

University of Massachusetts Amherst

ScholarWorks@UMass Amherst

Environmental Conservation Faculty Publication
Series

Environmental Conservation

2022

**SpORtl: The species originality and rarity index combines
phylogenetic and functional originality with rarity metrics to
provide a new perspective on species rarity**

Michael Cunningham-Minnick

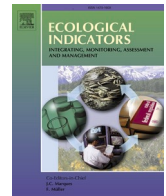
Joan Milam

David I. King

Follow this and additional works at: https://scholarworks.umass.edu/nrc_faculty_pubs



Part of the [Environmental Monitoring Commons](#), and the [Natural Resources and Conservation Commons](#)



Original Articles

SpORTI: The species originality and rarity index combines phylogenetic and functional originality with rarity metrics to provide a new perspective on species rarity

Michael J. Cunningham-Minnick^{a,*}, Joan Milam^a, David I. King^b

^a University of Massachusetts Amherst, Department of Environmental Conservation, 160 Holdsworth Way, Amherst, MA, USA

^b USDA Forest Service Northern Research Station, University of Massachusetts Amherst, Amherst, MA, USA



ARTICLE INFO

Keywords:

Apoidea
Life-history traits
Morphological features
Taxonomic relatedness
Bee conservation
Rarity weights

ABSTRACT

Methods used to assign rarity among species are fundamental to our ecological understanding and conservation of species that are most vulnerable to extinction or extirpation. Bees (Hymenoptera: Apoidea: Anthophila) are at the forefront of declines in pollinator diversity and a comprehensive understanding of their conservation requirements in any landscape is essential. Rarity is generally defined in terms of numerical abundance and geographical distribution, though aspects of species life history, such as degree of specialization and taxonomic relatedness, are also widely recognized as important. Incomplete information on the life histories of many taxa obliges ecologists to rely on species-level classifications of specialization provided by expert opinion or in published site- or region-specific studies. Descriptions of specialization are therefore rooted in characterization of the habitat and introduce subjectivity into rarity calculations through assumptions of how species perceive and use resources. An alternative approach that may reduce this level of subjectivity is to incorporate important life-history elements into species rarity assessments, which are traits of the organism itself and not its environment. Phylogenetic and functional originality are metrics which have been presented as useful for characterizing the uniqueness of species, and thus for developing a more informed index of species rarity. This study describes our Species Originality and Rarity Index (SpORTI) for bees that includes variables reflecting five rarity and originality metrics for each species: numeric rarity, geographic rarity, phenological rarity, phylogenetic originality, and functional originality. We compared species-specific rarity weights generated with this approach against other indices using a bee dataset collected over three years across the 520,000-km² land area of the Great Lakes Basin and within the United States and found that rankings using our approach differed significantly from other indices. Our index represents an improvement on previous approaches since it incorporates key information identified by other researchers and avoids potential subjectivity associated with assigning habitat specialization. Importantly, SpORTI has the added advantage to incorporate updated species life-history traits reported in the literature to allow for the most comprehensive and timely rarity index. This new index will aid researchers and practitioners in determining what species to focus conservation efforts on, as well as which management treatments and environmental factors affect our most vulnerable species of bees, or other taxa, so that limited resources can be applied to focal areas of conservation concern more effectively and efficiently.

1. Introduction

Ecological application of the ‘rarity’ concept includes designating some species as more important than others, particularly those at greater risk of extinction or extirpation (Flather and Seig, 2007). Land managers identify habitats of conservation concern and achieve conservation objectives with limited available resources by weighting the inherent value

of each species to identify those that potentially require greater conservation intervention (Capmourteres and Anand, 2016; Marris, 2007; Kremen, 1992). Diverse arthropod taxa, including insect pollinators such as bees, butterflies, and beetles, are in the conservation limelight following reports of declines in their global populations and pollination services in response to anthropogenic changes (Wagner et al., 2021; Eisenhauer et al., 2019; Seibold et al., 2019; Koh et al., 2016; Vanbergen

* Corresponding author.

E-mail addresses: mcunningham@umass.edu (M.J. Cunningham-Minnick), jmilam@umass.edu (J. Milam), david.king2@usda.gov (D.I. King).

<https://doi.org/10.1016/j.ecolind.2022.109339>

Received 1 July 2022; Received in revised form 12 August 2022; Accepted 17 August 2022

Available online 23 August 2022

1470-160X/© 2022 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

et al., 2013; Winfree et al., 2011; Kremen, 1992). The importance of accurately assigning rarity ranks to bee species is consequently essential to bee and pollinator conservation. Unfortunately, as our general understanding of factors that lead to the vulnerability of a species improves, so too does the complexity in producing a comprehensive method that establishes the relative rarity of a species.

By its simplest definition, rare species are those with lower abundances and smaller geographic range sizes relative to other species (Gaston, 1994; Preston, 1948), and prior characterizations of species rarity have incorporated these two metrics (Maciel, 2021; Harrison et al., 2019; Leitão et al., 2016; Leroy et al., 2011), but there are additional species-specific factors that influence species vulnerability (Konratyeva et al., 2019; Drever et al., 2012; Kunin and Gaston, 1997; Gaston, 1994). For example, species with short active seasons are more likely considered rare, suggesting that phenology may be important to include in species rarity calculations for bees and other taxa (Wilfahrt et al., 2021; Harrison et al., 2019; Flather and Seig, 2007; Reveal, 1981; Schoener, 1974). Phylogenetic comparisons have further demonstrated that species extinctions and local extirpations were not taxonomically random and thus, influential to species rarity even if unrelated to abundance (Grab et al., 2019; Hendrix et al., 2018; Silva et al., 2012; Cadotte and Davies, 2010; Schwartz and Simberloff, 2001; Purvis et al., 2000; Gaston, 1994). Since species functional traits largely determine behavior and resource use (Mori et al., 2013; Winfree et al., 2011), an informed rarity metric should also consider the uniqueness of species life-history, or functional, traits (Konratyeva et al., 2019; Vane-Wright et al., 1991), albeit in combination with other rarity metrics (Bartomeus et al., 2018).

Despite the importance of all five of these species qualities to characterizing species rarity, there is no single index for any taxon that incorporates them all: numeric rarity, geographic rarity, phenological rarity, phylogenetic originality, functional originality (Konratyeva et al., 2019). For example, MacLeod et al. (2020) used numeric rarity from museum data to determine rarity of crop-pollinating bee species. Volenec and Smith (2021) created a hybrid (weighted) metric based on numeric and phenological rarity to evaluate effects of urban land use on rare bees of forest fragments. The most comprehensive calculation of bee rarity to date included numeric, geographic, and phenological rarity to understand how rare bees differentially responded to forest, agriculture, and urban land uses (Harrison et al., 2019). Outside the bee literature, methods to include phylogenetics or species functional traits in weighting species for conservation have been developed (Pavoine and Ricotta, 2021; Cadotte and Tucker, 2018; Cadotte and Davies, 2010; Rosauer et al., 2009).

Perhaps the most popular approach to combine rarity and originality metrics in determining overall rarity was devised by Rabinowitz (1981) who used numeric and geographic rarity metrics to classify species as “generalists” or “specialists” to account for differences in specialization among species-habitat relationships in rarity calculations (overview of work since described in Maciel, 2021; Leitão et al., 2016; Rabinowitz et al., 1986). Maciel (2021) converted this approach to categorizing species based on rarity into a continuous index value using the inverse of the maximum number of habitat types occupied by a species as proxy for habitat specialization. However, basing habitat specialization on occurrences among habitat types conceptually increases subjectivity through the additional assumption that all species within the considered taxon interact within the landscape at the same scale and are responsive to the same general patterns of vegetation as defined by ‘habitat type’, which may or may not reflect required resources for species (Kirk et al., 2018; Krausman and Morrison, 2016). Using this approach will result in variation in the relative rankings of species within the rarity index depending on the resolution at which a taxon is evaluated even when scale is kept constant, which is particularly problematic for mobile taxa. For instance, the International Union for Conservation of Nature (IUCN) recognizes three hierarchical levels, or resolutions, of habitat types, many of which are still in development (IUCN, 2021a). Additionally, all

species would receive the same score for habitat specialization if they occurred in the same habitat types, and complications may arise if the habitat type of an area needs reclassified following land-use changes or profound effects from invasive species (Jung et al., 2020; Pyšek and Richardson, 2010). These issues can be eliminated by using species-centric metrics in the calculation of species rarity indices, rather than making assumptions about their specialization relative to habitat.

The methods used to calculate the metrics employed for characterizing species rarity have also varied, which may affect species rankings and their interpretation. A review of metric calculation methods is outside the scope of this paper, but conceptual differences among popular approaches deserve introduction. Numeric rarity is generally calculated using species abundances to represent population size (Gaston, 1994; e.g., Maciel, 2021; MacLeod et al., 2020; Leitão et al., 2016). However, taxa that exhibit different breeding systems, including the variable nesting aggregation behaviors or sociality observed in bees and birds, may be more accurately represented by species occurrences (e.g., Volenec and Smith, 2021; MacLeod et al., 2020; Harrison et al., 2019) since the distribution of individuals among assemblages that include these species will be fundamentally different (Estrada and Arroyo, 2012). There are two general approaches used to calculate geographical range sizes for species geographic rarity, including the extent of occurrence (e.g., Maciel, 2021; Harrison et al., 2019; Leitão et al., 2016), such as convex hulls that consider the area contained within extreme latitudinal and longitudinal occurrence points, and area of occupancy (Konratyeva et al., 2019; Gaston, 1994) which is the area of the summed sizes of the sampled plots. The most pragmatic choice is often a compromise between the two approaches that addresses the sampling completeness biases of both (Gupta et al., 2020; Konratyeva et al., 2019; Fleming et al., 2017; Gaston and Fuller, 2009; Burgman and Fox, 2003; Kunin and Gaston, 1997). Thus, the ideal method will find a balance between calculation ease and precision by using all species occurrence data and buffering those occurrences by a reasonable distance to create a geographic range that is largely unified yet can identify strong outliers in the dataset and potential physical barriers within the landscape without measuring them.

Calculations of phenological rarity among bee studies have varied as well. For instance, MacLeod et al. (2020) justified phenological exclusion based on previous studies that showed correlations between numeric and phenological rarity, while Volenec and Smith (2021) calculated numeric rarity as the maximum number of occurrences of a species within a month to account for species phenological differences. Indeed, singletons and doubletons (where only one or two individuals of a species are sampled, respectively) frequently comprise a large portion of species sampled in ecological studies of diverse taxa (Kunin and Gaston, 1997), which makes the accuracy of activity periods difficult to calculate in local and regional studies. Harrison et al. (2019) circumvented this issue by using museum specimens of bees specific to the study area to allow for temporal occurrences within a year to serve as an active flight window.

In general, originality metrics have not been used in previous studies of bee rarity largely due to the extensive knowledge required for input data. For example, advanced molecular and statistical techniques are needed to establish phylogenetic distances among species. The tree produced by Hedtke et al. (2013) established global relationships among, and branch lengths for, >1,300 bee and wasp species but would be impractical for use in most field studies as the included species were not chosen based on geographic overlap, while the more localized assemblage of apple orchards in the northeastern United States analyzed by Grab et al. (2019) may be too specific for application to other systems. Nonetheless, molecular studies of bee phylogenetics may be advantageously combined to understand taxonomic hierarchies regardless of scale. If the interpretation of these complex analyses could be simplified in terms of uniform distances among nodes instead of branch lengths of a phylogenetic tree, rarity indices may be able to incorporate phylogenetic originality as a composite metric comprised of many

studies (Kondratyeva et al., 2019; Vane-Wright et al., 1991).

Similarly, there are a variety of approaches to create a measure of functional originality from generalizable species traits (Kunin and Gaston, 1997; Gaston, 1994). Functional attributes of species have been widely applied in bee studies (e.g., Fortuin and Gandhi, 2021, Odanaka and Rehan, 2021, Bartomeus et al., 2013), but recent reviews and meta-analyses concerning ecological traits that represent vulnerability in bees and other pollinators have provided clarity on which species attributes are most influential: sociality, diet, nesting habits, and body size (Fortuin and Gandhi, 2021; Ghisbain et al., 2021; Buchholz and Egerer, 2020). Different reproductive strategies affect abundance or population size, as well as species range. For bees, this is best described in terms of sociality, which can directly affect the quantity of resources used and general interactions within the landscape (Kaluza et al., 2018; Müller et al., 2006). Degree of diet specialization further determines how many types of resources are needed for provisioning brood which can result in a network of causal effects on species in the ecosystem depending on floral resource availability (Kaluza et al., 2018; Ogilvie and Forrest, 2017; Torné-Noguera et al., 2014; Roulston and Goodell, 2011). Since bees are centralized foragers, nesting habits emphasize unique combinations of necessary nesting and food resources within sustainable foraging distances (Antoine and Forrest, 2021; Harmon-Threatt, 2020; Potts et al., 2005). Finally, body size is a determinant of dispersal ability, foraging distances, and energy needs of bees (Cholel et al., 2019; Greenleaf et al., 2007). Though these traits are interconnected, they are also complementary and collectively determine how species interact within the environment (Ogilvie and Forrest, 2017).

Given the need for a rarity index to inform conservation practices and ecological theory, as well as to address the potential limitations of previous approaches that did not include rarity and originality metrics together, we sought to design a rarity index that was more informed than other approaches through the evaluation of two criteria. First, additional and unique information must be included within the calculation of the new rarity index relative to other indices. Second, for the index to be considered more informed it must be deduced or inferred that this new information resulted in a different interpretation of species rarity. Therefore, we constructed a composite rarity index, the Species Originality and Rarity Index (SpORTI), for bees, encompassing five metrics and compared it to three other rarity indices that did not include originality metrics. The five metrics within SpORTI included: Numeric rarity to address relative commonness; geographic rarity to focus on spatial ranges that intersected the study area, phenological rarity to consider the temporal aspect of active flight seasons, phylogenetic originality to reflect the taxonomic uniqueness among species within the community, and functional originality based on a composite metric of nesting habits, diet specialization, body size, and reproductive strategy to include the ecological importance of unique combinations of traits known to affect the population (Fig. 1; Kondratyeva et al., 2019). Our approach first created a combined index for each species by standardizing species ranks such that the difference in rarity between any two consecutively ranked species was the same, and then the combined index was weighted based on species with greater rarity metric scores within each decile of the combined index. This process avoids the risk of misinterpretations from averaging weighted metrics (Maciel, 2021), yet still

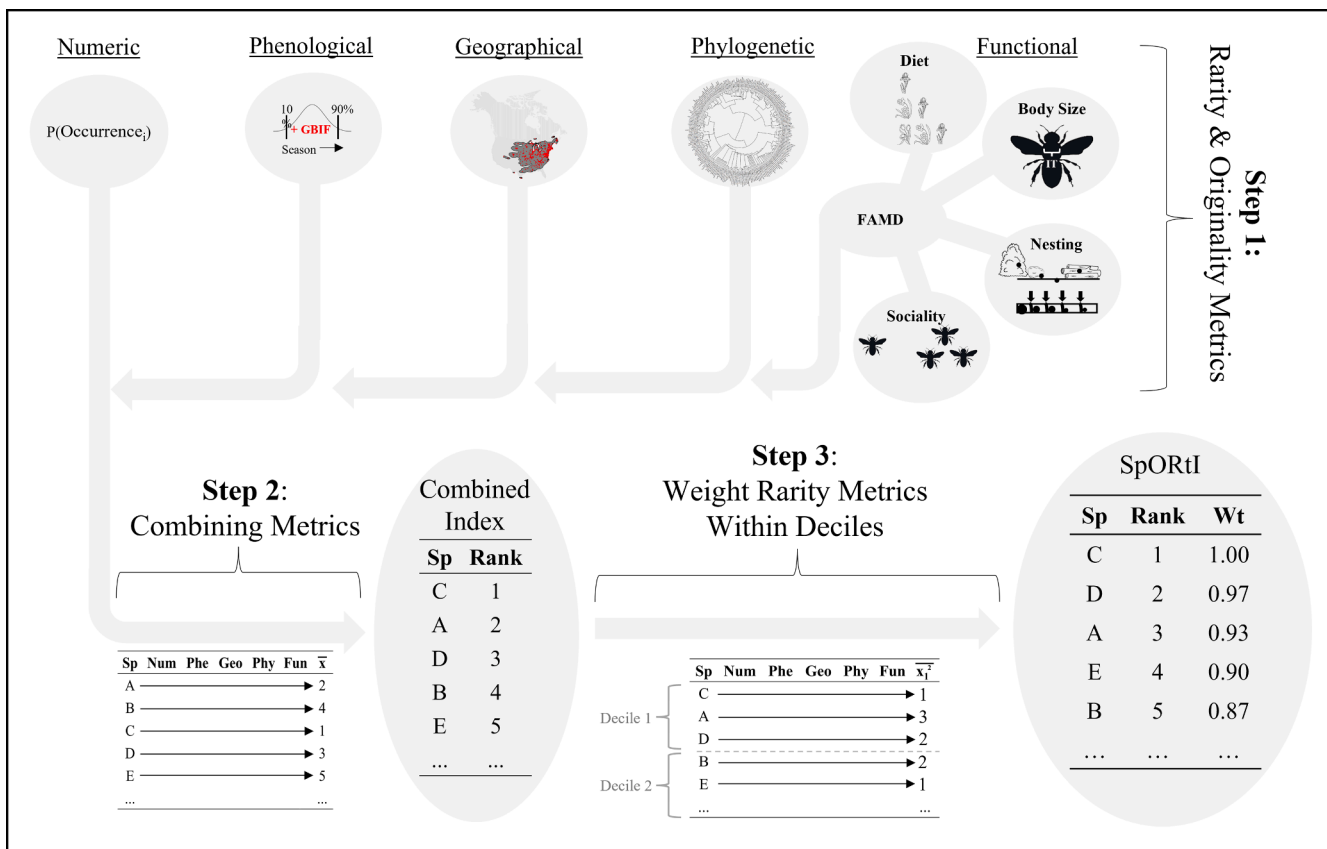


Fig. 1. Conceptual diagram of the process by which SpORTI was derived. In the first step, species scores were calculated for each metric, including: numeric rarity – probability of occurrence across samples; phenological rarity – middle 80 % of sampled dates augmented with GBIF (Global Biodiversity Information Facility) data; geographic rarity – proportion of land area within the Great Lakes Basin that overlaps species geographical range; phylogenetic originality – mean pairwise distance between nodes of composite phylogenetic tree; and functional originality – distance from centroid in multi-trait (diet specialization, body size, nesting habits, and sociality) space. In the second step, species scores were normalized and standardized between zero and one for each metric and a combined index was created by unweighted averaging across metrics. Within each decile of the combined index (n = 30 species in illustration), unstandardized scores of each rarity metric were raised to the third power and averaged in the third step to emphasize species with rare properties to create the Species Originality and Rarity Index.

emphasizes species that exhibit high rarity within a metric without allowing high or low rarity scores of any given metric to drive overall rarity rankings.

2. Methods

2.1. The data

We developed this approach using a dataset with 11,547 bees identified to 218 species collected on 100 plots that were sampled three times annually during 2017, 2018, and 2019 with a combination of standardized hand netting and deployment of pan traps painted blue, yellow, or left white (herein ‘bee bowls’). Sample plots were located within the Chequamegon-Nicolet, Finger Lakes, Hiawatha, Huron-Manistee, Ottawa, and Superior National Forests in the states of Michigan, Minnesota, New York, and Wisconsin and included a total of 492 samples. The sampled sites consisted of patches > 1 ha in size and > 1 km apart that had been recently (≤ 20 years) treated by mowing, prescribed fire or other means to enhance their value for wildlife, as well as reference sites that had experienced no management for >20 years. Full details of the experimental design along with the effects of management on bee communities will be published separately.

Due to the taxonomic difficulties of many specimens and the ongoing considerations in the taxonomy of certain groups of species, we grouped *Hylaeus affinis* and *H. modestus* into *H. affinis/modestus*, *Lasioglossum fattigi* and *L. paradmiraandum* into *L. fattigi/paradmiraandum*, and *L. ephialtum*, *L. oblongum*, *L. planatum*, *L. subviridatum*, and *L. taylorae* into a subgroup of *Lasioglossum* referred herein as ‘*L. viridatum*-subgroup’ following Gibbs et al. (2017) and treated each grouping as a species. By including all individuals that were identified either to species or species groups, our analytical approach to each rarity metric allowed flexibility to account for the multiple values of each metric. Each species within a species group was assigned a score for each metric, which were then averaged by species group before any indices were calculated. Since we introduced this approach in a conservation context, we removed all non-native species prior to analyses, including *Andrena wilkella* (27), *Apis mellifera* (301), *Lasioglossum leucozonium* (815), *Lasioglossum zonulum* (142), *Megachile rotundata* (2), *Osmia cornifrons* (7), and *Osmia taurus* (6). Therefore, information was used to calculate rarity metrics on 218 species, but the index includes 213 species, three of which are species groups. This approach to handle taxonomic issues lowered the number of species that were comparable within the final rarity index, which likely reduced the precision of the conclusions. Since the integrity of the data was retained by including trait comparisons among all 218 species, however, the relative species positioning within the index remained accurate. Alternatively, removing these species would have shifted the relationships, and thus the rarity ranks, among species, which could alter the interpretation of which species were more rare and potentially lead to less effective conservation recommendations and measures.

2.2. Rarity metrics

2.2.1. Numeric rarity

We calculated numeric rarity as the inverse of the occurrence frequency, which was based on the number of standardized sampling events ($N = 492$) and defined by a set of geographic coordinates, or plot, and date. Specimens caught by net and bee bowls during the same 24 h at a plot were considered to have been captured during the same sampling event.

2.2.2. Geographic rarity

We calculated geographic rarity using a maximum entropy method of kernel densities (area of occupancy) on occurrences of our dataset enhanced with the full dataset of historic occurrence records in the United States and Canada downloaded from the Global Biodiversity

Information Facility (GBIF) database publicly available at <https://www.gbif.org/what-is-gbif> (Table A1). Unique latitudinal and longitudinal sets of coordinates for each species were then extracted with the *stringr* package (Wickham, 2019) and used for all augmented calculations (Fig. A1a). We estimated kernel densities using the lowest confidence level of 0.0001 to represent an area of occupancy approach with minimal assumptions (Wickham, 2016). Boundary coordinates of the resulting ggplot-object were imported into ArcMap 10.8.1, where we recreated the density polygons using the extension Tools for Graphics and Shapes (available at https://www.jennessent.com/arcgis/shapes_graphics.htm) and clipped the density polygons to a detailed map of the Great Lakes Basin since this was the region from which the specimens were encountered, but also to illustrate that our approach is not limited by scale and can account for global commonness in assessments of species- or study-specific rarity. Therefore, geographic rarity was calculated as the inverse of the spatial range within the Great Lakes Basin (land area).

2.2.3. Phenological rarity

We derived phenological rarity using occurrence dates of our dataset enhanced with occurrence data from the GBIF database described previously. Since the flight season of bees varies geographically, we restricted the data enrichment to include only specimens encountered within the Great Lakes Basin (Fig. A1b). From the augmented dataset, we extracted the tenth and ninetieth percentile of the ordered Julian dates for each species to remove outliers from the dataset and focus on the primary flight period of bees in this region (Harrison et al., 2019). Thus, phenological rarity was calculated as the inverse of the number of days represented by the middle 80 % of occurrences within the study area.

2.2.4. Phylogenetic originality

We calculated phylogenetic originality using a composite approach and built a phylogenetic tree based on the combined work of others (e.g., Odanaka et al., 2022; Pisanty et al., 2022; Grab et al., 2019; Danforth et al., 2013; Gibbs et al., 2013; Rightmyer et al., 2013; Cameron et al., 2007) that depicted currently accepted positions of divergence events of bee species (Fig. A2). Specifically, we used the *ape* package (Paradis et al., 2019) and Grafen branch lengths ($\rho = 0.6$) assigned to species (Grafen, 1989) to derive our phylogenetic tree. From the tree, we calculated the average number of nodes between each species and every other species using the *distNodes* function in the *RRphylo* package (Castiglione et al., 2018). Species with incomplete phylogenies were automatically placed in the most precise hierarchical level (allowing multifurcation). This process was more sensitive to species with a more distinct, or unique, lineage (Mazel et al., 2016) and the mean pairwise distance among species served as the measure of phylogenetic originality. We used the *phytools* package (Revell, 2012) to create a visual of the tree (Fig. A2).

2.2.5. Functional originality

To calculate functional originality, we performed a factor analysis on mixed data (FAMD) using the *FactoMineR* package (Sebastien et al., 2008). The FAMD is unique in its ability to consider continuous and categorical variables while equalizing the contribution of each variable to the placement of species within multidimensional space. This analysis yielded species distances from the centroid in multi-trait space that collectively represented a gradient of functional uniqueness among species within the study, where the most functionally unique species were farthest from the origin and had larger values of functional originality.

Variables used within the analysis included standard life-history attributes that characterize species ecologically to address more analogous traits that phylogenetic relationships may not specifically account for, including factors that affect adults and offspring, and were demonstrated to influence species rarity: sociality (reproductive strategy),

nesting substrates (nesting habits), degree of diet specialization (diet requirements), and inter-tetragonal span (body size) (Ghisbain et al., 2021; Bucholz and Egerer, 2020; Table A2). We accounted for species that fell under multiple categories for a trait with multiple dummy species. We then averaged the distances of all trait combinations for each species in multivariate space to provide each species with a single functional uniqueness score. Information missing from the literature was either provided from the current study (body size measurements) or based on the typical attribute value of that group. For example, sociality of *Lasioglossum* (*Dialictus*) bees is quite diverse (Gibbs et al., 2013) but facultative or primitive social forms were most common of species in our dataset. Therefore, *Dialictus* species with unclassified sociality were considered as “social” (see below) for the analysis (Gibbs et al., 2012a).

The terminology describing bee sociality is inconsistent and in debate (Wcislo and Fewell, 2017; Costa and Fitzgerald, 2005; Michener, 1974). Here, we assigned the sociality of each bee species as ‘solitary’, ‘communal’, ‘social’, or ‘parasitic’, which is broadly relative to the global pool of social categories for bees as defined by Michener (2007, 1974) by focusing on the most common documented behaviors of the taxon. For instance, species that are typically solitary but may produce sister workers when resources are bountiful (known as facultative sociality) were considered both ‘solitary’ and ‘social’. We considered all species that exhibit primitive to advance sociality behaviors (reviewed in Shell and Rehan, 2018) as ‘social’. Brood (clepto) and social parasitism have evolutionary and ecologically different foundations (Litman, 2019; Sheffield et al., 2013; Gibbs et al., 2012b). However, the host knowledge gap of *Sphecodes*, a genus that exhibits both social and clepto-parasitism behaviors, is currently too great to warrant this division for our purposes. We also did not consider species that exhibit intraspecific usurpation or nest robbing due to the difficulties in discerning these species within the literature (Černá et al., 2013).

We considered degree of diet specialization for each bee species, which ranged in classifications from one species of one genus (monoleptic) to more than four families (polylectic or broadly polylectic) (Cane and Sipes, 2006). Specialist bees were demonstrated to be of greater conservation concern (Bogusch et al., 2020), defending a prioritization for bees with specialized diets. Yet the composition of pollen fed to brood is an ever-changing formula based on individual or colony needs and local availability of pollen which result in a large continuous gradient of generalist to specialist foraging behavior (Kelly and Elle, 2020; Wood et al., 2018; Smith et al., 2017; Danforth, 2002). Combined with recent DNA work showing higher floral species richness than previously thought in pollen provisions (reviewed in Lowe et al., 2022), this has likely led in part to the observed inconsistencies of where the oligolectic-polylectic boundary is (Table A2 & A3). Therefore, we relied on more recent publications to develop an ordinal classification system (most to least specialized) that accounts for the ‘gray’ areas of the intersection between polylects and oligolects as follows: highly specialized (1 genus), specialized (1 family), somewhat specialized (≤ 3 families), not specialized (> 3 families). Species with unrecorded foraging preferences were placed in the category ‘not specialized’. In addition, we classified diet specialization of parasitic species based on that of their known hosts since the ecological relevance of diet for any bee species pertains to effects of conditions, including pollen nutrition provisions, on developing offspring.

We categorized nesting habits of bees as joint categories of nesting substrates and partition material. Nesting substrate included soil (surface or below ground, including cavities or excavated), wood (cavities or excavated), twig (shaped pithy stems), and open (exposed to environmental elements). These categories are broad, yet still provide

information on the basic behavior, local preferences, and susceptibilities of species (Harmon-Threatt, 2020). *Osmia conjuncta* is unique in that it nests in snail shells, which for the purposes of our analyses, we categorized as ‘open’. Categories of nesting material focused on the partition of brood cells: leaves (leaf pieces or pulp), soil (all textures), resin, secretions (wax or polyester), wood. We did not incorporate waterproof cell-lining behaviors (Harmon-Threatt, 2020), though we discuss how including this and other information into the trait calculations is anticipated to affect rarity ranks while addressing flexibility and limitations of the index. We classified nesting substrates and materials of parasitic species based on those of their known hosts.

Finally, we considered body size as a continuous variable. Kendall et al. (2019) found bee body length, which is readily available in species descriptions, to be highly predictive of dry body mass ($R^2 = 0.92$), but more studies use intertegular distance as a measure of body size (Kendall et al., 2019; Burdine et al., 2018; Greenleaf et al., 2007; Bullock, 1999; Cane, 1987). We initially searched the literature for intertegular measurements (e.g., Bartomeus et al., 2018; Cariveau et al., 2016; Greenleaf et al., 2007; Winfree et al., 2007; Cane, 1987), but studies did not provide individual male and female widths, measurements for the same species varied greatly among studies, or intertegular distances for the target species were simply not included likely because other measurements, such as head width, wing length, and body length were the primary body measurements recorded for species descriptions (e.g., Gibbs, 2011, 2010; Mitchell 1962, 1960). Therefore, we measured and used the mean intertegular distance of up to three males and females of each species within the data set (Table A2) but note the correlation between body lengths from the literature and measured intertegular distance was > 0.91 and similar to the correlation within specimens measured by Kendall et al., (2019) of 0.95. Since each species received one score, the unweighted average body size of males and females were used if both were present in the study.

2.3. Combining individual metrics

Calculating the rarity index from the five rarity metrics included two steps. The first step involved combining the ranks of the individual metrics for each species to yield a single index value. The second step was to weight the combined index based on metric scores of species with greater rarity to adjust the species ranks and yield a final rarity index. To complete the first step and obtain the combined index, we scaled the raw scores of each metric between zero and one. This process normalized the metrics such that the value of one indicated the species with the least occurrences for numeric rarity (NRn), smallest spatial range for geographic rarity (GRn), shortest flight period for phenological rarity (PRn), greatest distance among nodes for phylogenetic originality (PON), or the greatest distance from the group centroid of trait combinations for functional originality (FOn). To standardize the metrics, we then rescaled the normalized scores into equidistant values between zero and one to produce proportional ranks (NRs, GRs, PRs, POs, FOs) such that a value of one always indicated the rarest species. For example, the 1st, 2nd, and 3rd most rare species within any metric received the proportional rank value of 1.000, 0.995, and 0.991, respectively, given the 213 species considered in the final rankings (see Fig. 1 for conceptual example). To account for the inter-dependence among the proportional ranks of rarity metrics (Kondratyeva et al., 2019; Gaston, 1994), we adjusted each one based on its correlation (Pearson’s) with the others as in Leitão et al. (2016). Thus, the combined index score I_i for the i th species was calculated as.

$$I_i = \frac{[(NRs_i \times w_{nr}) + (GRs_i \times w_{gr}) + (PRs_i \times w_{pr}) + (POs_i \times w_{po}) + (FOs_i \times w_{fo})]}{w_{nr} + w_{gr} + w_{pr} + w_{po} + w_{fo}}$$

where w_{nr} , w_{gr} , w_{pr} , w_{po} , and w_{fo} are weight parameters describing the relative independence of each ranked metric. For example, the ranked numeric rarity metric was weighted by w_{nr} , which was calculated as.

$$w_{nr} = \frac{1}{4} + \left[\left(\frac{1 - |r_{nrgr}|}{4} \right) + \left(\frac{1 - |r_{nrpr}|}{4} \right) + \left(\frac{1 - |r_{nrpo}|}{4} \right) + \left(\frac{1 - |r_{nrfo}|}{4} \right) \right],$$

where, for example, r_{nrgr} is the Pearson’s correlation coefficient between the proportional ranks of numeric rarity and geographic rarity. The combined index was then rescaled as proportional ranks between zero and one as before in preparation for the application of rarity weights.

2.4. Generating the final rarity index

Low ranks in several metrics are not as meaningful as a high ranking of rarity in any metric in terms of rarity and vulnerability of the species. For example, *Osmia inspergens* had high rarity scores (>0.9) for phylogenetic and functional originality but low scores for the other three metrics and an overall standardized score of 0.77 in the unweighted combined index while *Megachile brevis* was in the same index decile yet only demonstrated a high phylogenetic originality score and was still considered rarer than *O. inspergens* with a combined index value of 0.80. This situation occurred because the lower metric scores were still on average higher for *M. brevis* than the lower four scores for *O. inspergens*. Therefore, we developed a weighting system that adjusted the species ranks within deciles of the combined index by emphasizing species with high scores in rarity metrics by allowing rankings in the combined index to shift as a function of the normalized scores of each metric. We limited the effect of rarity weighting by applying weights to species within each decile of the unweighted combined index separately. Therefore, a species in the unweighted index and ranked within a decile could shift a maximum number of ranks such that that species remained in that decile. The final rarity index score $SpORt_{ij}$ for the i th species in decile j was thus calculated as:

$$SpORt_{ij} = \frac{1}{5} \left(NR_{ij}^{0.5x} + GR_{ij}^{0.5x} + PR_{ij}^{0.5x} + PO_{ij}^{0.5x} + FO_{ij}^{0.5x} \right),$$

where x is a positive whole number optimized such that the mean rank changes between all species in $SpORt_{ij}^x - SpORt_{ij}^{x-1}$ and $SpORt_{ij}^{x+1} - SpORt_{ij}^x$ for all j were not significantly different as determined by a paired Wilcoxon Rank Test. We found an optimization at $x = 6$ for our data and raised each normalized metric score to a power of three (Table 1). This process shifted the relative ranking of species on average 6.3 ranks to favor those with high rarity in some metrics, while preserving the general structure of species rarity yielded by the standardized and unweighted combined index. This means that, for instance, all species in the first decile (most rare) retained a rarer rank than the other 90 % of species following the weighting process. Continuing the previous example within a decile, *O. inspergens* increased in rarity 5

Table 1

Output of paired, two-sided, Wilcoxon Signed Rank Tests of the difference in the number of rank shifts from the precursor index to the final rarity index when weights were applied to scaled distances of each rarity metric with increasing values of the exponential parameter x . The optimal x was decided when the null hypothesis that there was no difference in rank shifts between x and $x + 1$ was not rejected.

x	Median	95 % CI	V-statistic	P-value
1	-3.0	-4.0 – -2.0	4819	< 0.0001
2	-1.5	-2.0 – -1.0	3620	< 0.0001
3	-1.0	-1.5 – -0.5	3170	< 0.0001
4	-1.0	-1.0 – -0.0	3099	< 0.001
5	-0.5	-1.0 – -0.0	2386	< 0.01
6	-0.0	-0.0 – 0.0	3015	0.68

ranks while *M. brevis* fell 9 ranks, which yielded a final rarity weight (index value) of 0.80 for *O. inspergens* and 0.76 for *M. brevis*. Thus, using rarity weights based on species-specific metric scores to adjust index values derived from metric ranks (normalized and standardized) removed the interpretation biases associated with weighted averaging but still allowed for prioritization of species with rare properties by constraining the weighting effects.

2.5. Comparing alternative approaches

We compared our approach that derives a species originality and rarity index (herein ‘SpORtI approach’) with three alternative approaches previously presented in the literature, which we refer to as the “classic approach”, the “r-metric approach” and the “habitat-approach”. The “classic approach” included the combination of only numeric and geographic rarity (Gaston, 1994). The “r-metric approach” included a combination of numeric rarity, geographic rarity, and phenological rarity (Harrison et al., 2019). Finally, the “habitat approach” was comprised of numeric rarity, geographic rarity, and the habitat specificity index, which considered the habitat type that each species occurred in (Maciel, 2021) to address the role of habitat descriptors in representing habitat specialization in lieu of species traits. We compared these metrics based on the relative positioning of species within each of the four approaches to better understand how the incorporation of different or additional information into the rarity index altered the interpretation of relative rarity among species.

We kept our calculation of each rarity metric and weight application procedure the same across approaches for valid comparisons, though it should be noted that these approaches in the literature used different calculations within their rarity metrics. For instance, Harrison et al. (2019) used a convex hull (extent of occurrence) method to calculate geographic rarity and maximum occurrences of museum data within a month for numeric rarity compared to our kernel density (area of occupancy) and sampling occurrence frequency method, respectively. Further, Maciel (2021) used maximum abundance within a month for numeric rarity. Such calculation differences do not affect our evaluation of how inclusion of these various rarity metrics affect an overall rarity index, however.

We relied on the IUCN terrestrial habitat type map created by Jung et al. (2020) to extract information for calculating the habitat specificity index (hsi) used in Maciel (2021). Specifically, we used Version ver004 of the level II IUCN habitat type classifications publicly available at <https://uploads.users.earthengine.app/view/habitat-types-map> to identify the habitat type at each location of the 492 samples. The accessed map was representative of habitat types as of 2015 with a resolution of 0.1 km and identified seven habitat types that were sampled in the bee dataset (Table 2). The habitat specificity index was then calculated as the inverse of the maximum number of occupied habitat types (h_{max}) for each species i . The normalization, standardization, and weighting process for this metric was performed as previously described.

If different approaches to calculate species rarity indices result in differently ordered species rankings, then the change in a species rank will alter the interpretation of the relative rarity of that species. It

Table 2

Distribution of the 492 bee samples among IUCN terrestrial habitat types – level II – per Jung et al. (2020) from most to least.

Habitat Type	Samples
Temperate Forest	286
Temperate Shrubland	152
Arable Land	30
Pastureland	17
Temperate Grassland	4
Plantations	2
Inland Wetland	1

follows that differences between approaches are responsible for the observed changes in relative rarity of a species between one approach and another. Therefore, to test the hypothesis that a species rarity index comprised of phylogenetic and functional originality in addition to rarity metrics provides a different interpretation, and thus a more informed index, of species relative rarity, we determined differences in species rankings among the four rarity index approaches with a series of Friedman tests on species rarity ranks using the *friedmanTest* function in the PMCMRplus package (Pohlert, 2021). Since the quantile threshold that defines a rare species is at most the first quartile but can vary otherwise depending on the study or resources available for conservation applications, we performed three Friedman Tests to address differences among deciles, quintiles, and quartiles between the ordered rarity rankings of each index and the corresponding rarity ranks of every other index, for a total of twelve Friedman Tests (Pohlert, 2021; Gaston, 1994). We then determined differences between approaches with pairwise comparisons at each quantile with post-hoc Conover-Tests on the same matrices used for the Friedman tests using the *frdAllPairConoverTest* function with a ‘holm’ correction for multiple comparisons in the same package.

3. Results

There were differences among the approaches to calculate species rarity indices when evaluated by deciles, quintiles, and quartiles (Table 3). Specifically, when evaluated by deciles, the SpORtI approach that included all five rarity and originality metrics ranked species differently from the classic approach (numeric and geographic rarity) as well as the r-metric approach (numeric, geographic, and phenological rarity). Although our SpORtI approach did not differ from the habitat approach, which included numeric and geographic rarity as well as habitat specificity, the habitat approach was different from the classic approach but did not differ from the r-metric approach. Only the SpORtI approach differed from the classic approach when evaluated by quintiles, though this difference was not significant ($p < 0.10$) when quartiles were considered. The r-metric approach did not differ from the classic approach in any quantile. Finally, visual examination of the distribution of differences within each decile between the classic approach and each of the three other approaches showed that the

Table 3

Friedman Test results on three degrees of freedom of differences among rarity index approaches (Chi-squared statistic, P-value) and post-hoc Conover Tests evaluating pairwise differences between approaches (t-statistic, P-value) with results of the reference approach in ranked order from most to least rare compared across deciles (9 degrees of freedom), quintiles (4 degrees of freedom), and quartiles (3 degrees of freedom). Significant results (<0.05) are emboldened, trends (<0.10) italicized, and non-significant results (NS) unmodified.

Quantile	Reference	Classic	Habitat	R-Metric	SpORtI
Decile	Friedman	30.0, 0.0001	18.4, 0.0005	16.3, 0.001	9.8, 0.05
	Classic	–	–3.4, 0.05	–1.7, NS	–5.1, 0.0005
	Habitat	2.9, 0.05	–	1.5, NS	–1.0, NS
	R-Metric	0.7, NS	–2.1, NS	–	–2.7, 0.05
	SpORtI	3.1, 0.05	1.4, NS	1.7, NS	–
Quintile	Friedman	15.0, 0.005	12.1, 0.01	3.5, NS	<i>7.1, 0.1</i>
	Classic	–	–2.4, NS	–1.2, NS	–3.6, 0.05
	Habitat	2.1, NS	–	0.5, NS	–1.9, NS
	R-Metric	–0.5, NS	–1.2, NS	–	–1.7, NS
	SpORtI	1.9, NS	1.9, NS	2.4, NS	–
Quartile	Friedman	12.0, 0.01	9.3, 0.05	2.7, NS	3.3, NS
	Classic	–	–2.1, NS	–1.1, NS	–3.2, <i>0.1</i>
	Habitat	1.8, NS	–	0.3, NS	–1.1, NS
	R-Metric	0.0, NS	–1.3, NS	–	–0.8, NS
	SpORtI	–1.3, NS	0.0, NS,	0.3, NS	–

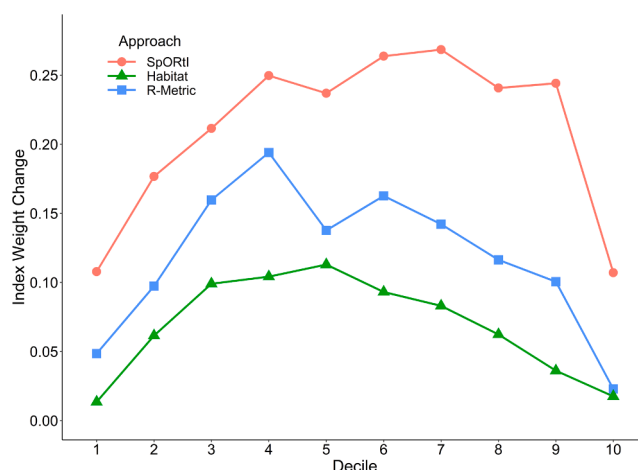


Fig. 2. Mean rank differences (as index values) within each decile between the classic approach (numeric and geographic rarity) and the r-metric (numeric, geographic, and phenological rarity), habitat (numeric and geographic rarity and habitat specificity index), and SpORtI (numeric, geographic, and phenological rarity, and phylogenetic and functional originality) approaches.

addition of the habitat sensitivity index or phenological rarity exhibited few differences in species rarity rankings for rare, as well as common, species (Fig. 2; Table A4).

4. Discussion

4.1. Rank differences among approaches

By comparing species rarity rankings among indices that differed in terms of the metrics included, we were able to identify metrics that did not have a discernable impact on species ranks and for which inclusion in rarity index calculations is not supported. For example, we found that combining all three rarity metrics (r-metric approach) did not provide a more informed rarity index than the classic approach. Since the difference between the r-metric and classic approaches was the addition of phenological rarity in the r-metric approach, including phenological rarity in the calculation did not produce a more informed index for bees. In contrast, all three metrics of the r-metric approach were also included in SpORtI. Therefore, the differences in relative species rarity between SpORtI and both the r-metric and classic approaches highlight the important role that functional and phylogenetic originality play in providing a more informed rarity index for bees since it provides additional and unique information and results in a different order of species rarity ranks.

Including a habitat specificity index (habitat approach) in addition to numeric and geographic rarity metrics resulted in different rarity rankings than the classic approach, but the similarity with the r-metric approach combined with its inability to demonstrate a difference with the classic approach across larger quantiles suggest limitations on the role of habitat type in providing new information to bee rarity indices. For instance, mean differences in species ranks between the habitat and r-metric approaches with the classic approach within the first two deciles were small and unlikely to shift those species into different deciles. Consequently, species considered rare (in the first quartile of rankings) in the classic rarity index were largely the same species that were considered rare using the habitat and r-metric approaches, suggesting that the inclusion of habitat sensitivity provides the least information on the rarest species on which conservation efforts will be focused.

Alternatively, SpORtI, which included rarity and originality metrics, provided enough new information to shift species ranks across all deciles compared to the classic approach, including those within commonly used rarity thresholds. Our index is based only on properties of the

species (Kondratyeva et al., 2019), and thus not subject to some of the limitations of previous rarity indices that were based on properties of the habitat, which required broad assumptions on the species-habitat relationships across species. For instance, the dataset used here was regional (520,000 km²) in scale yet two of the seven habitat types recorded – Temperate Forest and Temperate Shrubland – represented 89 % of the samples. This was undoubtedly due to the study design which sampled forest openings and illustrates a broader issue that the incorporation of habitat descriptors into rarity calculations can easily lead to biased interpretation since not all habitat types of a study region are likely to be equally represented in the dataset, which would be needed to accurately determine the relationship among species and number of habitat types. Biased representation of habitat types can also occur due to active management practices or natural processes (i.e. pollinator plantings, fires, floods, land-use change) during which species were sampled that eventually would alter community composition (Harrison et al., 2018; Leong and Roderick, 2015). Our findings also showed that 31 % of species were equally the most specialized to habitat type and therefore did not contribute much additional information to rare species already identified without the inclusion of habitat. It is possible that the hierarchical level of habitat type classification used in our calculation was too coarse, and that habitat types of finer resolution would yield greater variability in the habitat sensitivity index among species. However, it is not clear which hierarchical level of habitat types bees respond to best, and some areas are yet to be provided with finer resolution classifications. Relying instead on species traits to determine the relative order of species rarity circumvents these pitfalls.

4.2. The five rarity metrics and data augmentation:

We demonstrated for the first time a rarity calculation method that combines a comprehensive suite of individual components that encompassed rarity in terms of numeric, geographic, phenological, phylogenetic, and functional rarity and originality metrics into a single composite rarity index. Our approach provides solutions to difficulties associated with establishing rarity rankings for some taxa and addresses influential factors of rarity besides those included in previous calculations (Kondratyeva et al., 2019). For example, abundances or viable population sizes are widely used to calculate numeric rarity but can be difficult to estimate for species that are particularly difficult to sample and, consequently, for which abundance estimates are difficult to obtain. Additionally, taxa that exhibit multiple or plastic reproductive strategies, some of which are social or facultatively social, can skew the interpretation of differences in abundances among locations since multiple bees may represent multiple nests in some areas but not others, even within the same species (Harmon-Threatt, 2020). More complex calculations could address some of these issues for individual species assessments, but not for hundreds of species simultaneously (IUCN, 2021b; Maciel, 2021; Panjabi et al., 2020; Drever et al., 2012; Mace et al., 2008; Gaston, 1994). Relying instead on species occurrences for numeric rarity and accounting for reproductive strategy in the functional originality metric mitigated these issues by standardizing the interpretation of numeric rarity among species and separating species with varying socialities. For instance, 68 % of species in our dataset were solitary, which is representative of bee species more broadly (Kocher and Paxton, 2014). Every female of a non-parasitic solitary species has the potential to establish a nest. Fewer species are social, but every nest of a social species will be occupied by multiple individuals and therefore more likely to be represented. Since functional originality considers socialities that are less common to be more unique, social species will be generally considered rarer than solitary species for the reproductive strategy component of the functional originality metric. Thus, SpORTI removes some of the biases associated with social bees perceived as less rare because they may be encountered more often by chance.

Another advantage of SpORTI is its incorporation of phylogenetic and functional originality. Eliminating the need for chronological data by

focusing instead on the order of divergence events facilitated phylogenetic comparisons among the species of this study. This method illuminates the possibility for researchers without the genetic expertise, or the funds to conduct phylogenetic analyses on research specimens, to include phylogenetic originality in their rarity calculations (Kondratyeva et al., 2019). As previously discussed, other rarity indices largely avoided the inclusion of functional traits in deriving species-specific rarity weights due to the lack of extensive life-history knowledge needed of each species and the uncertainty of which traits to consider (Kondratyeva et al., 2019; Kunin and Gaston, 1997; Gaston, 1994). Most diverse taxa, including bees, comprise species with unknown life history traits. Our approach demonstrates that educated assumptions can provide a more informed rarity index than previous approaches that omitted functional originality by calculating functional originality as a composite metric.

For an extreme conceptual example, suppose a species of bee with unrecorded biology other than body size of the specimen was included in a dataset. Assigning a functional originality score based only on the body size may inaccurately represent the functional uniqueness of that species because a very large or small bee (in our dataset) would receive a high functional originality score regardless of other traits. Combining body size information instead with conservative assumptions regarding functional uniqueness prevents misrepresenting the contribution of the one known trait towards the functional originality score of the species while accounting for its incomplete profile by weighting that uncertainty with trait commonness. In our comprehensive approach, this species would be assigned the categories of highest probability – those most common – of sociality, nesting substrates, and diet specialization in addition to its measured body size. Our conservative treatment of this hypothetical species would not yield a high score of functional originality due to the commonness assigned to its unknown traits. Since functional originality is one of five metrics considered in the rarity index calculation, the influence of the unknown traits and their assignments of commonness would be restricted, allowing species with high scores of rarity in other metrics to still be evaluated as rare. Finally, as the natural history of this taxa continues to be unveiled, these assumptions will be removed and replaced with trait certainty of species which will result in a higher functional originality score. This process should then direct land managers to focus conservation efforts on a subset of species based on knowledge, while highlighting the need for study and empirical observations of species with incompletely documented life histories.

The calculation of our functional originality metric is advantageous because it considers the unique combination of species traits, each of which can influence the vulnerability of species, as they deviate from the most common combination of traits along a continuous axis. It is likely that the most common set of species traits represents species traditionally thought of as habitat generalists; however, an important distinction between our approach and those of studies that label species as generalists or specialists is that our calculations focus on the differences of trait combinations among species within the study, which may or may not align with the global habitat generalist – habitat specialist comparison. This approach keeps the metric relative among the species of the study area regardless of the scale, which is most relevant to land managers who need rarity information on species specific to their area of interest.

We also demonstrate an important application of publicly available biodiversity databases that we used to enrich our dataset to provide more complete spatial and temporal windows of activity for species of interest than what could be extracted from the project dataset alone. Other studies have also derived rarity indices from historic museum data (e.g., Harrison et al., 2019; Volenec and Smith, 2021), yet their inclusion of augmented numeric rarity calculations required the need for standardization of sampling efforts among the collections represented. The Species Originality and Rarity Index is not limited by this requirement, but takes advantage of the growing repositories of historic data for the other four rarity and originality metrics that are species-specific rather

than study-specific.

4.3. Index flexibility and limitations

Our rarity index was modeled from the metrics reviewed in Konratyeva et al. (2019). Therefore, the final list of species-specific rarity weights was composed of elements specific to species rather than habitat, emphasized rarity, and could be replicated in future studies of bees and other taxa. Although our procedure involved lumping species that were taxonomically uncertain and required assumptions on their life-history traits, these assumptions reflect the limitations of existing data rather than our approach. The extent to which these decisions influenced the rarity index values and the ensuing conservation recommendations is unclear, though we took steps to error towards a loss of precision to present originality scores that are conservative; thus, our choices are less influential to the final rarity index (Fig. A3). We argue that incomplete life histories of species do not justify the omission of originality metrics in the creation of a rarity index, which is supported by our findings that the inclusion of originality metrics provided a more informed rarity index than with a habitat specificity metric or only rarity metrics. Bees and other diverse taxa are historically difficult to evaluate for rarity due to under sampling, unresolved taxonomy, and ongoing investigations into the fundamental knowledge of their natural life histories (Chapman, 1999). Yet as our understanding of individual species increases, so will our knowledge of their phylogenetic and functional attributes, which will result in greater precision in the assignments of relative rarity through our approach, possibly shifting the values for individual species with respect to originality metrics. The fundamental nature of the five rarity and originality metrics considered in SpORtI emphasizes the potential to adapt our rarity index to calculate relative rarity in other taxa with complete and incomplete life history profiles.

Our work addresses a means to organize incomplete life history information by uniting a large body of literature focused on ecological and evolutionary processes while establishing ranks of species rarity in a community and study context. Though numeric rarity was derived only from our sampled dataset, the other four metrics represent a compilation of dozens of publications (Appendix A), which increased the scope and scale of input data for the index. For example, our index approach is not limited to the scale of the study area since the area of occupancy was calculated from augmented data that ranged throughout the United States and Canada. However, the calculation of geographic rarity only considers the overlap of the area of occupancy of a species with the study area to provide a local (study-relevant) understanding of geographically rare species. This suggests that studies of very localized areas may likely find a higher proportion of species to have 100 % coverage in their focal area without refining the resolution within the area of occupancy calculation. Also, the historic data used to augment geographic and phenological rarity were readily available and easily acquired through the GBIF repository, but data used to compute phylogenetic and functional originality metrics were obtained in a piece-meal manner, which may be perceived as a difficult task adopting this approach to new studies or inclusion in management decisions. Another advantage to our approach is that the baseline work for the originality metrics of these species is completed and included in the supplemental material. Therefore, future work that involves species which overlap the 218 species in this study will have less information to gather from the literature. If expanded, more studies could build on this baseline information by contributing phylogenetic positions and functional attributes of species into a centralized database that includes original sources of the data, which would streamline the extraction of these relationships and maintain consistent and accurate information on species traits for not only rarity studies but also others that utilize phylogenetic or functional attributes.

Our study represents the most comprehensive methodology for deriving a species rarity index for bees based on species traits; however,

there are aspects of bee ecology not included in our calculations that could influence species rarity. For instance, we based our numeric rarity calculations, as well as the species pool considered, on a regional dataset. Although this has the advantage of keeping applications and interpretations of SpORtI consistent with the effort of the study or survey, it has the disadvantage of possibly not including all known species of the study area as well as those absent due to sampling effort or intra- and inter-annual variation, which is true of most short-term bee surveys. These details are not considered explicitly within the calculations of SpORtI, but their effects would largely be limited to the calculation of numeric rarity. A solution to the issues associated with small sample size and studies of short duration is to base numeric rarity on multiple studies by standardizing sampling effort as in other bee-rarity studies that relied on Bartomeus et al. (2013), though the studies chosen and the standardization of sampling effort should be performed with care since the study areas may not overlap the region of interest and sampling methods may bias the collection of different species (Prendergast et al., 2020). We also did not consider subcategories of functional attributes, such as the full gradient of sociality classifications, oil or resin collecting and other specialized foraging behaviors, excavation or cavity nesting behavior within the substrate, preferences for soil textures or hard versus soft wood, polyester versus wax gland secretions, or cell linings of waterproof secretions, any of which may provide a more complete understanding of species rarity. Through our approach, additions or alterations in how the numeric rarity metric, or a component within the functional originality metric, is calculated are unlikely to greatly shift species positioning within the rarity index owing to the influence of the other four metrics and/or three components of functional originality (Fig. A3). We nevertheless recommend that these species-specific differences be considered when using SpORtI or deriving rarity indices.

The process by which the metrics were combined in our study differed from other rarity index calculations as well. Our calculations first created a combined index that averaged the normalized and standardized positioning of species within each metric while accounting for most non-independence between metrics before averaging (e.g. Maciel, 2021; Trevelin et al., 2017; Leitão et al., 2016) and then rarity weights, determined by the data, were applied to produce the final index. Alternatively, weighting metrics on rarity before averaging can result in a biased rarity index, especially if metrics were not standardized prior to weighting. For example, species abundances are naturally skewed distributions of many scarce species and few abundant species. Without first standardizing across metrics, many species with high scores of numeric rarity will likely receive a disproportionate weight compared to other metrics, resulting in a rarity index disproportionately influenced by numeric rarity following averaging. This can be mitigated by applying rarity weights to separate the cluster of, for instance, numerically rare species before averaging. However, these transformations are often arbitrary, vary among studies, and make the evaluation of species in terms of rarity difficult, especially when more than two metrics are involved or the metrics were not standardized (Maciel, 2021; Kunin and Gaston, 1997; Gaston 1994). Our approach lets the data determine the weights applied to species by limiting the influence of unstandardized rarity based on the decile in which species were ranked in the combined index. We chose to use deciles to constrain weighting effects rather than other quantiles to ensure that the index was founded on standardized calculations. For instance, using quartiles on a dataset of 100 species should shift species on average 8.3 % of the total number of rankings in a range of 0 to 24 ranks, while the expected rank shifts using deciles is 3.4 % with a narrower range of up to 9 ranks. It is unclear how our choice of deciles versus a different quantile would affect the overall rarity index and conservation recommendations, but conservation measures, and rarity indices, are focused on the rarer end of the rare-common spectrum, which typically ranges from 5 % up to 25 % (Gaston, 1994). Deciles, therefore, do a better job of preserving the unbiased ranking for species rarity at thresholds <25 % compared to, for example, quartiles and <20 % compared to quintiles and quartiles. Thus, SpORtI limits the

number of ranks that species can shift due to rarity weights and therefore is a rarity index that was largely a product of unweighted averaging with a higher resolution emphasis on high rarity scores in metrics.

The Species Originality and Rarity Index indicates the relative rareness of each species compared to all others in the index and is therefore conceptually based on general patterns of species-specific traits. Since the index value of any species is only informative in the context of the suite of species in comparison yet the occurrence of each bee species is dependent on plant phenology, geographic location, inter- and intra-annual variations in weather, climate, and other factors not explicitly considered in the index (Stemkovski et al., 2020), it is important to note that index values are not replacements for individual species assessments in the field. Rather, SpORTI can serve to inform conservation lists of species to consider for evaluation for protection or management. A set of species rarity weights applied to bee assemblages in an area of interest can identify hotspots of rarity and influential factors of the habitat, which can then provide land managers information on where rare bee species can be conserved as well as where to target management practices to enhance or restore rare species. Finally, although we did not consider non-native species in this analysis, SpORTI may provide a useful monitoring application of introduced species considering their often unique combination of traits and their anticipated growth in abundance and expansion in range.

5. Summary

The conservation practitioner dilemma of how to balance available resources while maximizing the likelihood of achieving conservation goals needs an approach that provides the most informed index of relative rarity among species possible (Vane-Wright et al., 1991). Validation of any rarity index would require comparable demonstrations of population declines in every species considered (standardized proof of vulnerability), which is infeasible. This paper instead debuted SpORTI, a novel rarity index that includes metrics of rarity on the commonness (numeric rarity), range size (geographic rarity), activity period (phenological rarity), phylogeny (phylogenetic originality), and ecological traits (functional originality) of species. These metrics are conceptually supported in the literature to collectively produce a more informed understanding of relative species rarity than approaches that do not include them, and our findings demonstrated that the additional information from originality metrics does result in a different interpretation of which species are most rare, and thus most likely in need of conservation intervention. The species rankings could be evaluated exactly as generated by SpORTI, or the index may be used to guide the focus of experts to a narrower list of candidate species for listed protection. The data for these five metrics of rarity exist for most taxa; therefore, we further suggest its exploration with bees as well as other taxonomic groups. Overall, the methodology used in SpORTI has the potential to streamline our understanding of how anthropogenic modifications to the landscape, including conservation management practices or other changes to environmental factors, affect rare species. It has the added promise to serve practitioners with conservation objectives focused on an individual taxon as well as those with more community-based conservation schemes. Thus, we anticipate that adoption of SpORTI will lead to better conservation decisions in the interest of conserving rare species.

CRedit authorship contribution statement

Michael J. Cunningham-Minnick: Conceptualization, Methodology, Formal analysis, Visualization, Writing – original draft, Writing – review & editing. **Joan Milam:** Resources, Writing – review & editing. **David I. King:** Conceptualization, Funding acquisition, Resources, Writing – review & editing, Supervision.

Declaration of Competing Interest

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

Data availability

All data and code to reproduce our analyses and associated figures are included within the [supplementary files](#).

Acknowledgements

We are grateful to Sierra Dawkins, Greg Flood, Tracy Grazia, Jack Greenlee, Phil Huber, Janet Kudell-Ekstrum, Matt Lark, Eric North, Linda Parker, Nicole Shutt, Dana Smith, Paul Thompson, and Sue Truell, of the United States Forest Service for managing bee surveys throughout the National Forests of the Great Lakes Basin. We thank Aliza Fassler for her organizational skills in curating specimens, building the database, and supervising summer interns, as well as Mike Arduser, Sam Droegge, Jason Gibbs, Rob Jean, and Michael Veit for verifying, and assisting in, the identification of specimens. We also thank the USFS Northern Research Station and University of Massachusetts – Amherst for hosting the research, as well as Amanda Klehr, Melanie Klein, and H. Patrick Roberts for brainstorming index names. Funding was provided by the Environmental Protection Agency's Great Lakes Restoration Initiative.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2022.109339>.

References

- [IUCN] International Union for the Conservation of Nature. 2021a. Habitats Classification Scheme. Version 3.1.
- [IUCN] International Union for the Conservation of Nature. 2021b. The IUCN red list of threatened species. Version 2021-2.
- Antoine, C.M., Forrest, J.R.K., 2021. Nesting habitat of ground-nesting bees: a review. *Eco Entomol.* 46 (2), 143–159. <https://doi.org/10.1111/een.12986>.
- Bartomeus, I., Ascher, J.S., Gibbs, J., Danforth, B.N., Wagner, D.L., Hedtke, S.M., Winfree, R., 2013. Historical changes in northeastern US bee pollinators related to shared ecological traits. *PNAS* 110, 4656–4660. <https://doi.org/10.1073/pnas.1218503110>.
- Bartomeus, I., Cariveau, D.P., Harrison, T., Winfree, R., 2018. On the inconsistency of pollinator species traits for predicting either response to land-use change or functional contribution. *Oikos* 127, 306–315. <https://doi.org/10.1111/oik.04507>.
- Bogusch, P., Bláhová, E., Horák, J., 2020. Pollen specialists are more endangered than non-specialised bees even though they collect pollen on flowers of non-endangered plants. *Arthropod Plant Interact* 14, 759–769. <https://doi.org/10.1007/s11829-020-09789-y>.
- Buchholz, S., Egerer, M.H., 2020. Functional ecology of wild bees in cities: towards a better understanding of trait-urbanization relationship. *Biodivers and Conserv.* 29, 2779–2801.
- Bullock, S.H., 1999. Relationships among body size, wing size and mass in bees from a tropical dry forest in México. *J. Kans. Entomol. Soc.* 72 (4), 426–439. <https://www.jstor.org/stable/25085929>.
- Burdine, J.D., Plummer, R., Seidel, M., McCluney, K.E., 2018. Mass-length relationships for 3 bee species in Northwest Ohio. *Ohio J. Sci.* 118 (2), 31–33. <https://doi.org/10.18061/ojs.v118i2.6433>.
- Burgman, M.A., Fox, J.C., 2003. Bias in species range estimates from minimum convex polygons: Implications for conservation and options for improved planning. *Anim. Conserv.* 6 (1), 19–28. <https://doi.org/10.1017/S1367943003003044>.
- Cadotte, M.W., Davies, T.J., 2010. Rarest of the rare: advances in combining evolutionary distinctiveness and scarcity to inform conservation at biogeographical scales. *Divers. Distrib.* 16, 376–385. <https://doi.org/10.1111/j.1472-4642.2010.00650.x>.
- Cadotte, M.W., Tucker, C.M., 2018. Difficult decisions: Strategies for conservation prioritization when taxonomic, phylogenetic and functional diversity are not spatially congruent. *Biol. Conserv.* 225, 128–133. <https://doi.org/10.1016/j.biocon.2018.06.014>.
- Cameron, S.A., Hines, H.M., Williams, P.H., 2007. A comprehensive phylogeny of the bumble bees (*Bombus*). *Biol. J. Linn. Soc.* 91, 161–188. <https://doi.org/10.1111/j.1095-8312.2007.00784.x>.
- Cane, J.H., 1987. Estimation of bee size using intertegular span (Apoidea). *J. Kans. Entomol. Soc.* 60 (1), 145–147. <https://www.jstor.org/stable/25084877>.

- Cane, J.H., Sipes, S., 2006. Characterizing floral specialization by bees. In Plant-pollinator interactions from specialization to generalization. Eds Waser, N.M., Ollerton, J. pp 99–122.
- Capmourtes, V., Anand, M., 2016. "Conservation value": a review of the concept and its quantification. *Ecosphere* 7 (10), e01476. <https://doi.org/10.1002/ecs2.1476>.
- Cariveau, D.P., Nayak, G.K., Bartomeus, I., Zientek, J., Ascher, J.S., Gibbs, J., Winfree, R., Rueppell, O., 2016. The allometry of bee proboscis length and its uses in ecology. *PLoS ONE* 11 (3), e0151482.
- Castiglione, S., Tesone, G., Piccolo, M., Melchionna, M., Mondanaro, A., Serio, C., Di Febraro, M., Raia, P., Cooper, N., 2018. A new method for testing evolutionary rate variation and shifts in phenotypic evolution. *Methods Ecol. Evol.* 9 (4), 974–983.
- Černá, K., Zemenová, M., Macháčková, L., Kolínová, Z., Straka, J., Korb, J., 2013. Neighbourhood society: nesting dynamics, usurpations and social behaviour in solitary bees. *PLoS ONE* 8 (9), e73806.
- Chapman, M.G., 1999. Are there adequate data to assess how well theories of rarity apply to marine invertebrates? *Biodivers. Conserv.* 8, 1295–1318. <https://doi.org/10.1023/A:1008909323840>.
- Cholel, H., Woodard, S.H., Bloch, G., 2019. Body size variation in bees: regulation, mechanisms, and relationship to social organization. *Curr. Opin. Insect Sci.* 35, 77–87. <https://doi.org/10.1016/j.cois.2019.07.006>.
- Costa, J.T., Fitzgerald, T.D., 2005. Social terminology revisited: Where are we ten years later? *Ann. Zool. Fenn.* 42, 559–564. <https://www.jstor.org/stable/123735870>.
- Danforth, B.N., 2002. Evolution of sociality in a primitively eusocial lineage of bees. *PNAS* 99, 286–290. <https://doi.org/10.1073/pnas.012387999>.
- Danforth, B.N., Cardinal, S., Praz, P., Almeida, E.A.B., Michez, D., 2013. The impact of molecular data on our understanding of bee phylogeny and evolution. *Ann. Rev. Entomol.* 58, 57–78. <https://doi.org/10.1146/annurev-ento-120811-153633>.
- Drever, C.R., Drever, M.C., Sleep, D.J.H., 2012. Understanding rarity: A review of recent conceptual advances and implications for conservation of rare species. *The For Chron* 88 (2), 165–175. <https://doi.org/10.5558/tfc2012-033>.
- Eisenhauer, N., Bonn, A., Guerra, C.A., 2019. Recognizing the quiet extinction of invertebrates. *Nat. Commun.* 10, 1–3. <https://doi.org/10.1038/s41467-018-07916-1>.
- Estrada, A., Arroyo, B., 2012. Occurrence vs abundance models: Differences between species with varying aggregation patterns. *Biol. Conserv.* 152, 37–45. <https://doi.org/10.1016/j.biocon.2012.03.031>.
- Flather, C.H., Sieg, C., 2007. *Species Rarity: Definition, Causes, and Classification. In Book: Conservation of Rare or Little-known Species: Biological, Social, and Economic Considerations.* Island Press.
- Fleming, C.H., Calabrese, J.M., Dray, S., 2017. A new kernel density estimator for accurate home-range and species-range area estimation. *Methods Ecol. Evol.* 8 (5), 571–579.
- Fortuin, C.C., Gandhi, K.J.K., 2021. Functional traits and nesting habitats distinguish the structure of bee communities in clearcut and managed hardwood & pine forests in Southeastern USA. *For Ecol. Manag.* 496, 119351. <https://doi.org/10.1016/j.foreco.2021.119351>.
- Gaston, K.J. (Ed.), 1994. *Rarity.* Springer Netherlands, Dordrecht.
- Gaston, K.J., Fuller, R.A., 2008. The size of species' geographic ranges. *J. Appl. Ecol.* 46 (1), 1–9. <https://doi.org/10.1111/j.1365-2664.2008.01596.x>.
- Ghisbain, G., Gérard, M., Wood, T.J., Hines, H.M., Michez, D., 2021. Expanding insect pollinators in the Anthropocene. *Biol. Rev.* 96, 2755–2770. <https://doi.org/10.1111/brv.12777>.
- Gibbs, J., 2010. Revision of the metallic species of *Lasioglossum (Dialictus)* in Canada (Hymenoptera: Halictidae, Halictini). *Zootaxa* 2591, 1–382. <https://doi.org/10.11646/zootaxa.2591.1.1>.
- Gibbs, J., 2011. Revision of the metallic species of *Lasioglossum (Dialictus)* of eastern North America (Hymenoptera: Halictidae: Halictini). *Zootaxa* 3073, 1–216. <https://doi.org/10.11646/zootaxa.3073.1.1>.
- Gibbs, J., Brady, S.G., Kanda, K., Danforth, B.N., 2012a. Phylogeny of halictine bees supports a shared origin of eusociality for *Halictus* and *Lasioglossum* (Apoidea: Anthophila: Halictidae). *Mol. Phylogenet. Evol.* 65, 926–939. <https://doi.org/10.1016/j.ympev.2012.08.013>.
- Gibbs, J., Albert, J., Packer, L., 2012b. Dual origins of social parasitism in North American *Dialictus* (Hymenoptera: Halictidae) confirmed using a phylogenetic approach. *Cladistics* 28, 195–207. <https://doi.org/10.1111/j.1096-0031.2011.00373.x>.
- Gibbs, J., Packer, L., Dumesh, S., Danforth, B.N., 2013. Revision and reclassification of *Lasioglossum (Evyllaesus)*, *L. (Hemihalictus)* and *L. (Sphécodogastra)* in eastern North America (Hymenoptera: Apoidea: Halictidae). *Zootaxa* 3672 (1), 001–117. <https://doi.org/10.11646/zootaxa.3672.1.1>.
- Gibbs, J., Ascher, J.S., Rightmyer, M.G., Isaacs, R., 2017. The bees of Michigan (Hymenoptera: Apoidea: Anthophila), with notes on distribution, taxonomy, pollination, and natural history. *Zootaxa* 4352 (1), 1–160.
- Grab, H., Branstetter, M.G., Amon, N., Urban-Mead, K.R., Park, M.G., Gibbs, J., Blitzer, E. J., Poveda, K., Loeb, G., Danforth, B.N., 2019. Agriculturally dominated landscapes reduce bee phylogenetic diversity and pollination services. *Science* 363, 282–284. <https://doi.org/10.1126/science.aat6016>.
- Grafen, A., 1989. The phylogenetic regression. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 326 (1233), 119–157. <https://doi.org/10.1098/rstb.1989.0106>.
- Greenleaf, S.S., Williams, N.M., Winfree, R., Kremen, C., 2007. Bee foraging ranges and their relationship to body size. *Oecologia* 153, 589–596. <https://doi.org/10.1007/s00442-007-0752-9>.
- Gupta, G., Dunn, J., Sanderson, R., Fuller, R., McGowan, P.J.K., 2020. A simple method for assessing the completeness of a geographic range size estimate. *Glob Ecol. Conserv.* 21, e00788.
- Harmon-Threatt, A., 2020. Influence of nesting characteristics on health of wild bee communities. *Annu. Rev. Entomol.* 65, 39–56. <https://doi.org/10.1146/annurev-ento-011019-024955>.
- Harrison, T., Gibbs, J., Winfree, R., 2018. Forest bees are replaced in agricultural and urban landscapes by native species with different phenologies and life-history traits. *Glob Chang Biol.* 24, 287–296. <https://doi.org/10.1111/gcb.13921>.
- Harrison, T., Gibbs, J., Winfree, R., 2019. Anthropogenic landscapes support fewer rare bee species. *Landsc. Ecol.* 34, 967–978. <https://doi.org/10.1007/s10980-017-0592-x>.
- Hedtke, S., Patiny, S., Danforth, B., 2013. The bee tree of life: a supermatrix approach to apoid phylogeny and biogeography. *BMC Evol. Biol.* 13, 138. <https://doi.org/10.1186/1471-2148-13-138>.
- Hendrix, S.D., Forbes, A.A., MacDougall, C.E.D., 2018. Variation in the phylogenetic diversity of wild bees at produce farms and prairies. *Agric. Ecosyst. Environ.* 259, 168–173. <https://doi.org/10.1016/j.agee.2018.03.005>.
- Jung, M., Dahal, P.R., Butchart, S.H.M., Donald, P.F., Lamo, X.D., Lesiv, M., Kapos, V., Rondinini, C., Visconti, P., 2020. A global map of terrestrial habitat types. *Sci. Data* 7, 256. <https://doi.org/10.1038/s41597-020-00599-8>.
- Kaluza, B.F., Wallace, H.M., Heard, T.A., Minden, V., Klein, A., Leonhardt, S.D., 2018. Social bees are fitter in more biodiverse environments. *Sci. Rep.* 8, 12353. <https://doi.org/10.1038/s41598-018-30126-0>.
- Kelly, T.T., Elle, E., 2020. Investigating bee dietary preferences along a gradient of floral resources: how does resource use align with resource availability? *Insect Sci.* 00, 1–11. <https://doi.org/10.1111/1744-7917.12785>.
- Kendall, L.K., Rader, R., Gagi, V., Cariveau, D.P., Albrecht, M., Baldock, K.C.R., Freitas, B.M., Hall, M., Holzschuh, A., Molina, F.P., Morten, J.M., Pereira, J.S., Portman, Z.M., Roberts, S.P.M., Rodriguez, J., Russo, L., Sutter, L., Vereecken, N.J., Bartomeus, I., 2019. Pollinator size and its consequences: Robust estimates of body size in pollinating insects. *Ecol. Evol.* 9, 1702–1714. <https://doi.org/10.1002/ece3.4835>.
- Kirk, D.A., Park, A.C., Smith, A.C., Howes, B.J., Prouse, B.K., Kyssa, N.G., Fairhurst, E.N., Prior, K.A., 2018. Our use, misuse, and abandonment of a concept: Whither habitat? *Ecol. Evol.* 8, 4197–4208. <https://doi.org/10.1002/ece3.3812>.
- Kocher, S.D., Paxton, R.J., 2014. Comparative methods offer powerful insights into social evolution in bees. *Apidologie* 45, 289–305. <https://doi.org/10.1107/s13592-014-0268-3>.
- Koh, I., Lonsdorf, E.V., Williams, N.M., Brittain, C., Isaacs, R., Gibbs, J., Ricketts, T.H., 2016. Modeling the status, trends, and impacts of wild bee abundance in the United States. *PNAS* 113 (1), 140–145. <https://doi.org/10.1073/pnas.1517685113>.
- Kondratyeva, A., Grandcolas, P., Pavoine, S., 2019. Reconciling the concepts and measures of diversity, rarity and originality in ecology and evolution. *Biol. Rev.* 94, 1317–1337. <https://doi.org/10.1111/brv.12504>.
- Krausman, P.R., Morrison, M.L., 2016. Another plea for standard terminology. *J. Wildl. Manage.* 80 (7), 1143–1144. <https://doi.org/10.1002/jwmg.21121>.
- Kremen, C., 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecol. Appl.* 2 (2), 203–217. <https://doi.org/10.2307/1941776>.
- Kunin, W.E., Gaston, K.J. (Eds.), 1997. *The Biology of Rarity.* Springer Netherlands, Dordrecht.
- Leitão, R.P., Zuanon, J., Villéger, S., Williams, S.E., Baraloto, C., Fortunel, C., Mendonça, F.P., Mouillot, D., 2016. Rare species contribute disproportionately to the functional structure of species assemblages. *Proc. Biol. Sci.* 283, 20160084. <https://doi.org/10.1098/rspb.2016.0084>.
- Leong, M., Roderick, G.K., 2015. Remote sensing captures varying temporal patterns of vegetation between human-altered and natural landscapes. *PeerJ* 3, e1141.
- Leroy, B., Petillon, J., Gallon, R., Canard, A., Ysnel, F., 2011. Improving occurrence-based rarity metrics in conservation studies by including multiple rarity cut-off points. *Insect Conserv Divers* 5 (2), 159–168. <https://doi.org/10.1111/j.1752-4598.2011.00148>.
- Litman, J.R., 2019. Under the radar: detection avoidance in brood parasitic bees. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 374, 20180196. <https://doi.org/10.1098/rstb.2018.0196>.
- Lowe, A., Jones, L., Witter, L., Creer, S., de Vere, N., 2022. Using DNA metabarcoding to identify floral visitation by pollinators. *Diversity* 14, 236. <https://doi.org/10.3390/d14040236>.
- Mace, G.M., Collar, N.J., Gaston, K.J., Hilton-Taylor, C., Akçakaya, H.R., Leader-Williams, H.N., Milner-Gulland, E.J., Stuart, S.N., 2008. Quantification of extinction risk: IUCN's system for classifying threatened species. *Conserv. Biol.* 22 (6), 1424–1442. <https://doi.org/10.1111/j.1523-1739.2008.01044.x>.
- Maciel, E.A., 2021. An index for assessing the rare species of a community. *Ecol. Ind.* 124, 107424. <https://doi.org/10.1016/j.ecolind.2021.107424>.
- MacLeod, M., Reilly, J., Cariveau, D.P., Genung, M.A., Roswell, M., Gibbs, J., Winfree, R., Peralta, G., 2020. How much do rare and crop-pollinating bees overlap in identity and flower preferences? *J. Appl. Ecol.* 57 (2), 413–423.
- Marris, E., 2007. What to let go. *Nature* 450, 152–155. <https://doi.org/10.1038/450152a>.
- Mazel, F., Davies, T., Gallien, L., Renaud, J., Groussin, M., Munkemüller, T., Thuiller, W., 2016. Influence of tree shape and evolutionary time-scale on phylogenetic diversity metrics. *Ecography* 39 (10), 913–920. <https://doi.org/10.1111/ecog.01694>.
- Michener, C.D., 1974. *The social behavior of the bees: a comparative study.* Belknap Press of Harvard University Press, Cambridge, MA.
- Michener, C.D., 2007. *The bees of the world.* Johns Hopkins University Press, Baltimore, MD.
- Mitchell, T.B. 1960. *Bees of the Eastern United States. Vol 1.* North Carolina Agricultural Experiment Station.

- Mitchell, T.B. 1962. Bees of the Eastern United States. Vol 2. North Carolina Agricultural Experiment Station.
- Mori, A.S., Furukawa, T., Sasaki, T., 2013. Response diversity determines the resilience of ecosystems to environmental change. *Biol. Rev.* 88, 349–364. <https://doi.org/10.1111/brv.12004>.
- Müller, A., Diener, S., Schnyder, S., Stutz, K., Sedivy, C., Dorn, S., 2006. Quantitative pollen requirements of solitary bees: Implications for bee conservation and the evolution of bee-flower relationships. *Biol. Conserv.* 130, 604–615. <https://doi.org/10.1016/j.biocon.2006.01.023>.
- Odanaka, K.A., Branstetter, M.G., Tobin, K.B., Rehan, S.M., 2022. Phylogenomics and historical biogeography of the cleptoparasitic bee genus *Nomada* (Hymenoptera: Apidae) using ultraconserved elements. *Mol. Phylogenet. Evol.* 170, 107453 <https://doi.org/10.1016/j.ympev.2022.107453>.
- Odanaka, K.A., Rehan, S.M., 2019. Impact indicators: Effects of land use management on functional trait and phylogenetic diversity of wild bees. *Agric. Ecosyst. Environ.* 286, 106663 <https://doi.org/10.1016/j.agee.2019.106663>.
- Ogilvie, J.E., Forrest, J.R.K., 2017. Interactions between bee foraging and floral resource phenology shape bee populations and communities. *Curr. Opin. Insect Sci.* 21, 75–85. <https://doi.org/10.1016/j.cois.2017.05.015>.
- Panjabi, A.O., Easton, W.E., Blancher, P.J., Shaw, A.E., Andres, B.A., Beardmore, C.J., Camfield, A.F., Demarest, D.W., Dettmers, R., Keller, R.H., Rosenberg, K.V., Will, T., Gahbauer, M.A., 2020. Avian conservation assessment database handbook, Version 2020. Partners in Flight Technical Series 8 (1). <http://pif.birdconservancy.org/acad.handbook.pdf>.
- Paradis, E., Schliep, K., Schwartz, R., 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* 35 (3), 526–528.
- Pavoine, S., Ricotta, C., 2021. On the relationships between rarity, uniqueness, distinctiveness, originality and functional/phylogenetic diversity. *Biol. Conserv.* 263, 109356 <https://doi.org/10.1016/j.biocon.2021.109356>.
- Pisanty, G., Richter, R., Martin, T., Dettman, J., Cardinal, S., 2022. Molecular phylogeny, historical biogeography and revised classification of andrenine bees (Hymenoptera: Andrenidae). *Mol. Phylogenet. Evol.* 170, 107151 <https://doi.org/10.1016/j.ympev.2021.107151>.
- Pohlert, T., 2021. PMCMRplus: Calculate pairwise multiple comparisons of mean rank sums extended. R package version 1 (9), 3. <https://CRAN.R-project.org/package=PMCMRplus>.
- Potts, S.G., Vuilliamy, B., Roberts, S., O'Toole, C., Dafni, A., Ne'Eman, G., Willmer, P., 2005. Role of nesting resources in organizing diverse bee communities in a Mediterranean landscape. *Ecol. Entomol.* 30, 78–85. <https://doi.org/10.1111/j.0307-6946.2005.00662.x>.
- Prendergast, K.S., Menz, M.H.M., Dixon, K.W., Bateman, P.W., 2020. The relative performance of sampling methods for native bees: an empirical test and review of the literature. *Ecosphere* 11 (5), e03076.
- Preston, F.W., 1948. The commonness, and rarity, of species. *Ecology* 29 (3), 254–283. <https://doi.org/10.2307/1930989>.
- Purvis, A., Agapow, P.M., Gittleman, J.L., Mace, G.M., 2000. Nonrandom extinction and the loss of evolutionary history. *Science* 288, 328–330. <https://doi.org/10.1126/science.288.5464.328>.
- Pyšek, P., Richardson, D.M., 2010. Invasive species, environmental change and management, and health. *Annu. Rev. Environ. Resour.* 35, 25–55. <https://doi.org/10.1146/annurev-enviro-033009-095548>.
- Rabinowitz, D., Cairns, S., Dillon, T. 1986. Seven forms of rarity and their frequency in the flora of the British Isles. Ed Soule, M.E., in *Conservation Biology: the science of scarcity and diversity*. Sinauer Associates, Sunderland, Massachusetts, pp. 182–204.
- Rabinowitz, D. 1981. Seven forms of rarity. Ed Synge H, in *The Biological Aspects of Rare Plant Conservation* pp. 205–217.
- Reveal, J.L., 1981. *The Concept of Rarity and Population Threats in Plant Communities*. Rare Plant Conservation. New York Botanical Garden, Bronx.
- Revell, L., 2012. An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.* 3, 217–223. <https://doi.org/10.1111/j.2041-210X.2011.00169.x>.
- Rightmyer, M.G., Griswold, T., Brady, S.G., 2013. Phylogeny and systematics of the bee genus *Osmia* (Hymenoptera: Megachilidae) with emphasis on North American *Melanosmia*: subgenera, synonymies and nesting biology revisited. *Syst. Entomol.* 38 (3), 561–576. <https://doi.org/10.1111/syen.12013>.
- Rosauer, D., Laffan, S.W., Crisp, M.D., Donnellan, S.C., Cook, L.G., 2009. Phylogenetic endemism: a new approach for identifying geographical concentrations of evolutionary history. *Mol. Ecol.* 18, 4061–4072. <https://doi.org/10.1111/j.1365-294X.2009.04311.x>.
- Roulston, T.H., Goodell, K., 2011. The role of resources and risks in regulating wild bee populations. *Annu. Rev. Entomol.* 56, 293–312. <https://doi.org/10.1146/annurev-ento-120709-144802>.
- Schoener, T.W., 1974. The compression hypothesis and temporal resource partitioning. *PNAS* 71, 4169–4172. <https://doi.org/10.1073/pnas.71.10.4169>.
- Schwartz, M.W., Simberloff, D., 2001. Taxon size predicts rates of rarity in vascular plants. *Ecol. Lett.* 4, 464–469. <https://doi.org/10.1046/j.1461-0248.2001.00241.x>.
- Sebastian, L., Josse, J., Husson, F., 2008. FactoMineR: An R package for multivariate analysis. *J. Stat. Softw.* 25 (1), 1–18. <https://doi.org/10.18637/jss.v025.i01>.
- Seibold, S., Gossner, M.M., Sions, N.K., Blüthgen, N., Müller, J., Ambarli, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J.C., Linsenmair, K.E., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E., Vogt, J., Wöllauer, S., Weisser, W.W., 2019. Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature* 574, 671–674. <https://doi.org/10.1038/s41586-019-1684-3>.
- Sheffield, C.S., Pindar, A., Packer, L., Winfree, P.G., 2013. The potential of cleptoparasitic bees as indicator taxa for assessing bee communities. *Apidologie* 44, 501–510. <https://doi.org/10.1007/s13592-013-0200-2>.
- Shell, W.A., Rehan, M., 2018. Behavioral and genetic mechanisms of social evolution: insights from incipiently and facultatively social bees. *Apidologie* 49, 13–30. <https://doi.org/10.1007/s13592-017-0527-1>.
- Silva, D., Silva, I., Batalha, M., 2012. Phylogenetic and phenotypic originality and abundance in a cerrado plant community. *Austral Ecol.* 37, 302–307. <https://doi.org/10.1111/j.1442-9993.2011.02277>.
- Smith, C., Weinman, L., Gibbs, J., Winfree, R., Resasco, J., 2019. Specialist foragers in forest bee communities are small, social or emerge early. *J. Anim. Ecol.* 88 (8), 1158–1167.
- Stemkovski, M., Pearse, W.D., Griffin, S.R., Pardee, G.L., Gibbs, J., Griswold, T., Neff, J. L., Oram, R., Rightmyer, M.G., Sheffield, C.S., Wright, K., Inouye, B.D., Inouye, D.W., Irwin, R.E., Coulson, T., 2020. Bee phenology is predicted by climatic variation and functional traits. *Ecol. Lett.* 23 (11), 1589–1598.
- Torné-Noguera, A., Rodrigo, A., Arnan, X., Osorio, S., Barril-Graells, H., da Rocha-Filho, L.C., Bosch, J., Ollerton, J., 2014. Determinants of spatial distribution in a bee community: nesting resources, flower resources, and body size. *PLoS ONE* 9 (5), e97255.
- Trevelin, L.C., Novaes, R.L.M., Colas-Rosas, P.F., Benathar, T.C.M., Peres, C.A., Russo, D., 2017. Enhancing sampling design in mist-net bat surveys by accounting for sample size optimization. *PLoS ONE* 12 (3), e0174067.
- Vanbergen, A.J., Baude, M., Biesmeijer, J.C., Britton, N.F., Brown, M.J.F., Brown, M., Bryden, J., Budge, G.E., Bull, J.C., Carvell, C., Challinor, A.J., Connolly, C.N., Evans, D.J., Feil, E.J., Garratt, M.P., Greco, M.K., Heard, M.S., Jansen, V.A.A., Keeling, M.J., Kunis, W.E., Marris, G.C., Memmott, J., Murray, J.T., Nicolson, S.W., Osborne, J.L., Paxton, R.J., Pirk, C.W.W., Polce, C., Potts, S.G., Priest, N.K., Raine, N. E., Roberts, S., Ryabov, E.V., Shafir, S., Shirley, M.D.F., Simpson, S.J., Stevenson, P. C., Stone, G.N., Termansen, M., Wright, G.A., 2013. Threats to an ecosystem service: pressures on pollinators. *Front. Ecol. Environ.* 11 (5), 251–259. <https://doi.org/10.1890/120126>.
- Vane-Wright, R.I., Humphries, C.J., Williams, P.H., 1991. What to protect – systematics and the agony of choice. *Biol. Conserv.* 55, 235–254. [https://doi.org/10.1016/0006-3207\(91\)90030-D](https://doi.org/10.1016/0006-3207(91)90030-D).
- Volenc, Z.M., Smith, C.M., 2021. Not all matrix habitat is created equal for rare bee species in forest habitat. *Ecol. Entomol.* 46, 926–935. <https://doi.org/10.1111/een.13029>.
- Wagner, D.L., Grooms, E.M., Forister, M.L., Berenbaum, M.R., Stopak, D., 2021. Insect decline in the Anthropocene: Death by a thousand cuts. *PNAS* 118 (2). <https://doi.org/10.1073/pnas.2023989118>
- Weislo, W., Fewell, J.H., 2017. In: *Comparative Social Evolution*. Cambridge University Press, pp. 50–83.
- Wickham, H., 2016. *ggplot2: Elegant graphics for data analysis*. Springer-Verlag, New York.
- Wickham, H., 2019. stringr: Simple, consistent wrappers for common string operations. R package version 1 (4). <https://CRAN.R-project.org/package=stringr>.
- Willfahrt, P.A., Asmus, A.L., Seabloom, E.W., Henning, J.A., Adler, P., Arnillas, C.A., Bakker, J.D., Biederman, L., Brudvig, L.A., Cadotte, M., Daleo, P., Eskelinen, A., Firn, J., Harpole, W.S., Hautier, Y., Kirkman, K.P., Komatsu, K.J., Laungani, R., MacDougall, A., McCulley, R.L., Moore, J.L., Morgan, J.W., Mortensen, B., Hueso, R. O., Ohlert, T., Power, S.A., Price, J., Risch, A.C., Schuetz, M., Shoemaker, L., Stevens, C., Strauss, A.T., Tognetti, P.M., Virtanen, R., Borer, E.T., 2021. Temporal rarity is a better predictor of local extinction risk than spatial rarity. *Ecology* 102 (11), e03504.
- Winfree, R., Griswold, T., Kremen, C., 2007. Effect of human disturbance on bee communities in a forested ecosystem. *Conserv. Biol.* 21 (1), 213–223. <https://doi.org/10.1111/j.1523-1739.2006.00574.x>.
- Winfree, R., Bartomeus, I., Cariveau, D.P., 2011. Native pollinators in anthropogenic habitats. *Annu. Rev. Ecol. Syst.* 42, 1–22. <https://doi.org/10.1146/annurev-ecolsys-102710-145042>.
- Wood, T.J., Kaplan, I., Szendrei, Z., 2018. Wild bee pollen diets reveal patterns of seasonal foraging resources for honey bees. *Front. Ecol. Evol.* 6, 21. <https://doi.org/10.3389/fevo.2018.00210>.