

Evolutionary Distinctiveness, Threat Status, and Ecological Oddity in Primates

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Abstract: *The EDGE (evolutionarily distinct and globally endangered) conservation program (www.edgeofexistence.org) uses a composite measure of threat and phylogenetic isolation to rank species for conservation attention. Using primates as a test case, we examined how species that rank highly with this metric represent the collective from which they are drawn. We considered the ecological and morphological traits, including body mass, diet, terrestriality, and home range size, of all 233 species of primates. Overall, EDGE score and the level of deviance from the mean of 20 different ecological, reproductive, and morphological variables were correlated (mean correlation $r = 0.14$, combined $p = 1.7 \times 10^{-14}$). Although primates with a high EDGE score had characteristics that made them seem odd, they did not seem to express more ancestral characteristics than expected. Sets of primate species with high EDGE scores will, therefore, collectively capture a broader than expected range of the biology of the clade. If similar patterns hold in other groups, the EDGE metric may be useful for prioritizing biodiversity for conservation.*

Keywords: conservation priorities, phylogenetic isolation, triage

Singularidad Evolutiva, Estatus de Amenaza y Rareza Ecológica en Primates

Resumen: *El programa de conservación EDGE (evolutivamente distinto y globalmente en peligro) (www.edgeofexistence.org) utiliza una medida compuesta de la amenaza y el aislamiento genético para clasificar especies para atención de la conservación. Utilizando primates como un estudio de caso, examinamos cómo representan especies que tienen alto valor con esta medida al colectivo de donde son tomadas. Consideramos características ecológicas y morfológicas, incluyendo masa corporal, dieta, terrestrialidad y extensión del rango de hogar, de las 233 especies de primates. En general, el valor EDGE y el nivel de desviación de la media de 20 variables ecológicas, reproductivas y morfológicas estaban correlacionadas (correlación promedio $r = 0.14$, p combinada = 1.7×10^{-14}). Aunque los primates con un valor EDGE alto tenían características que los hacían ver raros, no parecieron expresar más características ancestrales que lo esperado. Por lo tanto, los conjuntos de primates con valores EDGE altos colectivamente capturan un rango de la biología del clado más amplio que el esperado. Si se mantienen patrones similares en otros grupos, la medida EDGE puede ser útil para la priorización de la conservación de la biodiversidad.*

Palabras Clave: aislamiento filogenético, prioridades de conservación, triaje

Introduction

If this is the era of conservation triage (Marris 2007; Bottril et al. 2008; Joseph et al. 2009), then threatened species must be differentiated from each other so that the most important species can be attended to first. Attending to species on the basis of threat status is inefficient

and risks “unnecessary extinctions” (Joseph et al. 2009). Therefore, a prioritization system is needed that can objectively assign values to species. The London Zoological Society’s EDGE program (evolutionarily distinct and globally endangered) (Redding & Mooers 2006; Isaac et al. 2007) offers such a system. The program ranks species on the basis of their global threat status, taken directly

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from the International Union for Conservation of Nature (IUCN) Red List rankings (Mace & Lande 1991), and their evolutionary isolation to prioritize “those species that are both endangered and evolutionarily distinctive” (www.edgeofexistence.org).

The EDGE approach is comparable to the project prioritization protocol (Joseph et al. 2009), which uses a greedy algorithm to objectively select the optimal group of species that minimizes potential future extinctions within a fixed budget and maximizes taxonomic uniqueness if every selected species is conserved. The EDGE-listing procedure differs from the project-prioritization protocol because it is a two-stage procedure. First, a single, ranked EDGE list is published and those species that are receiving the least amount of attention from current conservation initiatives are selected as “focal species” (Isaac et al. 2007). Second, funds gathered primarily from private sources are allocated preferentially to these focal species, with the number of species allocated resources depending on the amount of funds gathered. The current EDGE process includes objective and subjective aspects; thus, it can be flexible to changes in the threat status of focal species.

The measure of evolutionary isolation in the EDGE score, evolutionary distinctiveness (ED), is one of a family of such measures (e.g., Vane-Wright et al. 1991; Crozier 1992; reviews in Pavoine et al. 2005; Redding et al. 2008). By assessing one clade at a time (e.g., order Primata), we used EDGE measures to preferentially rank those species within that clade that have fewer or more distant relatives. High-ranked species are candidates for higher conservation priority because they have potentially more unique genetic information (Redding & Mooers 2006), but they also have fewer close relatives and therefore less redundancy in the genetic information they contain.

Some suggest that species with high EDGE scores stand out as being unusual with respect to the other species in their clade (for a list of examples, see Supporting Information). For example, the platypus (*Ornithorhynchus anatinus*) has a high EDGE score and is very unusual. The platypus is an egg-laying, teatless, cold-blooded (32 °C) animal with poisonous spurs and a remarkable genome (Warren et al. 2008). It is part of a small clade (it and four species of echidna) that is the sister group to all (roughly 5400) other species of mammals. Although it seems justifiable to consider the platypus as an irreplaceable component of biodiversity, it is unknown whether it is representative of species with high EDGE scores.

If species with high EDGE scores are generally odd, where we define *odd* as absolute distance from the average phenotype (or in the case of categorical data, species that populate categories with few members), then a selection of species with the highest EDGE scores should represent a disproportionately broad set of biological characteristics from the overall group. Given that they are all

threatened, their imminent extinction would therefore result in a large loss of character diversity.

Character diversity itself is a valid measure of biodiversity (Faith 1992; Purvis & Hector 2000). Nevertheless, if evolutionarily distinct species have odd morphologies and such odd morphologies are associated with rare ecological roles, then groups of species with high EDGE scores may have increased functional importance (for related work with communities see Cadotte et al. 2008, 2009). From another perspective, if evolutionarily distinct species express predominantly relictual characters, then Erwin’s (1991) contention that species isolated on the tree of life are relictual is true and such species may therefore offer little to future evolutionary potential.

We first tested, solely within primates, for an overall correlation between EDGE score and biological oddness, as well as the correlations between EDGE’s two components (distinctiveness and endangerment) and oddness. We then determined whether the traits represented when choosing threatened and evolutionarily isolated species were likely to resemble those traits attributed to ancestral primates (i.e., whether the most threatened evolutionarily distinctive species were generally relicts).

Methods

From a variety of sources, we collected as much physical, ecological, and reproductive data as possible on the world’s 233 primate species (Wilson & Reeder 1993) (see Supporting Information for variables and references). We used this older taxonomy because it was used to create the EDGE list, although more-recent taxonomies include many more species (e.g., Groves 2001 [350 species]; Rylands & Mittermeier 2009 [424 species]). For each data point (e.g., adult male body mass for *Gorilla gorilla*), if there was more than one source the mean of the values was used. From approximately 85 data variables, those with <50% coverage of species or over 70% correlation with any other variable were removed, leaving 20 variables that we treated as independent in the final data set. For correlations, the variable with the highest average correlation coefficients over all other variables was the one removed. Finally, we discarded species that had no EDGE score (Isaac et al. 2007) (i.e., they were “data deficient” according to the IUCN Red List [IUCN 2009]), which left 217 species in our final data set.

For the 15 continuous variables, we transformed scales to remove the effect of outliers (e.g., by log transformation) and then calculated the absolute distance of each species’ score to the median score for that variable (Fig. 1a). For each of the five categorical variables, the value assigned to a species was the frequency of that category in the entire data set. So, for example, if we had a categorical data variable “coat color” that contained 100

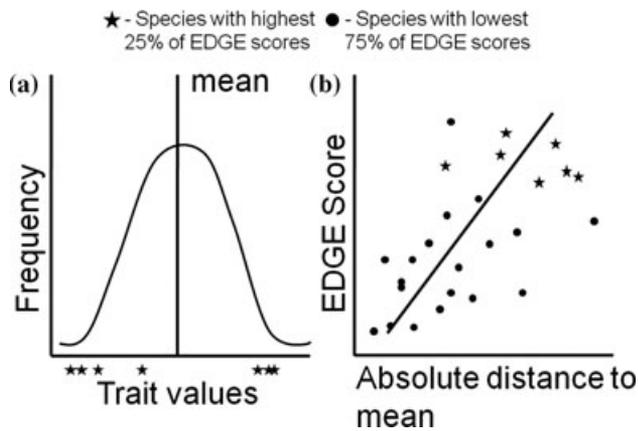


Figure 1. The relative position of species with high EDGE (evolutionarily distinct, globally endangered) scores. A high score within the distribution of species' values for a particular trait (e.g., body mass) can lead to a positive relationship between EDGE score and trait oddness. If species with high scores (star) tend to be far from a trait's average score, as shown in (a), and if species with lower EDGE scores (solid circles) tend to have a trait value nearer the mean, how unusual or infrequent a species value is for the given trait will be positively related to its EDGE score (b). The data points are illustrative and not part of the data set.

species, and 75 species had brown coats and 25 had black coats, the brown primates would all be given a value of 75 for that category, representing the frequency of brown coats across the data set, and, similarly, the black-coated species would be given a value of 25.

We then tested for a correlation (using `cor.test`; "base" package in R language) for each of the 20 variables between our statistical approximations of oddness and each species' EDGE score (Fig. 1b). A negative correlation coefficient for categorical data variables indicated a positive relationship between oddness and EDGE score. Because our correlations do not correct for phylogenetic relationships among the tips, the p values we report should not be seen as tests of the general hypothesis across other clades. Also, because we repeated the same test over 20 variables, the p value for a single test does not provide a valid probability of committing a type I (false-positive) error. Therefore, we used the false discovery rate to adjust the p values so they would take this into account (`p.adjust`; "stats" package in the R language; Benjamini & Hochberg 1995). This procedure accounted for the number of false-positive hypotheses that would be accepted with raw p values, given a predefined significance (α) value (in this case 0.05). This procedure ranked all the observed p values from each test and, working from the largest value down, accepted the null hypothesis only for those tests where $p \geq k \times \alpha/n$, where k is the rank of

the p value, α is the chosen level of significance, and n is the number of p values considered (García 2004).

To estimate the relationship between oddness and EDGE score over all 20 variables, we calculated the mean correlation coefficient and a combined p value with the Stouffer method (Whitlock 2005), which weighed the input values from each of the 20 independent tests on the basis of their sample size to give greater weight to correlations with more data points (Hunter & Schmidt 2004). Finally, we repeated all the analyses with the infraorder Lemuriformes removed to ensure the relationship was not entirely driven by this geographically peripheral, endemic clade (Spathelf & Waite 2007).

To assess whether traits represented by species with high EDGE scores were more likely to be ancestral, we attributed values for seven of the 20 variables to two hypothesized ancestral species (*Dryomomys szalayi* and *Ignacius clarkforkensis*) on the basis of recent fossil finds (Bloch et al. 2007). These species are members of the Plesiadapiformes, which are thought to be "stem primates" and thus to express characteristics that we expected to be exhibited by the ancestor to modern-day primates (Bloch et al. 2007). The seven traits were the variables that could be reasonably inferred from the fossil record: diet (from teeth shape), mass, length-to-mass ratio, tail-to-body length ratio, diurnality, terrestriality (mostly arboreal or mostly terrestrial), and habitat (forest or savannah-scrub). We scored a species as ancestral if it was placed in the same category (e.g., diet) as the ancestral species or, for continuous variables, if it was in the closest 15% of species when all species, including the ancestral ones, were placed in rank order by that variable. To test the sensitivity of this 15% value, we repeated the procedure three more times, coding the closest 5%, 10%, and then 20% of species in rank order as ancestral for the continuous variables. We then tested for a correlation (using `cor.test`; "base" package in the R language) between each species' ancestral score (ranging from 0, no ancestral traits, to 7, all traits ancestral) and its EDGE score.

Results

Overall, primate species' EDGE scores were positively related to trait oddness in 18 of the 20 variables and were significantly positively related to oddness for half of them (10 out of 20; Table 1). When all 20 tests were combined, the global result was a highly significant positive correlation (mean correlation = 0.14, $p = 1.74 \times 10^{-14}$). The mean correlation of only the variables with significant, adjusted p values was more strongly positive (mean $r = 0.36$). Lemuriformes did not drive this relationship because the patterns seen were very similar when they were removed (Table 1; combined $p = 4.3 \times 10^{-13}$).

Table 1. Pearson correlations (ρ) of the EDGE (evolutionarily distinct, globally endangered) scores for primate species and distance of species-specific traits from the average for the order.

Group ^a	Variable ^b	df	EDGE		
			ρ	p ^c	p ^d
M	female mass	216	0.158	0.039	0.051
M	tail length—body residuals	217	−0.007	0.918	0.762
M	body length—mass residuals	217	0.163	0.035	0.051
M	maximum age	146	0.068	0.552	0.327
M	sexual weight dimorphism	200	0.054	0.560	0.167
G	geographic range size	217	0.248	0.001	0.003
G	latitudinal midpoint	211	0.257	0.001	0.003
G	distance to continental centroid	217	0.347	0.000	0.003
BE	population density	143	0.293	0.001	0.025
BE	home range size	160	0.153	0.093	0.045
BE	group size	146	0.187	0.035	0.067
BE	solitariness	163	−0.230	0.011	0.000
BE	activity period	217	−0.188	0.015	0.051
BE	terrestriality	182	−0.102	0.282	0.051
BE	habitat	200	0.087	0.318	0.572
BE	diet class	217	−0.041	0.645	0.760
R	gestation duration	212	0.291	0.000	0.000
R	litter size	217	0.083	0.318	0.268
R	mating system	137	0.028	0.830	0.754
R	no. of males in group	174	0.014	0.895	0.754

^aAbbreviations: G, geographical traits; BE, behavioral and ecological traits; M, morphological traits; R, reproductive traits.

^bVariables described in Supporting Information (Appendix S2).

^cCorrected for multiple testing with the false discovery rate (Benjamini & Hochberg 1995).

^dCorrected value with Lemuriformes excluded.

Geographical traits were most significant (100%) and were followed in decreasing order by behavioral and ecological (50%), morphological (40%), and reproductive traits (25%) (Table 1).

Primate species with high EDGE scores did not appear to be more likely to express ancestral characters than low-scoring species because there was no relationship between the ancestral character score and EDGE score (Pearson product correlation coefficient $r = -0.003$, $n = 217$, $p = 0.96$). Using other cutoffs (5%, 10%, 15%, and 20%) to categorize species for the continuous variables as ancestral or not produced similar results (range of p values: 0.92–0.98).

When analyzing ED (evolutionary distinctiveness) and GE (threat) separately, for 13 of 20 variables oddness was significantly correlated to ED (mean correlation = 0.13, combined $p = 3.13 \times 10^{-27}$), whereas oddness was significantly correlated to GE for only three of the 20 variables (Table 2). There was a noticeably lower mean correlation coefficient for GE as well (mean correlation = 0.07), although the combined p value was still strongly significant ($p = 1.79 \times 10^{-7}$).

Discussion

For a large proportion of the traits we examined, we found a positive relationship between a primate species'

EDGE score and how far it is from the average morphological and ecological phenotype. Therefore, our approach to conservation evaluation prioritized a sample of the most evolutionarily isolated and threatened primates for conservation attention and captured a larger-than-expected proportion of the total ecological and phenotypic variation in the clade.

Our approach would have proven undesirable if, by choosing primate species with high EDGE scores, it had preferentially selected relictual species, at least if we accept that “ancestral” species might be less likely to contribute to future evolutionary radiations (Erwin 1991). If species with high EDGE scores harbor remnant ancestral characteristics, they may still be unusual compared with the rest of the clade. We found no strong tendency for species with high EDGE scores to have “ancestral” characteristics, which suggests they possess both rare and derived characters. There is no evidence yet, therefore, that these species are less likely to contribute to the future ecological landscape.

It is logical to ask how the two components of EDGE interact to produce the positive relationships we report here. As ED and GE are not correlated in primates (ED to GE correlation; Pearson's rho = 0.001, $n = 219$, $p = 0.89$), one might expect that for each of the traits we used in our analysis either ED or GE would drive the correlation with overall EDGE score. This proposition appears to hold generally (Table 2). Considering only the 10 traits that were significantly and positively correlated to EDGE, the

Table 2. Pearson correlations (ρ) of evolutionary distinctiveness (ED) scores (1, most threatened; 5, least threatened) and membership in IUCN (International Union for Conservation of Nature) threat categories (GE) for primate species, and distance from the average for the order.

Group ^a	Variable ^b	df	ED		GE	
			ρ	p ^c	ρ	p ^c
M	female mass	216	0.27	0.000	-0.01	0.957
M	tail length—body residuals	217	-0.05	0.554	0.05	0.642
M	body length—mass residuals	217	0.03	0.821	0.21	0.012
M	maximum age	146	0.12	0.195	-0.01	0.957
M	sexual weight dimorphism	200	-0.16	0.049	0.12	0.136
G	geographic range size	217	0.02	0.821	0.28	0.000
G	latitudinal midpoint	211	0.15	0.049	0.16	0.070
G	distance to continental centroid	217	0.17	0.040	0.32	0.000
BE	population density	143	0.19	0.049	0.20	0.070
BE	home range size	160	0.17	0.049	0.05	0.642
BE	group size	146	0.27	0.002	0.05	0.642
BE	solitariness	163	-0.62	0.000	0.10	0.330
BE	activity period	217	-0.72	0.000	0.15	0.074
BE	terrestriality	182	0.15	0.068	-0.14	0.126
BE	habitat	200	0.00	0.960	0.13	0.126
BE	diet class	217	-0.06	0.533	0.00	0.986
R	gestation duration	212	0.34	0.000	0.14	0.107
R	litter size	217	0.01	0.918	0.12	0.136
R	mating system	137	0.20	0.049	-0.05	0.642
R	no. of males in group	174	0.17	0.049	-0.05	0.642

^aAbbreviations: G, geographical traits; BE, behavioral and ecological traits; M, morphological traits; R, reproductive traits.

^bVariables described in Supporting Information (Appendix S2).

^cCorrected for multiple testing with the false discovery rate (Benjamini & Hochberg 1995).

ED score drove the relationship between trait oddness and EDGE score for seven traits: female mass, group size, latitudinal midpoint, gestation duration, activity period, population density, and solitariness. This relationship between trait oddness and ED is consistent with results from a few studies that show species in smaller taxonomic groups—compared with more species-rich groups at same taxonomic level—are found on the edge of multidimensional ecological and morphological space (Latiolais et al. 2006; Ricklefs 2006; Magnuson-Ford et al. 2009).

Threat status by itself was correlated with just two of the same 10 traits: geographic range and body shape (defined here as the residuals of a body mass - body length regression). Geographic range size is relatively straightforward to interpret. Small-range species are listed as threatened on the basis of their range size (Mace & Lande 1991), whereas species with large ranges are more likely to be affected by human encroachment (Blackburn & Gaston 2002; Cardillo et al. 2005). As for the latter correlation, we can think of no obvious mechanism that explains why primates with odd weight-to-size ratio (i.e., long with low mass or short with high mass) were at a higher risk of extinction. Particular body shapes could be associated with habitats (e.g., tall primary forests) that are more affected by human activities, but this remains to be tested.

“Distance to center of continent” was significantly related to both threat status and evolutionary isolation: species that were more threatened or that had fewer close relatives tended to be geographically peripheral. Although vertebrate threat status is unevenly distributed

globally (Grenyer et al. 2006), our results are the first to suggest that in some clades it may also be distributed toward a more-encompassing clade’s range edge. Potentially, the positive correlation between threat and distance to the center of the clade’s range is explained by preferential human development on coastlines. This relationship also may be affected by the observations that geographic range size gets smaller toward continental edges (e.g., Gaston 2003) and that smaller-range species are more likely to be listed as threatened (Mace & Lande 1991). Primates with high EDGE scores were also more likely to be found on the geographical edge of the continent on which they occur. Ricklefs (2005) suggests that such peripheral, evolutionarily isolated patterns may hold for passerine birds as well. This variable could act as a mechanism to drive some of the relationships we saw between EDGE score and the traits we tested in primates. If primate groups with higher average scores of evolutionary distinctiveness are geographically peripheral compared with their encompassing continental clades (e.g., macaques in Africa and tarsiers in Southeast Asia), they may also have developed unusual traits to survive and reproduce in habitats and seasonal regimes that are rare for the group as a whole.

The patterns we discovered need to be tested in other groups (Magnuson-Ford et al. 2009). Primates are somewhat restricted geographically and in their use of habitat (i.e., they are dominated by dwellers of tropical forests). These factors make it difficult to generalize all our findings to other mammal groups. For instance, we do not

know if clades with pole-to-pole latitudinal distributions will have the same relationship between ED score and distance to the center of the continent. We can think of no obvious reason, however, why the evolution of traits in primate species should be different overall from those of any other mammal group.

All geographic variables were significantly related to EDGE score, whereas only one of the reproductive traits was. This result was unexpected because reproductive traits often map well on to species phylogenies, whereas geographical traits do not (e.g., Gaston 2003). Nevertheless, whether or not a trait is strongly heritable is irrelevant to whether isolated species have unusual characteristics. Even with a perfectly inherited trait, the most unusual traits could be common to all the members of a small clade within a “bushy” (and therefore low-ED-scoring) part of the candidate tree.

The consensus for the variables we studied is that primate species on long branches are morphologically, ecologically, and behaviorally different from those on short ones. This finding, if found in subsequent analyses of other groups, may provide support for the suggestion that phylogenetic branch lengths can approximate gross phenotypic differences among species (Faith 1992, 2002). The frequency with which such a relationship is detected in other taxa depends on how well the topology of phylogenetic trees reflect the true evolutionary relationships among species and, more generally, whether branch lengths measured as the expected number of base substitutions within many different (often mitochondrial) genes all correlate similarly to the phenotypic differences among species. A strong and consistent relationship would be useful from a conservation perspective, potentially allowing maximization of the gross phenotypic diversity among a set of species.

Sets of primates that have high ED scores not only represent more biological diversity (the present study), but also represent a greater-than-expected proportion of the tree from which they are sampled (Redding et al. 2008). That is, as a collective, such species embody both higher-than-expected phylogenetic (Faith 1992) and ecological diversity. These two findings are interesting in light of a proposed “ideal” framework for conservation-evaluation ranking that includes a measure of phylogenetic (taxon by taxon), evolutionary (future evolutionary potential), and ecological (present-day ecosystem function) importance (Bowen 1999; Bowen & Roman 2005).

Bowen suggests that these three perspectives may often be in conflict. If, however, species with high evolutionary distinctiveness scores (Bowen and Roman’s first axis) represent a greater-than-random set of future evolutionary routes (Redding et al. 2008), then conserving them would be a logical bet-hedging strategy for retaining evolutionary potential, the second axis of conservation worth outlined by Bowen (1999; Bowen & Roman 2005). This means that Bowen and Roman’s first and sec-

ond axes need not conflict. Our results here suggest that, within primates, there is potential for some agreement between the first (phylogenetic) and third axes (ecosystem functioning). Interestingly, results of studies of artificially constructed communities suggest that “phylogenetic relatedness is an indicator of the ecological uniqueness of species” (Cadotte et al. 2008, 2009) such that evolutionarily isolated species are likely to be more ecologically distinct. Artificially constructed communities of less-related species in turn have higher ecosystem function (Maherali & Klironomos 2007; Cadotte et al. 2008, 2009).

Instead of communities of interacting species, ED methods have, so far, been predominately applied to clades. If, in future work, ED measures can be applied across communities and a link between evolutionary distinctiveness and ecological role is demonstrated, then using ED to rank at-risk species could retain a larger-than-expected selection of ecosystem functional diversity. So far, the EDGE framework seems to offer at least as much as advertised for conservation biology, and if our findings are replicated throughout the tree of life, perhaps more.

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Supporting Information

A list of articles from national news organizations that describe species with high EDGE scores as unusual (Appendix S1) and descriptions of the variables used and the data set (Appendix S2) are available as part of the online version of the article. The authors are responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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