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APPLICATION

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Generating species assemblages for restoration and experimentation: A new method that can simultaneously converge on average trait values and maximize functional diversity

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Abstract

1. Restoring resilient ecosystems in an era of rapid environmental change requires a flexible framework for selecting assemblages of species based on functional traits. However, current trait-based models have been limited to algorithms that select species assemblages that only converge on specified average trait values, and could not accommodate the common desire among restoration ecologists to generate functionally diverse assemblages.
2. We have solved this problem by applying a nonlinear optimization algorithm to solve for the species relative abundances that maximize Rao's quadratic entropy (Q) subject to other linear constraints. Rao's Q is a closed-form algebraic expression of functional diversity that is maximized when the most abundant species are functionally dissimilar.
3. Previous models have maximized species evenness subject to the linear constraints by maximizing the entropy function (H'). Maximizing Q alone produces an undesirable species abundance distribution because species that exhibit extreme trait values have the highest abundances. We demonstrate that the maximization of an objective function that additively combines Q and H' produces a more even relative abundance distribution across the trait dimension.
4. Some ecological restoration projects aim to restore communities that converge on one set of traits while diverging across another. The *selectSpecies* R function can derive assemblages for any size species pool that maximizes the diversity of any set of traits, while simultaneously converging on average values of any other set of traits. We demonstrate how the function works through examples using uniformly spaced trait distributions and data with a known structure. We also demonstrate the utility of the function using real trait data collected on dozens of species from three separate ecosystems: serpentine grasslands, ponderosa pine forests, and subtropical rainforests.

5. The quantitative selection of species based on their functional traits for ecological restoration and experimentation must be both rigorous and accessible to practitioners. The *selectSpecies* function provides ecologists with an easy-to-use open-source solution to objectively derive species assemblages based on their functional traits.

KEYWORDS
complementarity, community assembly, ecological restoration, functional diversity, R package, *selectSpecies*

1 | INTRODUCTION

Restoring ecosystems that are functionally resilient in an era of rapid environmental change is a key challenge facing land managers globally (Suding, 2011). While historical reference conditions have traditionally provided empirical data about how to define compositional targets for restoration projects, historical assemblages may not be well-adapted to future climate or novel environmental conditions (Harris, Hobbs, Higgs, & Aronson, 2006). This realization prompted the development of quantitative algorithms that derive species assemblages that exhibit traits to achieve specific functions (Laughlin, 2014a), such as optimizing pollinator habitat (M'Gonigle, Williams, Lonsdorf, & Kremen, 2016), invasion resistance (Yannelli, Karrer, Hall, Kollmann, & Heger, 2018), or drought resistance and fire tolerance (Laughlin, Strahan, Huffman, & Sánchez Meador, 2017).

One limitation of the original approach is that it tended to select assemblages of species that were functionally similar and therefore not functionally diverse. Restoration practitioners have long been interested in restoring diverse assemblages of species for conservation, and there has been increasing interest in selecting species that optimize functional diversity in restoration projects (Funk, Cleland, Suding, & Zavaleta, 2008; Ostertag, Warman, Cordell, & Vitousek, 2015; Giannini et al., 2016). Functional diversity may bolster the stability of a community (Hallett, Stein, & Suding, 2017), may enhance invasion resistance (Hooper & Dukes, 2010), and can be important to the delivery of multiple ecosystem services (Gagic et al., 2015). However, we have lacked the quantitative methods to select functionally-diverse species objectively, especially in high-dimensional cases when multiple traits are evaluated concurrently. Here we introduce a new approach that solves this problem. Our new R function assigns relative abundances to each species in the species pool to derive an assemblage that conforms with specified average trait values, maximizes the diversity of a trait, or achieves both simultaneously (Figure 1).

To generate assemblages that conform to average trait values, the model should derive an assemblage of species whose average trait value equals the specified 'optimal' trait value (see *x*-axis in Figure 2). In other words, the trait values of the community converge on this trait value (Figure 2). Basing a restoration on average trait values alone may lead to functioning communities under certain circumstances, but could lead to problems in others. For example, a community dominated by functionally similar species may not be resilient to unexpected disturbances. Therefore, to select species that are also functionally diverse, the model should derive an assemblage of species that maximizes the diversity of a trait (see *y*-axis in Figure 2). Practitioners may want to re-assemble communities that exhibit convergence toward an

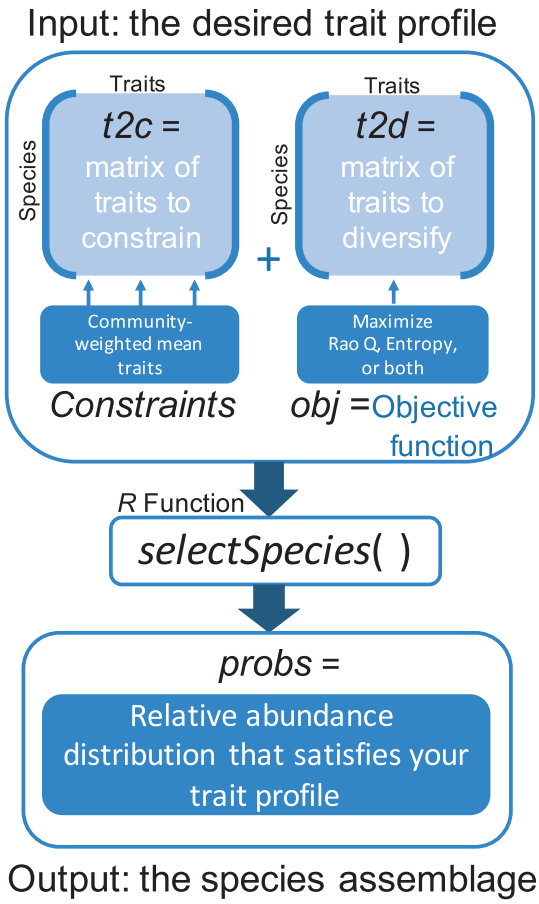

FIGURE 1 The input to *selectSpecies*() function is a user-specified trait profile of the desired community, which consists of a matrix of traits to constrain ('*t2c*'), a vector of *constraints* consisting of community-weighted mean (CWM) traits, a matrix of traits to diversify ('*t2d*', or alternatively a distance matrix), and the objective function ('*obj*') to maximize (quadratic entropy, entropy, or both). The output of the function ('*probs*') is a relative abundance distribution, i.e., proportional abundances for every species in the species pool

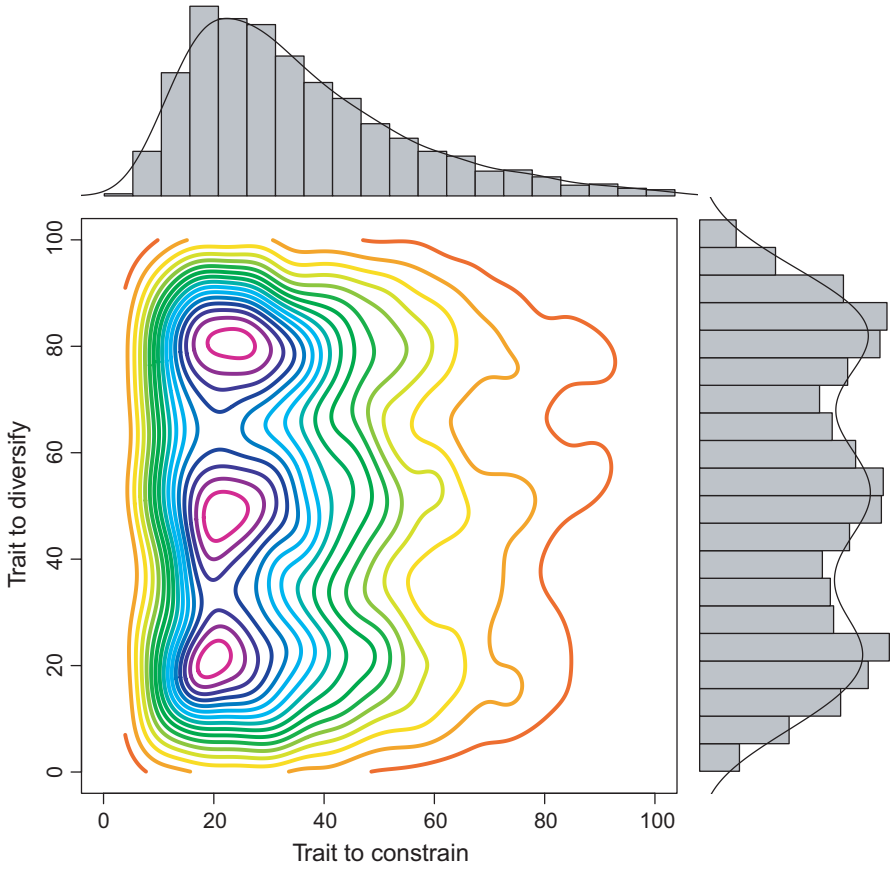

FIGURE 2 Hypothetical community-level trait distribution represented as a bivariate contour density plot, where red = low density and purple = high density. Marginal histograms are also shown for each trait axis. If the goal of the restoration is to re-assemble a community that exhibits convergence toward a specific value of one trait (i.e., the trait to constrain on the *x*-axis) and diversity of another trait (i.e. the trait to diversify on the *y*-axis), then the species that are selected for the project must reflect a complex multidimensional trait distribution

average value of one trait but simultaneously exhibit diversity of another trait. In these scenarios, the assemblage of species will need to reflect complex multidimensional trait distributions (Figure 2).

In this paper, we (1) describe the system of linear equations for constraining the assemblage to average trait values, (2) describe how the choice of objective function for optimization can be used to maximize functional diversity, and (3) present multiple examples that use the new *selectSpecies* function to optimize specific traits and functional diversity simultaneously to derive species assemblages for ecological restoration and experimentation.

2 | CONSTRAINING SPECIFIC TRAIT VALUES

Suppose we want to create a species assemblage drawn from a pool of S species. For each of these species, we know the mean trait value for K different traits. In addition, for each trait, we want the community-weighted mean (Shipley, Vile, & Garnier, 2006) of the assemblage to equal a predefined value that we believe will optimize survival in a given environmental condition (Laughlin, 2014a). To achieve this aim, we need to satisfy the following system of $K + 1$ linear equality constraints:

$$\sum_{i=1}^{s} t_{ik} p_i = \bar{T}_k \text{ for } k = 1,2,\ldots,K \quad (1)$$

$$\sum_{i=1}^{s} p_i = 1, \quad (2)$$

where t_{ik} is the known mean trait value of the kth trait for the ith species, p_i is the unknown proportion of the ith species within the assemblage, $\sum_{i=1}^{S} t_{ik} p_i$ is thus the community-weighted mean for trait k, $\bar{T}_k$ is the predefined value of the kth trait that we believe will optimize survival, and the unknown probabilities (i.e., relative abundances) must be non-negative and less than one ($0 < p_i < 1$, $i = 1, \ldots, S$). There must be fewer traits than species because if the number of equations ($K + 1$) exceeds the number of unknowns (S), this usually results in an overdetermined system with no solution. When $K + 1 < S$, then we have the desirable situation of an underdetermined system of equations with many possible solutions.

Shipley et al. (2006) proposed to select the solution that maximizes the following objective function:

$$H' = -\sum_{i=1}^{S} p_i \ln p_i \quad (3)$$

Equation 3 is the entropy function (H'), also known by ecologists as Shannon's diversity index. Maximizing the entropy function under the constraints of Equations 1 and 2 will produce an assemblage of species whose average trait values are equal to $\bar{T}_k$ and whose distribution is as even as possible given the trait value constraints.

The *selectSpecies* function in the R package Select (Laughlin & Chalmandrier, 2018) uses the general nonlinear optimization method

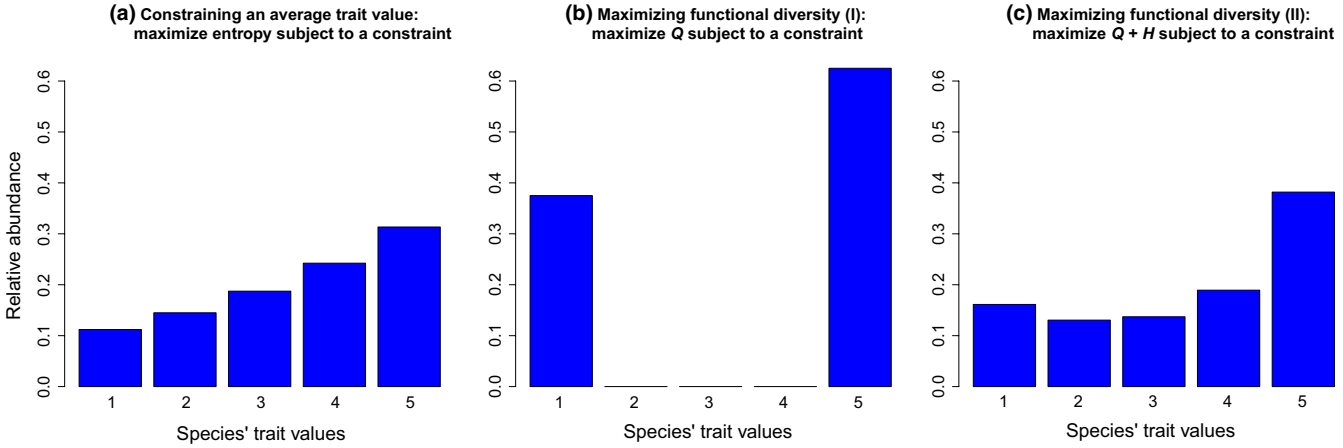

FIGURE 3 Species probability distributions (i.e., relative abundances) for five species whose trait values range uniformly between one and five. (a) Model results that constrained the assemblage to an average trait value ($\bar{T}$ = 3.5) by maximizing entropy (H'; Equation 3). (b) Model results that maximized functional diversity by maximizing quadratic entropy (Q; Equation 4) subject to the constraint that $\bar{T}$ = 3.5. (c) Model results that maximized Ω (i.e., $Q + H'$; Equation 6) subject to the constraint that $\bar{T}$ = 3.5

using augmented Lagrange multipliers (Ye, 1988), which has been implemented in the RSOLNP R package by Ghalanos and Theussl (2015). When entropy is maximized using the *selectSpecies* function, the results are virtually identical to the solutions obtained by the *maxent* function in the FD package of R (Laliberté, Legendre, & Shipley, 2014), which uses a different algorithm (Shipley et al., 2006). One advantage of the *selectSpecies* function over the *maxent* function is that *selectSpecies* can easily accommodate negative trait values (e.g., stable isotopes), whereas the latter requires a transformation because the values must be non-negative. Consider a pool of five species whose trait values range between one and five (Figure 3). The maximum entropy solution that constrains $\bar{T}$= 3.5 produces the most even distribution of relative abundances across all species given that constraint (Figure 3a). The R code for these examples are fully described in a vignette in the Supporting Information, which is also available in the R package on CRAN.

If enough information on intraspecific trait variability is available, then the Traitspace model (Laughlin, Joshi, van Bodegom, Bastow, & Fulé, 2012) could also be used to select species for restoration based on explicit parameterizations of community-level trait distributions. However, restoration practitioners rarely have enough intraspecific trait data to parameterize multidimensional trait distributions for multiple species, which is a requirement in the Traitspace model. Our goal was to develop a model that could be readily implemented by restoration practitioners and empirical ecologists. Average trait values per species are increasingly available, so we built a framework that could use species-level average trait values. Moreover, using a system of linear equations allows for the optimization of a well-known functional diversity index, which we now describe.

3 | OPTIMIZING FUNCTIONAL DIVERSITY

In the previous example, the community-weighted mean trait value of the model assemblage is the user-selected 'optimal' trait value $\bar{T}$ (Figure 3a). However, restoration practitioners often want to restore diverse assemblages of species that are functionally different. For example, if the goal is to restore habitat for a range of pollinators that are active at different times throughout the growing season, then practitioners want to maximize the diversity of flowering phenology (M'Gonigle et al., 2016). If the goal is invasion resistance and the maintenance of species coexistence by limiting the functional similarity of species, then trait diversity may be an important factor in designing the restored assemblage (Hooper & Dukes, 2010).

To achieve functionally diverse assemblages, we can maximize a different objective function:

$$Q = \sum_{i=1}^{S-1} \sum_{j=i+1}^{S} d_{ij} p_i p_j, \quad (4)$$

where d_{ij} is a dissimilarity metric between the trait value(s) of the i-th and j-th species. The *selectSpecies* function accepts either a numerical trait matrix, which is used to compute a Euclidean distance matrix, or a dissimilarity matrix defined by the user. This function, known as quadratic entropy (Q), is defined as the expected distance between two entities in a collection (Rao, 1982; Pavoine, 2012).

Quadratic entropy is maximized when the most abundant species are functionally dissimilar, and is widely used as a quantitative measure of diversity in ecology and evolution (Pavoine, 2012). Quadratic entropy is viewed as a multivariate measure of functional divergence (Mason, Mouillot, Lee, & Wilson, 2005) and is similar to functional dispersion (Laliberté & Legendre, 2010). When quadratic entropy is maximized using the *selectSpecies* function, the solution maximizes the relative abundances of the most functionally dissimilar species (Figure 3b). Note the absence of species in the middle of the trait axis in Figure 3b because the function maximizes trait divergence. This may not be a desirable property for selecting functionally diverse assemblages for restoration. Practitioners may want the species to span the full range of the trait axis, not just the two extremes (Figure 2). It has been demonstrated that this undesirable behaviour of Q can be avoided by using an ultrametric functional dissimilarity matrix, i.e., a matrix

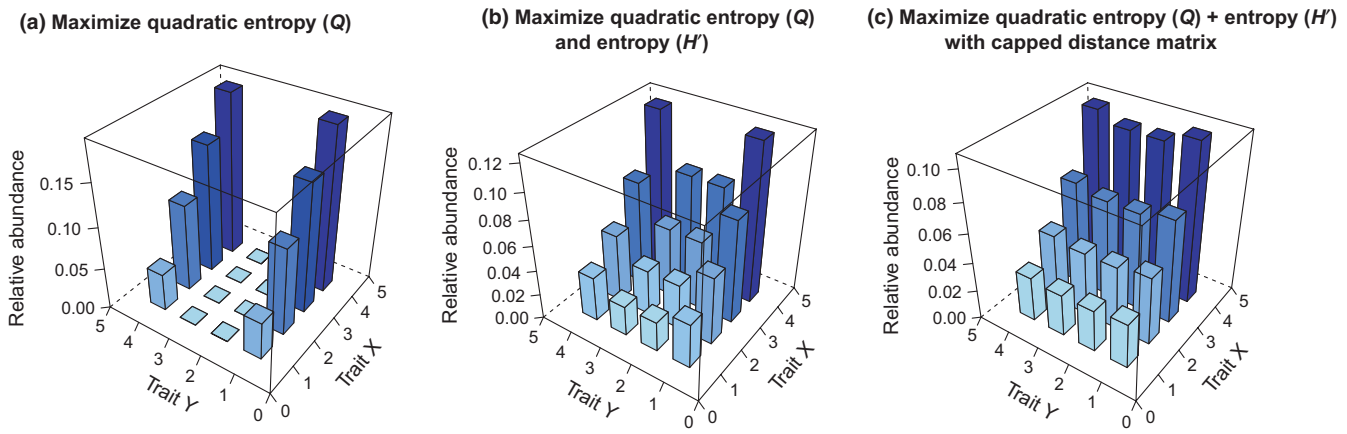

FIGURE 4 Species relative abundance distributions for 16 species whose trait values range uniformly between one and four. These model outputs describe when the desired trait profile is an assemblage of species that converges on a specific value of trait X but exhibits a diverse range of trait Y. Each bar represents one species and its location within the two-dimensional trait space. Two maximizations are illustrated: (a) maximize Q (Equation 4) only, (b) maximize Ω (Equation 6), and (c) maximize Ω (Equation 6) with a capped distance matrix

that reflects the branch lengths of an ultrametric functional tree where all end nodes are equidistant from the root of the tree (Pavoine, Ollier, & Pontier, 2005). However, raw trait data is rarely structured this way and building an ultrametric functional tree from trait data is non-trivial (Mouchet et al., 2008).

To produce an assemblage that spans the full range of a trait, we propose an alternative procedure to compensate this undesirable effect when the dissimilarity matrix is not ultrametric: maximize the functional diversity index and entropy simultaneously. Consider a new function, Ω, where quadratic entropy (*Q*) and entropy (*H′*) are additive:

$$\Omega = \varphi Q + (1-\varphi) H' \tag{5}$$

$$\Omega = \varphi \sum_{i=1}^{S-1} \sum_{j=i+1}^{S} d_{ij} p_i p_j + (1-\varphi) - \sum_{i=1}^{S} p_i \ln p_i \tag{6}$$

Each term in Equation 6 is weighted by the parameter phi (φ), which ranges from 0 to 1. The *selectSpecies* function by default sets φ = 0.5 so that both terms are weighted equally, but φ can be varied to place more weight on either *Q* or *H′*, depending on the objectives of the user. In fact, ecologists could vary φ systematically and compare the output of the model to natural vegetation in a future study to improve our understanding of trait distributions observed in nature. The output that maximizes Ω (Equation 6) illustrates two important features (Figure 3c): higher relative abundances still gravitate toward the extremes yet species in the middle of the trait axis are not ignored, and the solution still satisfies the constraint that $\bar{T}$ = 3.5.

4 | SIMULTANEOUSLY OPTIMIZING A SPECIFIC TRAIT VALUE AND FUNCTIONAL DIVERSITY

Practitioners may want to restore a community that converges on one trait but diverges on another (Figure 2). The *selectSpecies* function can be used to constrain the average to a specific value of one trait, while maximizing the diversity of another trait (Figure 4). Consider the idealized scenario where species are evenly distributed in a two-dimensional trait space and each trait ranges from one to four. One can constrain a specific value of trait *X* (e.g., $\bar{T}=3$), while optimizing the diversity of trait *Y*. The solutions that are obtained by optimizing *Q* (Equation 4) are illustrated in Figure 4a, whereas the solutions that are obtained by optimizing Ω (Equation 6) are illustrated in Figure 4b. Note that the potentially undesirable absence of species in the middle of the trait *Y* axis in Figure 4a is corrected in Figure 4b, but intermediate trait values are still not evenly represented in Figure 4b.

The *selectSpecies* function has an additional option to cap the distance matrix at $\bar{d}$, the average Euclidean distance between species in trait space, where

$$\bar{d} = \frac{2\sum_{i=1}^{S-1}\sum_{j=i+1}^{S} d_{ij}}{S(S-1)} \tag{7}$$

Capping the distance matrix at $\bar{d}$ yields species abundances that are more evenly distributed across the range of trait Y, as illustrated in Figure 4c. Note that the relative abundance distributions in Figure 4b,c are similar to the multidimensional trait distribution in Figure 2. Future studies can also determine which capped values (other than the mean distance) produce species abundance distributions that most closely approximate natural vegetation or produce the most even distribution of traits.

We leave it to the user to decide whether to varyφ or to cap the distance matrix at $\bar{d}$, but the choice depends on the objectives. To maximize trait divergence, set φ to 1 (or equivalently select *Q*, rather than *Q* + *H′*, as the objective function) and do not cap the distance matrix (Figure 4a). To achieve a balance between functional divergence and species evenness, then set φ = 0.5 (the function default) and do not cap the distance matrix (Figure 4b). To achieve a balance between species evenness and an even distribution of trait values in the assemblage, we recommend setting φ = 0.5 and capping the distance matrix at $\bar{d}$ (Figure 4c).

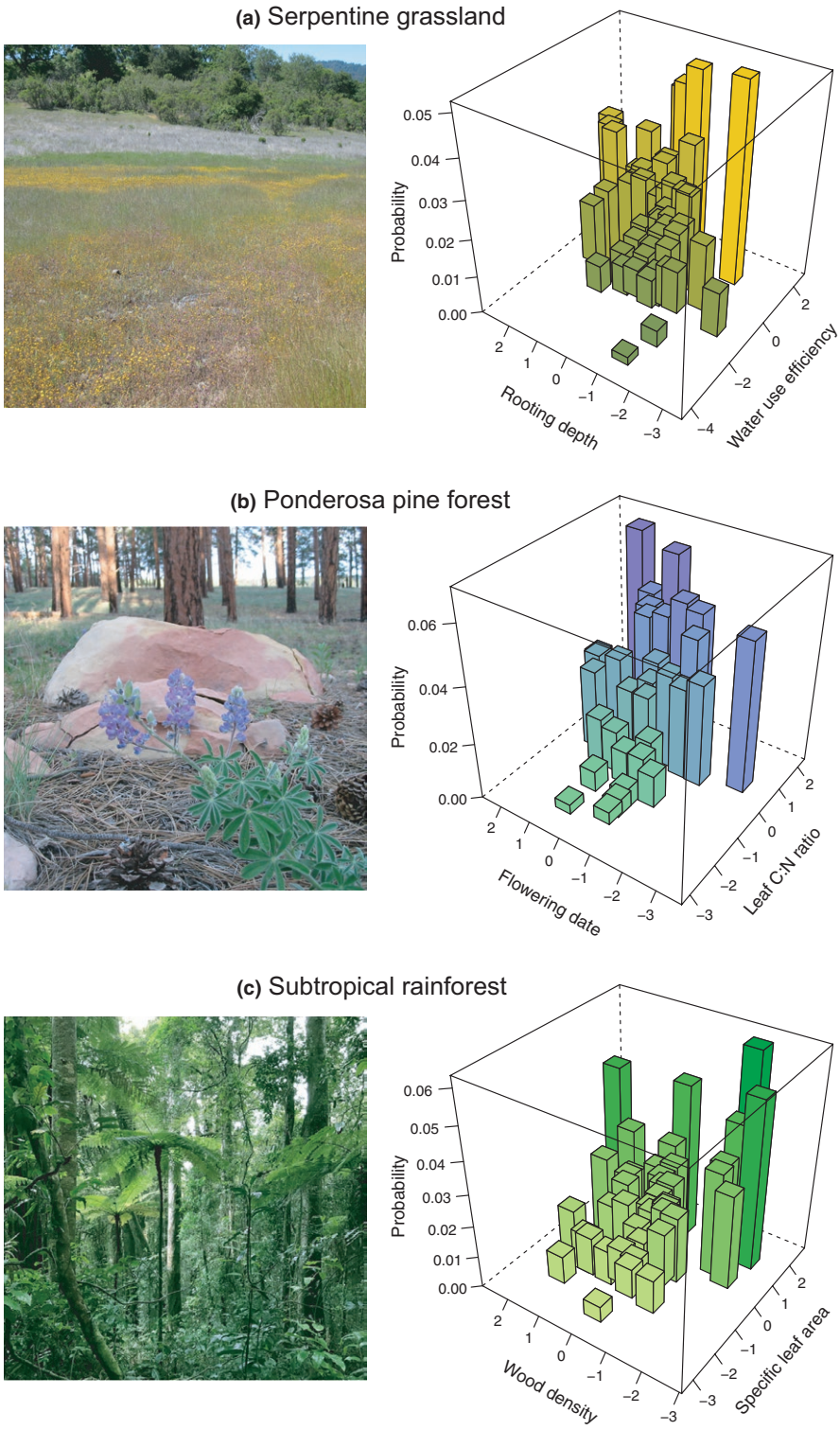

FIGURE 5 Examples of species assemblages (i.e., discrete probability distributions) derived from the *selectSpecies* R function that simultaneously constrain one trait and diversify another within (a) serpentine grassland in California, USA (photo: J.L. Funk), (b) ponderosa pine forest in Arizona, USA (photo: D.C. Laughlin, and (c) subtropical rainforest in Queensland, Australia (photo: Brandon Clark). Each bar represents one species and its location within the two-dimensional trait space

5 | EXAMPLES

5.1 | Optimizing drought tolerance in a Serpentine grassland

Three examples demonstrate how to use this function with real data (Figure 5). Restoring ecosystems that are resilient to drought is often an important management goal (Funk, Hoffacker, & Matzek, 2015). Drought tolerant plants can exhibit high water use efficiency (WUE), the rate of carbon assimilation per unit of water used (Noy-Meir, 1973). Therefore, selecting species with traits that converge on high water use efficiency can be one restoration objective. Rooting depth also influences drought tolerance, but a drought-resilient community would likely exhibit a diversity of rooting depths to optimize complementary water use throughout the soil profile (Hooper et al., 2005). Therefore, selecting species that optimize rooting depth diversity would be important. Using

a dataset of 48 species from a serpentine grassland in California (Funk & Wolf, 2016), we normalized traits by first taking the logarithm of log-normally distributed traits and then standardized each variable to unit variance. We used the *selectSpecies* function to derive an assemblage with a high average WUE by constraining the assemblage to the 67th percentile of the distribution of WUE, but diversified the range of rooting depths by optimizing Ω with a capped distance matrix $\bar{d}$ (Figure 5a). This output can be used to design a seed or planting mix for a restoration project by selecting species with the highest relative abundances.

5.2 | Optimizing pollinator habitat in low fertility soil

Restoration practitioners may wish to plant species that maximize the range of flowering times to provide floral resources for pollinators throughout the growing season, while simultaneously constraining the list to species that can tolerate infertile soil conditions. Using a dataset of 34 forb species from a ponderosa pine forest in Arizona, we determined the median flowering date (day of year) of each species using local floras, and we used leaf carbon-to-nitrogen (C:N) ratio as an indicator of each species ability to tolerate infertile soil conditions. High leaf C:N ratios are indicative of a resource-conservation strategy. We used the *selectSpecies* function to derive an assemblage with a diverse range of flowering times by diversifying flowering date, but constraining leaf C:N ratio to the 67th percentile of the distribution of leaf C:N ratio (Figure 5b). This output can be used to design a seed or planting mix for a restoration project by selecting species with the highest relative abundances.

5.3 | Optimizing seedling growth rate and canopy stratification in a tropical forest

Restoration practitioners who are restoring rainforests by planting tree seedlings directly into clearings may wish to plant species with high specific leaf area to promote fast seedling growth and rapid canopy closure. However, they may also want the canopy to stratify after reaching the sapling stage. Species with greater carbon allocation to dense wood tissue will exhibit slower growth than species with low wood density. Therefore, canopy stratification may be achieved by planting species with a diversity of wood densities. Using a dataset of 41 tree species from a subtropical rainforest in Queensland Australia (McCarthy, 2018), we derived an assemblage with a diverse range of wood densities, but a high average specific leaf area (Figure 5c). This output can be used to design a planting mix to optimize initial growth rates and early canopy stratification.

6 | CONCLUSION

In this paper, we have used examples where species assemblages were derived using only two traits for illustrative purposes. However, the *selectSpecies* function can derive species assemblages based on any number of traits: there is no upper limit to the number of trait values used as constraints (equation 1) and there is no upper limit to the number of traits when maximizing functional diversity (equation 4-6). However, there must be fewer traits than species (i.e., $K + 1 < S$) because mathematical systems with more equations than unknowns usually have no solution (Lay, 2006). We recommend using traits that exhibit low correlation and reflect independent aspects of organism function to maximize the information content of the traits (Laughlin, 2014b).

The *selectSpecies* R function provides ecologists with an easy-to-use open-source solution to the problem of objectively selecting species based on their functional traits. In the case of experimental restoration ecology, contrasting trait values can be selected to design alternative restoration assemblages to test which trait values perform best under a range of experimental conditions (Laughlin, 2014a). The SELECT package version 1.3 under license GPL (≥2) is available on CRAN (cran.r-project.org) and is compatible with version 3.3.0 of R and above.

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AUTHORS' CONTRIBUTIONS

D.C.L. wrote the first draft of the paper, D.C.L. and L.C. wrote the R package with conceptual contributions from C.J., M.R., J.M.D., and J.L.F.; J.L.F., J.M.D. and D.C.L. provided data and photos for Figure 5; all authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

The datasets and code used in this paper are available in the R package 'SELECT' version 1.3, which is available on CRAN at https://CRAN.R-project.org/package=Select. After installing the R package and loading the library '*Select*', datasets can be accessed using the data() function, where the name of the three datasets (serpentine, pineforest, and tropicalforest) can be entered within the parentheses.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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