

Evolutionary distinctiveness and conservation priorities in a large radiation of songbirds

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Keywords

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Abstract

Human-induced impacts such as climate change and habitat alterations, coupled with limits on funding, have forced conservation actions into a mode of triage. Although no current method has been agreed upon as the best approach to select species for conservation, many studies have demonstrated the utility of incorporating phylogenetic diversity into these decisions. In many cases, degree of phylogenetic relatedness is thought to provide a measure of functional diversity, and greater phylogenetic distinctiveness is likely linked to ecosystem stability. Despite recent debate over the validity of this notion, phylogenetic information remains an important factor to consider in evaluating species and regions for conservation attention. Emberizoidea is a large radiation of 830 species, representing roughly 17% of all songbirds and 8% of all birds. Species in this clade are found throughout the Americas and occur in all terrestrial biomes in the region. The large distribution of this clade, coupled with its morphological and ecological diversity, makes it an important radiation to study from an evolutionary and conservation perspective. This study provides conservation priorities for all species in Emberizoidea using evolutionary distinctiveness (ED) and Evolutionarily Distinct and Globally Endangered (EDGE) values from a pseudoposterior distribution of time-calibrated supertrees. We found that threat level is not correlated with degree of ED, indicating that the most threatened species do not represent a disproportionate amount of ED. In addition, threatened species are slightly clustered across the phylogeny, indicating similar threats may be affecting groups of closely related species such as island radiations or geographically restricted radiations in highly disturbed regions.

Introduction

The planet is currently experiencing a serious extinction event driven largely by anthropogenic factors (Barnosky *et al.*, 2011; De Vos *et al.*, 2015). This is true in birds, where extinction rates far exceed that of the benchmark rate prior to human effects (Pimm *et al.*, 2006). Limits on available resources for conserving species, or protecting areas that are facing threats, necessitate a prioritization system (Marris, 2007). Typical methods suggest defining areas for conservation using hotspots, which are often calculated using a variety of criteria, such as species richness or endemism. These differences in criteria often produce inconsistent results and the proposed hotspots do not always reflect known threat levels (Orme *et al.*, 2005). As molecular data are becoming easier to collect, more studies are incorporating phylogenetic information into conservation evaluations (Isaac *et al.*, 2007; Jetz *et al.*, 2014; Redding, Mazel & Mooers, 2014). Implementing a phylogenetic approach into these measures ensures the largest amount of phylogenetic diversity is protected for

a given conservation proposal. Additionally, this method may be an improvement over criteria such as species richness for adequately conserving functional diversity, as greater phylogenetic distinctiveness may be linked to ecosystem stability (Cadotte, Cardinale & Oakley, 2008; Cadotte, Dinnage & Tilman, 2012).

Recent studies have demonstrated that, under certain scenarios, phylogenetic diversity may not always maximize functional diversity (Kelly, Grenyer & Scotland, 2014; Mazel *et al.*, 2017). By simulating trait evolution under a variety of models and tree topologies, Mazel *et al.* (2017) suggests that maximizing phylogenetic diversity captures as much, or more functional diversity than might be expected by random under a majority of trait evolution model/tree topology combinations. This indicates that for many scenarios, phylogenetic diversity can be a valuable approach to conservation prioritizations for its representation of trait diversity. However, for a significant area of model space, phylogenetic diversity captures less functional diversity than might be captured by a random selection of species. This occurs when traits evolve

under a speciation model (where traits only evolve at speciation events) on an unbalanced tree topology. For these scenarios, conserving phylogenetic diversity would not maximize functional diversity. Despite this, we argue, like others (e.g. Rosauer & Mooers, 2013), that phylogenetic diversity remains an informative characteristic for conservation. The primary goal of conservation is to preserve biodiversity, and genetic diversity is one of the most fundamental measures of biodiversity. Thus, using phylogenetic information acts as a useful objective tool for identifying a genetically diverse set of organisms for conservation. Additionally, these measures can act as one of many tools in a single conservation strategy, and can provide an objective approach to further prioritize species that have been identified by other conservation approaches, such as the IUCN Red List [e.g. Evolutionarily Distinct and Globally Endangered (EDGE) values; see below].

Two commonly used measures are evolutionary distinctiveness (ED), which prioritizes species on their evolutionary uniqueness, and the EDGE metric, which weights a species ED value by its threat of endangerment (Isaac *et al.*, 2007). The latter metric has seen widespread application across many groups of taxa in multiple studies (Mammals, Isaac *et al.*, 2007; Amphibians, Isaac *et al.*, 2012; Plants, Huang *et al.*, 2016; Squamata, Tonini *et al.*, 2016), and has seen one application to birds (Jetz *et al.*, 2014). While Jetz *et al.* (2014) sampled across all Aves, studies of this scale often necessitate a trade-off between size and accuracy. Because conservation actions based on these calculations can operate at the species-level, it is critical to ensure the accuracy of individual species relationships, many of which were inferred in Jetz *et al.* (2014) from classifications rather than phylogenies. Therefore, it is important to revisit subclades within Aves, where more attention can be afforded to these relationships as better phylogenetic data become available.

Emberizoidea is one of the largest radiations of birds. At *c.* 830 species, it represents roughly 17% of all songbirds, and 8% of all birds (Clements *et al.*, 2017). This group is often referred to as the 'New World nine-primaried oscines'; however, the radiation includes a major clade (Emberizidae) that back dispersed to the Old World. Additionally, members of this clade have a present, though greatly reduced tenth primary, making the name unrepresentative of the clade as a whole (Hall, 2005). The Emberizoidea lineage is hypothesized to be the result of a trans-Beringian land bridge dispersal to the New World about 20 million years ago (Mayr, 1964; Barker *et al.*, 2004, 2015). Subsequent diversification has resulted in six large, well-studied crown radiations: Thraupidae (tanagers), Cardinalidae (cardinals), Passerellidae (New World sparrows), Icteridae (blackbirds), Parulidae (wood-warblers) and Emberizidae (Old World buntings). In addition to the larger clades, Emberizoidea contains multiple low diversity lineages, such as the monotypic *Rhodinocichla* (Barker *et al.*, 2013, 2015). Classification of these species has previously faced many challenges, owing largely to a wide range of morphological and plumage diversity. This radiation includes birds that vary in size from over 490 g (*Psarocolius bifasciatus*) to 6 g (*Oreothlypis luciae*;

Dunning, 2008). The clade includes a variety of bill shapes and associated feeding morphologies, from the large, blunt seed-eating bill of the Large Ground Finch *Geospiza mag-nirostris*, to the long, thin nectar-feeding bill of the Purple Honeycreeper *Cyanerpes caeruleus* (Burns, Hackett & Klein, 2002, 2003). These species also exhibit large amounts of plumage variation, from the uniformly brown California Towhee *Melospiza crissalis*, to the multi-colored Paradise Tanager *Tangara chilensis* (see Burns & Shultz, 2012). Emberizoidea occurs in almost all latitudes and across a wide variety of habitats, from the high Arctic (*Plectrophenax nivalis*), to tropical forest (*Lanio versicolor*). While it can be difficult to understand the drivers that are responsible for producing different patterns in niche, the extreme ranges in temperature, elevation and diet suggest this radiation contains diverse adaptations (Pyron *et al.*, 2015). Thus, diversity in ecological niche, together with diversity in morphology, may represent underlying functional diversity, and is likely an indicator of large amounts of genetic diversity throughout Emberizoidea. The unbalanced tree structure suggests variation in diversification rate (Barker *et al.*, 2013), and as a result, some lineages may harbor a large amount of unique evolutionary history. Thus, this clade is not only interesting to study from an evolutionary perspective, but is an important lineage on which to focus conservation prioritizations, particularly in the Americas where it is the dominant lineage of songbird. In this study, we examine the ED of Emberizoidea species and prioritize them for conservation using EDGE values calculated from recently published phylogenies based on genetic data. Additionally, we look for patterns in how threatened species are distributed across the phylogeny to better understand how evolutionary and geographic factors contribute to a species susceptibility to threat.

Materials and methods

Taxon sampling and phylogenetic tree construction

Tree construction (Appendix S1) largely followed Barker *et al.* (2015), except that we used a more recent taxonomy (Clements *et al.*, 2017) to identify species-level taxa appropriate for this study. Sampling followed Clements *et al.* (2017), and we used the IUCN (BirdLife International, 2017) to assign threatened (including extinction) status. Because ED and EDGE values rely in part on a branch length calculation to prioritize taxa, it is important that all taxa are extant, and of the same classification level. Thus, seven taxa (*Atlapetes gutturalis*, *Basileuterus hypoleucus*, *Myiothlypis roraimae*, *Icterus chryscephalus*, *Passerculus rostratus*, *Spizella taverneri* and *Sturnella lilianae*) included in a recent phylogenetic study of Emberizoidea (Barker *et al.*, 2015) that currently rank below the species level by Clements *et al.* (2017) were dropped from the species list. In addition to these subspecific taxa, we also dropped one species, *Quiscalus palustris*, which is currently listed as extinct (BirdLife International, 2017). The Bachman's Warbler *Vermivora bachmanii* also represents a species that is largely thought to

be extinct, although the IUCN does not currently list this species as extinct. The IUCN reports the last unconfirmed sighting occurred in 1988, and last confirmed breeding record occurred in 1937, but maintains its status at Critically Endangered due to unconfirmed records requiring additional investigation (BirdLife International, 2017). To maintain consistency in following the IUCN classifications, we retained this species in our study. These changes resulted in a taxon set of 830 species (Table S1).

Posterior distributions of ultrametric trees have previously been generated for all major crown clades of Emberizoidea (Lovette *et al.*, 2010; Burns *et al.*, 2014; Klicka *et al.*, 2014; Powell *et al.*, 2014; Barker *et al.*, 2015), as well as absolute time-calibrated generic-level backbones of the phylogeny (Barker *et al.*, 2013). These trees are based on two mitochondrial loci (CYTB and ND2), and four nuclear loci (ACO1-I9, FGB-I5, MB-I2 and RAG1), resulting in molecular data for 782 of the 830 species included in this study. The posterior distribution for each crown clade was combined with the backbones to construct a pseudoposterior distribution of supertrees using tree distributions from Barker *et al.* (2015).

Forty-eight species lacked molecular data and were added manually to all trees in the pseudoposterior distribution. When available, we used hypotheses of closest relative from previous studies. The species was then attached randomly to the branch subtending its closest relative or closest sister clade. For 17 species, no information was available for placement (Table S1). Thus, these species were added randomly to the clade containing other members of the genus using the *add.species.to.genus* function of the 'phytools' package in R (Revell, 2012).

Clade assessments: phylogenetic clustering of threatened species

The IUCN (2016) Red List classifies 11 species from Emberizoidea as 'Critically Endangered', 35 as 'Endangered', 50 as 'Vulnerable', 55 as 'Near Threatened' and 678 as 'Least Concern'. We used these data to examine how threatened species are distributed across the phylogeny. Specifically, we used the phylogenetic species variability (PSV) and phylogenetic species clustering (PSC) metrics (Helmus *et al.*, 2007) to test whether threatened species are distributed in a clustered, random, or overdispersed pattern. Both metrics were calculated for the complete phylogeny, as well as each of the six major family-level clades (greater than six species) to examine if the overall pattern differed from finer scale patterns. PSV averages the shared branch lengths of all species pairs contained in a given set of species, to result in an average overall relatedness (Helmus *et al.*, 2007). PSC is a similar metric but is adapted to look specifically at the degree of tip clustering of the species set. The calculation of this metric differs from PSV in that it averages only the maximum relatedness value across all species in the set (Appendix A pg. E79 of Helmus *et al.*, 2007). As a result, PSC only examines the most closely related species to any other given species, and thus can be

thought of as a standardized analog of the Nearest Taxon Index (Webb, 2000). These metrics have been successful in recovering clustered patterns of threat in a recent study of Squamata (Tonini *et al.*, 2016) and are calculated similarly here. Both metrics examine patterns of a set of species across a phylogeny as defined by an unspecified shared neutral trait. Patterns are quantified on a scale from 0 to 1, with 0 representing a species set that is maximally related (clustered), and 1 representing a community that is maximally unrelated (i.e. all species form a polytomy; overdispersed). Threatened species which are distantly related may indicate threat is being driven by geographical overlap, as altered or degraded habitat has the potential to affect distantly related species equally. Threatened species which are more closely related may also indicate geographical overlap (e.g. degraded habitat across a localized radiation), but may also result from a phylogenetically shared trait which is or has become disadvantageous. PSV and PSC were calculated using the 'Picante' package in R (Kembel *et al.*, 2010).

Threat level was treated as a binary trait, with species classified by the IUCN as 'Least Concern' and 'Near Threatened' considered not-threatened, and species classified as 'Vulnerable', 'Endangered' or 'Critically Endangered' considered threatened (IUCN 2016). Fifteen species from Emberizoidea that fall into the threatened category currently lack molecular data. Both PSV and PSC are dependent on the topology of the tree for which the values are being calculated. In order to standardize our values to the topology of the specific tree, we calculated a range of values by randomly selecting 100 different sets of species from within Emberizoidea, and for each family. If the value for the actual set of threatened species fell outside the range of values produced by the random sets, we considered the pattern to differ from what would be expected by random. To incorporate phylogenetic uncertainty, both metrics were calculated across 100 random trees from the pseudoposterior.

Species assessments: ED and EDGE

We calculated distinctiveness values for each species using the ED and EDGE metrics (Isaac *et al.*, 2007). ED is calculated by adding the branch lengths that lead from a tip to the root, with internal branches divided by the number of species subtending it. ED calculations were performed using the *ed.calc* function of the 'caper' package in R (Orme *et al.*, 2013) and were averaged across all trees from the pseudoposterior distribution. ED values were also examined across Red List threat levels to determine if species facing higher levels of threat represent a disproportionate amount of ED. We calculated a standard analysis of variance using average ED grouped by threat level using the 'stats' package in R (R Core Team, 2013).

Globally endangered (GE) values were calculated for all species using the IUCN Red List threat levels (IUCN, 2016), converted as follows: 'Least Concern' = 0, 'Near Threatened' = 1, 'Vulnerable' = 2, 'Endangered' = 3 and 'Critically Endangered' = 4. *Emberiza vincenti*, currently unassessed by the IUCN, was given a GE value of 0. EDGE

values were calculated using ED and GE values with the equation: $EDGE = \ln(1 + ED) + GE \times \ln(2)$ (Isaac *et al.*, 2007).

Results

Taxon sampling and phylogenetic tree construction

Our tree included 830 species and a pseudoposterior distribution of 9595 trees. Because our analyses used largely the same backbone and crown clade tree sets as Barker *et al.* (2015), our maximum clade credibility (MCC) tree (Fig. 1;

constructed using Letunic & Bork, 2016) was highly congruent with the MCC tree of Barker *et al.* (2015) with most differences relating to the randomly added taxa. Thus, details regarding the tree will not be discussed further here.

Phylogenetic clustering of threatened species

Using PSV, threatened species were distributed throughout Emberizoidea in a phylogenetically clustered pattern (PSV = 0.881; Table 1), with the PSV value for the threatened species set falling just below the range of values produced by the random sets of species (0.883–0.888). The

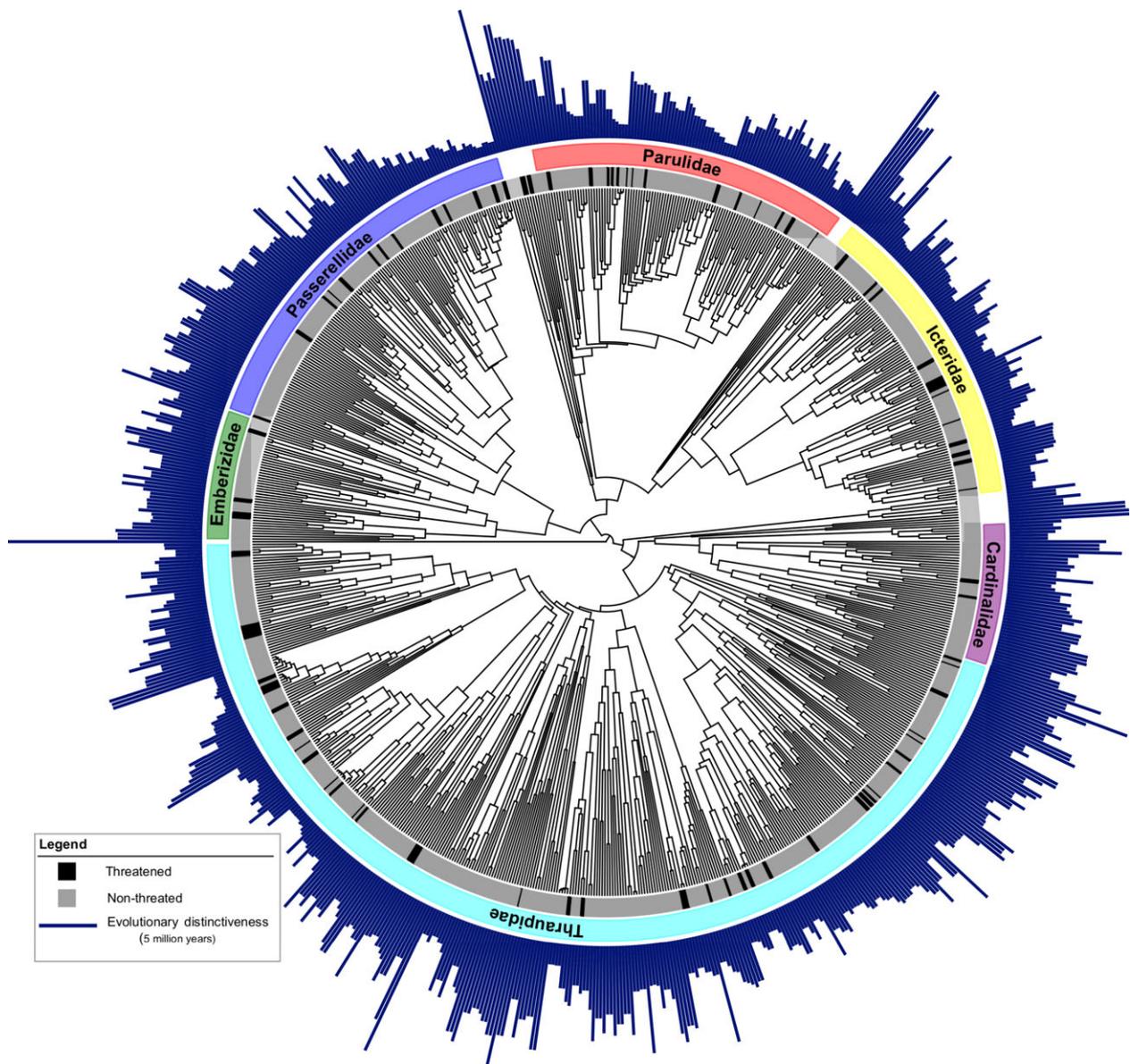


Figure 1 Maximum clade credibility tree of Emberizoidea supertrees. Ring around tips of phylogeny indicate non-threatened (gray) or threatened status (black) according to the IUCN. Blue bars represent evolutionary distinctiveness. The six major families are indicated.

Table 1 Results from the (a) phylogenetic species variability (PSV) and (b) phylogenetic species clustering assessments (PSC) for Emberizoidea as a whole and each of the six major families within Emberizoidea

Clade	Species richness	Number threatened	Empirical	Null	Pattern	Support, %
(a) PSV						
Emberizoidea	830	96	0.881	0.883–0.888	Clustered	86
Cardinalidae	48	2	0.949	0.574–0.913	Overdispersed	99
Emberizidae	44	4	0.889	0.817–0.871	Overdispersed	33
Icteridae	104	14	0.774	0.761–0.801	Random	100
Parulidae	108	14	0.755	0.711–0.752	Overdispersed	93
Passerellidae	127	13	0.768	0.827–0.900	Clustered	100
Thraupidae	373	47	0.927	0.935–0.941	Clustered	100
(b) PSC						
Emberizoidea	830	96	0.3112	0.176–0.349	Random	100
Cardinalidae	48	2	0.9486	0.309–0.738	Overdispersed	100
Emberizidae	44	4	0.6683	0.311–0.659	Overdispersed	48
Icteridae	104	14	0.4344	0.191–0.449	Random	87
Parulidae	108	14	0.4827	0.271–0.494	Random	83
Passerellidae	127	13	0.449	0.253–0.486	Random	100
Thraupidae	373	47	0.3742	0.222–0.457	Random	100

Empirical = value calculated on the maximum clade credibility (MCC) tree for the actual set of threatened species; Null = range of values obtained by calculating PSV and PSC for 100 random sets of species across the Emberizoidea MCC tree; Support = percent of trees sampled from the posterior that produced the same pattern as the MCC tree when comparing the empirical set of threatened species to a null distribution for that specific tree.

PSC value was inside the range of values produced by the sets of random species (0.176–0.349), indicating that threatened species are not likely to be more closely related at the tips of the phylogeny than would be expected by chance alone. Tests across trees from the pseudoposterior supported these results, with 86% of the examined trees exhibiting a clustered pattern for PSV, and 100% exhibiting a random pattern for PSC.

Patterns of clustering among threatened species within families was highly variable (Table 1). Cardinalidae and Emberizidae show threatened species to be overdispersed, though these are the smallest clades, and contain only two and four threatened species respectively. Additionally, values calculated from the Emberizidae posterior indicated strong conflict in threat pattern, with only 33% of trees exhibiting overdispersed PSV and 48% exhibiting overdispersed PSC. This lack of support indicates there may be a large amount of phylogenetic uncertainty underlying the topology of the MCC tree for this family. The four remaining clades all show random PSC, with over 80% of trees from the posterior supporting this pattern for all families; however, these clades differ in their PSV pattern, with Icteridae exhibiting a random pattern, Parulidae exhibiting an overdispersed pattern, and both Passerellidae and Thraupidae showing a clustered pattern. These patterns were all well supported across the sampled posterior.

ED and EDGE

ED values (Table S1) were approximately log-normally distributed with a median of 3.581, ranging from 0.707 (*Sporophila hypochroma*; the least evolutionarily distinct species) to 13.680 (*Rhodinocichla rosea*; the most evolutionarily

distinct species). Large differences in the size of families results in unequal levels of variance; however, ED values were approximately proportional across families with Cardinalidae representing the highest average ED (4.77) of the major families and Parulidae representing the lowest average ED (2.80; Table 2). Nineteen species do not belong to one of the six major families. Instead, current classifications place these into nine smaller families ranging from 1 to 6 species (Barker *et al.*, 2013; Chesser *et al.*, 2017). These 19 species have an average ED of 8.31 and 16 of them are among the top 40 ED species (Table 3). Thus, many of these species contain above average levels of unique evolutionary history, and represent species that diverged early in the radiation with little subsequent diversification. Their high distinctiveness is likely correlated with the previous difficulty placing them in a phylogenetic context.

ED values do not differ significantly by IUCN threat level ($P = 0.199$; Fig. 2), indicating that the most threatened species do not represent a disproportionate amount of ED. Similarly, only five of the top 40 highest ED species are threatened (Table 3). This percentage is approximately equal to the proportion of threatened species across Emberizoidea.

EDGE values (Table S1) were log-normally distributed with a median of 1.617, and ranged from 0.534 (*Sporophila pileata*), to 4.884 (*Conothraupis mesoleuca*). Thus, *C. mesoleuca* represents the most EDGE species within the Emberizoidea lineage. Of the top 40 species (5% of included species; Table 4), 11 are listed by the IUCN as critically endangered, and 23 are listed as endangered. Six species in the top 40 were placed on the tree using taxonomic constraints and lack character-state data (*Conothraupis mesoleuca*, *Nemosia rourei*, *Atlappetes blancae*, *Tangara cabanisi*, *Amaurospiza carrizalensis* and *Basileuterus griseiceps*).

Table 2 Summary of evolutionary distinctiveness (ED) and Evolutionarily Distinct and Globally Endangered (EDGE) values according to family

Family	Species richness	Species percent	Number threatened	Percent threatened	ED sum	ED percent	ED average	Top 40 EDGE
Calcariidae	6	0.72	0	0.00	24.76	0.78	4.13	0
Calyptophilidae	2	0.24	2	1.00	17.84	0.57	8.92	2
Cardinalidae	48	5.78	2	4.17	228.90	7.26	4.77	2
Emberizidae	44	5.30	4	9.09	192.69	6.11	4.38	2
Icteridae	104	12.53	14	13.46	291.90	9.25	2.81	7
Ictariidae	1	0.12	0	0	10.82	0.34	10.82	0
Mitrospingidae	4	0.48	0	0	33.42	1.06	8.35	0
Nesospingidae	1	0.12	0	0	10.40	0.33	10.40	0
Parulidae	108	13.01	14	12.96	302.27	9.58	2.80	4
Passerellidae	127	15.30	13	10.23	428.73	13.59	3.38	4
Phaenicophilidae	4	0.48	0	0	31.20	0.99	7.80	1
Rhodinocichlidae	1	0.12	0	0	13.68	0.43	13.68	0
Spindalidae	4	0.48	0	0	21.56	0.68	5.39	0
Teretistridae	2	0.24	0	0	16.25	0.52	8.12	0
Thraupidae	373	44.94	47	12.60	1518.76	48.15	4.07	18
Zeledoniidae	1	0.12	0	0	10.88	0.34	10.88	0

Similar to ED, all major families contain a percentage of top EDGE species roughly proportional to their size (Table 2). Despite proportionally low total ED and a low average ED, Icteridae contains the highest proportion of species in the top 40 EDGE rankings with seven of its 104 total species. Thraupidae exhibits the next highest proportion with 18 of its 373 total species ranking in the top 40 EDGE.

Discussion

We present here a phylogenetic conservation assessment for a large, widespread radiation representing roughly 17% of all songbirds, and 8% of all birds. This assessment was based on a complete phylogeny with molecular data for almost 95% of taxa and represents the most complete conservation assessment for this group from a phylogenetic perspective.

EDGE values calculated here provide an updated assessment of species rankings for conservation based on distinctiveness and threat. These rankings can be useful as an objective tool for conservation prioritizations. Top priorities based on this metric, *Conothraupis mesoleuca* and *Nemosia rourei*, both occur in regions with high levels of land use change and that have been previously recognized as biodiversity hotspots (Myers *et al.*, 2000). These species both exhibit extremely low population sizes (<250 mature individuals; BirdLife International, 2017) and each underwent long periods lacking confirmed records. *Nemosia rourei* was rediscovered in 1998 (with a probable sighting in 1995) in southern Espírito Santo, Brazil after being unreported for 57 years (Bauer *et al.*, 2000), and *Conothraupis mesoleuca* was rediscovered in 2003 in Goiás, Brazil after 64 years without a confirmed report (Candia-Gallardo, Silveira & Kuniy, 2010). Two species included in this study (*Vermivora bachmanii* and *Leucopeza semperi*) rank among the highest EDGE species (third and fourth respectively), yet are likely extinct. *Vermivora bachmanii* is currently listed as 'Critically Endangered' by the IUCN, but has not been reported since 1988,

and has not had a confirmed breeding record since 1937 (BirdLife International, 2017). *Leucopeza semperi* is also listed as critically endangered, but has no confirmed record since 1961 (BirdLife International, 2017). These species are retained in this study due to small amounts of suitable habitat that remain poorly surveyed, and to maintain consistency with IUCN classifications.

Currently, the Zoological Society of London (ZSL) provides lists of both ED and EDGE values. These values are derived from a calculation of both metrics for all birds from Jetz *et al.* (2014). Massive efforts, such as conservation and distinctiveness studies of all birds, are important steps to initiate conservation actions. However, as new data become available, it is crucial that conservation assessments are updated to reflect our best understanding of current conservation needs. This is especially true for metrics such as ED and EDGE because these metrics operate on the species level. Thus, small changes to either phylogenetic placement, or threat status, have the potential to result in large changes in individual prioritizations. The values calculated in this study are based on phylogenetic estimates using the latest molecular data, and the most recent assessment of threat status, for a large number of passerine birds. Our comparison to current values has focused primarily on the ranking of species relative to each other. A simple correction to these values by rescaling the root of the phylogeny would make them directly comparable to the current values of other related clades. Only with this rescaling would these values be suitable as an update to the ZSL ED and EDGE values for the species of Emberizoidea.

The Emberizoidea radiation has taken place relatively recently in the evolution of birds, with diversification beginning about 20 million years ago. Because of their age, many of these species are less distinct than other birds in the ZSL's top 100 EDGE species. Values for the top 100 EDGE species range from the Plains-wanderer *Pedionomus torquatus* at 6.46, to the Pernambuco Pygmy-owl *Glaucidium*

Table 3 Top 40 highest ranking evolutionary distinctiveness (ED) species

Species	Family	IUCN	ED
<i>Rhodinocichla rosea</i>	Rhodinocichlidae	LC	13.68
<i>Charitospiza eucosma</i>	Thraupidae	NT	11.16
<i>Zeledonia coronata</i>	Zeledoniidae	LC	10.88
<i>Icteria virens</i>	Icteriidae	LC	10.82
<i>Catamblyrhynchus diadema</i>	Thraupidae	LC	10.73
<i>Nesospingus speculariferus</i>	Nesospingidae	LC	10.40
<i>Volatinia jacarina</i>	Thraupidae	LC	9.59
<i>Calyptophilus tertius</i>	Calyptophilidae	VU	8.92
<i>Calyptophilus frugivorus</i>	Calyptophilidae	VU	8.92
<i>Tersina viridis</i>	Thraupidae	LC	8.85
<i>Xanthocephalus xanthocephalus</i>	Icteriidae	LC	8.67
<i>Dolichonyx oryzivorus</i>	Icteriidae	LC	8.52
<i>Mitrospingus cassinii</i>	Mitrospingidae	LC	8.47
<i>Mitrospingus oleagineus</i>	Mitrospingidae	LC	8.47
<i>Cyanicterus cyanicterus</i>	Thraupidae	LC	8.44
<i>Tachyphonus surinamus</i>	Thraupidae	LC	8.33
<i>Cnemoscopus rubrirostris</i>	Thraupidae	LC	8.28
<i>Wetmorethraupis sterrhoapteron</i>	Thraupidae	VU	8.28
<i>Lamprospiza melanoleuca</i>	Mitrospingidae	LC	8.24
<i>Orthogonys chloricterus</i>	Mitrospingidae	LC	8.24
<i>Xenospingus concolor</i>	Thraupidae	NT	8.18
<i>Piezorina cinerea</i>	Thraupidae	LC	8.18
<i>Calochaetes coccineus</i>	Thraupidae	LC	8.17
<i>Teretistris fornsi</i>	Teretistridae	LC	8.12
<i>Teretistris fernandinae</i>	Teretistridae	LC	8.12
<i>Amblycercus holosericeus</i>	Icteriidae	LC	8.01
<i>Sicalis citrina</i>	Thraupidae	LC	7.96
<i>Spiza americana</i>	Cardinalidae	LC	7.91
<i>Xenoligea montana</i>	Phaenicophilidae	VU	7.91
<i>Microligea palustris</i>	Phaenicophilidae	LC	7.91
<i>Rhodospingus cruentus</i>	Thraupidae	LC	7.75
<i>Phrygilus fruticeti</i>	Thraupidae	LC	7.73
<i>Tachyphonus delatrii</i>	Thraupidae	LC	7.72
<i>Oreothraupis arremonops</i>	Passerellidae	VU	7.71
<i>Phaenicophilus poliocephalus</i>	Phaenicophilidae	NT	7.69
<i>Phaenicophilus palmarum</i>	Phaenicophilidae	LC	7.69
<i>Xenodacnis parina</i>	Thraupidae	LC	7.69
<i>Chlorophanes spiza</i>	Thraupidae	LC	7.67
<i>Iridophanes pulcherrimus</i>	Thraupidae	LC	7.67
<i>Orchesticus abeillei</i>	Thraupidae	NT	7.66

LC, least concern; NT, near threatened; VU, vulnerable.

mooreorum at 4.88 (Zoological Society of London, 2018). While many are lower, some scores within Emberizoidea, such as *Conothraupis mesoleuca* (4.88) approach the scores of the top 100 EDGE species, and suggest the incorporation of these values can have an impact on conservation actions. A scatterplot of the current and newly calculated values for species in this study (Fig. 3) shows a lack of a tight correlation and identifies several taxa with major changes in priority. Four species are not found in the 99th percentile of both EDGE lists (Fig. 3a). Two species, *Gubernatrix cristata*, and *Poospiza rubecula*, occur in the 99th percentile of our values, but are not present in the same percentile of the current values. Additionally, *Icterus oberi* and *Catharopeza bishopi*

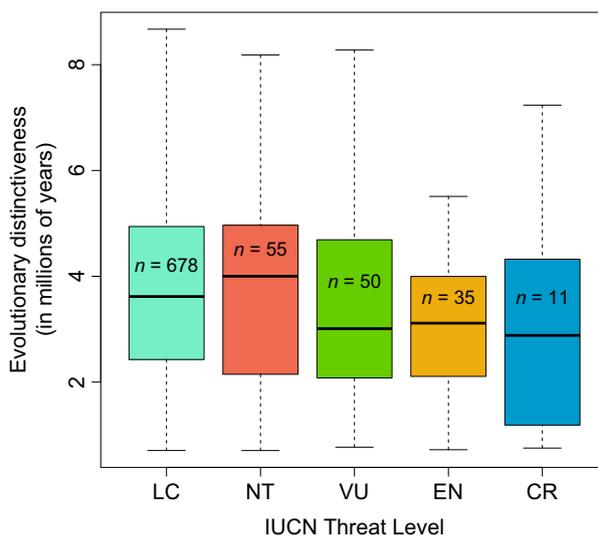


Figure 2 Boxplot of evolutionary distinctiveness in millions of years grouped by IUCN threat level category. Category abbreviations correspond to LC, least concern; NT, near threatened; VU, vulnerable; EN, endangered and CR, critically endangered. Numbers inside the boxes indicate number of species in that category.

are placed in the 99th percentile of the current list of values, but do not occur in the same percentile of the values we have calculated here. Using the same approach, 12 species are identified as having noticeable changes in ED value (Fig. 3b). *Rhodinocichla rosea*, *Charitospiza eucosma*, *Nesospingus speculariferus*, *Volatinia jacarina*, *Calyptophilus tertius* and *Calyptophilus frugivorus* all place in the 99th percentile of ED values calculated here, but not in the current values, and *Rhynchophanes mccownii*, *Calcarius lapponicus*, *Parkerthraustes humeralis*, *Xenoligea montana*, *Spiza americana* and *Microligea palustris* place in the 99th percentile of the current values, but not those calculated here. Therefore, we found important differences between the two lists, with our results providing improved, updated values.

Threatened species in the Emberizoidea radiation show a weak signal of phylogenetic clustering, as indicated by PSV. While this indicates that, on average, some groups of threatened species are closely related, PSC results suggest this pattern retained some degree of randomness within these clusters. Thus, threatened species may be closely related to other threatened species, but are not more likely to be each other's closest relative. Additionally, the amount of deviation of the empirical values from the null distribution of values was typically low, indicating the signal for these patterns was likely weak. Obtaining a clustered pattern in only the larger clades likely indicates that the overdispersed pattern seen in some of the families may be an artifact of small clade size, or few threatened species. This results in high variance across trees from the posterior, and a large range of values in the null distribution.

While PSV results suggest low levels of clustering, the random pattern in tip clustering recovered from the PSC

Table 4 Top 40 highest ranking Evolutionarily Distinct and Globally Endangered (EDGE) species

Species	Family	IUCN	EDGE
<i>Conothraupis mesoleuca</i>	Thraupidae	CR	4.88
<i>Nemosia rourei</i>	Thraupidae	CR	4.78
<i>Vermivora bachmanii</i>	Parulidae	CR	4.48
<i>Leucopeza semperi</i>	Parulidae	CR	4.40
<i>Amaurospiza carrizalensis</i>	Cardinalidae	CR	4.25
<i>Gubernatrix cristata</i>	Thraupidae	EN	4.16
<i>Rowettia goughensis</i>	Thraupidae	CR	4.13
<i>Poospiza rubecula</i>	Thraupidae	EN	3.95
<i>Nesopsar nigerrimus</i>	Icteridae	EN	3.95
<i>Torreornis inexpectata</i>	Passerellidae	EN	3.93
<i>Cnemathraupis aureodorsalis</i>	Thraupidae	EN	3.93
<i>Icterus oberi</i>	Icteridae	CR	3.85
<i>Catharopeza bishopi</i>	Parulidae	EN	3.83
<i>Habia atrimaxillaris</i>	Cardinalidae	EN	3.80
<i>Emberiza jankowskii</i>	Emberizidae	EN	3.79
<i>Anumara forbesi</i>	Icteridae	EN	3.69
<i>Emberiza aureola</i>	Emberizidae	EN	3.68
<i>Calyptophilus tertius</i>	Calyptophilidae	VU	3.68
<i>Calyptophilus frugivorus</i>	Calyptophilidae	VU	3.68
<i>Icterus northropi</i>	Icteridae	CR	3.68
<i>Tangara cabanisi</i>	Thraupidae	EN	3.66
<i>Xenospiza baileyi</i>	Passerellidae	EN	3.65
<i>Wetmorethraupis sterrhopteron</i>	Thraupidae	VU	3.61
<i>Agelaius tricolor</i>	Icteridae	EN	3.60
<i>Spizella wortheni</i>	Passerellidae	EN	3.59
<i>Melanospiza richardsoni</i>	Thraupidae	EN	3.58
<i>Xenoligea montana</i>	Phaenicophilidae	VU	3.57
<i>Bangsia aureocincta</i>	Thraupidae	EN	3.57
<i>Oreothraupis arremonops</i>	Passerellidae	VU	3.55
<i>Coryphaspsiza melanotis</i>	Thraupidae	VU	3.53
<i>Diglossa venezuelensis</i>	Thraupidae	EN	3.50
<i>Compsospiza garleppi</i>	Thraupidae	EN	3.49
<i>Poospiza alticola</i>	Thraupidae	EN	3.47
<i>Macroagelaius subalaris</i>	Icteridae	EN	3.44
<i>Diglossa gloriosissima</i>	Thraupidae	EN	3.43
<i>Camarhynchus heliobates</i>	Thraupidae	CR	3.42
<i>Buthraupis wetmorei</i>	Thraupidae	VU	3.41
<i>Basileuterus griseiceps</i>	Parulidae	EN	3.39
<i>Camarhynchus pauper</i>	Thraupidae	CR	3.35
<i>Agelaius xanthomus</i>	Icteridae	EN	3.34

VU, vulnerable; EN, endangered; CR, critically endangered.

results indicates this pattern is not likely due to a disadvantageous trait imparted by shared ancestry. Instead, it appears this signal is the result of localized radiations in areas now facing high levels of disturbance and habitat alterations. Threatened lineages represent many different localities, including regions throughout all of the Americas, as well as multiple Old World localities (*Emberiza* spp.). One example is the *Sporophila* seedeaters, with six closely related species (*S. palustris*, *S. cinnamomea*, *S. falcirostris*, *S. frontalis*, *S. maximiliana* and *S. nigrorufa*) currently elevated in threat status. These six species are distributed in close geographic proximity throughout south-central and south-eastern Brazil. It is unsurprising these species are all faced with elevated

threat levels, as this region is known to be highly disturbed (see da Fonseca, 1985) and is often a highly ranked biodiversity hotspot (Myers *et al.*, 2000).

Another prevalent pattern among threatened species of Emberizoidea is island endemism, with 20 of the threatened species occurring as island endemics (out of 71 total island endemics in the radiation). Similar to *Sporophila* seedeaters, some radiations have resulted in phylogenetic clusters of threatened species due to speciation across islands. Island populations are often considered more susceptible to the effects that lead to endangerment (e.g. stochastic effects on small populations; Pimm, 1991) and this is likely the case for some species clusters throughout Emberizoidea, such as species in the genera *Icterus* and *Camarhynchus*. *Camarhynchus* is perhaps the best example of an island endemic radiation leading to clustering of threatened species. This group, along with the closely related taxon *Pinaroloxias inornata*, represents a radiation across the Cocos and Galápagos Islands, with five species listed as threatened (*Camarhynchus heliobates*, *C. pauper*, *C. pallidus*, *C. psittacula* and *Pinaroloxias inornata*). Like many others, these island species face threats resulting from introduced species and human impact (Dvorak *et al.*, 2012). Recently, the dipteran nest parasite *Philornis downsi* has become a serious threat to Galápagos species, with up to 76% nestling mortality attributed to its presence (Fessl, Sinclair & Kleindorfer, 2006). Overall, the patterns of threat clustered across localized radiations is consistent with expectation from our clustering analysis and suggests many closely related species may be facing high levels of threat due to co-occurrence in degraded and impacted habitats.

Consistent with previous studies, ED values for Emberizoidea show no difference across threat level categories, indicating that, when compared with more phylogenetically similar lineages, unique lineages are not more susceptible to population declines from potential impacts. The slight clustering pattern recovered for Emberizoidea is consistent with a previous calculation of dispersion for all 'Endangered' and 'Critically Endangered' birds (Jetz *et al.*, 2014). Jetz *et al.* (2014) measured dispersion by calculating a *D* metric in which values near one represent randomness, values below one represent clustering, and values above one represent overdispersion. They report a value of $D = 0.887$, indicating very low levels of clustering, potentially approaching a pattern of randomness, similar to the pattern reported here.

The incorporation of ED into the EDGE metric is beneficial for numerous reasons, including its ability to incorporate a taxon's unique evolutionary history, its potential as a proxy for functional diversity (Cadotte *et al.*, 2012) and as an informative measure of biodiversity more generally (Rosauer & Mooers, 2013). However, these metrics can be sensitive to changes in taxonomy. One of the biggest potential challenges in the conservation of this radiation is unrecognized diversity, especially in lesser studied species or regions of the Neotropics. As additional phylogeographic and population genetic studies investigate these areas, it is likely new species will be described, and existing taxa will be split. Until the most recent assessment, numerous species

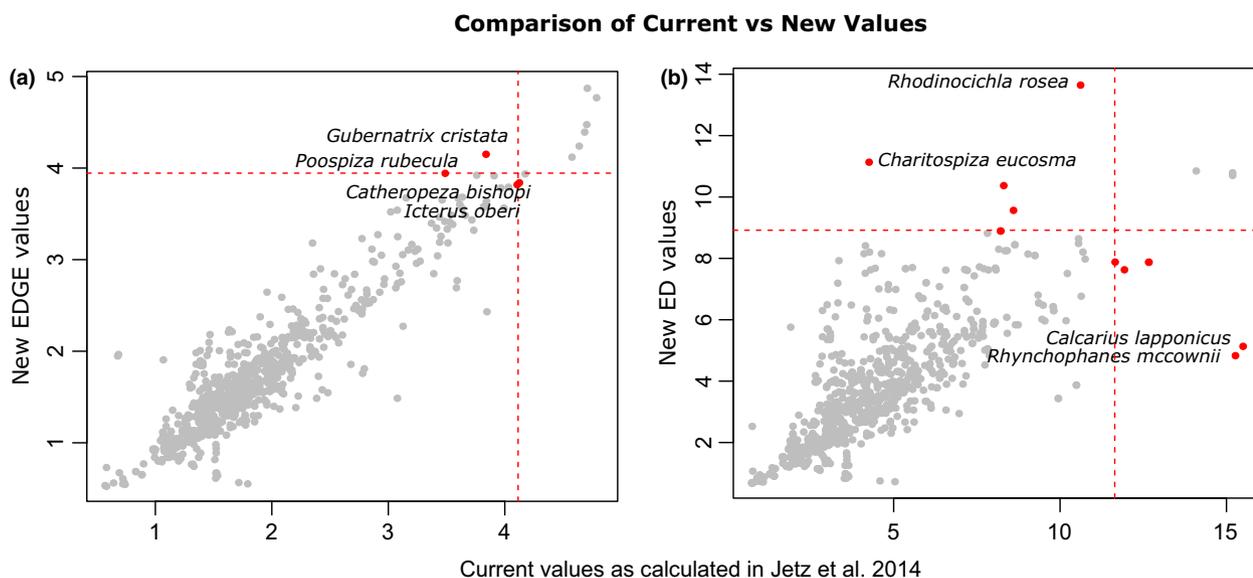


Figure 3 Comparison of previously calculated values to those calculated in this study for (a) Evolutionarily Distinct and Globally Endangered (EDGE) values, and (b) evolutionary distinctiveness (ED) values. Dashed red lines indicate the 99th percentile cutoffs. Red points indicate species that fall above this cutoff in one list of values, but below the cutoff in the other list of values. The names of the largest outliers have been included.

from this radiation lacked a Red List assessment due to unrecognized splits. One species that ranks highly in ED but previously lacked a threat status is the Western Chat-Tanager *Calyptophilus tertius*. This species ranks 8th in average ED with a value of 8.9, and is one of only two species in the family Calyptophilidae (Chesser *et al.*, 2017). The most recent IUCN assessment classified this species as ‘Vulnerable’ (BirdLife International, 2017). Due to its high-ranking ED value, changing the status from unassessed to threatened moves this species from the 120th ranked EDGE species to 18th. This exemplifies the large impact taxonomy can have on these rankings. Future taxonomic changes that result in splitting high ED species may have similar impacts as those on *C. tertius*, if the split results in a drastic change in extinction probability (e.g. smaller population size, range restrictedness; Rimmer *et al.*, 2005).

Emberizoidea represents a speciose and diverse radiation of songbirds that harbors a large amount of phylogenetic diversity and potential for functional diversity. EDGE values presented here help to guide further conservation efforts by prioritizing distinct species that are currently threatened with extinction. Additionally, threatened species within this radiation show low levels of phylogenetic clustering, and may be the result of localized radiations. Future research should conduct fine scale geographic analyses to thoroughly examine these patterns and highlight areas of co-occurrence across a large number of species. Because threatened species may be closely related to one another, habitat degradation and human impact on a single area has the potential to affect multiple species from the same clade. Therefore, further research into modeling different extinction scenarios may be able to test various conservation strategies by incorporating shared geography into measures of phylogenetics and

distinctiveness. These assessments, combined with the ones calculated here, will help provide the objective and comprehensive measures that are needed to ensure the persistence of biodiversity in increasingly threatened environments.

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Supporting information

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

Table S1. List of species included in this study, including name, family, threat classification, ED value, and EDGE value.

Appendix S1. Supplemental methods.