from each taxonomic Family (34 total) within the defined species pool	For this objective, a species from each taxonomic family is selected randomly to represent a null representation of taxonomic richness	(The Plant List, 2013)
Frequency (1)	Here, we use frequency of occurrence values obtained from the European Vegetation Archive to estimate which species are the most frequently occurring within these habitats on a European-wide scale, we then use this as a proxy for species 'Dominance' here. Frequency of occurrence values was used to rank species, and then the top *n* frequent species were selected to match the *n* of species required for the Comprehensive objective (Table 2)	Dominance is associated with a contribution to carbon, nutrient and water cycling (Grime, 1998). Dominant species are often selected in plant species mixes for restoration, as they are known to represent key species of habitats or be helpful facilitators. We use this as another 'null' model for comparison with prioritized objectives	(Chytrý et al., 2016; Schaminée et al., 2016)
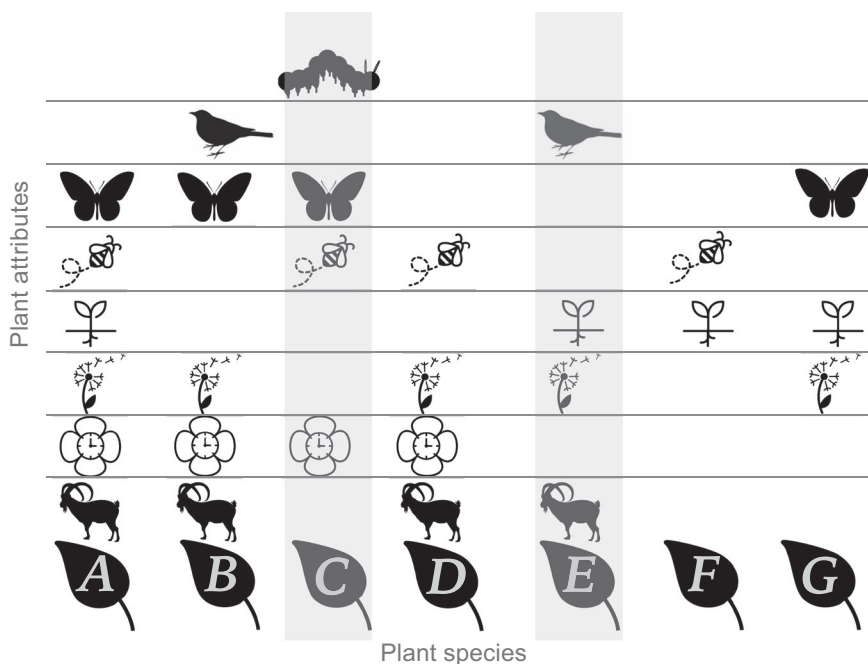
FIGURE 1 Conceptual framework of plant species prioritization for attributes that enable ecosystem services: a simplified example. Every plant species A–G represented in each vertical column has a unique combination of attributes in the plant species-attribute matrix which are represented in each horizontal row. Plant species C and E capture each attribute just one time when selected together. This represents a comprehensive species mix that captures all desired attributes within the plant species selected. All images sourced from The Noun Project

for example, by weighting the importance of attributes among plant species. Here, we maintain a binary classification scheme of attributes to maintain comparability across objectives.

2.3 | Objective construction, comparison lists and prioritization

To construct objectives, we first set targets and create problems to be solved (Figures 1 and 2). We constructed five objectives

for prioritizing species based on setting targets which deliver (a) all desired attributes within the plant species selected (Figure 1) ('Comprehensive', *N* = 163 attributes); (b) specific processes and taxa that play key roles in ecosystem regeneration, specifically, species-specific seed dispersal and pollination for birds ('Bird', *N* = 48 attributes) and (c) Lepidoptera Relationships (pollination and herbivory) ('Lepidoptera Relationship', *N* = 82 attributes; Figure 2), (d) representation of both levels of taxonomic plant richness in combination with Lepidoptera relationships ('Pairwise Lepidoptera + Plant Rich Family', *N* = 116 attributes including plant families counted as an
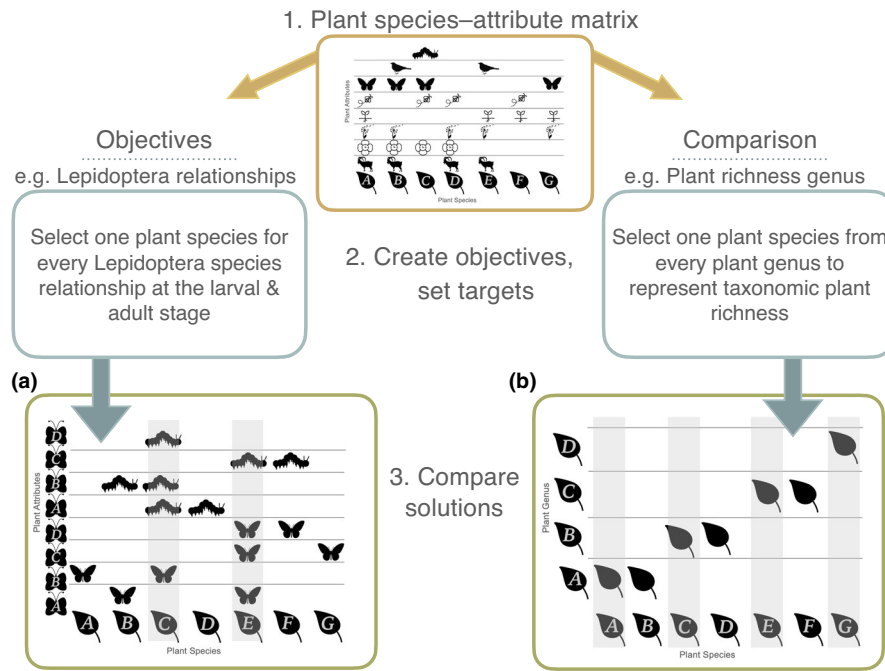
FIGURE 2 Conceptual framework showing the workflow for this method and two simplified visualizations of objectives used in this study. Panel (a) visualizes the 'Lepidoptera relationships' objective. In this example, attributes are Lepidoptera species A–D at both the larval and adult stage and each has a relationship with plant species A–G. Panel (b) visualizes the 'Plant richness genus' comparison objective. In this example, attributes are the genus a plant species belongs to, and plant species are selected randomly, one to represent every genus to represent taxonomic diversity. In these simplified visualizations, grey shaded bars represent selected plant species for solutions that meet the objectives using the minimum number of plant species

attribute) and (5) ('Pairwise Lepidoptera + Plant Rich Genus', *N* = 197 attributes).

We compared the outcomes of these five objectives to four comparison lists—plant species selections meant to serve as plausible opportunistic approaches for creating species mixes. These include (a) a fixed list of the most frequent species occurring in these habitats at a biogeographical scale, as a proxy for dominant species ('Dominants', *N* = a fixed list of 37 plant species), (b) a representation of plant diversity through taxonomic richness at the family ('Plant Rich Family', *N* = 34 families) (c) genus level ('Plant Rich Genus', *N* = 115 genera; Figure 2) and (d) selecting plant species at random ('Random'; see Table 2).

To compare a species mix of dominant species to prioritized objectives, we sorted dominant species by frequency of occurrence values, and created a fixed list of 'dominant' species equal to the number of species in the Comprehensive solutions for direct comparison between the performance of the two species lists in terms of representing attributes that potentially support particular ecosystem functions and services. We consider a single presence of an attribute so that objectives and comparisons could be directly contrasted.

To efficiently find the smallest number of plant species that met the target-based objectives (Table 1), we used the 'minimum-set' problem formulation which is commonly applied to spatially explicit decision-making that cost-efficiently meet targets for conservation features (e.g. habitats, species ranges or ecological

processes; Possingham et al., 2000). We adapted inputs to apply it to our non-spatial problem (Hill et al., 2014; see Appendix S1). To do so, we replaced geographical spatial units with individual plant species, and replaced the features found in those geographical units with the functional attributes assigned to each plant species, resulting in a plant species-attribute matrix (Figure 1). Each plant species had a unique set of attributes, each attribute with a binary value of '0' or '1', and these values were summed to produce a 'attribute sum' for every plant species, that is, the number of attributes that characterize each plant species. For each objective, complementary sets of plant species were identified where collective attributes achieved the minimum targets set (where we considered a minimum target of 1; Table 2). We set equivalent costs across species (value of 1) so that we could test the outcomes of prioritizing plant species across different objectives independent of costs.

Once objectives were set, all problems were solved using the R package PRIORITIZR (Hanson et al., 2019), with Gurobi 9.0 as an algorithmic solver (Gurobi Optimization Inc., 2018). For each prioritized objective, we set problems in prioritizr with an optimality gap of zero, and the 'add_gap_portfolio' function to produce a portfolio of 100 different solutions, where the first solution is the optimal solution to the original data formulation, and every solution thereafter meets targets within the pre-specified optimality gap. This relative gap specifies a threshold worst-case performance for solutions in the portfolio, so in this case, we chose to accept 100 solutions no matter

TABLE 2 Summary of how the nine ecological restoration prioritization objectives were implemented in the decision-support software prioritizr, showing the details of the attributes within each objective, and the number of attributes targeted to be included in the selection of plant species for each objective. Each prioritized objective (Comprehensive, Bird, Lepidoptera Relationship, Pairwise Lepidoptera + Plant Rich Family, Pairwise Lepidoptera + Plant Rich Genus) aims to select the fewest number of plant species, while meeting all objective targets. These five prioritized objectives are then compared to four species selections that can serve as a null comparison (Dominants, Plant Rich Family, Plant Rich Genus, Random)

Objective	Attributes description	Objective targets
Prioritized objectives		
Comprehensive	163 attributes, including all attributes from Table 1 specified to the species level	Ensure all 163 single species-specific attributes are represented at least once
Bird	49 attributes representing 28 species of alpine grassland birds, under three broad ecosystem function categories: herbivores (20 bird sp.), insectivores (28 bird sp.) and bird shelter (1 attribute)	Ensure all 49 bird-related attributes are represented at least once
Lepidoptera Relationship	82 attributes representing 76 unique species of butterflies and moths (Lepidoptera) under two broad ecosystem function categories: pollinators (18), larval (64). 6 Lepidoptera species have multiple life-stage requirements represented in the dataset	Ensure all 82 species-specific Lepidoptera-relationship-related attributes are represented at least once
Pairwise Lepidoptera + plant rich Family	34 plant taxonomic families + 82 plant–pollinator relationships as attributes	Include 1 plant species belonging to every family, and all 49 plant–pollinator-related attributes are represented at least once
Pairwise Lepidoptera + plant-rich Genus	115 plant taxonomic genera + 82 plant–pollinator relationships as attributes	Include 1 plant species belonging to every single genus, and all 82 plant–pollinator-related attributes are represented at least once
Comparison objectives		
Dominants	Species frequency of occurrence on a biogeographical scale identified and rank ordered in terms of dominance (Chytrý et al., 2016; Schaminée et al., 2016)	Include the n most frequent plant species to match n species required for the Comprehensive selection, as a single fixed list to allow direct comparison
Plant Rich Family	34 plant taxonomic families in the dataset	Include 1 randomly selected plant species belonging to every family to represent 'plant biodiversity' at the Family level
Plant Rich Genus	115 plant taxonomic genera in the dataset	Include 1 randomly plant species belonging to every genus to represent 'plant biodiversity' at the genus level
Random	Select plant species randomly in intervals of 5, ranging from 5 to 120 species	No attribute targets

the performance relative to the optimal (gap = 0). For all random solutions for comparison, we used 'add_shuffle_portfolio' (instead of the gap portfolio). This randomly reordered data prior to solving problems, so plant species were selected under different data formulations to produce a random selection process. These problems can also be solved using MARXAN, and we provide more details on using these applications for these applications in the Supplementary Information (see Appendix S1).

2.4 | Evaluation

In comparing and evaluating approaches to plant species selections for species mixes, prioritizr produces two important outputs: optimal solutions to meet targets for objectives (in this case, a plant species list); the feature representation indicating the number of plant attributes represented by a solution, relatively (to possible maximums) or absolutely (total number). We used the first

optimal solution of each objective to compare the attribute sum of the plant species selected (see Table S1). We compared the mean values of the attribute sum using a Kruskal–Wallis chi-square test to assess differences in the total number of attributes (attribute sum).

We calculated the selection frequency of plant species across all 100 solutions generated to identify the relative irreplaceability of each plant species within a species mix to meet targets for each objective. Where a plant species had a selection frequency of 100 across solutions, we categorized it as '*irreplaceable*'. Irreplaceability can be interpreted as an index of the likely overall value of a feature, or in this case a plant species, in achieving an objective (Smith et al., 2018). Where a species was chosen between 1 and 99 times, we categorized it as '*variable*', and where it was chosen zero (0) times it was categorized as '*redundant*'.

We evaluated each objective's ability to capture the nine broad ecosystem functions and service categories defined in Table 1. To do so, we took the species identified in all 100 solutions for each

objective (see Supporting Information), identified the full list of attributes present (see Table S1) and calculated the percentage of attributes captured compared to the total number of attributes possible for selection in each broad attribute category (Table 1).

We compared our results to an ad-hoc selection of species that we approximated using a random species selection process. We selected plant species at random in intervals of 5 (ranging from 5 to 125 plant species) and calculated the proportions of attribute provision captured across the same nine broad ecosystem function categories. We considered the mean (50%), upper (75%) and lower quantiles (25%) of each random species selection across all solutions for comparison across objectives.

All prioritizations, figures and analyses were conducted using the R Studio version 1.3.1056 and R version 4.0 environment and language for statistical computing and graphics (R Core Development Team, 2019).

3 | RESULTS

Across the five ecological objectives, the number of plant species needed to meet each objective's targets varied widely. For example, the targets for the 'Bird' objective were met with only

five plant species, targets for the 'Pairwise Lepidoptera + Plant Rich Genus' objective required 119 plant species (Figure 3). We also found high variability in the number of attributes (the attribute sum) captured by the individual plant species selected in the solutions (max:59; min:2; see Table S1). The plant species selected in the 'Comprehensive' and the 'Lepidoptera Relationship' objective had a significantly higher attribute sum overall (Kruskal–Wallis $s^2 = 146.68$, $p = <0.001$, Table S3, Figure 4, see Figure S1) than found in the other objectives.

This prioritization approach favours plant species with a high attribute sum, yet also prioritizes plant species that supports unique or rare attributes, as these species may be considered irreplaceable (Figure 4). In the case of the Comprehensive and the Lepidoptera Relationship objective, many plant species were irreplaceable, representing specialist relationships. In contrast, in the bird objective, many plant species were of variable importance, and thus could be interchangeable (Figure 4; Table S4).

Figure 5 illustrates the number of plant species selected across the first solutions for each objective and the percentage of the attributes captured relative to the total number of attributes in each ecosystem function category. This demonstrates the trade-off between the number of plant species selected and the provision of minimum sets of attributes. It also examines how well a single objective
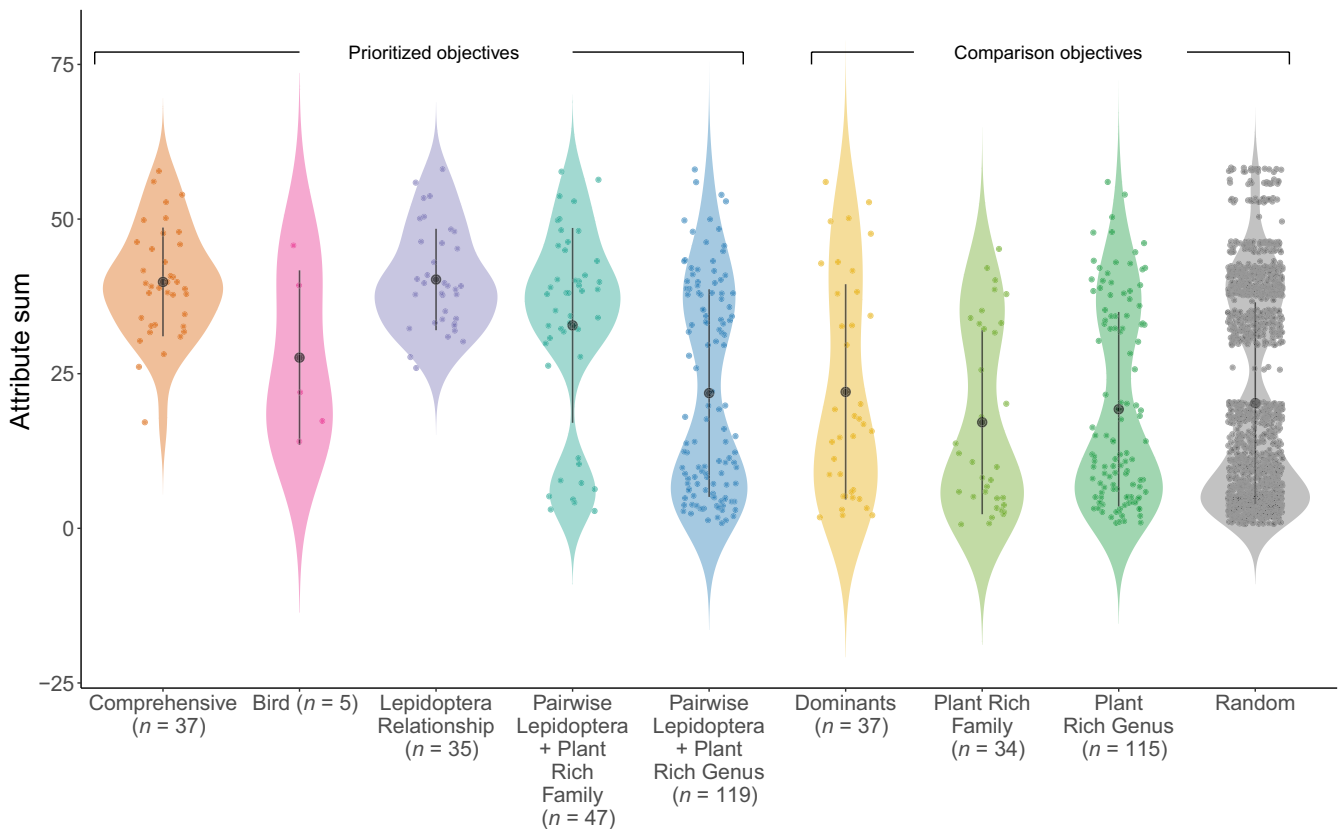
FIGURE 3 The attribute sum (total number of attributes per plant species) captured by each plant species in the first optimal solution of every objective. Each objective solution is labelled along the x-axis, and reflects the selection of species needed to meet the targets of that objective. Each point is a plant species. The large black points represent the mean and the bars represent the standard error around the mean. The shaded area represents the spread and the density of the data. n: number of plant species in the solution of every objective
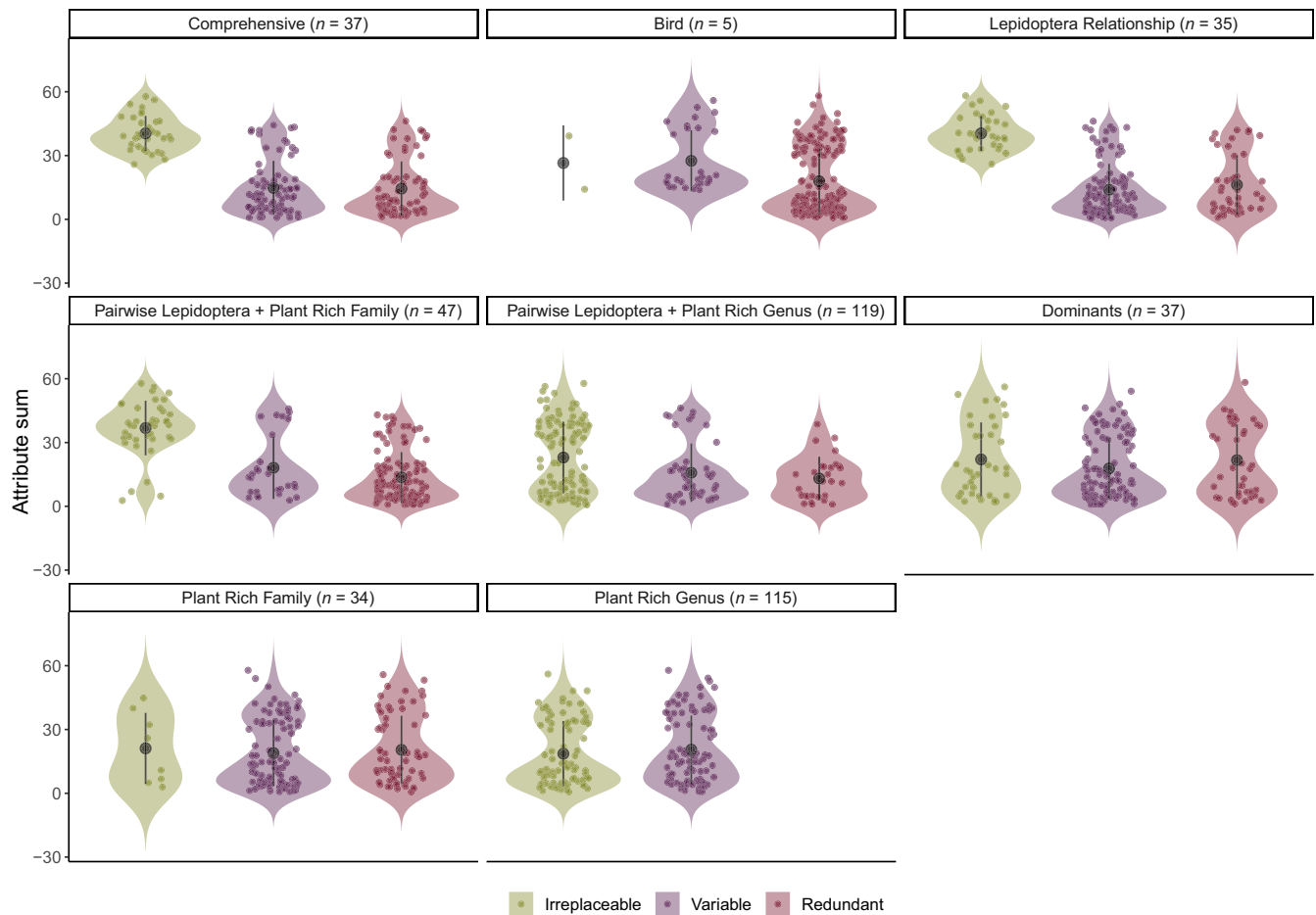
FIGURE 4 The attribute sum (total number of attributes per plant species) captured by each plant species for each objective, for plants species that were Irreplaceable (selection frequency (SF) = 100/100), Variable (SF = 99 > 1/100), or Redundant (SF = 0). Each point is a plant species. The black points represent the mean and the bars represent the standard error around the mean. The shaded area represents the spread and the density of the data

captures broad ecosystem function and services compared to the performance of other objectives.

Objectives that did not set out to prioritize a specific category of ecosystem function had variable performance. For example, the 'Bird' objective performed poorly for all plant–pollinator-related ecosystem functions, capturing <25% of the attributes needed to support plant–pollinator, nectar and larval functions (Figure 5). This is unsurprising given the 'Bird' objective only needed five plant species to achieve the targets. Alternatively, the 'Comprehensive' objective, which aimed to represent each of the 163 attributes found across the entire plant species pool once (and did so with 37 plant species), met 100% of targets set (1 of every attribute). However, the species prioritized in this objective performed no better than the random species selection for representing Genus and Family levels of plant taxonomic diversity representation (Figure 4).

Overall, the random selection of plant species performed well for ecosystem functions that are supported by common attributes across plant species (e.g. bird trophic, bird herb, bird shelter), but worse than our prioritization when the ecosystem function is supported by a highly specialized attribute (e.g. plant–pollinator relationships; see Figure S2). In general, the smaller the number of

randomly selected plant species, the worse the performance for providing ecosystem functions and services. Even when large numbers of randomly selected plant species are considered, provision of some trophic relationships or ecosystem function and service groups was found to be low (see Figure S2).

4 | DISCUSSION

Plant species have a unique combination of functional attributes that contribute to important ecosystem processes and trophic relationships in different ways. Here, for the first time, we have developed and tested an approach for prioritizing plant species to represent multiple plant attributes that potentially support trophic complexity and ecosystem services and functions in species mixes for active restoration treatments. Our results show that species selection approaches targeting for taxonomic richness, dominant species and/ or with a random approach may not support higher trophic levels and the ecosystem functions and services they provide as efficiently as our objective-based approaches. Critically, our results illustrate that higher trophic levels and ecosystem functions can, in some
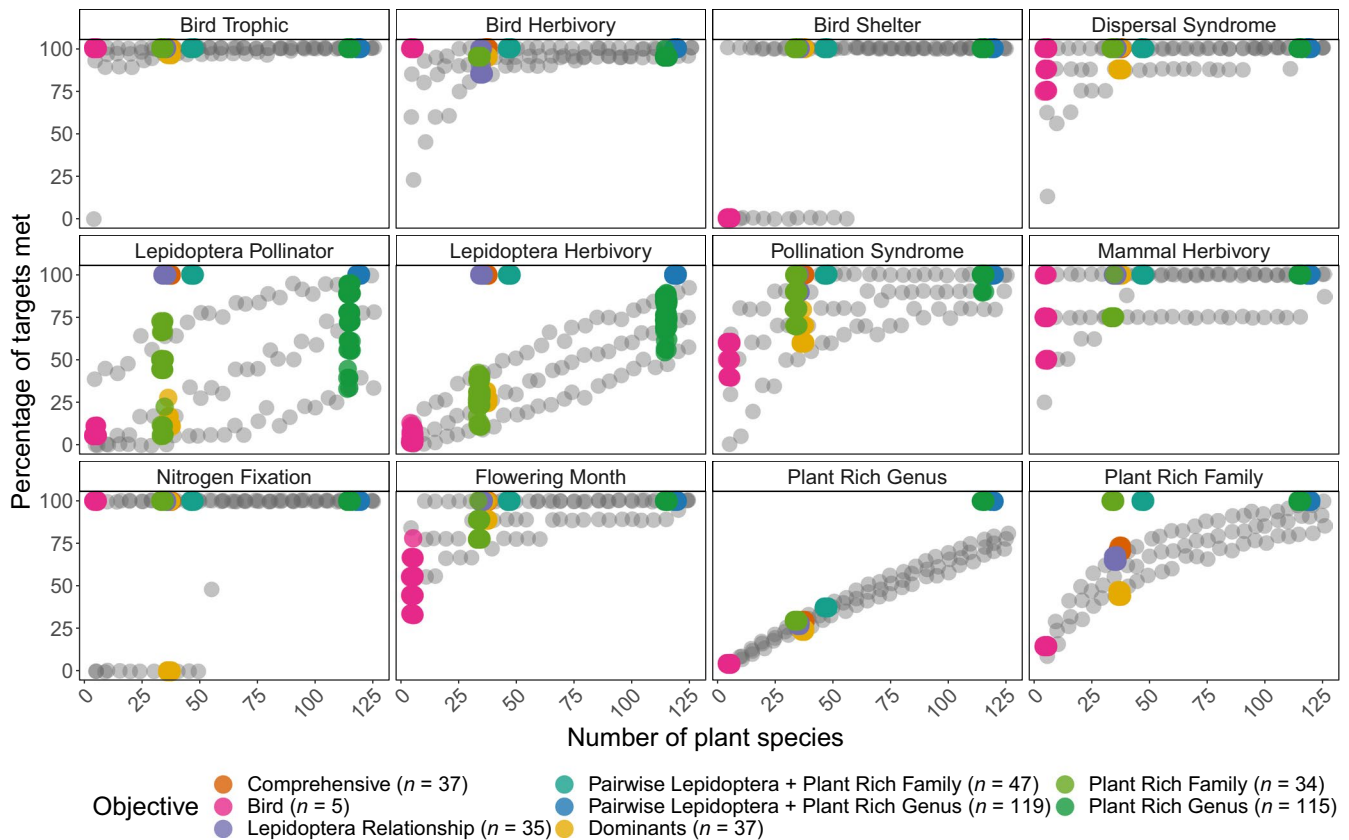
FIGURE 5 Trade-offs between number of plant species selected for each objective, and the corresponding proportion of ecosystem function targets captured compared across objectives. Optimizations were run 100 times for each targeted coloured objective and all unique runs are shown here as points. Grey points represent the mean, upper (75%) and lower (25%) quantiles of runs for randomly selected species in intervals of 5 from 5 to 120 plant species

instances, be supported well when plant species richness is relatively low. Conversely, trophic relationships, ecosystem functions and services can in some cases be unsupported and low while plant species richness is high. We confirm that a random draw of plant species from the regional plant species pool cannot be assumed to support other trophic groups and ecosystem functions and services. This has important implications for the design and implementation of species mixes for restoration projects which aim to reach multiple restoration objectives such as plant diversity, higher trophic levels and certain ecosystem functions and services tied to plant species identities.

4.1 | Prioritizing functional attributes

Some ecosystem functions and services are captured by plant species selections easily, even when these are not the targets of the objective. In these cases, the functional plant attribute is abundant (e.g. wind dispersal syndrome) within the plant species pool. For example, bird diets are often generalized to a plant genus or family (e.g. Asteraceae), so minimum diet requirements for the bird species represented here do not require many plant species to meet minimum provisional targets. By randomly selecting species from the species

pool, these attributes are often captured in a minimum amount of plant species. The bird objective only requires five plant species to provide a minimum diet for 28 species of alpine birds, and in practice a species mix designed for birds would benefit from higher representation of these plant functional attributes and diet options.

In other cases, where a specialist relationship between an attribute and a plant species exists, targets are not captured well, unless an objective is prioritized for such. For example, relationships between plants and insect herbivores are often specialized, making many plant species irreplaceable when optimizing the plant community for herbivores. The objectives for plant taxonomic richness, for dominant species and for randomly selecting species do not meet minimum targets for plant–pollinator relationships, even when up to 125 plant species are selected. The fewer plant species that are selected, the higher the risk that resources for herbivores and pollinators will not be provided within the plant species mix. However, when targeted, all Lepidoptera species relationships with particular plant species in terms of larval herbivory or pollination (82 Lepidoptera relationships total) can be represented at least once within a species mix with 35 targeted plant species. Negative changes within ecosystems can lead to trophic cascades (Knight et al., 2005), and in restoration, there is the opportunity to directly support these connections between organisms positively facilitate regeneration

processes and ecological networks (Harvey et al., 2017; Valiente-Banuet et al., 2015) through this framework. When considered this way, one can ask if the species pool used in restoration is providing adequately for the species pool of other trophic levels within that habitat while balancing multiple targeted outcomes.

Conversely, depending on how plant taxonomic diversity is defined (representing one species from every taxonomic Family or Genus), it is not always represented well by objectives prioritized for attributes, or by randomly selecting species, but can be captured efficiently through targeted selection. Additionally, both attributes and plant biodiversity can be captured efficiently together when both are set as targets (Pairwise objectives). Seed mixes matter for restoration success and can be optimized according to many factors (Barr et al., 2016), but require the balancing of multiple targets which is a complex multivariate decision-making task that can make use of decision-support tools as demonstrated here.

Additionally, seeding and planting treatments for restoration are restricted by many confounding constraints including budgets, labour and project size and so restoration species mix treatments are often quite low (Barr et al., 2016). Where constraints are present, prioritizing plant species to optimize particular targets can be a potentially beneficial method to decide which species to include in low-diversity treatments. This method has similarities to methods for filtering plant species lists based on particular targets (Brudvig & Mabry, 2008). This method also has similarities to selecting plant species to optimize functional diversity, or for the convergence of targeted plant trait representations for particular environments (e.g. traits that increase chances of survival in dry, harsh environments; Laughlin et al., 2018; Wang et al., 2020, 2021). However, our approach presented here is distinct from these other approaches, and it offers the unique advantage of optimizing targets according to flexible constraints and offers quantitative support for comparing different options easily both in terms of targets and cost. There is surely opportunity for future work to combine these approaches in the future.

4.2 | Indications and further development

To test this proof-of-concept, it was necessary to make some simplifying assumptions. Focusing on a study system with relatively good knowledge on frequently occurring plant species, we selected attributes based on available data in the target system. Rare plant species, which have not been thoroughly studied, are often documented as having few attributes, resulting selection bias towards representing common species. A prioritized solution can only be as good as the data available, and the prioritization objectives set out here are limited by the available data. Generalized data on pollination syndromes or seed dispersal syndromes of plant species can be limiting, as these relationships can be habitat specific. Although we used the best data available from a trait database and field guides, we recognize that next steps should include an improvement on data used. These data include plant–insect associations for additional insect taxa (e.g. wild

bees as pollinators or plant and leafhoppers as herbivores), and of improved occurrence data (for our work, no data on the altitudinal occurrence of moths were available). Local entomological specialists can help to compile realistic lists of plant–insect interactions, and we postulate that this method could also make excellent applied use of pollinator network or food web data across trophic levels.

A 'Comprehensive' species mix (Figure 1, Comprehensive objective) is one that captures all desired attributes within the plant species selected. Here, we focused on comparing the comprehensive approach to others to answer our questions and to demonstrate this proof-of-concept. In our approach, targets were set to ensure a minimum of one attribute was present in solutions, allowing for a direct comparison between objectives, but this means other plant species were categorized as redundant when not selected. In practice, including several species with the same attributes may be desirable as an insurance plan for species that do not germinate or that exhibit intraspecific variation. By including some redundancy of attributes, one can minimize the chance that this attribute will not be represented in the realized restored community. Three types of abundance are relevant for reaching restoration objectives: the species mixes used, including quantity and quality of each species (Frischie et al., 2020; Shaw et al., 2020), the final abundance of each species in a restored plant community and the final expression of each species attribute (including interspecific variation). Our approach can be adapted to consider abundances of attributes at all three levels, which may be a subject of further research.

Similarly, we assume that the cost of including a plant species is the same to test our questions independent of costs, but the approach can and should account for cost variation to acquire, store and reproduce seeds as this will likely hold great influence on prioritized solutions in practice (Jiménez-Alfaro et al., 2020). Reporting on the costs of conservation and management actions is largely inadequate and non-standardized (Iacona et al., 2018), and we know from previous research that only a small proportion of seeds are usually available for purchase (Ladouceur et al., 2018), and must be collected by hand, which is costly (Pedrini et al., 2020). Here, while we use the 'minimum-set problem', objectives can also be created that meet targets best within cost constraints. Prioritization approaches could also guide future efforts for native seed supply and policy by informing collection, farming and storage for an expanded restoration species pool. Furthermore, including these real costs in decision-making frameworks can help to plan efficient projects, and can be used to communicate budget constraints and needs in a robust way.

5 | CONCLUSIONS

This proof-of-concept is the first step towards framing future empirical research in optimizing species mixes for the ecological restoration of natural ecosystems. We call for empirical field tests for this approach to take place, which will require bringing together interdisciplinary collaboration across subfields of ecology and conservation. We provide a transparent and robust approach

that could move restoration efforts towards prioritizing plant species to maximize targets and minimize costs offering quantitative decision-making support. This approach could be applied to any system and/or targets which could also contributed to many stages of restoration decision-making and could play an important role in delivering efficient, targeted solutions. However, similar approaches will need robust ecological data to be applied to specific cases studies and restoration targets, preferably at regional or local scales.

AUTHORS' CONTRIBUTIONS

E.L., B.J.-A., P.H. and H.P. conceived the idea; E.L. and B.J.-A. designed the case study, defined and selected the plant species pool, and made a data collection plan; E.L., D.S. and R.v.K. identified, collected and requested appropriate data; P.P. and J.H.C.C. donated plant trait data; E.L. performed the analysis. J.M., H.P. and P.H. provided guidance on analyses and interpretation; E.L. and J.M. wrote the manuscript. All authors contributed to editing and shaping the manuscript into the final version.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.rjdfn2zbj (Ladouceur et al., 2021). Code necessary to reproduce results is available in a GitHub repository (https://github.com/emma-ladouceur/Prioritize-Species-Restoration) and archived with Zenodo (https://doi.org/10.5281/zenodo.4897014).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.