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Finding the perfect mix: An applied model that integrates multiple ecosystem functions when designing restoration programs

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ABSTRACT

We present an applied model that helps restoration practitioners select an ideal mix of species to plant in order to meet their restoration objectives. The model generates virtual plant communities designed to optimize the delivery of multiple ecosystem functions. We used an optimization approach to find the most cost-effective combinations of species to plant to optimize the delivery of four ecosystem functions: *rapid establishment of vegetation cover, soil building, biological soil health* and *resistance to invasion.* We used trait-function relationships to characterize species' effects on ecosystem functions. This model accounts for key operational constraints selected by the user, including budget, the number of species to plant, and which functions to consider. The user can also decide whether or not to maximize the functional diversity of the species mix to increase its *resilience to global environmental change.* To demonstrate the practicality of this approach, we derived optimal species mixtures for the restoration of forests damaged by Cu-Ni smelters in the City of Greater Sudbury (Ontario, Canada). The species mixtures generated by the model varied according to which functions and operational constraints were selected. Results show that the species mixtures that were the most effective at delivering multiple functions were also cost-effective, but were less functionally diverse. This tool provides restoration practitioners with cost-effective restoration strategies for managing the recovery of multi-faceted socio-economic and environmental values in disturbed landscapes.

1. Introduction

Decades of resource development have profoundly altered ecosystems in North America (Dudley et al., 2018; McClung and Moran, 2018) and caused drastic changes in biodiversity and ecosystem function (Bongaarts, 2019). Ecosystem restoration is a promising method to mitigate the impacts of resource extraction and provides an opportunity to enhance the ecosystem functions and services that communities benefit from (Hobbs et al., 2009; Jones, 2017). Vegetation re-establishment is typically the first step to initiate ecosystem recovery (Colloff et al., 2010; Vaughn et al., 2010). However, restoring a diverse suite of ecosystem functions can be a challenge. Restoration practitioners require robust tools to help them incorporate multiple restoration objectives (Costanza et al., 2017) and provide guidance on which plant species to include in their restoration species mix. These tools need to be flexible enough to account for site-specific objectives (Day et al., 2006). For instance, practitioners may want to enhance functional diversity to improve ecosystem resilience to global environmental change (Timpane-Padgham et al., 2017). Alternatively, in the case of acid-generating mine tailings, promoting functional diversity may not be desirable. In this case, planting functionally similar agronomic grasses might be preferred, because they can stabilize soils effectively, tolerate harsh growing conditions, and prevent the growth of deep-rooting species that could facilitate oxygen migration into reactive tailings (Guittonny-Larchevêque et al., 2016; Proteau et al., 2020). Tools also need to account for potential trade-offs between multiple restoration priorities (Burnett et al., 2019). For example, restoration activities intended to re-establish vegetation in Cu-Ni smelter damaged landscapes, including the application of lime to reduce soil acidity and soil metal availability, can have negative effects on culturally important

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wild blueberry species (City of Greater Sudbury, 2018). Applying a robust framework for the management of functional recovery can clarify goals and define priorities prior to selecting plant species to include within a restoration species mix (Williams and Lonsdorf, 2018).

Typically, species selection for restoration is based on species composition of a reference ecosystem (i.e., historical restoration; Burnett et al., 2019), or guided by expert knowledge on species' habitat preferences and their ability to achieve functional goals (Laughlin, 2014). Species selection may also depend largely on what is commercially available (Macdonald et al., 2015). These methods are limited in their ability to balance various management goals, and may not fully consider the financial constraints of restoration programs or the potential trade-offs between management objectives (Williams and Lonsdorf, 2018). To improve the integration of ecosystem functions in restoration programs, researchers have begun incorporating plant functional traits into decision-support tools (Rayome et al., 2019). Plant functional traits are morphological, physiological or phenological characteristics that drive ecosystem function and/or determine an individual's fitness (Violle et al., 2007). By providing a direct link between species identity and their functional role within the ecosystem, plant traits can provide a mechanistic approach to describe the influence species assemblages have on a particular ecosystem function (Jones, 2017). Trait-function relationships are not species-specific, and can be generalized over large geographic regions with different pools of candidate species (Shipley et al., 2016). For instance, the *Restoration Ecosystem Service Tool* (Rayome et al., 2019) was designed to test different plant species combinations using ordination techniques, and allows species to be selected iteratively based on their positions in a multivariate space of ecosystem functions. Alternatively, Ladouceur et al. (2021) developed a quantitative framework to select species for restoration that achieve multiple ecosystem functions and service targets based on both plant attributes and functional traits. Their approach minimizes the cost of restoration by determining the fewest species needed to meet specific restoration objectives. Both of these approaches identify the species that are most likely to meet such restoration objectives, but do not determine the relative abundance of each species that should be planted to achieve restoration goals. Laughlin et al. (2018) developed the *selectSpecies* R program that generates plant species assemblages. Assemblages are derived for only two restoration objectives at a time, including enhancing the functional diversity of the restored community and one other desired ecosystem function (such as pollinator habitat quality).

Multi-criteria decision analysis (MCDA) is another approach used to develop optimal species combinations for ecological restoration. MCDA has been widely used in natural resource management scenarios (Carpentier et al., 2016) and includes several techniques to integrate multiple sources of qualitatively distinct data into a single-dimensional metric (Feron et al., 2004; Linkov et al., 2009, 2011). Reubens et al. (2011) used this approach to select tree species that could achieve multiple environmental and socio-economic restoration objectives in degraded semi-arid regions. However, their tool does not factor in the cost to plant or prepare a site and does not find optimal species combinations required to achieve desired restoration goals within a limited budget.

In this study, we present a model that incorporates both a plant functional trait approach and MCDA principles to generate species combinations that optimize the delivery of multiple ecosystem functions in disturbed plant communities in need of restoration. The model accounts for key operational constraints, such as the budget, the number of species to plant, and the ecosystem functions to prioritize in the model. The model also allows the user to decide whether or not to maximize the functional diversity of the resulting species mix to create a community that is more likely to be *resilient to global environmental change*. We applied this model to derive optimal species mixtures for restoration of forests damaged by Cu-Ni smelters in the City of Greater Sudbury, Ontario, Canada. We demonstrate the practicality of this approach for designing cost-effective landscape restoration programs by providing examples of virtual plant communities generated by the model for a range of common restoration scenarios in our study region. We discuss how customizing operational constraints to reflect site-specific objectives affects the composition of optimal species mixtures and the delivery of ecosystem functions they provide. Lastly, we discuss how solutions (i.e., species mixtures and associated relative abundances) generated from this model can be used to inform restoration programs.

2. Methods

2.1. Description of the study region

Our model was developed to generate optimal species mixtures for the restoration of upland forests damaged by Cu-Ni smelter emissions in the City of Greater Sudbury, Ontario, Canada. This region is known for heavily degraded industrial landscapes characterized by shallow, metal-contaminated soils, and sparse vegetation cover (Winterhalder, 1995). In recent decades, forests in this region have recovered significantly following major reductions in smelter emissions beginning in the 1970s and the implementation of large-scale restoration programs (Watson et al., 2012, see full study area description in Appendix A1). Nevertheless, many plant communities remain affected by elevated soil metals, high soil acidity, and the lack of soil organic matter (Wren et al., 2012).

The forests of our study region are located at the northern edge of the deciduous forest ecozone in Northeastern Ontario (Goldblum and Rigg, 2010). We first derived a list of 130 candidate species for restoration based on plant taxa found in the Sudbury region and species planted by Sudbury's Regreening Program (City of Greater Sudbury, 2016, 2017; SARA Group, 2009). We then further limited our list to 108 species that are suitable for planting on dry-to-mesic upland sites.

2.2. Stakeholder engagement for model development

Good restoration planning requires an understanding of the restoration objectives of stakeholders and community members. To identify restoration goals, we held a workshop in November 2016 with 17 local experts representing industry, academia, municipal and provincial governments, and community partners (see Appendix A2). Stakeholders selected five ecosystem functions as key restoration objectives*: rapid establishment of vegetation cover, soil building, biological soil health, resistance to invasion by exotic plant species*, and *plant community resilience to future global environmental change* (see definitions in Box 1). Ecosystem functions in this study were broadly defined as ecological processes that act at an ecosystem level and generate ecosystem services (La Notte et al., 2017).

Promoting the *rapid establishment of vegetation cover* and enhancing *soil building* processes were selected by stakeholders because of the historic loss of vegetation cover and extensive soil erosion within this region (Courtin, 1994). Improving *biological soil health* was prioritized because unrestored sites close to Cu-Ni smelters have been found to have low microbial biomass (Nkongolo et al., 2016) and slow litter decomposition rates (SARA Group, 2009). Planting species that improve an ecosystem's *resistance to invasion by exotic plant species* was selected because disturbed habitats tend to be more susceptible to colonization by non-native weeds (Hobbs and Huenneke, 1992).

Restoring biodiversity is a major priority in the study area due to the low diversity of Sudbury's smelter damaged forests (Santala et al., 2015). Furthermore, stakeholders emphasized the importance of the restored forest being able to resist and recover from the wide range of disturbances associated with global environmental change, such as anticipated increases in prolonged drought periods, fire events, and pest outbreaks. Hence, *plant community resilience to future global environmental change* was selected as another priority ecosystem function.

Box 1

Definitions of the five key ecosystem functions prioritized during stakeholder engagement.

- **Establishment of vegetation cover:** The rapid development of a healthy vegetation cover. This function is characterized as the presence (or dominance) of plant species that colonize sites rapidly, grow quickly, and develop a large canopy area.
- **Soil building:** The accumulation of organic matter through plant litter influx to create a substrate that can support plant establishment and growth. Slow litter decomposition results in the build-up of organic matter (Melillo et al., 1989).
- **Biological soil health:** This function indicates the capacity of soil to serve as a living system (Doran and Zeiss, 2000). High soil respiration rates indicate greater microbial activity and good biological soil health (Schloter et al., 2018).
- **Resistance to invasion by exotic plant species (hereafter Resistance to invasion):** The ability of a plant community to resist invasion by an exotic plant species. This function is based on the theory of limiting similarity, which proposes that species invasion is unlikely if another species with similar functional traits is already present in the community, or if all available ecological niches are occupied (Funk et al., 2008).
- **Plant community resilience to future global environmental change (hereafter Ecosystem resilience):** Following the insurance hypothesis (Naeem and Li, 1997; Yachi and Loreau, 1999), functionally diverse communities are better able to conserve multiple ecosystem functions and resist or recover from a broad range of environmental disturbances associated with global environmental change (i.e., changes in pattern and frequency of pest outbreaks, fire, and drought; Gladstone-Gallagher et al., 2019). Functional diversity is therefore considered a good indicator of ecosystem resilience (Messier et al., 2021; Timpane-Padgham et al., 2017).

2.3. Linking traits and selected ecosystem functions

We used restoration objectives prioritized by the stakeholders to develop a conceptual framework that links key plant traits to ecosystem functions (Table 1). Trait-function associations in plant communities are complex and a particular ecosystem function can be controlled by multiple plant traits, or vice-versa (de Bello et al., 2010). For example, leaves from species with high leaf lignin concentration decompose more slowly and create a thick organic layer, but they can also reduce microbial activity and negatively affect *biological soil health* (Eviner and Chapin III, 2003). Literature used to support these linkages between trait-ecosystem function relationships are shown in Appendix A4.

The functions *soil building* and *biological soil health* involve several interacting biological, physical, and chemical factors related to both plant and decomposer traits (Handa et al., 2014; Makkonen et al., 2012). Several studies have linked elevated concentrations of metals in smelter-disturbed soils with reduced rates of forest litter decomposition, but failed to describe mechanisms that cause this effect (Johnson and Hale, 2004). To complement trait information from the literature, we conducted a field experiment to identify plant traits that best explain these two functions within the study area. We determined the microbial respiration rates of soil collected from the study area mixed with leaf litter from one of 43 plant species (see Appendix A3). Species selected vary widely in litter quality within the study region, providing us with a broad gradient of 21 chemical and structural litter traits. This experiment allowed us to identify traits controlling respiration within this Cu-Ni damaged landscape. We found that microbial respiration rate in the litter-soil mix was best explained by lignin and nitrogen concentrations of senesced leaves. These traits were then selected to characterize *soil building* and *biological soil health* functions (Table 1).

Several trait-based approaches have been proposed as effective methods to control invasive plant species. MacDougall et al. (2009) suggests that successful invaders become competitively dominant because they have a fitness advantage, and they occupy a different niche space than resident species allowing them to exploit untapped resources. However, empirical evidence regarding the contribution of different traits to niche differentiation and the ability to supress and tolerate competitors is limited (Semchenko et al., 2018). For this study, we employed the concept of “limiting similarity” as the process that governs competitive exclusion in the model (Yachi and Loreau, 1999). This process has been empirically demonstrated to be effective at preventing the invasion of exotic forbs (Price and Pärtel, 2013). We used garlic mustard (*Alliaria petiolata* L.) as our invasive species of concern for this study because it is considered one of Ontario’s most invasive forest weeds (OFAH/ONDMNRF Invading Species Awareness Program, 2021) and is currently present in isolated areas in the study region. To quantify *resistance to invasion by exotics*, we generated a single metric that captures the similarity between an exotic species’ niche and the candidate species’ niche. We calculated the similarity in trait dimensions between *A. petiolata*, and each candidate species following the approach of van der Sande et al. (2020). This approach uses the Gower index (Gower, 1971), which we calculated using the ‘daisy’ function in the ‘cluster’ package in R (Maecher et al., 2016). The Gower index describes the distance between each pair of species in terms of key traits related to a competitive ability and nutrient use efficiency (see Appendix A4). High trait dissimilarity values indicate that the candidate species has traits distinct from *A. petiolata*. Hence, we inverted the dissimilarity values and re-scaled them to a range between 0 and 1, so that candidate species with values close to 1 indicated a greater trait similarity with *A. petiolata*.

Restoration programs are increasingly incorporating strategies to mitigate the negative impacts of global environmental change (von Holle et al., 2020). Functionally diverse communities are known to be generally more resilient to disturbances resulting from changes in temperature, precipitation patterns, fire regimes, and pest outbreaks (Messier et al., 2021; Timpane-Padgham et al., 2017). However, in extremely disturbed sites, harsh growing conditions could make it difficult to promote species diversity (Guittonny-Larchevêque et al., 2016; Proteau et al., 2020). Furthermore, in certain situations where an environmental stressor is already known (e.g., an area susceptible to drought stress), functional diversity may be less effective at promoting *ecosystem resilience* than selecting species with traits adapted for stressor-specific tolerance (Boisvert-Marsh et al., 2020). For these reasons, e*cosystem resilience* was not included in the model as a function per se, but can be accounted for with a user-defined constraint depending on their specific context.

2.4. Collection of plant trait data

Trait values were obtained from field measurements, online databases, and literature (see Table 1). Trait values and sample collection locations for field measurements are presented in Appendix B and in Fig. C.1 in Appendix C. Specific leaf area and leaf dry matter content measurements followed Cornelissen et al. (2003) and Ryser et al. (2008). In 2016, fresh foliar samples were collected in June, and freshly senesced material was collected during the main period of leaf fall (late August to mid-November). Concentrations of C and N in fresh and senesced leaf material were determined using a NCS Vario EL III combustion analyzer

Table 1

Description of plant traits and their relationships to the five selected ecosystem functions.

Trait	Description	Relationships to Ecosystem Functions				
		Resistance to Invasion	Establishment of Vegetation Cover	Biological Soil Health	Soil Building	Ecosystem Resilience
Raunkiaer life form†	The relation of the perenniating tissue (e.g., overwintering tissues) to the ground surface					✓
Typical maximum height†	Shortest distance between upper boundary of the main photosynthetic tissues and ground of a mature individual	✓	↑			✓
Specific leaf area₴	One sided area of a fresh leaf divided by its oven-dry mass	✓	↑↓	↑	↓	✓
Leaf dry matter content₴	Oven dry mass of a leaf divided by its water-saturated fresh mass			↓	↑	✓
Growth rate†	Rate of growth expressed as slow, moderate, and rapid	✓				✓
Seed mass†	Number of seeds per kilogram. Seed does not include minor covering structures	✓	↑			✓
Seed production†₴	Number of seeds produced by an individual per year	✓	↑			✓
Seed dispersal distance†	Distance seed travels from the parent plant	✓	↑			✓
Lateral extension†	Lateral spread by means of vegetative organs	✓	↑			✓
Vegetative propagation†	Number of methods of vegetative propagation used by a species to reproduce		↑			✓
Root depth†	Maximum rooting depth	✓				✓
Foliar nitrogen concentration₴	Total amount of nitrogen per unit of leaf dry mass	✓		↑↓	↑↓	✓
Foliar carbon concentration₴	Total amount of carbon per unit of leaf dry mass	✓		↑↓	↑↓	✓
Foliar phosphorus concentration₴	Total amount of phosphorus	✓				✓
Leaf area index₴	One-sided green leaf area per unit ground surface area	✓	↑↓			
Canopy area₴	Spread of an individual plant crown over an area	✓	↑			
Clonal propagation†	Species' ability to reproduce vegetative using clonal organs		↑			
Lignin₴	Fallen leaf litter lignin			↓	↑	
Litter biomass₴	Total foliar dry mass of a single individual plant			↑	↑	
Allelopathy†[*]	Species' ability to produce phytochemical compounds that limits seedling growth				↑↓[*]	

See Appendix A4 for a detailed version of this table that includes references for trait relationship to ecosystem functions and trait unit and value ranges.

For each trait listed, symbols correspond to whether the data was acquired through the literature (†) or field measurements (₴). Signs indicate the relationship between the described trait and the ecosystem function (↑, positive relationship with function; ↓, negative relationship with function; ↑↓, no clear directional relationship; ✓, associated with function). Citations used to support the relationship for a given plant trait to each ecosystem function is provided in Appendix A4.

[*] Species that exhibit allelopathic properties by producing compounds in senesced leaves that can inhibit the growth of other species (Rice, 1984).

(Elementar Americas Inc., Mt. Laurel, NJ). Total elemental concentrations of fresh and senesced leaf material were determined with a Varian Vista simultaneous axial inductively coupled argon plasma (ICAP) emission spectrometer (Varian Analytical Instruments, Walnut Creek, CA) after microwave digestion with HNO_3 and HF. Hemicellulose, cellulose, and lignin concentrations were obtained from a series of chemical digestions using three replicates (NDF, ADF, ADL) with a Fiber Analyzer 2000 (Van Soest et al., 1991). Methods used to measure canopy area, annual production of foliar biomass, and leaf area index are described in Appendix A5.

Raunkiaer life form, typical maximum vegetative height, seed mass, seed production, seed dispersal distance, lateral extension, vegetative propagation potential, root depth, and clonal propagation ability were acquired from the TOPIC database (Aubin et al., 2020). Plant characteristics for growth rate and allelopathy were acquired from the literature. Missing trait values were estimated as the average values for the genus and represented <14% of cases.

2.5. *Quantifying ecosystem function scores*

We first integrated plant traits that serve as indicators of ecosystem functions *establishment of vegetation cover, soil building,* and *biological soil health* into a single function score to rank the ability of each candidate species to deliver each function using multi-criteria decision analysis (MCDA). We used a multi-criteria aggregation technique that does not require criteria weights of individual traits, but instead employs the concept of nested multi-attribute frontiers in dimensions of the individual criterion (Yemshanov et al., 2013). Elements in each frontier were assigned a function score equal to the volume of the criteria space under the multi-criteria frontier (see description in Appendix A6). These function scores were used to rank the ability of each candidate species to deliver a given ecosystem function. Since we intended to use these scores in the model, we rescaled the function score values between 0 and 1, with 1 representing the highest function delivery.

The trait-function relationships identified in our conceptual framework (Table 1) reveal common traits between some of our functions, creating the potential for multicollinearity between ecosystem functions. To explore potential correlations between function scores of the 108 candidate species, we computed Kendall's Tau between the functions: *establishment of vegetation cover, soil building, biological soil health,* and *resistance to invasion*. Kendall's tau (τ) is a measure of rank-order correlation and was used because of the many tied scores in the data (Sokal and Rohlf, 1995). The function *resistance to invasion* correlated positively with scores for *biological soil health* (tau $= 0.23$, $p = 0.001$, $n = 108$), and negatively with *soil building* (tau $= -0.28$, $p < 0.001$, $n = 108$). All other function scores were not found to be significantly correlated to one another (Fig. C.4 in Appendix C). The list of the species function scores is presented in Figs. C.2a and C.2b in Appendix C.

2.6. *Finding an optimal species mixture for restoration*

We developed an optimization model to find cost-effective species combinations for restoration. Our model includes four ecosystem functions with specific delivery target values. The model considers the importance of each function to be equal in the model simulations. Some of the candidate species are known to produce allelopathic compounds in their leaves and roots that eventually end up in their litter. Litter with high concentrations of allelopathic compounds can inhibit the growth of other species (Rice, 1984). We found that when delivery of the *soil building* function was high, virtual plant communities generated by the model were dominated by species with allelopathic properties, such as *Pteridium aquilinum,* or coniferous species from the genus *Pinus* or *Picea* that are known to cause litter-induced changes in soil quality and limit the establishment of other species (Dolling, 1996; Teixeira da Silva et al., 2015). We introduced an allelopathy threshold that limits the abundance of these species in the species mixture. This constraint is applied only when the delivery of the *soil building* function is high and cannot be modified by the user (see Appendix A7, and Fig. C.4 in Appendix C). A full description of the model is provided in Appendix A7.

2.7. *User-defined model constraints*

We defined the model such that the user can select the operational constraints to be included. The budget constraint limits the total restoration cost per hectare. The cost to plant each species was based on the cost of propagation material, transportation, and labour provided by the City of Greater Sudbury Regreening Program (McCaffrey, Personal Communication, January 2018) (see Appendix B). Early-successional species capable of colonizing sites naturally were assumed to have low site preparation cost. The user can also select the number of overstory (trees and large shrubs) and understory (herbaceous plants and small shrubs) species in the mixture separately, as well as which functions to include in the model.

The model also allows the user to maximize the functional diversity of the resulting species mix. To characterize functional diversity, we first created a dissimilarity metric $\mathbf{q_{ij}}$ for each pair of species $\boldsymbol{i}$ and $\boldsymbol{j}$ based on the Gower index. This index describes the distance between each species pair in terms of key trait values related to their ability to respond to a broad range of potential disturbances (Table 1). We used the matrix of $\mathbf{q_{ij}}$ values to quantify functional diversity. If the goal is to create a functionally diverse community, then the abundance of the most functionally distinct species in the plant community is maximized based on a quadratic entropy equation (Pavoine, 2012; Rao, 1982). Alternatively, if creating a functionally diverse community is not a priority, then the plant community composition is maximized using Shannon's entropy, creating an even species composition (Shipley et al., 2006).

2.8. *Model outputs*

Given a particular set of user-defined constraints, the model solutions provide the most cost-effective species combinations while

Fig. 1. Examples of practical restoration scenarios for our study region. Scenario 1 prioritizes a single ecosystem function (*establishment of vegetation cover*). Scenario 2 prioritizes *resistance to invasion* and *biological soil health*, which are priorities for the restoration of urban woodlands at risk for invasion by competitive plants. Scenario 3 prioritizes the *establishment of vegetation cover* and *building soil* over other functions which are of particular importance for the restoration of rocky barrens with sparse vegetation and shallow soils.

maximizing the delivery of ecosystem functions selected by the user. Solutions consist of a list of species and their relative abundances. The model considered understory and overstory species as separate species pools and generates two distinct sets of species each with a maximum abundance of 100%. These are ultimately combined to create a complete species mixture with a total cover of 200%. Each solution provides an estimate of how much it could cost to plant the species mix, as well as a theoretical estimate of expected function delivery. The delivery values for each function range from 0 to 2, where 2 is the maximum value a single function can theoretically achieve. Finally, the functional diversity for each species mix was calculated based on whether or not it is applied as a constraint. The model generated either globally optimal solutions that satisfy all constraints set by the user, or feasible solutions that achieve its functional objectives, but fail to satisfy one or all of the user-defined constraints (i.e., the species number and budget constraints).

2.9. *Examples of model applications to restoration scenarios*

In order to demonstrate how differences in restoration priorities affect solutions generated by the model, we provide here three examples of practical restoration scenarios for our study region (Fig. 1). For each scenario, we set the user-defined community to 15 species (six in overstory and nine in understory). These numbers reflect the average richness of overstory and understory species found in undisturbed sites within the study region (SARA Group, 2009). We also set an unlimited budget to allow the creation of virtual communities without financial constraint. For each scenario, we demonstrate how the decision to maximize functional diversity affects optimal species combinations. We also compare how operational constraints impact the delivery of ecosystem functions and the functional diversity of the generated species mix. This was done because trade-offs between these two performance measures may affect the "ideal" solution selected by the user.

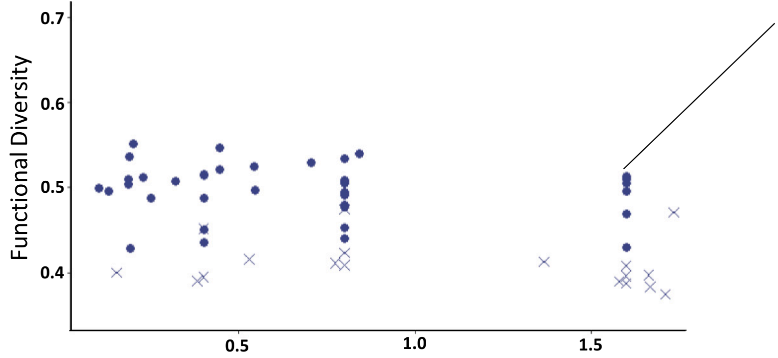
We explored model behaviour using three practical scenarios. Scenario 1 provides a simplified example of our model results. It prioritizes a single function, the *establishment of vegetation cover* (Fig. 1). This ecosystem function was selected because it was the highest-ranking restoration priority in our study region. Scenario 2 creates an optimal species mixture for the restoration of urban woodlands, which typically have adequate canopy cover and soil development but are at greater risk for invasion by exotic plants. Scenario 2 therefore prioritizes the functions *resistance to invasion* and *biological soil health* over other functions included in the model (Fig. 1). Scenario 3 creates an optimal species mixture for the restoration of the Sudbury Rocky Barrens, which is the dominant plant community type in the study area and requires active restoration (Fig. 1). The Rocky Barrens are characterized by shallow soils and sparse vegetation cover because of past industrial disturbance that caused vegetation dieback and soil erosion (Rumney et al., 2021). For this scenario, we prioritized *establishment of vegetation cover* and *building soil* over all other functions (Fig. 1).

3. Results

Our examples of practical model applications for our three restoration scenarios showed that the species mixtures generated by the model varied according to the ecosystem functions considered. The solutions for Scenario 1, which prioritized *establishment of vegetation cover,* consisted primarily of fast growing, light-demanding early-successional forest species, such as the overstory species *Populus grandidentata* (41%), *Betula papyrifera* (31%), and the understory species *Chamaenerion*

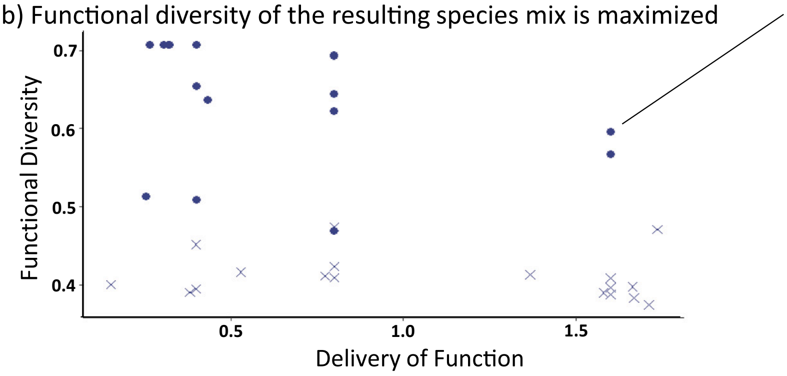
Scenario 1: Simplified example

a) Functional diversity of the resulting species mix is not maximized



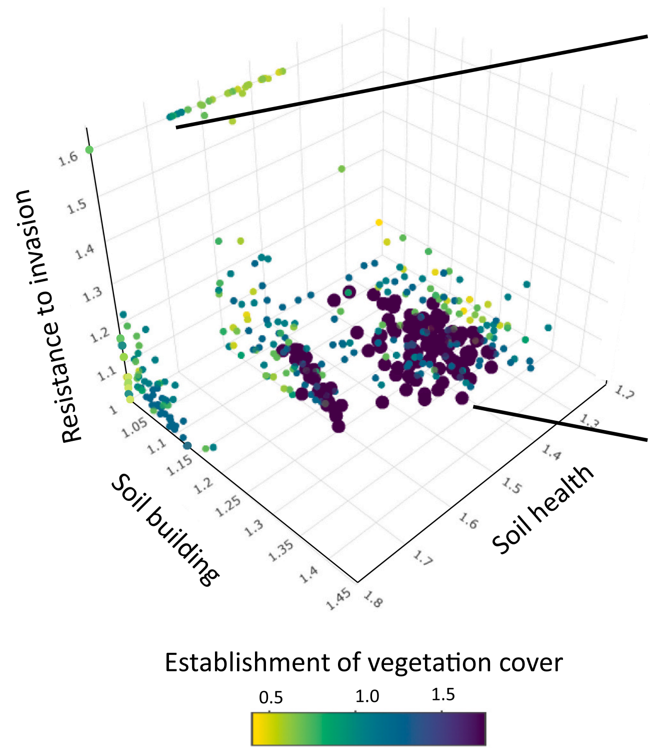
Species name	Relative abundance (%)
Overstory	
Populus grandidentata	41
Betula papyrifera	31
Populus tremuloides	12
Acer spicatum	5
Sambucus racemosa	5
Understory	
Chamaenerion angustifolium	50
Polygonatum pubescens	15
Anaphalis margaritacea	5
Apocynum androsaemifolium	5
Fragaria vesca	5

b) Functional diversity of the resulting species mix is maximized



Species name	Relative abundance (%)
Overstory	
Populus balsamifera	53
Populus tremuloides	23
Sambucus racemosa	9
Betula papyrifera	5
Pinus strobus	5
Understory	
Polygonatum pubescens	44
Rumex acetosella	21
Cornus canadensis	5
Epigaea repens	5
Chamaenerion angustifolium	5

Fig. 2. Model solutions for Scenario 1 for a user-defined community of 15 species (six in the overstory and nine in the understory), an unlimited budget and one ecosystem function (*establishment of vegetation cover*). See Fig. 1 for scenario description. Delivery of the function ranges from 0 to 2, where 2 is the maximum value that can be achieved. Panel a) presents optimal species mixtures generated when functional diversity is not maximized in the model; panel b) when functional diversity is maximized. Circles represent optimal solutions that satisfy all model parameters, and crosses show feasible solutions that fail to satisfy the species number or budget constraints. For each panel, we provide as an example of an optimal solution the five most abundant species in the overstory and understory.



Scenario 2: Urban Woodlands

Species name	Relative abundance (%)
Overstory	
Populus grandidentata	37
Sambucus racemosa	32
Populus tremuloides	16
Betula papyrifera	5
Rhus typhina	5
Understory	
Polygonatum pubescens	36
Aster ciliolatus	24
Fragaria vesca ssp. *americana*	10
Taraxacum officinale	5
Chamaenerion angustifolium	5

Scenario 3: Rocky Barrens

Species name	Relative abundance (%)
Overstory	
Populus grandidentata	30
Betula papyrifera	28
Populus balsamifera	27
Pinus banksiana	5
Sambucus racemosa	5
Understory	
Chamaenerion angustifolium	35
Polygonatum pubescens	23
Rumex acetosella	13
Anaphalis margaritacea	5
Apocynum androsaemifolium	5

Fig. 3. The delivery of ecosystem functions for optimal solutions (i.e., species mixture and associated relative abundances) when functional diversity of the community was not maximized. Solutions generated for a user-defined community of 15 species (six in overstory and nine in understory), and an unlimited budget when four ecosystem functions are optimized *(establishment of vegetation cover*, *soil building*, *biological soil health* and *resistance to invasion*). The delivery of each function ranges from 0 to 2, where 2 is the maximum value of delivery a single function can theoretically achieve. Solutions with higher function values for the *establishment of vegetation cover* are represented by darker colours, and solutions with a function value above 1.5 are represented by larger points. The relative abundance of the five most abundant overstory and understory species are shown for the restoration scenarios 2 and 3 (see Fig. 1 for scenarios description).

angustifolium (50%) (Fig. 2a). Solutions for Scenario 2, which aims to restore urban woodlands, included fast-growing species with high competitive ability and the capacity to produce large amounts of fast-decomposing leaf litter, including *Populus* species (53%) and *Sambucus racemosa* (32%) (Fig. 3). The species solutions for Scenario 3, designed to restore Rocky Barrens, included fast growing, light-requiring early-successional species with leaf litter that decompose more slowly, such as the overstory species *P. grandidentata* (30%), *B. papyrifera* (28%), *Populus balsamifera* (27%), and the understory species *C. angustifolium* (35%), and *Polygonatum pubescens* (23%) (Fig. 3).

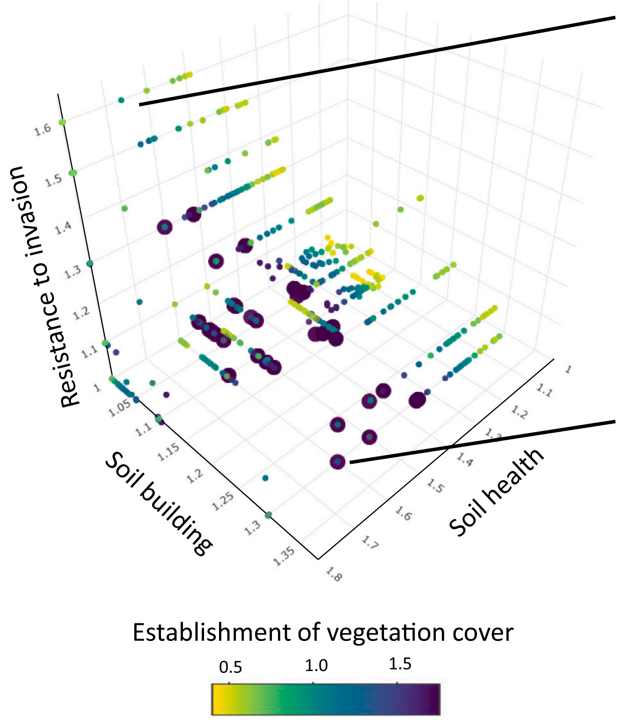
Optimal species combinations for each scenario were found to change based on whether or not functional diversity was maximized within the model. For example, Scenario 1, our simplified example, consisted mainly of early-successional *Populus* species (76%) in the overstory, but had an understory dominated by the late-successional species *P. pubescens* (44%) when functional diversity was maximized (Fig. 2b).

The solutions that satisfied the functional objectives of the model (i.e., were able to meet target values for functional delivery) but failed to satisfy other constraints set within the model (species number, budget constraints, represented by crosses in Fig. 2) were characterized by an extreme dominance of *Populus grandidentata* in the overstory and *C. angustifolium* in the understory, regardless of whether or not the functional diversity of the resulting mix was maximized within the model.

Regardless of the ecosystem function considered, we found that solutions with low functional diversity were able to provide higher delivery values for specific functions better than more functionally diverse species mixtures (Figs. 2 and 5). Furthermore, solutions with fewer species (eight species) were able to achieve similar function delivery values as those with higher numbers of species (20 species, Fig. 5). This is mainly because a few of our candidate species had a particular suite of traits that made them more efficient at providing better function delivery. When functional diversity is maximized, the model is forced to select species that are less effective at providing specific functions. We found that the solutions achieving highest delivery values also had lower restoration costs per hectare (i.e. \$1000 ha^{-1}) in comparison to solutions with a higher budget (i.e. \$8000 ha^{-1}). When functional diversity is not maximized, high budget solutions were required to create more functionally diverse solutions (Fig. 5). When functional diversity was maximized, communities with 20 planted species were more functionally diverse regardless of the budget.

4. Discussion

Results generated by our model provide restoration practitioners with a scalable approach to overcome the challenge of selecting a cost-effective species mix that also optimize the delivery of multiple ecosystem functions. The species mixtures generated by the model vary according to which functions are included, and by the operational constraints set by the user. By providing custom species mixtures for a particular set of site-specific objectives, this model can account for a wide range of restoration goals. We used solutions generated from the model to develop PlantR, an interactive planning tool that provides resource managers with a science-based approach to selecting an ideal mix of species to plant to meet their restoration objectives. This tool was



Scenario 2: Urban Woodlands

Species name	Relative abundance (%)
Overstory	
Populus tremuloides	54
Sambucus racemosa	18
Populus balsamifera	13
Betula papyrifera	5
Populus grandidentata	5
Understory	
Polygonatum pubescens	41
Chamaenerion angustifolium	19
Taraxacum officinale	10
Phleum pratense	5
Aster ciliolatus	5

Scenario 3: Rocky Barrens

Species name	Relative abundance (%)
Overstory	
Populus balsamifera	58
Sambucus racemosa	13
Betula papyrifera	13
Pinus strobus	5
Populus grandidentata	5
Understory	
Polygonatum pubescens	43
Rumex acetosella	20
Epigaea repens	6
Achillea millefolium	5
Brachyelytrum erectum	5

Fig. 4. The delivery of ecosystem functions for optimal solutions (i.e., species mixture and associated relative abundances) when functional diversity of the community was maximized. Solutions generated for a user-defined community of 15 species (six in overstory and nine in understory), and an unlimited budget when four ecosystem functions are optimized. Ecosystem functions optimized are *establishment of vegetation cover*, *soil building*, *biological soil health* and *resistance to invasion*. The delivery of each function ranges from 0 to 2, where 2 is the maximum value a single function can theoretically achieve. Solutions with higher function values for the *establishment of vegetation cover* are represented by darker colours, and solutions with a function value above 1.5 are represented by larger points. The relative abundance of the five most abundant overstory and understory species is shown for the restoration scenarios 2 and 3 (see Fig. 1 for scenarios description).

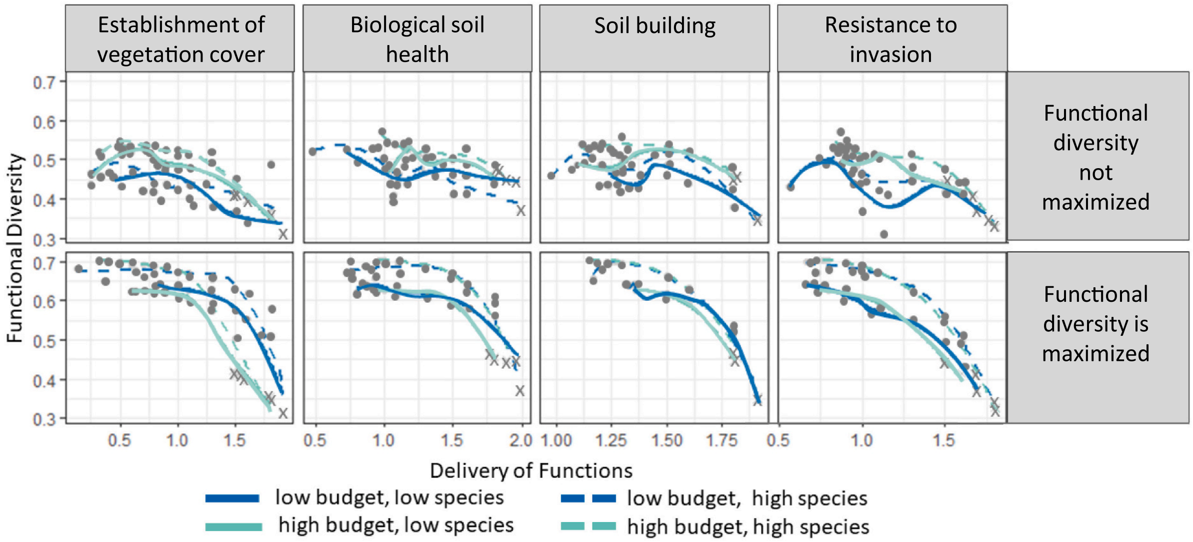


Fig. 5. Functional diversity and delivery of ecosystem functions of solutions under contrasting management scenarios. Management scenarios intended to demonstrate how contrasting budget, species number and functional diversity constraints affects the performance measures of solutions. Low species number included three species in overstory and five in the understory (eight total), and high species number included eight species in overstory and twelve in the understory (20 total). Low restoration budget was set to $1000 per hectare, and high budget was $8000 per hectare. Circles represent optimal solutions that satisfy all model parameters and crosses represent feasible solutions that fail to satisfy all model constraints (i.e., the species number and the budget constraints).

developed on the Power BI intelligence platform (Microsoft, 2021) and is available upon request (Appendix A8).

4.1. Virtual communities as a guide for selecting a species mix

Our model allows the user to select one or more ecosystem functions for their restoration goals and provides them with a set of optimal solutions that users can explore to find a species mix that best meets their needs. In our examples, when only one function was the main objective (i.e., *establishment of vegetation cover*), the species mixture of the optimal solution resembled natural plant communities dominated by a few post-fire early-successional forest species in the region. The species mixture included *Populus grandidentata* and *B. papyrifera* in the overstory and *C. angustifolium* in understory (Pavek, 1992; Uchytil, 1991; Fig. 2). However, maximizing the delivery of a single restoration goal can have negative impacts on the delivery of others. For example, in intensively managed forests there are well known trade-offs between maximizing wood volume and stand-level biodiversity (Duncker et al., 2012). Also, restoration practices intended to improve soil quality in landscapes damaged by smelter activity can be detrimental to culturally important species, such as blueberry species (*Vaccinium* spp.). Blueberry harvesting is a traditional socio-economic activity in the region (City of Greater Sudbury, 2018). Resource managers must be aware of the trade-offs that can arise from conflicting management objectives (Carpentier et al., 2016).

One advantage of combining a trait-based approach with optimization modeling is that it allows for potential trade-offs among multiple socio-economic and environmental objectives to be assessed early in the restoration program (Fiedler et al., 2018). For example, when the objective was to *rapidly establish vegetation cover* that promotes *soil building,* as in our Rocky Barrens scenario, the mix generated included fast-growing, early-successional plant species with some recalcitrant litter to improve soil development and vegetation recovery in areas that had experienced vegetation dieback and soil erosion (Rumney et al., 2021) (Fig. 3). For our urban woodlands scenario, where *resistance to invasion by exotics* was the main concern, along with improving *biological soil health,* the optimal species mix included fast-growing, competitive species able to create large amounts of fast-decomposing litter with high nitrogen concentration (Fig. 4) (Kazakou et al., 2006).

In some circumstances, our model created novel species assemblages that practitioners may not usually consider. This tended to be the case when we maximized functional diversity (Figs. 1b and 4). Some of these virtual communities included both early- and late-successional species (Kraft et al., 2004). Such combinations are not typically found together in natural forest types described for the study region (Chambers et al., 1997; Northern Ontario Plant Database, 2019). The most functionally dissimilar species in our candidate species mix included fast-growing species with resource acquisition traits adapted for early-successional habitats and slow-growing species with resource conservation traits adapted to late-successional forests (Huston and Smith, 1987). Novel communities generated by the model may be more suitable for achieving particular restoration goals. However, novel communities could conflict with the socio-cultural objectives of restoration programs, particularly if stakeholders aim to restore communities to resemble natural forests in their region (Standish et al., 2013).

While there are concerns regarding the use of novel communities in restoration, there is growing evidence of their usefulness, particularly in areas with considerable environmental degradation (Perring et al., 2014). For example, hybrid poplar (*Populus* spp.) and red pine (*Pinus resinosa*) plantations that are substantially different from natural forest types in Ontario, have been used as effective nurse crops to promote natural succession of late successional forest herbs (Boothroyd-Roberts et al., 2013; Parker et al., 2008). Transplanting late-successional understory species beneath the mature canopy of early-successional trees has also been demonstrated as a sound approach to overcome barriers associated with poor dispersal abilities of late-successional species (Ontario Government, 2000; Santala et al., 2015). Novel communities created by our model could be used to maintain key ecosystem functions in heavily disturbed areas as ecosystems recover.

4.2. Species-rich and functionally diverse communities did not improve delivery of functions

Several studies have suggested that species-rich communities are better at delivering multiple ecosystem functions (Kanowski and Catterall, 2010; Suter et al., 2021). In our model solutions, the highest levels of functional diversity could only be achieved at the expense of the delivery of one or more functions (Figs. 2 and 5). Furthermore, solutions with only eight species could achieve similar functional delivery values as communities with 20 species. This is largely because a few species in our candidate species list possess traits that are proficient at providing certain functions. When the model is required to select functionally distinct species, it is forced to select species that are less efficient at providing these functions (Fig. 5). Similar findings have been reported in European forests, where tree diversity was found to positively relate to multifunctionality at moderate levels of function delivery, but was negatively related when high function delivery was required (van der Plas et al., 2016). This suggests that restoring communities with a few key, functionally productive species may be sufficient for sustaining ecosystem functions (Cardinale et al., 2006; Gaston, 2010). Managing for beta-diversity (i.e., a patchwork of functionally different plant communities) has also been suggested as a more effective approach to managing diversity within restored landscapes than maximizing alpha-diversity (i.e., local-scale diversity) (Grman et al., 2018).

4.3. It does not cost more to improve the delivery of functions

Designing restoration programs to provide multiple ecosystem functions did not cost more. The model was able to generate low-cost restoration species mixtures capable of delivering high levels of ecosystem functions. In our study area, the species with the highest delivery levels for each of the ecosystem functions were the least expensive to plant, mainly because of their ability to colonize sites naturally following site preparation. Many native colonizing species are favourable for restoration due to the role they play in ecosystem re-establishment (Brown and Amacher, 1999). Cost savings from using inexpensive species mixtures could provide incentives to expand restoration to a larger area (Williams and Lonsdorf, 2018).

4.4. Limitations and next steps

Our modeling approach provides a science-based method to formally integrate multiple restoration goals when developing restoration programs. It provides guidance when considering which species to include within a restoration mix, but solutions should not be viewed as prescriptive. More work is needed to test the ability of model-generated species mixtures to effectively deliver ecosystem functions. This could include field studies to explore how habitat type influences the delivery of functions by altering trait values, or by exploring how competition between species affects the long-term stability of the restoration mix (Williams and Lonsdorf, 2018). Large-scale restoration efforts may also be constrained by logistical challenges such as the availability of propagation material identified by the model as capable of delivering multiple ecosystem functions. Further research is needed to explore the use of native species for ecological restoration, and to improve production capacity of nurseries for such material (White et al., 2018).

Our model uses data and operational constraints specific to our study region. For example, some species were inexpensive to plant (e.g., natural colonizers such as *Populus* spp. and *Betula papyrifera)*. However, this may not be the case in other regions. This work could be expanded to address other restoration contexts, additional restoration objectives, and habitat types. Potentially, one could also test alternative assumptions related to the delivery of ecosystem functions, such as the principle of competitive hierarchies (Semchenko et al., 2018), to quantify the functional resistance to invasion by competitive plants, or by considering competitive traits of juvenile exotic species rather than mature individuals (Schuster et al., 2018). We could also adapt the model to select species with traits adapted for specific climate-related stressors (e.g., drought; Boisvert-Marsh et al., 2020).

There is increasing demand from practitioners and policy makers for knowledge and decision support tools that improve the integration of socio-economic and environmental values in restored landscapes. Our model provides a first step that links knowledge of trait-function relationships with optimization techniques to improve our capacity to restore multiple ecosystem functions. Our integrative approach is generalizable and can be adapted to a variety of socio-ecological restoration contexts to improve strategies used to effectively manage the recovery of multiple restoration goals in disturbed landscapes.

Declaration of Competing Interest

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

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Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoleng.2022.106646.

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