

RESEARCH ARTICLE

Common, showy, and perennial species dominate a restoration species pool

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Native seed vendors are a primary source of germplasm for restoration projects; however, most plant species are not commercially available. Preferences in the types of species that vendors grow and sell may limit the similarity between reference communities and reconstructed ones established from seed mixes. We tested whether a restoration species pool shows preference for certain groups of species, focusing on the Ozark Highland Ecoregion (midcontinent United States). We identified the pool of 1,082 candidate herbaceous plant species appropriate for restoration projects on upland habitats in this region, and then surveyed nine regional seed vendors to assess their commercial availability. Commercially available species were more likely to be forbs over graminoids, perennials over annuals, and common species with larger ranges and moderate conservatism scores. Within forbs, taller species and those with longer bloom durations were favored. Species with affinity to open habitats (e.g. grassland) were more likely to be available from multiple vendors than those from woodlands and forests. Encouragingly, 454 (42%) of the species in this regional pool were available. However, this means that most species in the region are not likely to be included in seed mixes, unless they are hand-collected from remnant populations. This restoration pool favors common and showy species, which is consistent with previous studies showing these kinds of species tend to dominate seed mixes and restored plant communities. We identified 39 species that were not available from any of the vendors surveyed, which we recommend as candidates for expansion of the Ozark restoration species pool.

Key words: conservatism, functional traits, seed mix, seed producer, seed vendor

Implications for Practice

- Seed vendors in the midcontinent United States encouragingly supply over 400 species native to the Ozark Highlands Ecoregion. However, since this is less than half of the restoration pool, restoration with species reintroductions may require a combination of purchased and hand-collected seed.
- Species with larger ranges are more widely available, so we recommend that seed producers prioritize species with locally endemic ranges which producers are less likely to select in other regions.
- Commercially available species tend to be perennials, and forbs that are taller or bloom longer.
- Ruderal species with low conservatism are the most likely natives to recruit as volunteers, and highly conservative species often fail to establish in restored communities, but species with moderate conservatism are often also the most abundant in reference sites and are good candidates for inclusion in restoration species pools.

in assessing whether current seed production infrastructure can meet the needs of restoration practitioners (Pedrini et al. 2020; Gibson-Roy et al. 2021). Seed availability represents a primary limitation to restoring populations of desirable native plant species in degraded terrestrial habitats. In recent years, the native plant seed industry has grown rapidly, and demand for native seed is expected to increase substantially over the next decade (Tangren et al. 2022). However, most native species remain commercially unavailable (Merritt & Dixon 2011; White et al. 2018). If degraded ecosystems lack species found in historical reference ecosystems, native seed vendors and seed production areas (SPAs) can fill this gap by supplying native seed for restoration seed mixes (Ladouceur et al. 2018; Jones 2019; Zinnen & Matthews 2022a). As the primary supplier of native

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Introduction

The native seed industry is crucial for supporting the capacity for large-scale restoration projects to achieve global conservation targets (Cross et al. 2020; National Academy of Sciences 2023). Although seed-based restoration is a critical part of the UN Decade on Restoration, substantial barriers remain

plant species, the seed industry can comprise over half of seed used for species reintroductions (Barak et al. 2022). Although hand-collecting seeds from remnant sites is a common alternative to purchasing seeds from vendors, this practice poses potential risks of overharvesting from small populations or altering diversity in remnant plant communities (Meissen et al. 2015; Tangren et al. 2022). Thus, SPAs represent the best option for sustainably matching restoration demand for most species (Nevill et al. 2016; Pedrini et al. 2020; Zinnen et al. 2021). Despite the key role the native seed industry plays in building restoration capacity, significant questions remain as to how this industry can best support the specific biodiversity needs of restoration projects (Merritt & Dixon 2011; Broadhurst et al. 2016).

A “regional pool” describes all of the species that can colonize and occupy a given region, whereas the “restoration pool” represents a subset of native species from the regional pool that are commercially available from vendors or suppliers (Ladouceur et al. 2018; Zinnen & Matthews 2022a). For most ecosystems, the number and characteristics of native species in the restoration pool remains poorly known. In the United States, studies of the restoration pool have focused mostly on grasslands rather than on woodlands and forests, which are a dominant ecosystem throughout the eastern and central United States (e.g. White et al. 2018). Assessing the size and characteristics of the restoration pool represents the first step in evaluating the capabilities of commercial vendors to support seed-based restoration activities in a specific region. Of the approximately 25,000 native vascular plant species in the United States, only 26% are commercially available according to recent estimates (White et al. 2018). Similar evaluations for grasslands in Europe and tropical forests in Brazil found that only 32% and 38–44% of species were commercially available, respectively (Ladouceur et al. 2018; Vidal et al. 2020). If restoration projects source only commercially available seed, then they may exclude a majority of native species from the regional pool.

Although the restoration pool has grown substantially in many regions, commercially available species may represent a selective subset of the regional pool. Restoration practitioners often select species with high seed availability and reintroduction success, over species that more closely approximate historical communities or promote life-form diversity (Leger & Baughman 2015; Oldfield & Olwell 2015; Holl et al. 2022). If commercially available species represent a nonrandom subset of the regional pool, this could influence the composition and diversity of seed mixes employed in restoration (Ladwig et al. 2020; Zinnen & Matthews 2022b). In turn, this may partially explain why restored communities often differ markedly in composition and diversity from reference ones (Fagan et al. 2008; Barak et al. 2017; Newbold et al. 2020). In the few studies that have assessed commercial seed availability for restoration, herbaceous (vs. woody), and rare species are less likely to be available, and some plant families are disproportionately represented, depending on the region (White et al. 2018; Vidal et al. 2020). Continual demand for widely available species over rare species found in reference systems might select for the restoration pool, and resulting mixes and reconstructions, to contain a less diverse composition of species (Weber 1999).

The goal of this study is to assess the capacity of the native seed industry to support ecological restoration across terrestrial habitats in the Ozark Highlands Ecoregion of the midcontinental United States. Specifically, our objectives are to: (1) determine the regional pool of native herbaceous vascular plant species appropriate for restoration of terrestrial habitats (e.g. grassland, woodland, savanna, and forest); (2) define the restoration pool by surveying the native herbaceous species available from commercial seed vendors; (3) characterize the restoration pool with respect to growth form, rarity, habitat affinity, and selected functional traits; and (4) identify candidate species that are not commercially available, but should be prioritized due to their importance in Ozark ecosystems.

We developed four nonexclusive predictions about which types of species would be better represented in the restoration pool (Table 1).

- (1) The “showiness” hypothesis: Compared to other growth forms, forbs will be preferred because the aesthetic value of restoration projects is often a high priority, and forbs tend to have larger and more colorful flowers than graminoids, so will have value as “showier” species (e.g. Lindemann-Matthies & Bose 2007). Similarly, taller species and those with a longer bloom period may be selected preferentially because their blooms are more apparent to both humans and pollinators.
- (2) The “duration” hypothesis: perennial species will be preferred over annual or biennial ones based on the common restoration goal of accelerating succession toward a persistent and resilient native plant community.
- (3) The “commonness” hypothesis: We expect that species with smaller geographic ranges or more exacting habitat preferences are less likely to be commercially available due to their lower demand or perceived lower chances of establishment success. Species with a high conservatism score tend to have more specific habitat preferences. Those with low scores naturally occur across a broad range of habitats, but may be perceived as less desirable weedy/ruderal species because of their fidelity to heavily or frequently disturbed areas. Based on this pattern, we expect species with a moderate conservatism score, larger range size, and higher conservation rank (less concern for conservation) to be more commonly available from seed vendors.
- (4) The “Open habitat/SPA suitability” hypothesis: In the United States, the commercial seed market for grassland (prairie) plant species has grown rapidly in recent years (White et al. 2018). Based on this and because it may be more difficult to grow shade-loving species using common agronomic methods, we expect that species with affinities to open habitats, including glades, prairies, and savannas, are more likely to be commercially available than species with affinities to woodlands and forests. Similarly, as warm-season C₄ grass species tend to dominate open habitats, we predict that proportionally more warm-season rather than cool-season C₃ grasses will be commercially available. In a seed production context, it may be easier to grow species that tend to occur on drier soils rather than ones that require saturated or wet soils, so we expect species with a higher (drier) wetness rating will be more widely available.

Table 1. Distribution of species among factor levels for assessing patterns in species likelihood in representation in the Ozark Highlands restoration pool.

Scope	Variable	Type	Description	Hypothesis	Predicted Preference
All species	Physiognomy	Categorical	Annual forb, biennial forb, perennial forb, perennial grass, perennial sedge	Showiness, duration	Forbs > grasses, perennial > other
All species	Conservatism	Categorical	Low, moderate, high	Commonness	Moderate
All species	Habitat affinity	Categorical	Open, closed, generalist	SPA suitability	Open
All species	Wetness rating	Categorical	-3, 0, 3, 5	SPA suitability	Higher
All species	Range size (EOO)	Continuous	10–2,574 counties	Commonness	Higher
All species	State Conservation rank	Categorical	SR1, SR2, SR3, SR4/SR5, other	Commonness	Higher rank
Forbs	Max height	Continuous	4–500 cm	Showiness	Taller
Perennial forbs	Bloom duration	Continuous	1–9 months	Showiness	Longer
Grasses	Photosynthesis type	Categorical	C ₃ , C ₄	SPA suitability	C ₄ > C ₃

Methods

Defining the Species Pool

We examined commercial seed availability in the Ozark Highlands, a 41,078-km² (15,560 mi²) Level III ecoregion in central United States (Omernik 1995). Ecoregions are spatially defined zones based on ecosystem type, quality, and response to disturbances, designed to facilitate assessment, research, and monitoring of geographical areas (Bryce et al. 1998). Although ecoregions are defined within four nested levels, Level III ecoregions consist of operationally manageable units and potential seed transfer zones for restoration (Bower et al. 2014). The Ozark Highlands covers nearly the bottom third of Missouri and extends into NW Arkansas, NE Oklahoma, and a very small portion of SE Kansas (Chapman et al. 2002). This region experiences a humid subtropical climate (Köppen classification) with approximately 1,070–1,270 mm (42–50 inches) of annual precipitation (30-year 1981–2010 USDA climate normals). The soils are derived mostly from cherty carbonate rocks and a bedrock of dolomite, sandstone, or limestone (Chapman et al. 2002). Much of the region is topographically dissected, but there are also large swaths of rolling hills and plateaus. The dominant ecosystems are fire-maintained oak or mixed oak-pine forests, woodlands, and savannas, while bottomland forests, prairies, and glades (rocky grasslands) are also present (Nelson 2010). Restoration of the herbaceous flora in these systems is a priority for land management, especially in the woodlands and forests, which have lost herbaceous species due to densification and mesofication (McCarty 1998; Reid et al. 2020; Kaul et al. 2023). Thus, we focus our analysis on herbaceous angiosperms in upland habitats, given their priority for restoration.

We developed a targeted list of herbaceous plant species relevant for potential restoration projects in the Ozark Highlands by combining existing databases and excluding species that were not appropriate for the scope of this study. Regional species pools can be too large to use as a restoration guide, so filtering for traits desirable for restoration facilitates identifying a targeted species pool that can be used to improve restoration success (Bader 2001; Brudvig & Mabry 2008). We started with a digitized database from The Ecological Checklist of the

Missouri Flora (Ladd & Thomas 2015). The checklist of Missouri flora has 2,961 entries corresponding to taxa at the species, subspecies, or variety level. To identify our target species pool, we removed all adventive (non-native) taxa ($n = 906$), as well as all shrubs ($n = 114$), trees ($n = 145$), woody vines ($n = 39$), and ferns ($n = 73$), leaving only native forbs, grasses, and sedges. From the remaining 1,684 taxa we removed all obligate wetland species (Missouri wetness rating of “-5”; $n = 332$). Here, we focus on upland plant species because emergent species are less common in the dominant habitats of this region, wetland plants are often introduced as plugs or in vegetation mats, and seed-based restoration techniques are less developed for wetlands (Tarsa et al. 2022). We excluded species that occur within the state of Missouri, but not within the Ozark ecoregion, by consulting range maps and descriptions in the Flora of Missouri (Yatskievych 1999, 2006, 2013) and in the Biota of North America Program (BONAP) Taxonomic Data Center website (Kartesz 2015). Based on available species range data from these two sources, we removed 174 taxa because they did not occur in the Ozark ecoregion ($n = 155$), only had a historic range in the Ozark ecoregion ($n = 13$), were classified as non-native in the Ozark ecoregion ($n = 3$), or were classified as native, but as noxious weeds ($n = 3$). The resulting pool contained 1,178 taxa. We then collapsed taxa identified as varieties or subspecies into a single species. Our regional pool for upland habitats within the Ozark ecoregion contained 1,082 species.

Species Traits and Commercial Availability

To determine which species from the restoration pool are commercially available, we identified and surveyed vendors representing appropriate potential sources of seed for restoration in the Ozark Highlands. We focused only on vendors in, or near our study region, because sourcing seed from a “local” provenance is often a priority for restoration projects (Bucharova et al. 2017; La Tour et al. 2020; Goldsmith et al. 2021). We identified seven native seed vendors in Missouri, as well as five large and reputable vendors outside the state. We acquired information on which native species each vendor produces from their respective websites, or if they did not have a website, then through personal communication. We were unable to obtain

species lists from three vendors in Missouri. In total, we obtained species lists from nine vendors, including four seed vendors within Missouri, four regional seed vendors located in Iowa, Minnesota, and Kentucky, and a large vendor that produces seed for regions all across all the United States (Supplement S1). While nine vendors may seem like a small sample from a large industry, our analysis (see following text) indicates that this sampling adequately captures the restoration pool in this ecoregion, and smaller vendors tend to sell a subset of species also offered by larger ones (Table S4; Fig. S1). Native vendors often sell a combination of seeds and potted plants (Zinnen & Matthews 2022a). For this study, we focus only on seed availability, because seed additions are the most common approach for operational scale restoration of herbaceous communities (e.g. Cross et al. 2020).

To test our predictions on whether rarity, conservation status, habitat affinity, and traits relate to the likelihood a species is commercially available, we compiled data for each species in our regional pool using multiple sources. We assigned each of the species a wetness rating, coefficient of conservatism, and to one of seven physiognomic groups, based on duration and growth form, according to Ladd and Thomas (2015). The physiognomic groups included annual forbs, annual sedges, annual grasses, biennial forbs, perennial forbs, perennial sedges, and perennial grasses. A coefficient of conservatism (C-score) is an integer value 0–10 assigned to each species locally by expert botanists, and meant to designate fidelity to intact versus heavily disturbed or human-modified environments (Swink & Wilhelm 1994; Taft et al. 1997; Ladd & Thomas 2015). Since C-scores are subjectively assigned and can vary depending on the author or region, here we follow the convention of binning C-scores into more ecologically interpretable groups including low (0–3), moderate (4–6), and high (7–10) conservatism (e.g. Maginel et al. 2016). We quantified rarity as the number of counties in the United States with documented occurrence in the BONAP database (Kartesz 2015). This measure is analogous to an area of occupancy, rather than extent of occurrence (EOO) measure of geographic range (Gaston & Fuller 2009). We assessed conservation status based on the Missouri state conservation rank (Missouri Natural Heritage Program 2020). State ranks (SR) are as follows: SR1, critically imperiled; SR2, imperiled; SR3, vulnerable; SR4, apparently secure; and SR5, secure. For species given a range of values (e.g. SR2/SR3), we assigned them the lower of the two values. We binned species into five categories including SR1, SR2, SR3, SR4/SR5, and other, which includes unranked species that lacked data and species with only historic ranges in the state. We developed a habitat affinity variable by qualitatively assigning each species to one of three groups, “open-habitat specialists,” “closed-habitat specialists,” or “generalists,” based on habitat descriptions in the Flora of Missouri. Due to a lack of available information, we were unable to assign a habitat designation for 135 species. We extracted trait data from the Flora of Missouri on maximum height (cm) for all forb species, and bloom time duration (number of months) for perennial forbs. We determined the photosynthetic pathway for all grasses (Poaceae) at the species level, or inferred it from congeners when species-level information was

unavailable in Waller and Lewis (1979). To assess whether hemiparasites (independent of physiognomy) are present in the restoration pool we cross-referenced our regional pool with the USDA Animal & Plant Health Inspection Service parasitic plant list, and identified 16 hemiparasitic species.

To determine the commercial availability of dominant species that characterize major terrestrial habitat types in the Ozark Highlands, we used data in the The Terrestrial Natural Communities of Missouri (Nelson 2010). For each habitat type described in this text, the author provides short lists of “dominant,” “matrix,” and “restricted” plant species. We compiled a list of all species listed as dominant in any habitat that occurs within the Ozark Highlands ecoregion within the broader categories of forest, woodland, savanna, prairie, and glade ($n = 37$ habitat types). We then assessed which of these 117 dominant species are commercially available.

Statistical Analyses

All analyses were conducted using R version 4.1.0. and R studio version 1.3.1073. Our nine explanatory variables included six predictors for all plant species in the target pool, and three predictors developed for a subset of species (Table 1). We assessed whether any of the six predictors for availability of all species were correlated, by selecting the species with data available for all variables ($n = 933$), then using chi-squared tests for each pair of categorical variables, and Kruskal–Wallis tests to assess whether range size differed between levels of categorical variables. We used factorial analysis of mixed data (FAMD), a method for reducing data dimensionality with categorical and continuous variables, to describe and visualize relationships between the six predictors for all species (“FactoMineR” package; Lê et al. 2008). Due to uneven sample sizes among explanatory variables (Tables 1 and S6), and highly uneven distribution of species among factor level combinations (Tables S1–S3), we were unable to fit a generalized linear model including all explanatory variables. For each of nine explanatory variables separately, we used hurdle models to sequentially test our predictions about which species were most likely to be available from at least one vendor (binomial response—available or not), and then how many vendors sell each commercially available species (count response—Poisson distribution) (hurdle function in “pscl” package; Zeileis et al. 2008, Jackman 2020). We evaluated significance of explanatory variables using likelihood ratio tests, which compare the goodness of fit between nested models with the explanatory variable included, versus a model only including the intercept using the “lmeTest” package (Zeileis & Hothorn 2002). For significant categorical variables, we assessed pairwise differences between factor levels with Tukey-adjusted z -ratio tests using the “emmeans” package (Lenth 2022). This type of analysis accounts for variation in sample size among factor levels to assess which groups have higher predicted availability. We removed annual sedges ($n = 15$) and annual grasses ($n = 28$) from the analysis of physiognomy, since zero sedges, and only one annual grass was commercially available.

Results

We identified a regional pool of 1,082 species, mostly composed of perennial (52.5%) and annual forbs (20.4%), which are of potential interest for restoration of upland habitats in the Ozark Highlands (Fig. 1A). From this pool, we found that 454 (42%) species were commercially available from at least one vendor. Of these, 149 (33%) were available only from one of the nine vendors. The vendor with the most species in our pool had 376 species available (86% of the total), with 97 species unique to only this vendor (Table S4; Fig. S1). Three vendors accounted for over 97% of the 454 available species (Fig. S1).

The regional pool included 73 plant families across 29 orders (Table S5). Most species in the regional and restoration pools belonged to only a handful of families, and these patterns were

consistent across both species pools (Fig. 2). The four largest families, Asteraceae, Poaceae, Cyperaceae, and Fabaceae, together accounted for 46% ($n = 500$), and 53% ($n = 241$) of species from the regional and restoration pools, respectively (Fig. 2). Seventeen families (23.3% of families), containing a combined 87 species (8% of pool), had no representation in the restoration pool by any vendor surveyed (Table S5). Most of these families were only represented in the regional pool by one or two species. However, some families including the Orchidaceae ($n = 27$), Convolvulaceae ($n = 14$), and Solanaceae ($n = 12$) contained several species in the regional pool, but were absent from the restoration pool. Proportional availability of species within families was unrelated to the total number of species in the family (Fig. S2). The regional pool contained

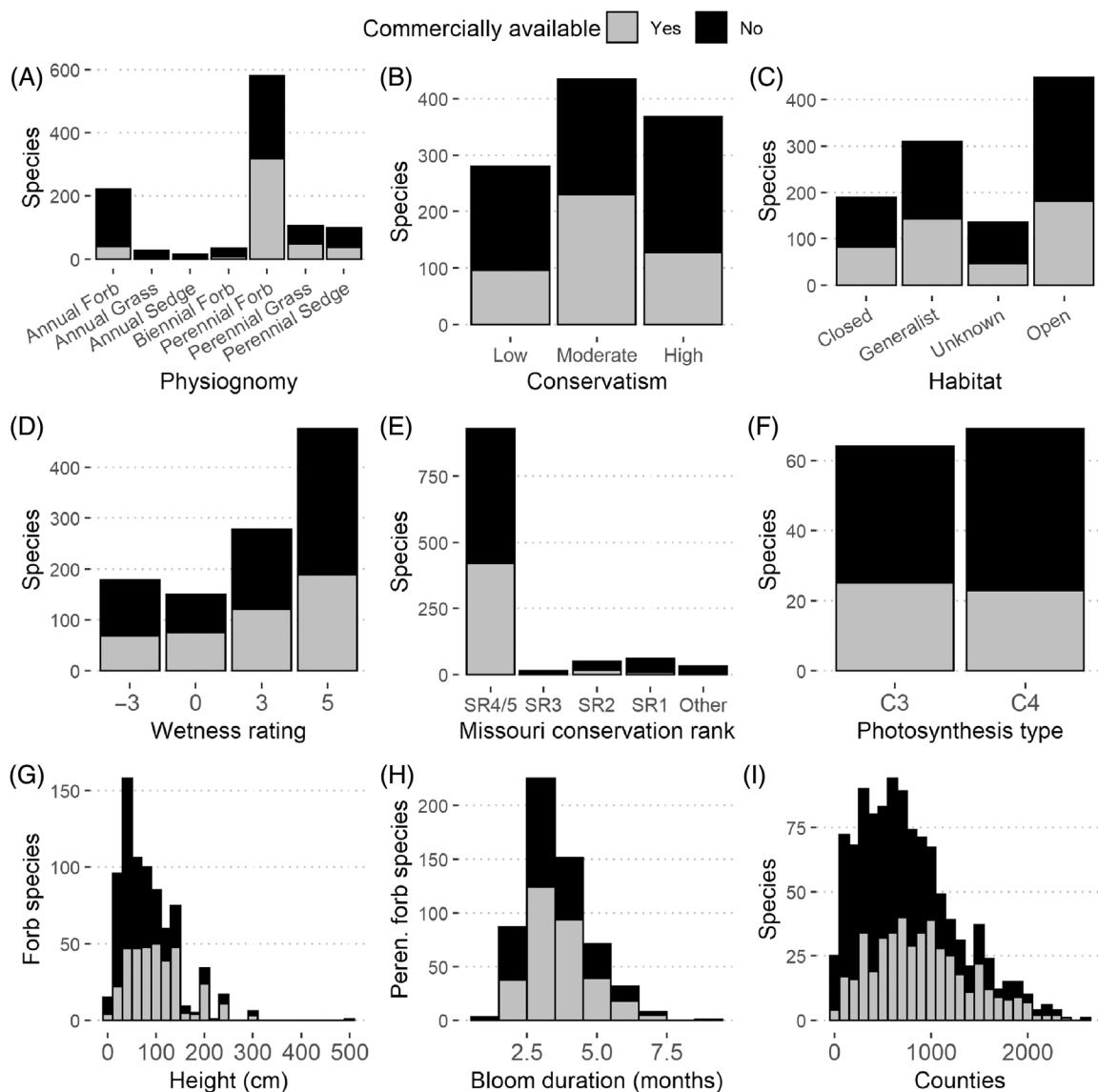


Figure 1. Frequency diagrams for each predictor variable showing the proportional availability of species based on (A) physiognomic categories combining growth form and duration; (B) conservatism groupings; (C) habitat specialization; (D) soil wetness affinity; (E) conservation designation for Missouri; (F) photosynthetic mode for grasses; (G) forb height; (H) perennial forb bloom duration; and (I) range size as measured by the number of U.S. county occurrences.

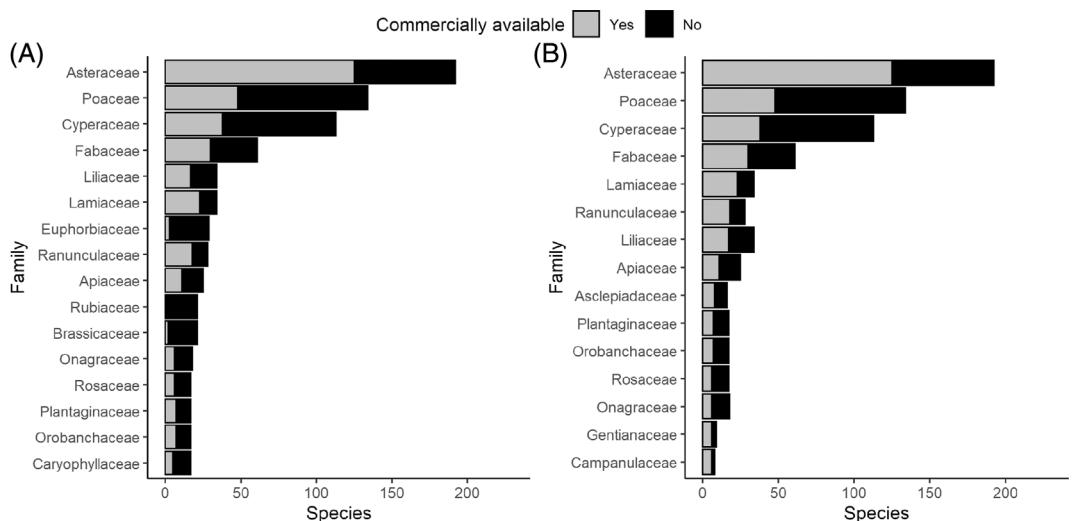


Figure 2. (A) Top 16 families by species richness in the regional pool (total bar length) and (B) top 15 families by species richness available in the restoration pool (gray bar length).

16 species of hemiparasites across three families, and eight (50%) of them were available in the restoration pool.

Predictors of Species Availability and Representation Across Vendors

Considering all species, physiognomy, conservatism, state conservation rank, and range size significantly predicted commercial availability (Table S6). Perennial forbs were the best represented group, being significantly more likely to be selected than all nonperennial species, two times more likely to be available than annual and biennial forbs, and the only functional group with over 50% predicted probability of availability (Fig. 3A). Perennial grasses had the second highest availability of any group, whereas no annual grasses were commercially available. Conservatism scores also significantly predicted commercial availability (Table S6). Most species (74%) in the regional pool had moderate or high conservatism (Fig. 1B). Moderately conservative species had around 18% higher probability of availability than those with low or high conservatism (Fig. 3B). Species also differed in likelihood of commercial availability based on the Missouri conservation rank, with the species of lowest conservation concern (SR4/SR5) having over two and a half times the predicted availability rate as those with the highest conservation concern (SR1) (Table S6; Fig. 3C). Range size varied between species by two orders of magnitude (Fig. 1I). Species with larger total ranges were more likely to be commercially available (Table S6; Fig. 3D). Height and bloom duration both predicted forb availability (Table S6). For all forb species (Fig. 1G), taller forbs were more likely to be available (Table S6; Fig. 3E), and considering only the perennials, species that have longer bloom periods were more likely to be available (Table S6; Fig. 3F). Habitat affinity, Missouri wetness rating, and grass photosynthetic pathway were unrelated to commercial availability (Table S6).

For commercially available species, physiognomy, conservatism, habitat affinity, wetness rating, range size, and state conservation rank were significant predictors of the number of vendors from which species were available (Table S6). Number of vendors selling a species was related to physiognomic groups, but differently so than when considering only binary availability. Perennial grasses were available from the most vendors, having significantly higher representation than perennial sedges or annual forbs (Fig. 4A). Perennial forbs were also available from more vendors than annual forbs (Fig. 4A). Highly conservative species were available from fewer vendors than less conservative species (Fig. 4B). Similar to the binary availability, species with a low conservation concern (rank SR4/SR5) were the most likely to be available from many vendors (Fig. 4C). Habitat affinity predicted the representation of species across vendors, with species found in more open habitats having greater availability than generalists, or closed-canopy specialists (Fig. 4D). Generalists also had greater representation than species from closed-canopy habitats. Species with a wetness rating of "0" (facultative) were available from more vendors than those with a rating of "5" (upland obligate; Fig. 4E). Species with larger ranges were more likely to be available from a greater number of vendors (Fig. 4F). Taller forb species, and those with a longer bloom duration are more likely to be available from more vendors (Fig. 4G & 4H). Grass photosynthesis type was unrelated to number of vendors (Table S6).

Our FAMD plots show distinct clusters of factor levels among predictor variables (Fig. 5A). The first two dimensions accounted for 12.4% and 8.7% of variance among species respectively (cumulative = 21.1%). We chose to present the first two dimensions, since they were easily interpretable with two of the six variables loading heavily onto each of the two dimensions. The three remaining dimensions explained a low amount of variance and had high contributions from variables already loading heavily on one of the first two dimensions. Dimension 1 separated species based on conservatism (33.1%)

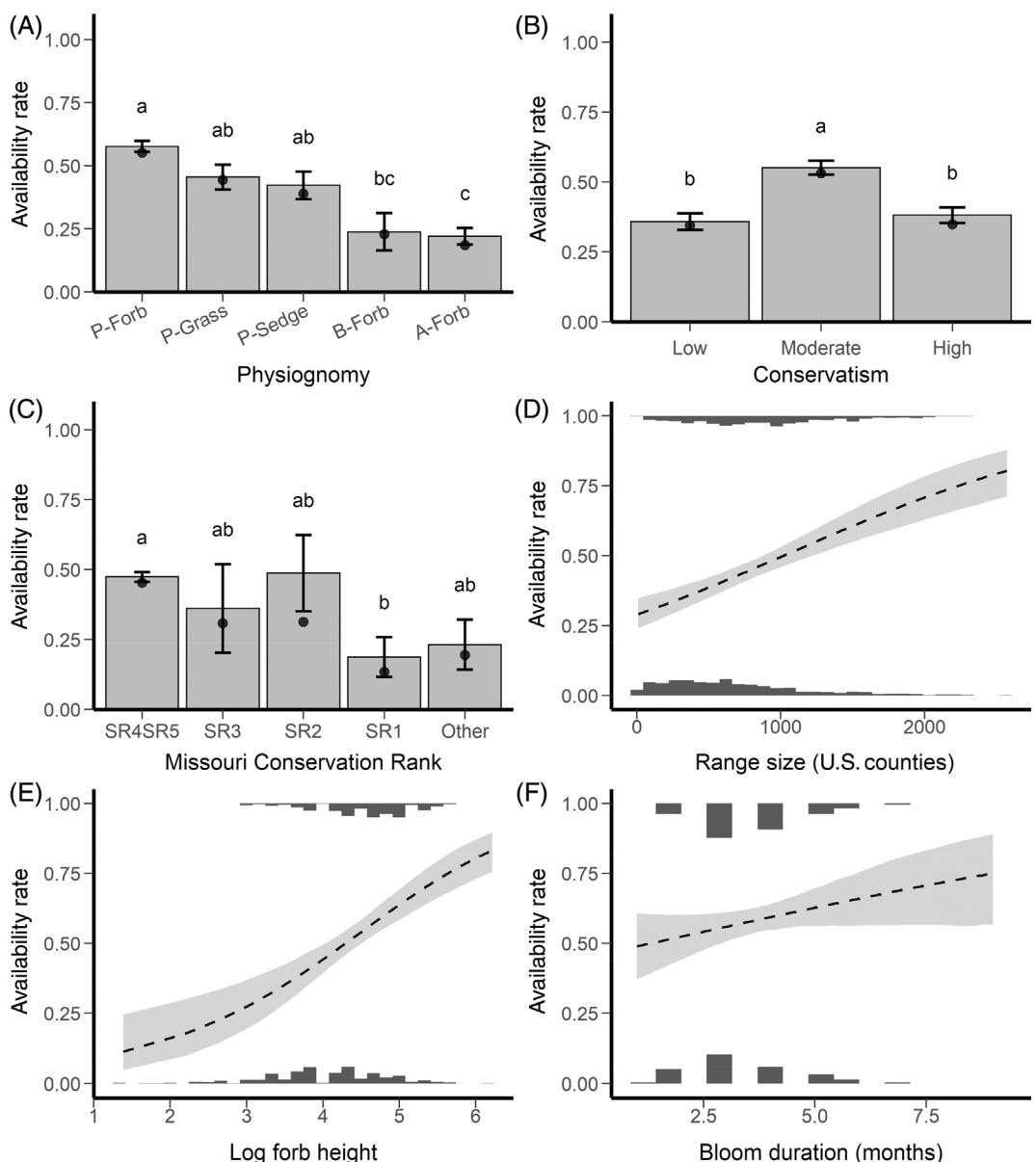


Figure 3. Commercial availability of Ozark herbaceous species available from native seed vendors is predicted by (A) physiognomy (duration and growth form; P = perennial, B = biennial, A = annual); (B) conservatism (low C = 0–3, moderate C = 4–6, high C = 7–10); (C) the state-level conservation rank; (D) the range size within the United States; (E) when only considering forbs, taller plants are more likely to be available from vendors; and (F) for perennial forbs, species with longer bloom duration are more likely to be available. Plots (A)–(C): factor levels that share a letter are not different ($p > 0.05$); points and lines, respectively, show raw and model-predicted values. For plots (D)–(F), histograms show distribution of binary responses, and lines display model-predicted availability with bootstrapped 95% CI.

and range size (26.0%), and dimension 2 had high contributions from physiognomy (32.8%) and habitat (28.5%). Groups of species with the highest availability and representation among vendors tended to group near the origin, with space near the periphery corresponding to lower availability (Fig. 5B & 5C). Plots isolating each variable illustrate how factor levels group in this ordination space, and particularly how conservatism, wetness, habitat affinity, and Missouri conservation rank covary with range size on dimension 1 (Table S3; Fig. S3A–S3F).

Ozark Dominant Species

The list of dominant species for terrestrial habitats in the Ozarks includes 117 species with low conservation risk (all SR4/SR5; Table S7). Of these, 64% have moderate conservatism, with high or low conservatism species each representing 18%. These dominant species are mostly forbs (53% perennial, 15% annual) and perennial grasses (17%), with the remaining 15% composed of perennial sedges, annual grasses, and one biennial forb. One third ($n = 39$) of these dominant species were not available from

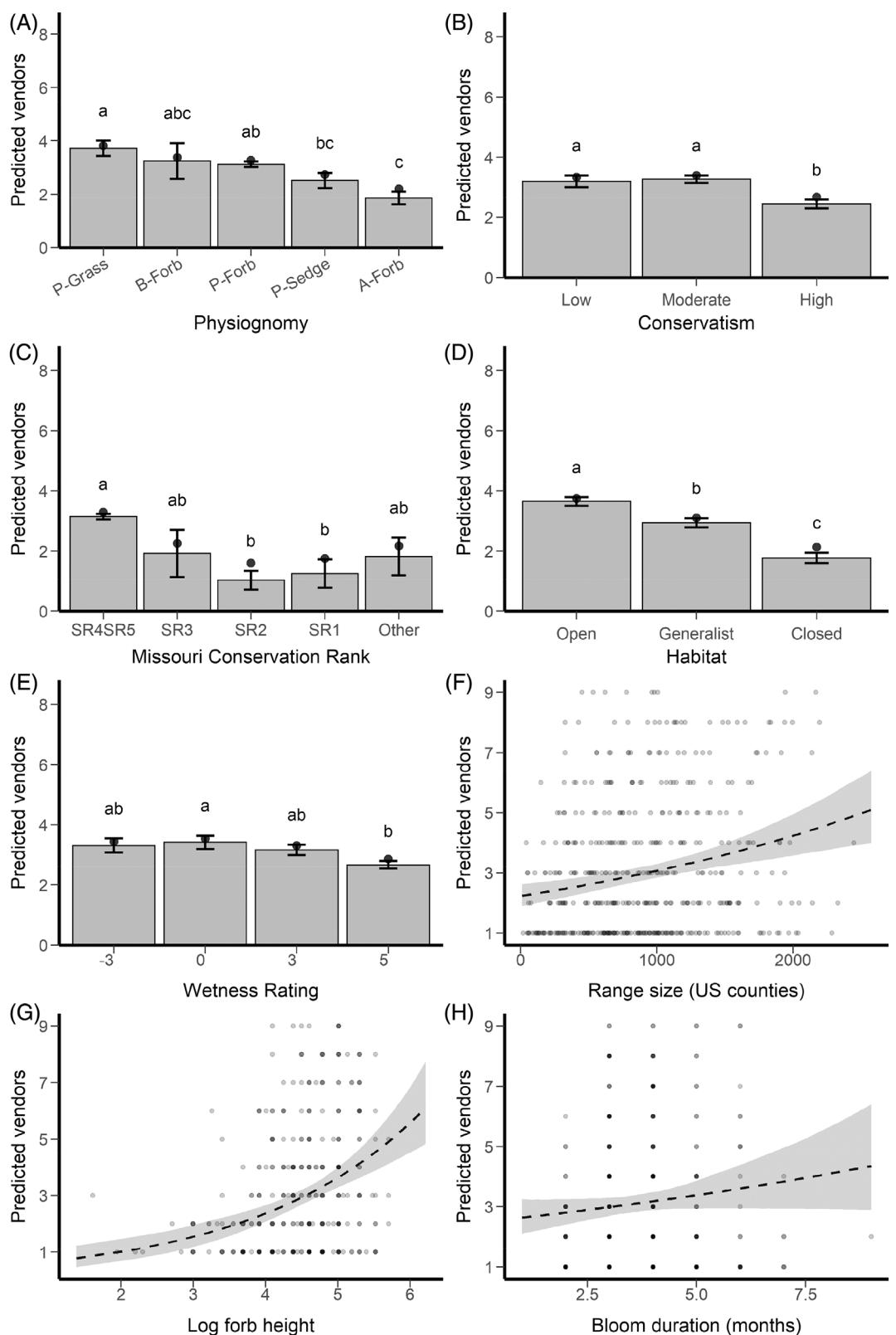


Figure 4. Ozark herbaceous species are more likely to be available from more vendors based on (A) physiognomy (duration and growth form; P = perennial, B = biennial, A = annual); (B) conservatism (low C = 0–3, moderate C = 4–6, high C = 7–10); (C) the state-level conservation rank; (D) habitat affinity; (E) wetness rating; (F) the range size within the United States; (G) when only considering forbs, taller plants are more likely to be available from more vendors; and (H) perennial forbs with longer bloom duration are more likely to be available from more vendors. Plots (A)–(E): factor levels that share a letter are not different ($p > 0.05$); points and lines, respectively, show raw and model-predicted values. For plots (F)–(H), lines display model-predicted number of vendors with bootstrapped 95% CI.

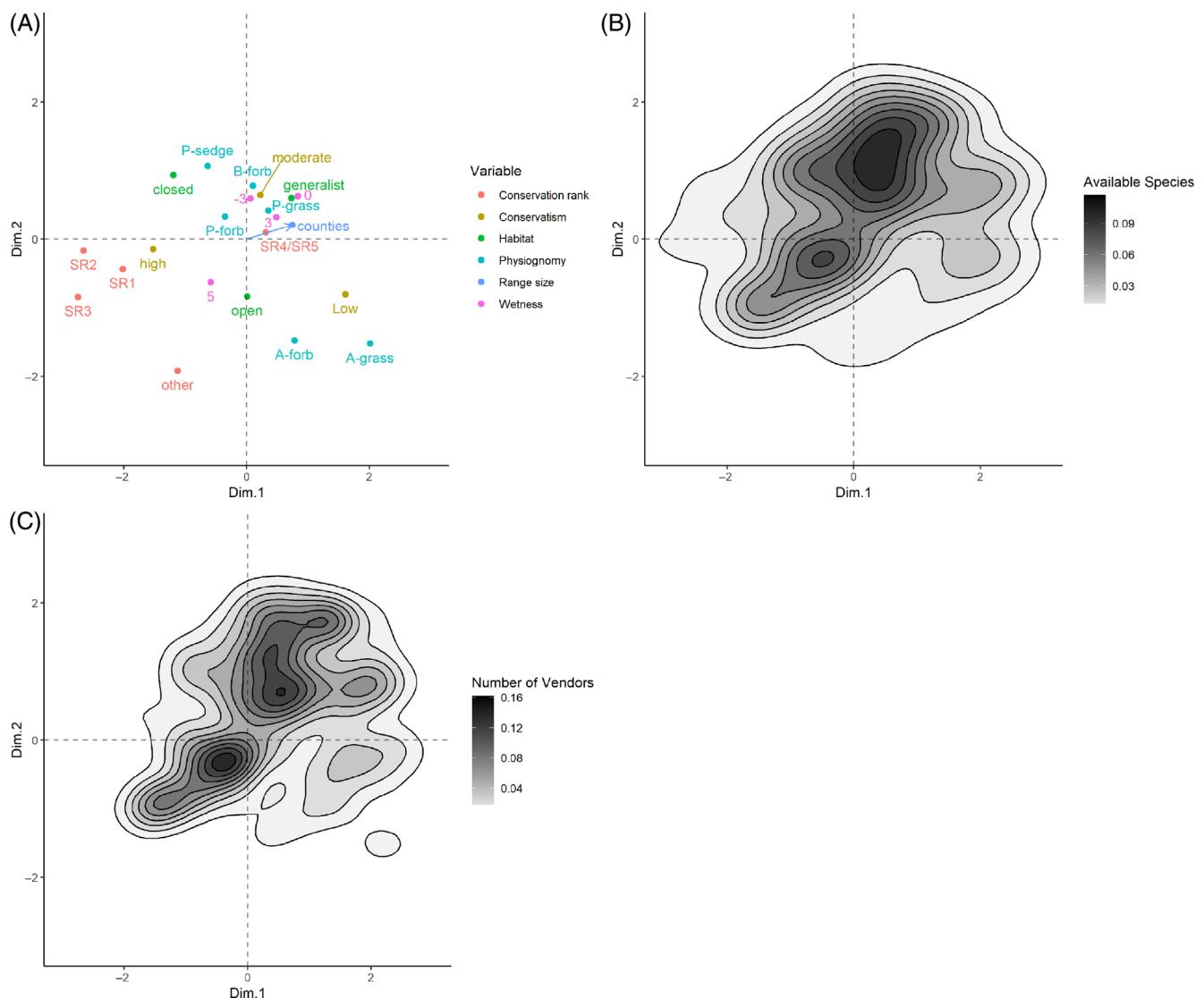


Figure 5. Factorial analysis of mixed data (FAMD) ordination plots visualizing (A) relationships between six explanatory variables including all levels of five active factors, and one continuous variable (range size); (B) density of commercial availability (407/933 are available); and (C) density of number of vendors for each species.

any vendor (Table S7). These 39 species belong to 18 plant families and are roughly distributed as expected from the regional pool across categorizations based on physiognomy, conservatism, habitat affinity, and wetness rating (Fig. 1).

Discussion

Previous work has documented that SPAs tend to over- or undervalue certain types of species, with the most common “workhorse” species being those that have high agronomic suitability, seed production, establishment success, and low cost (Dunne & Dunne 2003; Leger & Baughman 2015; Zinnen et al. 2021). Conversely, underutilized species may be those that establish poorly from seed, are difficult to cultivate at scale, produce few seeds, or are not perceived as priority species for

restoration (Jones 2019). Our results demonstrate clear patterns in how species traits and commonness relate to workhorse versus underutilized status.

We found support for our hypotheses that commonness, showiness, and longer duration are positively associated with species’ representation in the restoration pool. We found the strongest trends supporting the prediction that species differ in their likelihood of commercial availability based on physiognomy (growth form and duration). Perennial species were nearly twice as likely to be available as shorter-lived annual or biennial species, and as predicted, forbs were more widely available than grasses or sedges. Forbs may be considered showier than graminoids because of their larger or more brightly colored flowers. Also consistent with our showiness hypothesis, we found that taller forbs were favored over shorter ones, and perennial forbs

that bloom for longer are more likely to be available and are offered by more vendors. Forbs may also have higher commercial availability because they are increasingly prioritized in restoration seed mixes due to their value as hosts and food sources for wildlife and insects (e.g. Harmon-Threatt & Hendrix 2015). We also found support for our commonness hypothesis, with respect to specific predictions for conservatism, range size, and conservation rank. The FAMD ordination showed species with larger ranges, moderate conservatism, and least conservation concern (SR4/SR5) clustered together, indicating a syndrome of traits for common species with the highest commercial availability. This result is consistent with previous work showing that the broader U.S. seed market shows preference for species with higher global conservation ranks (G4, G5; White et al. 2018). Species with moderate conservatism scores were more likely to be available than those with high or low conservatism, and species with high conservatism were available from fewer vendors. This may be because species of low conservatism are perceived as “weedy,” and thus either may be undesirable for restoration applications, or for species that are desirable, may be expected to recruit into restored areas as volunteers from the seed bank or local dispersal. Species with low conservatism scores also tend to be shorter-lived annuals and biennials, which are not generally prioritized for seed mixes, but may provide important functions in restoration such as rapid revegetation. On the other hand, highly conservative species may be difficult to grow for seed production, or have a smaller range, and thus limited restoration demand. Land managers tend to choose more dominant species for purchase (Oldfield & Olwell 2015; Holl et al. 2022), so demand for species of moderate conservatism might precipitate an increase in inventory for these species. The higher availability of common species may be explained by ease of production, where rarer species may be harder to collect from appropriate wild populations, or harder to propagate based on differences in reproduction methods or conditions (Lesage et al. 2018; Holl et al. 2022). Additionally, this restoration pool may also be influenced by demand from individual buyers who want seed for native plant gardening rather than for large-scale restoration applications (De Vitis et al. 2017). For example, seeding native annual plants may be a useful strategy to rapidly establish cover in a restoration context, but these species may be less appealing for home gardeners. Similarly, the choice of species for native plant gardens may be driven by consumers’ perceived value to pollinators (Majewska & Altizer 2020), which could explain demand-driven selection for forbs, especially in certain families (e.g. Lamiaceae, Asclepiadaceae) which are frequently advertised for these purposes.

We predicted that species with affinity to open habitats might have greater proportional representation in the restoration pool due to the high demand and ease of production for prairie species in the Midwest (White et al. 2018). Although open-habitat species represented the largest habitat group in both the regional and restoration pools, commercial seed availability was proportional to species of closed and generalist habitats. However, for commercially available species, those from open habitats were sold by more vendors than the generalist or closed-habitat species, consistent with the high demand for common

prairie obligate species reported previously (Zinnen & Matthews 2022b). In contrast to our prediction, warm and cool season grass species exhibited similar commercial availability, with about a third of all species belonging to each group being available. In open grasslands, hemiparasitic species can be ecosystem engineers suppressing dominant species (usually grasses) and increasing community evenness, are often missing from restored communities, and may improve restoration outcomes when reintroduced (Barak et al. 2017; Chaudron et al. 2021; Hodžić et al. 2022). Since half of the hemiparasites in the regional pool were available in the restoration pool, this suggests that the lack of hemiparasites in restored grasslands may be due to difficulty of establishment (e.g. Mudrák et al. 2014) or lack inclusion in seed mixes, more than seed availability.

Quantifying characteristics of the restoration pool as we have done, may aid with interpreting where different forms of selection occur between species in a regional pool and those that occupy restored communities. The restoration pool describes a subset of the regional pool, and seed mixes contain a subset of the restoration pool. Several studies describe general relationships between seed mixes and the composition and diversity of restored plant communities (Grman et al. 2015; Barber et al. 2019; Kaul & Wilsey 2021). However, only a few studies have quantified the characteristics of species selected for seed mixes from the larger restoration pool (Ladwig et al. 2020; Zinnen & Matthews 2022b) or described what factors influence mix design from a practitioner perspective (Goldsmith et al. 2021; Barak et al. 2022). Consistent with previous reports indicating availability of species is a major constraint on seed mix design (Barak et al. 2022; National Academy of Sciences, Engineering, and Medicine 2023), our results suggest that some patterns previously described in seed mixes may be attributable to constraints on restoration pools, rather than on selection of species from within them. For example, Zinnen and Matthews (2022b) found that “showy” forbs dominate prairie seed mixes in the Midwest United States, which is consistent with our characterization of the broader restoration pool in the Ozarks. Additionally, we found similar taxonomic patterns in families that were missing or poorly represented from this restoration pool, and the families that were missing from seed mixes for Midwestern savannas, including the Brassicaceae, Cistaceae, Ericaceae, Orchidaceae, Solanaceae, Polygalaceae, Rubiaceae, and Urticaceae (Ladwig et al. 2020). Future work should address why these families are underrepresented in restoration pools and mixes, and seek to remove barriers to sourcing seeds for restoration.

While it was not within the scope of this project to explicitly test for specific taxonomic biases in the restoration pool, we did find that the representation of species availability varied widely among plant families. Notably, 17 families from the regional pool were completely lacking from the restoration pool, and several species-rich families in the regional pool including Euphorbiaceae, Rubiaceae, Brassicaceae, and Caryophyllaceae, had remarkably low representation from seed vendors. The absence of orchids and other families may partially explain the lack of representation of these families in communities restored using

seed mixes (Barak et al. 2017). Perhaps unexpectedly, we found no relationship between plant families' total species richness in the regional pool, and the proportional availability of species within a family. This may be considered a positive outcome, as it suggests there is no bias in the restoration pool toward larger or smaller families.

Ozark Highlands in Context

We found that 42% of the regional pool is available from appropriate vendors, which represents a higher availability than the total of 26% vascular plant availability reported across the United States, but is not as high as the estimate of 74% availability for the Midwestern tallgrass prairie seed market (White et al. 2018). This positions the Ozark seed market as above the national average yet still lacking the majority of Ozark biodiversity—more similar to the 32% availability in European grasslands (Ladouceur et al. 2018) and the 38–44% availability reported in southeastern Brazil (Vidal et al. 2020). The Asteraceae and Poaceae were the best-represented families in the Ozark restoration pool, consistent with their dominance previously reported in the broader U.S. seed industry (White et al. 2018).

The final goal of this project was to identify candidate species to recommend as valuable for restoration potential in this region. Of the 120 species identified by Nelson (2010) as dominant in upland Ozark habitats, 78 (66%) were commercially available. This is encouragingly high; however, there are still 39 species that would be difficult for restoration practitioners to acquire without hand collecting them from wild populations. These 39 species represent important plants that have not been commercially selected, likely for a variety of species-specific reasons. For example, the annual species, *Sporobolus vaginiflorus* (C = 0; dominant in limestone glades) and *Plantago elongata* (C = 1; sandstone glades) may be perceived as weedy natives that readily establish on their own. In contrast, *Hypericum hypericoides* (C = 8; dry sandstone woodlands) may be difficult to produce because it is a highly conservative shade-loving species. Violets dominant in woodlands (*Viola palmata*) and prairies (*V. sagittata*) may be missing because violet seed production is difficult due to several factors including a long fruiting duration, explosive dehiscence, low seed number, and dormancy (Bartow 2014; Kilgore et al. 2022). Interestingly, almost half of these 39 missing species are annuals, indicating the value of this group may be underappreciated by the restoration community that produces and purchases seeds. This highlights how missing taxa from the restoration pool could potentially make assembling a high-quality seed mix more difficult, if the species for sale represent those that are easiest to cultivate, rather than being the ones that have biological significance to restoration.

There is an enormous opportunity to improve seed-based restoration capacity, especially for woodlands in the Ozark ecoregion. Seeds for woodland species in this region are generally hand harvested in wildlands, which is the only option when species are not included in SPAs (Pedrini et al. 2020; Reid et al. 2020; Kaul et al. 2023). Understory species grow slower,

need shadier conditions, and may be more difficult to harvest using mechanical methods, making it hard to scale up profitably for vendors.

Restoration projects often prioritize the use of genetically diverse and locally adapted ecotypes for seed sources used in revegetation. Most seed vendors do not label products at taxonomic ranks below the species level. However, conservation goals are sometimes identified for subspecies or varieties. The extent to which these taxa are commercially available is difficult to assess. Additionally, many restoration projects call for seed from a local provenance, but obtaining information on ecotypes of native seed lots from vendors can be difficult. While over 400 species from this regional pool are commercially available, the number of species that are available from an Ozark ecotype is likely much lower.

Here, we are only scratching the surface in terms of identifying ways in which seed availability in the restoration pool enables conservation efforts, and may have downstream effects on the diversity, composition, and functioning of restored plant communities. Mismatches in temporal supply and demand from restoration practitioners may also explain patterns in species' availability, as seed vendors cannot succeed when producing seed for species that are not purchased (Goldsmith et al. 2021; Barak et al. 2022; Tangren et al. 2022). We were unable to find published data on the habitats where some species in the Ozark regional pool tend to grow. We suggest that publishing species' habitat affinities at regional scales would facilitate research and practice of species conservation and seed mix development. In the future, we recommend continued collaboration between seed vendors, restoration practitioners, and conservation scientists to identify the limitations of available seed stocks and to better align supply and demand for native seeds.

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Accumulation of total ($n = 454$) species available from at least one vendor across the nine vendors included in this study.

Figure S2. Commercial availability of species by family is not related to total richness of species in the family.

Figure S3. Distribution of 933 species (jittered points) in FAMD ordination plots.

Supplement S1. Names and website information for the nine seed vendors used to assess commercial availability of native herbaceous species in the Ozark Highlands.

Table S1. Chi-square tests to assess whether categorical variables are independent.

Table S2. Kruskal–Wallis rank sum tests determining whether the continuous variable range size differs by 5 categorical variables.

Table S3. Post hoc pairwise Dunn tests determining whether the continuous variable range size differs by 5 categorical variables.

Table S4. Total and singleton species from the regional Ozark species pool available from each of nine seed vendors.

Table S5. Representation of 73 plant families available from nine US native seed vendors.

Table S6. Likelihood ratio tests assessing influence of predictor variables on commercial availability.

Table S7. Native plant species designated as “Dominant” in any Ozark habitat in The Terrestrial Natural Communities of Missouri.

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