

Conservation prioritization based on trait-based metrics illustrated with global parrot distributions

Evsey Kosman¹ | Kevin R. Burgio^{2,3}  | Steven J. Presley^{2,3} | Michael R. Willig^{2,3} | Samuel M. Scheiner⁴ 

¹Institute for Cereal Crops Improvement, Tel Aviv University, Tel Aviv, Israel

²Center for Environmental Sciences and Engineering, University of Connecticut, Storrs, Connecticut

³Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut

⁴Division of Environmental Biology, National Science Foundation, Alexandria, Virginia

Correspondence

Samuel M. Scheiner, Division of Environmental Biology, National Science Foundation, Alexandria, VA.
Email: sscheine@nsf.gov

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Abstract

Aim: Conservation planning and prioritization generally have focused on protecting taxa based on assessments of their long-term persistence or on protecting habitats and sites with high species richness. An implicit assumption of these approaches is that species are equally different from each other. We propose metrics for conservation planning and prioritization that include consideration of differences among taxa in their functional characteristics to ensure long-term maintenance of ecosystem functioning and services.

Innovation: We define metrics of functional distinctiveness, irregularity and singularity for a species. Functional distinctiveness is the mean distance in trait space of a species to all other species in a community. Functional irregularity is the variation in the proportional distances of a focal species to all other species based on a Hill function. Functional singularity is the product of those two metrics. These metrics can be weighted based on proportional abundance, biomass or frequency of occurrence. The metrics can be used to prioritize particular species for conservation based on their functional characteristics or to identify functionally distinct priority areas for conservation using the mean functional distinctiveness, irregularity and singularity of a set of species in an area. The metrics can be compared to the species richness of that area, thereby identifying areas that might have low species richness, but whose species are especially functionally distinct, providing important information of conservation relevance.

Main conclusions: Applying these metrics to data on the global distributions of parrots, we identified species that are not of current conservation concern because they are geographically widespread, but which might be prioritized due to their functional singularity (e.g., the scarlet macaw). We also identified areas that are species poor and not generally considered noteworthy for their parrot fauna, but that contain a fauna that is functionally singular (e.g., Chile). Together, these metrics broaden the criteria used for conservation prioritization.

KEYWORDS

functional distinctiveness, functional diversity, functional irregularity, functional singularity

1 | INTRODUCTION

1.1 | General context

Conservation action at a time of increasing human population size and per capita consumption is particularly challenging for preserving biodiversity. Already there has been extensive species extinction, as well as the near complete loss of some habitat types (e.g., North American prairie, Atlantic rain forests of South America) that now persist only as small isolated fragments. Indeed, species loss is so great as to represent the sixth major global extinction of earth's history (Ceballos et al., 2015). Within this context, it is increasingly important to identify and prioritize taxa and habitats to optimize the efficacy of conservation action within the limitations of available financial resources, increasing human populations, uncertain political motivations and diminishing time before effects become irreversible.

Historically, conservation efforts have focused on protecting taxa based on assessments of threats to their long-term persistence (e.g., endangered species) or on protecting habitats and sites with high species richness. The subsequent development of siting algorithms (Andelman, Ball, Davis, & Stoms, 1999; Andelman & Willig, 2002) provided a critical tool for conservationists to prioritize areas for protection based on their species richness and irreplaceability (i.e., the degree to which inclusion of a site into a conservation network was necessary to attain predefined conservation goals). A fundamental and implicit assumption of these approaches is that species are equally different from each other (e.g., a site containing two frugivorous parrot species belonging to the same genus deserves the same prioritization as a site containing a frugivorous species and a nectarivorous species from that genus or two frugivorous species from different genera). The expansion of concepts of biodiversity beyond consideration of species richness to include consideration of differences among taxa in their characteristics (e.g., abundances, genetics, phylogenetic histories, or functional attributes), provides additional perspectives that can be used to prioritize species conservation based on essential species differences (Cadotte, Carscadden, & Mirotchnick, 2011; Devictor et al., 2010; Flynn, Mirotchnick, Jain, Palmer, & Naeem, 2011). This focus on functional characteristic of species has received increasing attention in the past decade (Brum et al., 2017; Decker, Linke, Hermoso, & Geist, 2017; Maire, Buisson, Biau, Canal, & Laffaille, 2013; Pollock, Thuiller, & Jetz, 2017; Strecker, Olden, Whittier, & Paukert, 2011). However, all but one of these efforts use a community-level metric of functional importance. In this paper, we present a species-level metric that allows for prioritization of particular species, not just places.

1.2 | Conservation prioritization

An operational challenge for conservation is to choose from among a set of biological units (e.g., OTUs, germplasms, species, communities, landscapes) a subset that preserves the greatest amount of genetic, functional, phylogenetic or other variability. Because it is impossible to equally protect everything, methods are required to

prioritize each candidate element based on its contribution to the total variability of a biota. To address this challenge, we present metrics based on trait values that can be used to estimate the amount of variation in trait characteristics preserved by each species in a given set. Such an approach can improve conservation outcomes by maximizing the functional diversity of a set of species to enhance ecosystem function or the long-term sustainability of a clade or assemblage (Pavoine, Bonsall, Dupaix, Jacob, & Ricotta, 2017; Violle et al., 2017). Our metrics are built on the assumption that trait values are an effective proxy for functions performed by species so that maximizing the variability of such traits will maximize the functional diversity of a community or larger assemblage. We illustrate the utility of these metrics by using data on the global distribution of parrots (Order: Psittaciformes).

Our efforts are an extension of the recent work of Violle et al. (2017) and Pavoine et al. (2017) aimed at assessing the conservation value of particular species, and of our own work on community-level functional diversity metrics (Presley, Scheiner, & Willig, 2014; Scheiner, Kosman, Presley, & Willig, 2017). Metrics of functional diversity or the functional value of particular species are based on the arrangement of the species in a hyperspace defined by trait values that are presumed to reflect the functional roles of species within ecosystems. Using the terms "rarity" and "originality," respectively, Violle et al. (2017) and Pavoine et al. (2017), explored the notion of identifying species that have functional characteristics that differ from those of other species in a biota by using the mean distance in trait space of a focal species from all other species. Here, we add consideration of a second property for estimating functional differences among species: variability in distances. A species is functionally different from other species not only when it is distant from them on average, but when it is consistently different. For example, a species might be, on average, quite distant from most species but functionally similar to one other species. The conservation priority for such a species might be lower than that of a species with the same average distance to other species but that is also consistently different from all other species (i.e., a species without a close neighbour in functional space). Violle et al. (2017) address this property with their measure of functional uniqueness, the minimum pairwise distance between a focal species and the other species. Our metric differs in that one of the components is based on variation in distances to all other species, not just the nearest neighbour in trait space.

Previously, Scheiner et al. (2017) proposed metrics of functional diversity based on the magnitude of the distances among species, termed "dispersion," and the variability in those distances, termed "equability," including a composite metric that captured both properties (see also Gregorius & Kosman, 2018). In this paper, we develop similar metrics to evaluate species-specific contributions to the functional uniqueness of a biota. We follow Pavoine et al. (2017) and Violle et al. (2017) in the use of mean distance, and follow the terminology of Violle et al. for that mean distance, "functional distinctiveness." For variability in those distances, we use a metric based on Hill numbers (Hill, 1973), which we term

“functional irregularity.” We also define a composite metric that captures both of these properties, which we term “functional singularity.” We present versions of these metrics based solely on functional trait information and based on functional trait information weighted by the relative frequency of occurrence or similar measures such as the relative abundance or proportional biomass. Although we present our metrics with regard to species-level trait information, the same approach can be used for variation at lower levels in the biological hierarchy such as subspecies, strains or individuals. For example, allelic differences can be used for making conservation decisions regarding the preservation of germplasm stocks.

Our approach to prioritization differs significantly from the typical approach of using community-level metrics (Brum et al., 2017; Decker et al., 2017; Maire et al., 2013; Pollock et al., 2017; Strecker et al., 2011). Those metrics provide a measure of how diverse all of the species within a particular community (or other conservation unit) are relative to the within-community diversity of other communities. The approach advocated here and by Violle et al. (2017) provides a way to prioritize individual species regardless of the diversity of the communities within which they are located. Such prioritization is consistent with the IUCN approach to threat assessment, thereby allowing functional information to be added to that assessment.

Our approach also allows the conservation value of a community to be measured relative to the total species pool. With community-level metrics, a community that includes just one or two species that are functionally similar to each other would be assessed as less diverse than a community with more, functionally different species, even if those two species are highly, functionally distinct from all of the others in the species pool. With our approach, the functional conservation value of a particular community is realized in two steps. First, the functional singularity is determined for each species in the species pool. Then, the community conservation value is computed as the mean functional singularities of its constituent species. Using this approach, a community consisting of just two species that are highly, functionally distinct from all other species would be given a high prioritization value.

1.3 | Parrots: a vertebrate order of global conservation concern

To demonstrate how our metrics can be used to inform conservation decisions, we apply them to data on the global distributions of parrots (Psittaciformes). Parrots are the most threatened order of birds (Olah et al., 2016). Over 40% of the species are listed by the IUCN as near-threatened or worse (IUCN, 2014). In addition to threats to species persistence that are associated with habitat loss and climate change, the capture of specimens for the pet trade enhances the likelihood of extinction, at least locally (Olah et al., 2016; Snyder, McGowan, Gilardi, & Grajal, 2000). Moreover, parrots are keystone mutualists as they provide important ecosystem functions, including

invertebrate pest management, pollination, seed predation and seed dispersal (Blanco et al., 2016; Blanco, Hiraldo, Rojas, Dénes, & Tella, 2015; Tella et al., 2015). Because the global distribution and functional characteristics of parrot species are well known, the order represents an ideal taxon for exploring conservation issues based on considerations of functional characteristics. We use our metrics to identify species that could be the target of conservation efforts because of their functional characteristics and to select locations that are rich in such species. These species or locations might differ from those identified using contemporary approaches based on the geographic range of a species or numbers of species in a location.

2 | METHODS

2.1 | Identifying the conservation priority of a species

We begin by defining metrics of functional distinctiveness, irregularity and singularity for a species. The functional distinctiveness of a species is the mean distance of that species from all other species in a community. For ease of presentation, we use the term “community” to designate the set of species, but emphasize that these metrics apply equally to species at any spatial extent. Let d_{ij} represents the dissimilarity in trait space between the i th and j th species, with traits scaled so that $0 \leq d_{ij} \leq 1$, $d_{ij} = d_{ji}$, and $d_{ii} = 0$. (See Supporting information Appendix S1: Section 1 for a discussion of how traits are scaled.) As in Violle et al. (2017), the mean difference of the i th species from all other species is:

$$M_i(T) = \sum_{j=1, j \neq i}^S d_{ij} / (S-1), \quad (1)$$

where S is the number of species in the community. This metric has a range of [0,1] and measures the dispersion of the i th species relative to all other species in a community. We use the notation “ T ” to emphasize that the metric is based on trait values.

Functional irregularity is based on variation in the proportional distances of a focal species from all other species using the Hill function (see Supporting information Appendix S1: Section 3). The overall difference of the i th species from all other species is $d_i = \sum_{j=1}^S d_{ij}$, so that the proportional contribution of the j th species to the cumulative difference is $f_{ij} = d_{ij}/d_i$, where $\sum_{j=1, j \neq i}^S f_{ij} = 1$, and functional irregularity is:

$${}^qFI_i(T) = \left(\sum_{j=1, j \neq i}^S f_{ij}^q \right)^{\frac{1}{1-q}} / (S-1) \quad (2)$$

(This function is undefined for $q = 1$; see Supporting information Appendix S1: Equation 3A for the limit form in that case.) If $d_{ij} = 0$ for all j (i.e., the trait profiles for all species are identical), f_{ij} is undefined and ${}^qFI_i(T) = 0$ by definition. The metric ranges from 0 when the trait profiles for all species are identical, to 1 when the other $S - 1$ species

are equally distant from the i th species. The exponent q alters the weighting of the proportional distances. As q increases, the metric gives greater weight to larger distances. When $q = 0$, all trait differences are weighted equally and ${}^0F_i(T) = (S - 1)/(S - 1) = 1$. If one or more of the other species have trait values that are identical to that of the focal species ${}^0F_i(T) = S_j/(S - 1)$, where S_j is the number of species with trait profiles that differ from that of the i th species.

From these two metrics, we define a metric that combines functional distinctiveness and irregularity, functional singularity:

$${}^qFS_i(T) = M_i(T) \times {}^qF_i(T), \quad (3)$$

which also has a range of $[0,1]$. For two species with equal values of functional irregularity, the species with the greater functional distinctiveness will have the greater functional singularity, and vice versa for differences in functional irregularity. This composite metric identifies the extent to which a particular species is different from all other species $[M_i(T)]$ and the variability (or homogeneity) of those differences $[{}^qF_i(T)]$, thus determining the most consistently different species in a given community.

2.2 | Weighted metrics

The metrics just described are based on trait values alone. However, differences among species in proportional abundance, biomass or frequency of occurrence provide additional information that may be relevant to conservation action. Frequency of occurrence is a measure of geographic range size, with large values corresponding to broadly distributed species and small values corresponding to microspatial or endemic species. We illustrate the procedure of weighting with respect to abundance and later provide an empirical example of weighting based on frequency of occurrence. Let n_j be the abundance (number of individuals) of the j th species in a set of S species. Assuming that all individuals of a particular species have identical trait values, as per Violle et al. (2017) the mean abundance-weighted difference of the i th species from all other species is:

$$M_i(TA) = \frac{\sum_{j=1, j \neq i}^S n_j d_{ij}}{\sum_{j=1, j \neq i}^S n_j}. \quad (4)$$

This metric has a range of $[0,1]$. We use the notation "TA" to emphasize that the metric is based on trait values that are weighted by abundance. However, it is important to note that the metric is not weighted by the abundance of the focal species; rather it is weighted by the abundances of each of the other species in the community. The functional distinctiveness of the focal species decreases as the abundances of species with similar trait values increase. When all species are equally abundant, the metric reduces to $M_i(T)$.

Similarly, we can define an abundance-weighted measure of functional irregularity:

$${}^qF_i(TA) = \left[\sum_{j=1, j \neq i}^S (n_j \hat{f}_{ij})^q \right]^{1/(1-q)} / (S - 1), \quad (5)$$

where \hat{f}_{ij} is the proportional contribution of an individual of the j th species to the overall difference of an individual of the i th species to all individuals of the other species (Supporting information Appendix S1: Section 6). A limit formula is required when $q = 1$ (see Supporting information Appendix S1: Equation 16A). The metric ranges from 0 when the trait values for all species are identical (by definition), to 1 when abundance-weighted distances to the other species are identical ($n_j d_{ij} = n_k d_{ik}$, for all j and k), such as when all other species are equally abundant and equally distant from the i th species. When all species are equally abundant, the metric reduces to ${}^qF_i(T)$. Our composite metric of abundance-weighted functional singularity is:

$${}^qFS_i(TA) = M_i(TA) \times {}^qF_i(TA), \quad (6)$$

which has a range of $[0,1]$. Again, when all species are equally abundant, the metric reduces to ${}^qFS_i(T)$.

2.3 | Identifying functionally distinct priority areas for conservation

Use of the previously described metrics at global or continental extents facilitates the identification of species that should be considered for protection if the maintenance of functional diversity is a conservation goal. Often, though, conservation efforts are based on protecting sites and the communities that occupy them. One such site-based approach involves the identification of areas with exceptionally high numbers of species (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000). Similarly, our metrics can identify priority areas of functional singularity, ones that comprise an appreciable number of functionally distinct and singular species.

Assume that S species are distributed among H units, and each community contains a set (C_h) of S_h species ($h = 1, 2, \dots, H$). Then, the aggregate functional singularity for each community can be represented as the sum of the corresponding values of the species in that community:

$${}^qFS_h(T) = \sum_{i \in C_h} {}^qFS_i(T). \quad (7)$$

Similar sums can be calculated for functional distinctiveness $[{}^qM_h(T)]$ and functional irregularity $[{}^qF_h(T)]$ (see Supporting information Appendix S1: Section 4). Each of these metrics has a range of $[0, S]$ and is greater when a unit is either more species-rich or is rich in species that are highly functionally distinct or functionally irregular. However, an area might be species poor and the metric would have a moderate value, even if that area includes exceptionally functionally singular species. We can address this by adjusting the metric relative to local species richness:

$${}^q\overline{FS}_h(T) = {}^qFS_h(T) / S_h. \quad (8)$$

These mean values identify areas that have a high proportion of functionally singular species, even if that area is not particularly species-rich. Such areas might otherwise be overlooked if priorities

are based on species richness alone. These community metrics can also be weighted by abundance or frequency of occurrence (see Supporting information Appendix S1: Section 7).

2.4 | Application to conservation of parrots

To demonstrate how functional distinctiveness, irregularity or singularity can be used to inform conservation action, we applied them to data on the global distributions of parrots. We used our metrics (a) to identify species that could be the target of conservation efforts because of their functional characteristics and (b) to select locations that comprise species that cumulatively represent considerable functional diversity. These species or locations might differ from those identified using conventional approaches based on the geographic range of a species or numbers of species in a location.

We used current range maps for all 398 extant parrot species (BirdLife International & NatureServe, 2014), following the taxonomy of Del Hoyo, Collar, Christie, Elliot, and Fishpool (2014). We counted the number of 50 × 50 km grid cells on a global map occupied by each species; 25,081 grid cells contained at least one species. We estimated functional diversity using two types of data: categorical (binary) and continuous attributes. For each data type, we used a suite of 24 continuous or categorical traits that reflect particular niche axes and define functional components. Functional components included ingestible food size (culmen length), diet (carrion, invertebrates, snails, pollen, nectar, seeds, nuts, fruit, flower, vegetation, roots, fungi), foraging strategy (dig, scavenge, flower probe, glean, excavate, graze) and foraging location (water, ground, vegetation, subcanopy, canopy). For culmen size, we used the average value for each species based on measurements of multiple adults, when available. These data were standardized to a range of [0,1]. For each categorical attribute, a species received a “1” if it exhibited the characteristic and a “0” if it did not.

We obtained trait data for all parrot species from the literature (BirdLife International, 2015; Forshaw, 1989; Del Hoyo, Elliot, & Sargatal, 1997; Juniper & Parr, 1998). We estimated missing culmen length measurements using linear regressions based on congeners (or tribe members, if there were few or no congeners with such data). To address missing trait data for diet, foraging location and foraging strategy, we substituted the traits of the most closely related congener, as these traits generally are conserved phylogenetically (Peterson, 2011). In total, 30 species had missing data and we estimated 4.5% of trait values (410 of 9,142). See for more information.

To determine the functional distance between each parrot species, the simple mismatch dissimilarity was calculated for each of the three groups of binary traits (diet, foraging strategy and foraging location), and the mean character difference was calculated for culmen length. Then the combined distance (d_{ij}) between species was determined by an equal-weight averaging of the four group-specific distances. Functional metrics were calculated according to Equations 1–8. To visualize the distribution of species in trait space, we used the first two dimensions from a nonmetric multidimensional scaling (NMDS) based on the combined distance matrices for all 398 species of parrot.

The NMDS analyses were conducted using the R package “ecodist” (Goslee & Urban, 2007). These two dimensions accounted for 75% of the total variation among parrots for the 24 functional traits.

3 | RESULTS

3.1 | Global patterns

Parrots are distributed circumtropically, with the greatest species richness in southeastern Australia, Papua New Guinea, Amazonia and northeastern South America (Figure 1). Based on endemism alone, conservation efforts might focus on species such as the Saint Vincent parrot (*Amazona guildingii*) that is endemic to the island of Saint Vincent in the Lesser Antilles, or the Seychelles black parrot (*Coracopsis barklyi*) that is endemic to the Seychelles, or the Chatham parakeet (*Cyanoramphus forbesi*) that is endemic to the Chatham Islands of New Zealand (Supporting information Appendix S1: Table S1). The IUCN status of each of these three species is “vulnerable.”

Use of functional trait information leads to consideration of other species for conservation prioritization. Species at the periphery of functional trait space (Figure 2) generally have high values of functional singularity. Some also have limited distributions, such as the kea (*Nestor notabilis*) or the Antipodes parakeet (*Cyanoramphus unicolor*), each a New Zealand endemic. The former has an IUCN status of “endangered,” and the latter has a status of “vulnerable.” They are also functionally very different from most other parrot species, the kea being the world's only alpine parrot and the Antipodes parakeet being one of only five ground-dwelling parrots. However, some of the functionally distinct species are currently widespread. For example, the scarlet macaw (*Ara macao*) is one of the most widely distributed parrots in the world and can be found in humid evergreen forests across Central and South America; its IUCN status is “least concern.” Similarly, two functionally distinct species, the Finsch's pygmy parrot (*Micropsitta finschii*) that is native to Micronesia and the slender-billed parakeet (*Enicognathus leptorhynchus*) that is endemic to southern Chile, have a much smaller geographic distributions and have an IUCN status of “least concern.” The species with the greatest functional singularity, the hyacinth macaw (*Anodorhynchus hyacinthinus*), is one of the world's largest parrots; its geographic range is intermediate in size; it occurs across central and eastern South America, and has an IUCN status of “vulnerable.” Clearly, some of these species are currently prioritized for conservation, whereas others are not, even though their functional singularities suggest additional consideration is warranted.

The parrot data show how the components of functional singularity—functional distinctiveness and functional irregularity—provide complementary information (Figure 3; Supporting information Appendix S1: Figures S2, S3). Because of the aggregated distribution of species in trait space (Figure 2), some near the center is very close to many other species, resulting in a low mean distance to other species (functional distinctiveness) and a high variation in

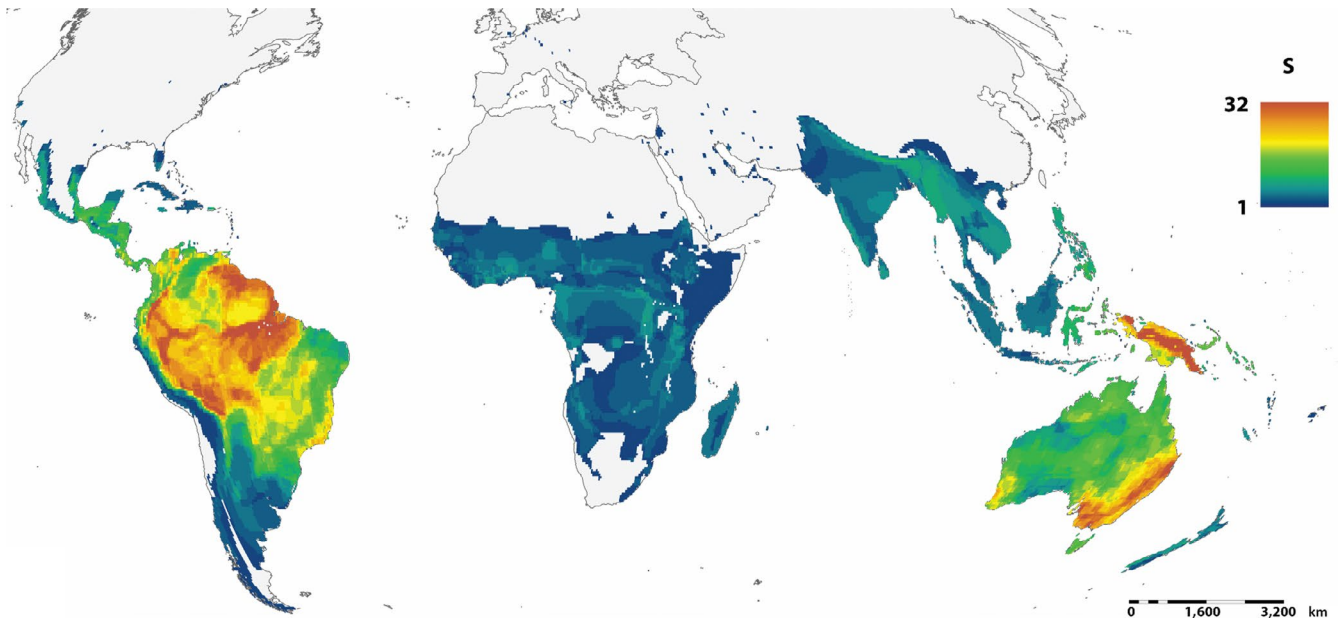


FIGURE 1 Global variation in parrot species richness (S) at a grain of 50×50 km grid cells. Map projection: Mollweide Equal Area

distances (functional irregularity). Other species also near the center are more separated from any others, or are in a cluster of only two or three species, resulting in low mean distance and low variation in distances. As a result, functional distinctiveness and functional irregularity are correlated only weakly (the Spearman rank correlation of $M_i(TA)$ and $FI_i(TA)$ is 0.44). The correlation between the metrics is not driven by associations with frequency of occurrence, as different frequency categories are equivalently distributed in all regions of trait space (Supporting information Appendix S1: Figure S1).

In addition to prioritizing species based on their functional attributes, functional singularity can be used to identify regions of conservation priority that would be ignored if we focused solely on species richness. Mean functional singularity $\left[{}^q\overline{FS}_h(T)\right]$ highlights regions whose species are especially distinct from a functional perspective (Figure 4). They include species-rich regions, such as Australia, but also ones that are species poor, for example New Zealand and Chile. In the case of Chile, only one of its five species—the slender-billed parakeet—is exceptionally distinct, but when taken as a whole the fauna is noteworthy for its functional singularity. A useful method for highlighting such areas is a plot of standardized differences in species richness and functional singularity (Figure 5). Doing so makes evident other areas with exceptional functional singularity such as the Sierra Madre Occidental of Mexico and the island of Java. It also emphasizes that western Australia, besides being moderately species-rich (Figure 1), is especially rich in functionally distinct species. The inclusion of endemism information further emphasizes the potential for conservation prioritization of such areas (compare Supporting information Appendix S1: Figures S2 and S4, Figures S3 and S5, Figure 4 and Supporting information Appendix S1: Figures S6 and see S7).

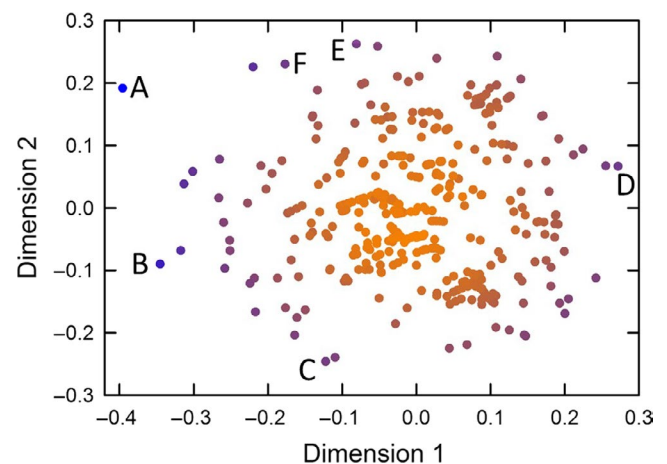


FIGURE 2 The distribution of 398 parrot species (circles) with respect to the first two axes from NMDS based on 24 functional traits. Points are colour coded by functional singularity weighted by frequency of occurrence $\left[{}^1\overline{FS}_i(TA)\right]$; orange indicates the smallest values and blue the largest values. The labelled points are as follows: (a) the hyacinth macaw (*Anodorhynchus hyacinthinus*), (b) the kea (*Nestor notabilis*), (c) the scarlet macaw (*Ara macao*), (d) Finsch's pygmy parrot (*Micropsitta finschii*), (e) the Antipodes parakeet (*Cyanoramphus unicolor*) and (f) the slender-billed parakeet (*Enicognathus leptorhynchus*)

4 | DISCUSSION

4.1 | Expanding the prioritization process in conservation

Considerations of functional traits complement and expand current prioritization practices for the conservation of species and sites. Beyond considerations of species that are threatened due to small geographic

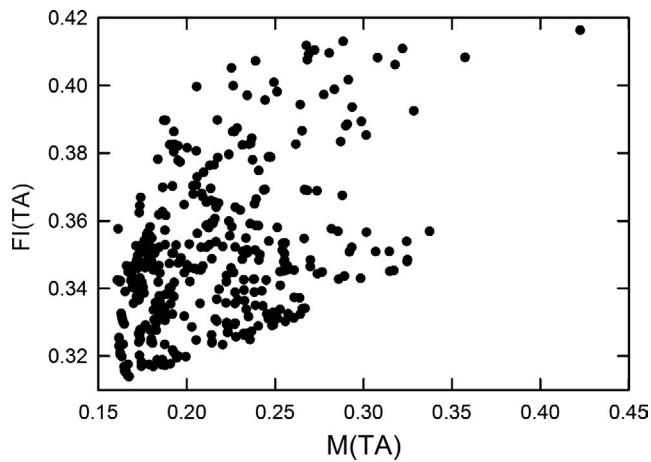


FIGURE 3 The empirical association between functional distinctiveness [$M_i(TA)$] and functional irregularity [${}^1F_i(TA)$] for 398 parrot species

ranges or small population sizes, metrics of species distinctiveness, irregularity and singularity identify species that are functionally different and worthy of increased scrutiny, even if they are currently widespread and common (e.g., the scarlet macaw). Moreover, such information can be used to identify regions that are particularly rich in functionally singular species (e.g., Chile) and can be combined with measures of species abundance or frequency of occurrence to inform conservation action. Our intent is not to replace current prioritization practices that focus on species abundance or species richness, but to complement them with additional information. We highlight ways to explicitly consider abundance and functional attributes of species to make conservation decisions that better address long-term goals of ecosystem sustainability.

Our metrics (Table 1) advance those advocated by Violle et al. (2017). Both approaches consider functional distinctiveness to be an

important characteristic for identifying species of conservation concern. Violle et al. (2017) use two approaches to address the concept of species-level functional distinctiveness, which they term “functional rarity”: functional uniqueness (U_i), which measures the distance of a focal species to its nearest neighbour in functional trait space, and functional distinctiveness (D_i), which is based on the mean distance of a focal species to all other species in functional trait space. However, neither of these measures capture variation in the functional distances between species. By considering only a single distance between nearest neighbours, functional uniqueness ignores information about the overall location of a focal species relative to all other species in functional trait space that is captured by functional irregularity (Supporting information Appendix S1: Figure S8). Additionally, functional uniqueness can be subject to large changes in value by the addition or removal of a single species that is functionally similar to the focal species. Functional uniqueness can be considered a special case of functional irregularity for q equal to negative infinity (effectively weighting nearest neighbours to solely influence functional irregularity). We advocate the use of functional singularity for conservation decisions because it (a) combines information on functional distinctiveness and irregularity, and (b) can be combined with abundance or frequency of occurrence information. Moreover, functional singularity can be used regardless of the spatial extent of the data, rather than using different metrics at local and regional extents as suggested by Violle et al. (2017). A metric that is applicable at all spatial extents means that the same prioritization process for conservation action can be used without having to arbitrarily decide whether an area under consideration represents a single community, a landscape or a region.

Importantly, the aggregate community-level functional singularity metric that we propose (Equation 7), as well as this metric relative to local species richness (Equation 8), are conceptually different from

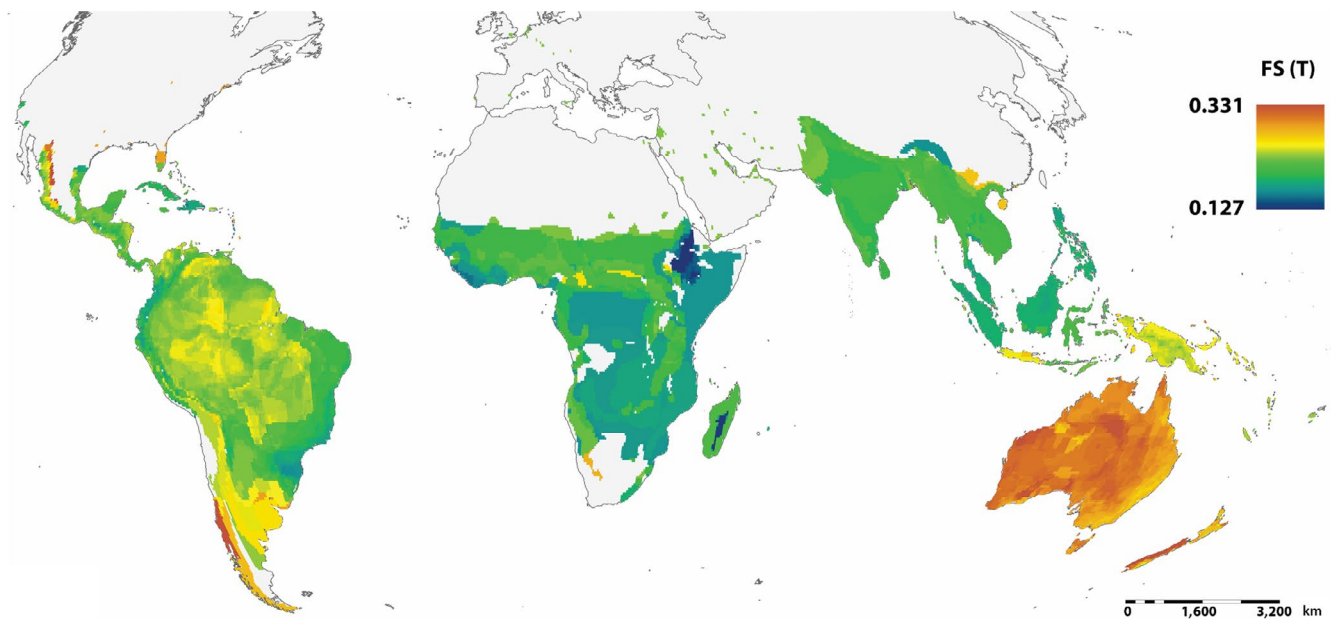


FIGURE 4 Global variation in the mean functional singularity of parrots [${}^1\overline{FS}_h(T)$] at a grain of 50×50 km grid cells. Map projection: Mollweide Equal Area

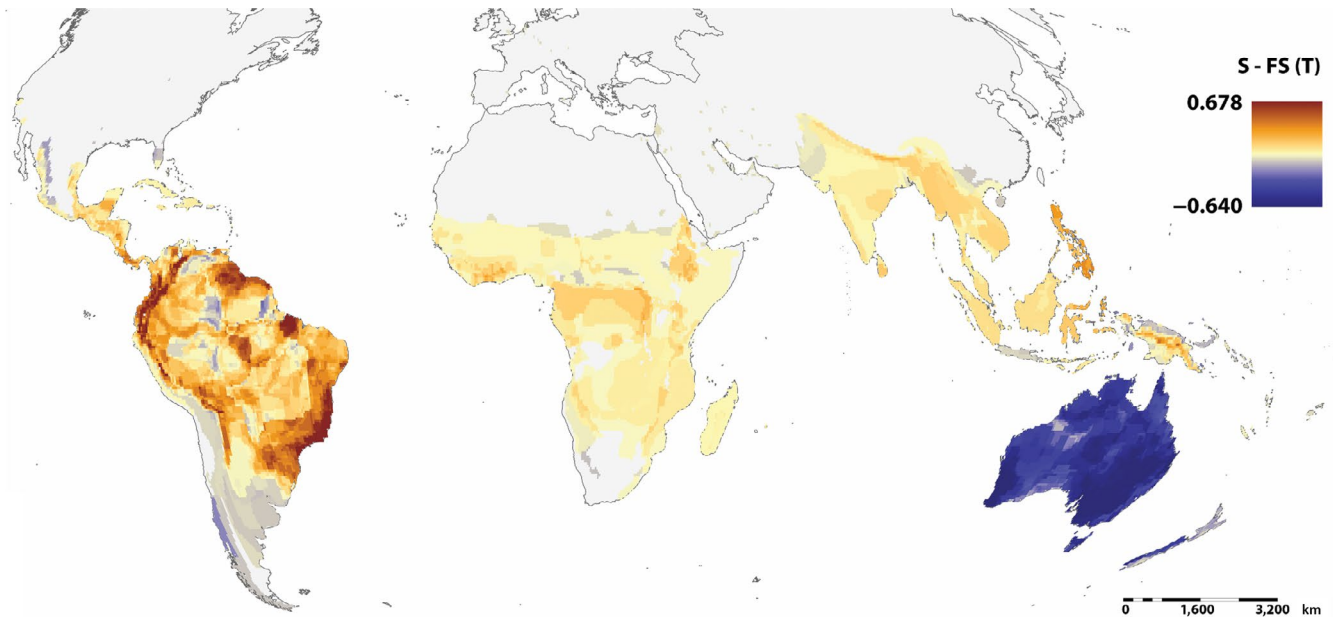


FIGURE 5 The difference in species richness $[S]$ and mean functional singularity $[{}^1\overline{FS}_h(T)]$ of parrots at a grain of 50×50 km grid cells. Both variables for each grid cell were first z-transformed, which computes a mean-centred difference in standard deviation units so that very high values of richness or singularity have large positive values and low values of richness or singularity have large negative values. The difference in those z-scores was then computed and plotted. Areas that are very species-rich with average to low singularity values appear dark orange, and areas that have high singularity values with low species richness appear dark blue. Map projection: Mollweide Equal Area

TABLE 1 Metrics of species' functional value

Equations	Metric	Symbol	Formula
1	Functional distinctiveness	$M_i(T)$	$\frac{\sum_{j=1, j \neq i}^S d_{ij}}{(S-1)}$
2	Functional irregularity	${}^qF_{I_i}(T)$	$\frac{\left(\sum_{j=1, j \neq i}^S \left(\frac{d_{ij}}{\sum_{k=1, k \neq i}^S d_{ik}} \right)^q \right)^{\frac{1}{1-q}}}{(S-1)}$
3	Functional singularity	${}^qFS_i(T)$	$M_i(T) \times {}^qF_{I_i}(T)$
4	Abundance-weighted functional distinctiveness	$M_i(TA)$	$\frac{\sum_{j=1, j \neq i}^S n_j d_{ij}}{\sum_{j=1, j \neq i}^S n_j}$
5	Abundance-weighted functional irregularity	${}^qF_{I_i}(TA)$	$\frac{\left(\sum_{j=1, j \neq i}^S \left(\frac{n_j d_{ij}}{\sum_{k=1, k \neq i}^S n_k d_{ik}} \right)^q \right)^{\frac{1}{1-q}}}{(S-1)}$
6	Abundance-weighted functional singularity	${}^qFS_i(TA)$	$M_i(TA) \times {}^qF_{I_i}(TA)$
7	Aggregate functional singularity	${}^qFS_h(T)$	$\sum_{i \in C_h} {}^qFS_i(T)$
8	Mean functional singularity	${}^q\overline{FS}_h(T)$	$\frac{{}^qFS_h(T)}{S_h}$

Notes. d_{ij} : standardized distance in trait space between the i th and j th species; S : number of species; n_j : the abundance of the j th species; q : the weighing factor of the proportional distances; C_h : the set of species contained in community h ; S_h : the number of species in community h .

community-level metrics of functional diversity that measure variation within a particular community (Chiu & Chao, 2014; Laliberté & Legendre, 2010; Villéger, Mason, & Moullot, 2008). Our metrics are based on the functional singularity of each species (Equations 3, 6) compared to a larger operational unit (e.g., region or global pool), whereas the latter is a result of relationships among species within a given community without any direct evaluation of the contribution of each constituent species to the total variation.

4.2 | Insights from applications to global parrot data

The data on parrots show how species richness and functional singularity provide different and complementary types of information. For example, both Amazonia and Australia are species-rich (Figure 1), but the latter region also has very functionally distinct species whereas the former harbours mainly "typical" parrots (Figures 4 and 5). Those differences could lead to differences in conservation strategies for Amazonia

and Australia. For example, in Amazonia, the focus might be on maximizing the average functional diversity of a suite of local sites. Doing so likely would capture adequately the range of functional singularity in the region. In contrast, in Australia, the focus might be on maximizing the total functional diversity of the region, so as to ensure that the entire range of functional diversity is represented in conserved areas.

4.3 | Extensions to biogeography, ecology, and evolutionary biology

Standardized community metrics (Equation 8) quantify the per species contribution of functional distinctiveness, irregularity or singularity at a site. Areas with high values of these metrics mostly comprise functionally unusual species. Consequently, they may be useful in guiding comparative investigations in biology. Examining the relationship between these metrics and local site characteristics such as the frequency or intensity of disturbance, productivity, soil or climatic factors, or along biogeographic gradients of latitude, elevation or depth might tell us about mechanisms of species sorting from the regional species pool. Comparisons with measures of ecosystem function might tell us the roles that “typical” and “unique” species play in a community.

Values of functional distinctiveness, irregularity or singularity for species can be mapped onto a phylogeny and reveal the extent of evolutionary conservatism in these measures of species function, and how competition among congeners, colonization of new regions or vicariance might drive trait evolution. Phylogenetic diversity is often touted as a proxy for functional diversity and is advocated for use in conservation prioritization (Cisneros et al., 2014; Mouquet et al., 2012). Examining how these functional metrics are distributed across a phylogeny, and comparing functional and phylogenetic distance measures, would provide tests of that supposition. If they are only weakly correlated (Kluge & Kessler, 2011; Narwani, Alexandrou, Oakley, Carroll, & Cardinale, 2013; Purschke et al., 2013), conservation prioritization procedures will need to take into account both phylogenetic and functional information.

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DATA ACCESSIBILITY

The data used in this paper were previously published (Burgio et al., in press) and are available on Figshare: <https://figshare.com/s/6cdf8cf00793deab7ba6>.

ORCID

Kevin R. Burgio  <https://orcid.org/0000-0002-8375-2501>

Samuel M. Scheiner  <https://orcid.org/0000-0003-1677-9752>

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BIOSKETCH

Evsey Kosman is a mathematician. He develops general and logically consistent approaches and metrics for measuring and decomposing genetic, functional and phylogenetic variability to address a wide range of topics in population genetics, ecology and conservation. His research interests also include analysing structural relationships of operational units at different hierarchical levels of biological organization and at various spatiotemporal scales.

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SUPPORTING INFORMATION

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

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