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## Research

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# Phylogenetic and functional diversity in large carnivore assemblages

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Large terrestrial carnivores are important ecological components and prominent flagship species, but are often extinction prone owing to a combination of biological traits and high levels of human persecution. This study combines phylogenetic and functional diversity evaluations of global and continental large carnivore assemblages to provide a framework for conservation prioritization both between and within assemblages. Species-rich assemblages of large carnivores simultaneously had high phylogenetic and functional diversity, but species contributions to phylogenetic and functional diversity components were not positively correlated. The results further provide ecological justification for the largest carnivore species as a focus for conservation action, and suggests that range contraction is a likely cause of diminishing carnivore ecosystem function. This study highlights that preserving species-rich carnivore assemblages will capture both high phylogenetic and functional diversity, but that prioritizing species within assemblages will involve trade-offs between optimizing contemporary ecosystem function versus the evolutionary potential for future ecosystem performance.

## 1. Introduction

The expansion of the human environmental footprint over the past 100 years has been accompanied by dramatic declines in components of the Earth's biodiversity [1]. This biodiversity decline can have radical impacts on humanity by altering ecosystem properties, and the subsequent goods and services provided [2,3]. Uneven spatial distribution of diversity coupled with limited resources available for conservation has generated a large body of work identifying biodiversity conservation priorities [4]. However, many of these approaches rely on taxonomic richness as a proxy for diversity [5]. This is a potentially serious shortcoming, because the ecological significance of diversity is also influenced by the relative functional attributes of different organisms [6].

Both phylogenetic (PD) and functional (FD) diversity have been related to ecosystem function [7], and it is now generally accepted that ecosystem function may differ substantially between species assemblages with the same taxonomic richness [8,9]. Unfortunately, there are still no unified metrics that includes all aspects of biodiversity [10], and the use of PD as a proxy for FD is not unequivocally supported [2,11,12]. Because it may not be possible to simultaneously optimize conservation of all aspects of biodiversity, it is important to recognize the value of each component. For instance, because one of the fundamental advantages of genetic variation is the potential to adapt to future conditions [13], we can regard phylogenetic diversity, which generally is closely related to genetic diversity, to describe the potential for future FD and hence future ecosystem performance [14]. This would then stand in contrast to FD, which primarily relates to present ecosystem function.

Large terrestrial carnivores are critically important for ecosystem dynamics [15], and have high cultural values and public appeal [16–18]. However, they are often extinction prone owing to high levels of human persecution coupled with low population densities and slow growth rates [19]. Recent carnivore conservation efforts typically target protection of local populations, and although there have been suggestions for taxonomic and functional prioritizations both

on regional [20] and global scales [21], simultaneous evaluations of PD and FD between and within carnivore assemblages are lacking.

I used an adaptation of a carnivore super-tree [22,23] combined with a dendrogram-based measure of FD [24] to quantify PD, FD and functional redundancy (FR) across the global and continental assemblages of large carnivores, as well as to quantify relative species contributions to these diversity components. I included species whose body mass averages 10 kg or more, hence both including large carnivores (as defined from energetic models [25]) and mesocarnivores [21] in the assessment.

## 2. Material and methods

I followed the conventional definition of the world as consisting of seven continents, i.e. Africa, Asia, Europe, North America, South America, Australasia and Antarctica. I did not include data from Australasia and Antarctica, because neither of these two continents has any indigenous species within contemporary Carnivora. North America was defined as containing USA, Canada, Mexico and the Central American countries, and I delineated Europe as continental Europe eastwards until the Black Sea. I included Russia in the Asian continent.

Species definitions as well as global and continental conservation status for each species were taken from the IUCN red list [26]. The continental conservation statuses for European species were complemented by a mammal status survey for Europe, because this provided a more refined regional assessment for this continent [27].

### (a) Measurement of phylogenetic diversity and species contributions

I used a previously published complete carnivore composite super-tree [22], with the amendment that skunks and stinkbadgers were regarded as a monophyletic Mephitidae rather than as part of Mustelidae [23,28]. I selected this hypothesis over more recent molecular ones [22,29,30] because it contained all species identified as large carnivores in this study and, therefore, provided a more complete evaluation of phylogenetic diversity for the analyses.

I calculated the evolutionary distinctiveness (ED) for each species as the sum of all branches along each species phylogenetic trajectory where each branch were weighted by the number of species sharing it [31], and the unique phylogenetic contribution (PC) of a species as the length of each species terminal branch (see the electronic supplementary materials, figure S1). I estimated the ED of each assembly as the sum of the ED of contributing species, and the unique PC of each assembly as the sum of the PCs of species endemic to that assemblage. For ease of interpretation, continental values of ED and PC were scaled so that they represent the proportion of total phylogenetic diversity contained within Carnivora. To quantify the contribution of individual species to the ED and PC of assemblages, I scaled species contributions by the total ED and PC within each assemblage. Phylogenetic calculations were conducted using the Tuatara package for the phylogenetic software MESQUITE (v. 2.74; [31,32]).

### (b) Measurement of functional diversity, redundancy and functional species contributions

My aim was to measure the FD with regard to predation processes. I, therefore, compiled data on a set of traits that all relate to predation effects in some way; diet, body size, hunting group

size, and area use (see the electronic supplementary materials, tables S1 and S2). Although these traits may not directly quantify all functional aspects of predation by large carnivores, the traits were selected because there is quantified trait data for all included species and they all relate to a wide range of predation related ecosystem effects. In addition, because hunting mode may indirectly influence the effects of predators in addition to direct predation effects [33], I also added a palaeomorphological classification of carnivore functional groups [21,34]. Although this classification is based on skeletal morphology, it is closely related to the hunting mode of the respective species [34] and may, therefore, provide information regarding predation effects caused by anti-predatory responses of prey.

I quantified FD and redundancy using dendrograms created from cluster analyses on continental trait matrices [24]. Such dendrograms can be used as both an index of relative FD and FR of species assemblages, as well as to measure individual contribution to FD and FR [9,24]. Each continental trait matrix was converted into a distance matrix that was clustered into a corresponding dendrogram. I used Gower's distance method because I had data containing both numerical and categorical variables [35], and the unweighted pair-group method using arithmetic averages (UPGMA) clustering method because this method generated the highest cophenetic correlation [36,37]. I followed the usual protocol of standardizing trait matrices so that each trait had a mean of 0 and a standard deviation of 1 before they were used to produce distance matrices. I used the Xtree function contributed by J. Schumacher ([http://owenpetchey.staff.shef.ac.uk/Code/Code/calculatingfd\\_assets/Xtree.r](http://owenpetchey.staff.shef.ac.uk/Code/Code/calculatingfd_assets/Xtree.r)) to transform the output from each cluster analyses into the appropriate species-branch matrices and branch-length vectors [38].

Analogous to calculations of ED and PC, I calculated the FD contribution of each species as the sum of all contributed branches where each branch were weighted by the number of species sharing it, and unique functional contribution (FC) as the length of the terminal branch (see the electronic supplementary materials, figure S1). I calculated contribution to FR as the sum of all branch fractions that was shared with other species (i.e. total branch length—FD, electronic supplementary materials, figure S1). I calculated the FD of each assemblage as the sum of all species' FD values (i.e. the sum of all branches [24]), FR as the sum of all species FR values (i.e. the sum of all species total branch lengths—their FD values [9]) and FC as the sum of the terminal branch length of endemic species (see the electronic supplementary materials, figure S1).

To account for the relative amount of space that species occupy in the calculations of the functional metrics of each assemblage, I also calculated functional metrics scaled by the proportional geographical range size for each species. This was done by replacing the binary coding in the species-branch matrices with the proportional range size of each species. The proportional range sizes were based on species distribution polygons from IUCN [26]. Each set of species polygons was first projected according to the EASE-Grid equal area coordinate system [39] and then cropped to be contained within each continental border. Proportional range sizes were calculated as the ratio of the area of all species polygons for a given species within a continent divided by the total land area for that continent. Continental borders were obtained from political country borders available from Blue Marble Geographics (<http://www.bluemarblegeo.com/products/worldmapdata.php?>). Only species polygons classed as 1 (extant) and 2 (probably extant) were included in the analyses [26].

For ease of interpretation, I scaled FD, FC as well as the geographically scaled values to range between 1 and 0, where 1 was the FD for the global assemblage. With this scaling, the value of each assemblage thus reflects FD in relation to the total FD of large carnivores on Earth [37]. I scaled FR to represent the

**Table 1.** Evolutionary distinctiveness (ED), phylogenetic contribution (PC), functional diversity (FD), functional redundancy (FR) and functional contribution (FC) of assemblages of large carnivores (greater than 10 kg). Functional indices are presented both for data not taking geographical distribution of species into account as well as metrics scaled by proportional continental range sizes for each species.

	total species	endemic species	ED (%) <sup>a</sup>	PC (%) <sup>a</sup>	raw <sup>b</sup>			scaled <sup>c</sup>		
					FD <sup>d</sup>	FR <sup>e</sup>	FC <sup>f</sup>	FD <sup>d</sup>	FR <sup>e</sup>	FC <sup>f</sup>
global	43		17.6	11.2	1	0.73		0.23	0.30	
Africa	16	9	7.84	3.38	0.62	0.65	0.20	0.30	0.48	0.09
Asia	22	10	9.37	2.97	0.70	0.60	0.15	0.24	0.14	0.05
Europe	7	1	2.12	0.09	0.45	0.42	0.02	0.19	0.11	0
North America	10	5	2.81	0.54	0.58	0.42	0.16	0.28	0.22	0.11
South America	5	3	1.98	0.96	0.40	0.20	0.20	0.18	0.06	0.07

<sup>a</sup>Represent percentage of total phylogenetic diversity within Carnivora.

<sup>b</sup>Raw values refer to indices that had not been scaled by geographical range sizes.

<sup>c</sup>Scaled values refer to indices that had been scaled by geographical range sizes of individual species.

<sup>d</sup>FD was scaled by the global assemblage so that values represent the functional diversity relative to the total functional diversity of large carnivores on Earth.

<sup>e</sup>FR was scaled so that values represent redundancy in relationship to the overall diversity in each assemblage.

<sup>f</sup>FC was calculated as the unique FC of endemic species within each continental assemblage, scaled by the total functional diversity contained within the global assemblage.

proportion of redundancy for each assemblage in relation to the sum of all individual branch segments. This value, therefore, represents the proportion of the total ecosystem function within an assemblage that is overlapping among species. Although such overlapping functionality previously was regarded as superfluous, it is now generally regarded as a desirable component of ecosystems because it increases resilience to environmental perturbations [9]. Within assemblages, I calculated the proportional contribution of species to the FD and FR of each specific assemblage, and the proportion of FD that was uniquely contributed by each species. Because the species contributions within assemblages are heavily influenced by species richness (i.e. species in a species poor assemblage will make larger individual contributions than species in a species-rich assemblage), I have presented species contributions as the deviation from equal contribution of each species. Species contributions to both phylogenetic and functional metrics are given for all species in the electronic supplementary material, table S3.

### (c) Statistical analyses

To evaluate if the PD or FD of continental assemblages deviated from expectations based on random assemblages with the same corresponding species richness, I tested the observed values for each continental assemblage against predictions from distributions of ED, PC, FD and FR values calculated on 10 000 bootstrapped assemblages containing the same number of species as the empirical assemblages. The species for each bootstrapped assemblage were drawn from the global species pool without replacement. The FC and PC were calculated on a random number of selected species within each bootstrapped assemblage, to also enable randomization of the number of endemic species within assemblages.

I evaluated the relationships between functional and phylogenetic metrics in carnivore assemblages as well as relationships between species contributions to phylogenetic and functional components of diversity in respective assemblage using Spearman rank correlations. Because I repeated correlations on raw and geographically scaled functional metrics, as well as on global and continental assemblages, I adjusted the statistical significance of these multiple tests according to the false discovery rate method

[40]. I similarly adjusted the significance from the bootstrap analyses to account for simultaneous evaluations across all continents for a single metric. All functional calculations as well as statistical analyses were conducted using the statistical software package R v. 2.15.1 for Linux (<http://www.r-project.org>).

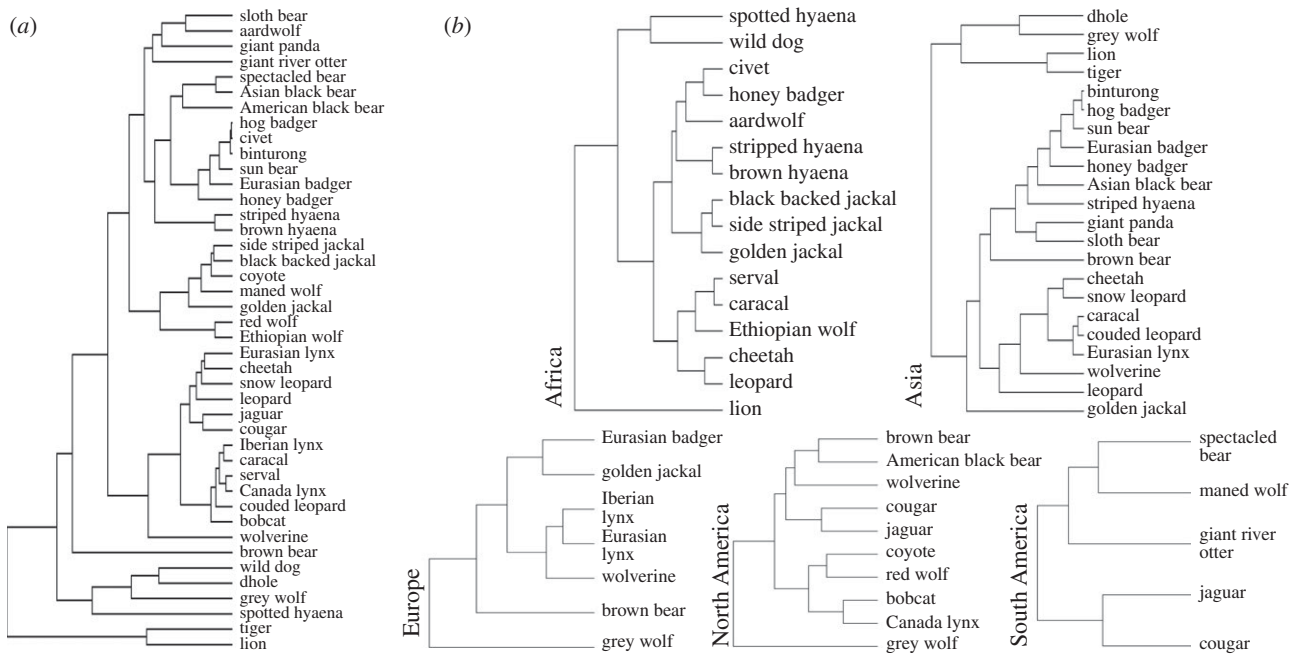
## 3. Results

### (a) Assemblage comparisons

Large carnivores contain 18 per cent of the total PD within Carnivora, and uniquely contribute to 11 per cent of this diversity. Scaled by species geographical range sizes, the global carnivore assemblage only retained 23 per cent of its FD (table 1). Although the total FR within the global assemblage was high (73%), it was reduced by more than half after geographical scaling (30%). Asia and Africa contain the two most species-rich assemblages, the highest number of endemic species and the highest level of phylogenetic diversity and contribution as well as FD and redundancy (table 1). Europe had very low PC and FC caused by its single endemic species (Iberian lynx, *Lynx pardinus*).

Species richness in continental assemblages was positively correlated to both ED ( $r_s = 1.00$ ,  $p = 0.02$ ) and FD ( $r_s = 1.00$ ,  $p_{adj} = 0.03$ ), but not to PC ( $r_s = 0.60$ ,  $p = 0.35$ ) or any of the other functional metrics (FD<sub>scaled</sub>:  $r_s = 0.70$ ,  $p_{adj} = 0.23$ ; FR:  $r_s = 0.87$ ,  $p_{adj} = 0.10$ ; FR<sub>scaled</sub>:  $r_s = 0.70$ ,  $p_{adj} = 0.35$ ; FC:  $r_s = -0.15$ ,  $p_{adj} = 0.95$ ; FC<sub>scaled</sub>:  $r_s = 0.10$ ,  $p_{adj} = 0.95$ ). ED was positively correlated to FD ( $r_s = 1.00$ ,  $p_{adj} = 0.03$ ), but not to either geographically scaled FD ( $r_s = 0.70$ ,  $p_{adj} = 0.23$ ) or to FR (FR:  $r_s = 0.87$ ,  $p_{adj} = 0.10$ ; FR<sub>scaled</sub>:  $r_s = 0.70$ ,  $p_{adj} = 0.23$ ). Similarly, PC was not correlated to FC (FC:  $r_s = 0.41$ ,  $p_{adj} = 0.27$ ; FC<sub>scaled</sub>:  $r_s = -0.10$ ,  $p_{adj} = 0.95$ ).

Neither ED (Africa:  $z = 1.57$ ,  $p_{adj} = 0.23$ ; Asia:  $z = 0.20$ ,  $p_{adj} = 0.84$ ; Europe:  $z = -1.48$ ,  $p_{adj} = 0.23$ ; North America:  $z = -2.19$ ,  $p_{adj} = 0.14$ ; South America:  $z = -0.25$ ,  $p_{adj} = 0.84$ ) nor PC differed from expectations based on species richness in any of the continental assemblages (Africa:  $z = 1.57$ ,



**Figure 1.** Functional relationships between species in (a) the global and (b) the continental assemblages of large carnivores (greater than 10 kg). The functional dendrograms were constructed from a data matrix of 10 traits related to predation effects.

$p_{\text{adj}} = 0.29$ ; Asia:  $z = 0.45$ ,  $p_{\text{adj}} = 0.70$ ; Europe:  $z = -0.77$ ,  $p_{\text{adj}} = 0.70$ ; North America:  $z = -1.63$ ,  $p_{\text{adj}} = 0.29$ ; South America:  $z = 0.38$ ,  $p_{\text{adj}} = 0.70$ ).

The African ( $z = -5.10$ ,  $p_{\text{adj}} < 0.001$ ) and Asian ( $z = -7.05$ ,  $p_{\text{adj}} < 0.001$ ) assemblages had lower FD than expected from their species richness, and there was a trend for the European assemblage to have lower than expected FD ( $z = -2.07$ ,  $p_{\text{adj}} = 0.06$ ). The FD in North ( $z = -1.38$ ,  $p_{\text{adj}} = 0.21$ ) and South America ( $z = -1.12$ ,  $p_{\text{adj}} = 0.26$ ) did not differ from random expectations. The Asian assemblage had lower than expected ( $z = -2.50$ ,  $p_{\text{adj}} = 0.03$ ) and the South American assemblage had higher than expected ( $z = 2.51$ ,  $p_{\text{adj}} = 0.03$ ) FC. The FC did not differ from random expectations in either of the other continental assemblages (Africa:  $z = -1.03$ ,  $p_{\text{adj}} = 0.38$ ; Europe:  $z = -1.03$ ,  $p_{\text{adj}} = 0.38$ ; North America:  $z = 0.08$ ,  $p_{\text{adj}} = 0.94$ ), nor did FR (Africa:  $z = 1.86$ ,  $p_{\text{adj}} = 0.31$ ; Asia:  $z = -1.29$ ,  $p_{\text{adj}} = 0.49$ ; Europe:  $z = 0.70$ ,  $p_{\text{adj}} = 0.60$ ; North America:  $z = -0.379$ ,  $p_{\text{adj}} = 0.71$ ; South America:  $z = -1.02$ ,  $p_{\text{adj}} = 0.51$ ).

## (b) Species contributions

Large species generally had large FCs. For instance, the lion (*Panthera leo*) provided unique function to the African assemblage and the grey wolf (*Canis lupus*) to the assemblages in Europe and North America (figure 1). The smaller bodied mesocarnivores typically clustered together exhibiting large functional overlap (figure 1).

Within the global assemblage, there were significant negative correlations between species contributions to ED and FD (raw:  $r_s = -0.32$ ,  $p_{\text{adj}} = 0.04$ ; geographically scaled:  $r_s = -0.33$ ,  $p_{\text{adj}} = 0.04$ ; figure 2a,b), and there was a trend for a negative correlation between species values of PC and FC ( $r_s = -0.31$ ,  $p_{\text{adj}} = 0.09$ ; figure 2e). However, there were no significant correlations between species contributions to ED and FR (raw:  $r_s = 0.23$ ,  $p_{\text{adj}} = 0.27$ ; geographically scaled:  $r_s = 0.16$ ,  $p_{\text{adj}} = 0.32$ ; figure 2c,d) not between PC and scaled

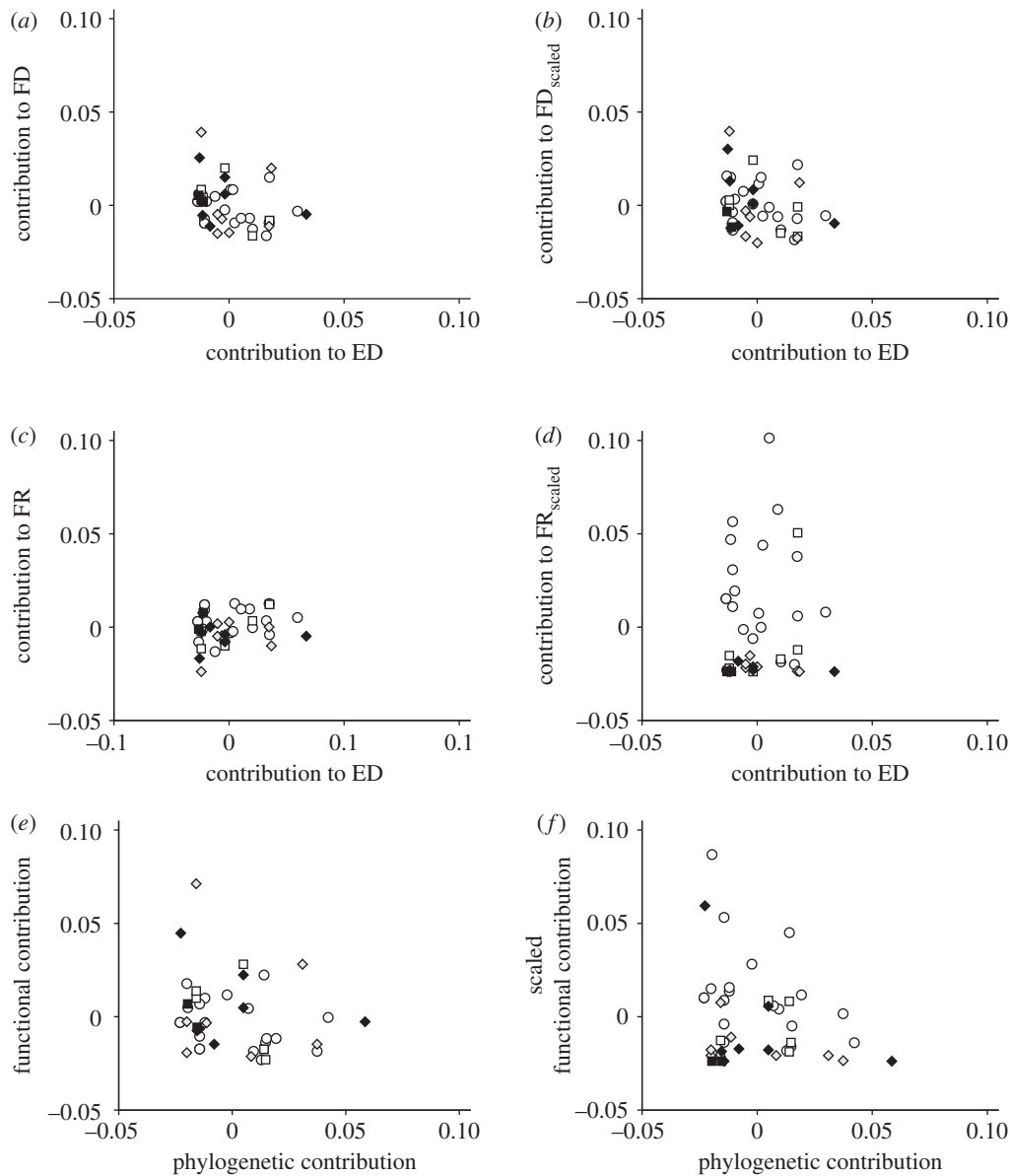
FC ( $r_s = -0.20$ ,  $p_{\text{adj}} = 0.21$ ; figure 2f). Within continental assemblages, there were no significant correlations between species contributions to ED and either FD (raw:  $r_s = -0.04$ ,  $p_{\text{adj}} = 0.76$ ; geographically scaled:  $r_s = -0.05$ ,  $p_{\text{adj}} = 0.76$ ; figure 3a,b) or FR (raw:  $r_s = 0.08$ ,  $p_{\text{adj}} = 0.59$ ; geographically scaled:  $r_s = 0.07$ ,  $p_{\text{adj}} = 0.59$ ; figure 3c,d), nor between unique species contributions to phylogenetic and FD (raw:  $r_s = -0.13$ ,  $p_{\text{adj}} = 0.40$ ; geographically scaled:  $r_s = -0.11$ ,  $p_{\text{adj}} = 0.40$ ; figure 3e,f).

## (c) Relationships between raw and geographically scaled functional diversity

Among assemblages, there were no significant correlations between raw and geographically scaled FD ( $r_s = 0.70$ ,  $p = 0.23$ ), FR ( $r_s = 0.82$ ,  $p = 0.09$ ) or FCs ( $r_s = 0.67$ ,  $p = 0.22$ ). However, within both the global ( $r_s = 0.90$ ,  $p_{\text{adj}} < 0.001$ ) and continental ( $r_s = 0.73$ ,  $p_{\text{adj}} < 0.001$ ) assemblages, there were positive correlations between species contributions to raw and geographically scaled FD (figure 4a,b). Although there was a positive correlation between species contributions to raw and geographically scaled FR ( $r_s = 0.61$ ,  $p_{\text{adj}} < 0.001$ ) and a trend for a significant positive correlation between unique species contributions to raw and geographically FD ( $r_s = 0.33$ ,  $p_{\text{adj}} = 0.06$ ) in the global assemblage, there were no significant correlations within continental assemblages (FR:  $r_s = 0.22$ ,  $p_{\text{adj}} = 0.326$ ; unique FC:  $r_s = 0.14$ ,  $p_{\text{adj}} = 0.12$ , figure 4c–f).

## 4. Discussion

My results suggest that prioritizing species-rich assemblages of large carnivores simultaneously will capture high PD and FD, as well as FR and associated resilience [9]. This study thus confirms previous theoretical and empirical studies, which similarly have highlighted a positive relationship between species richness and FD [9,24,41]. Dalerum *et al.*

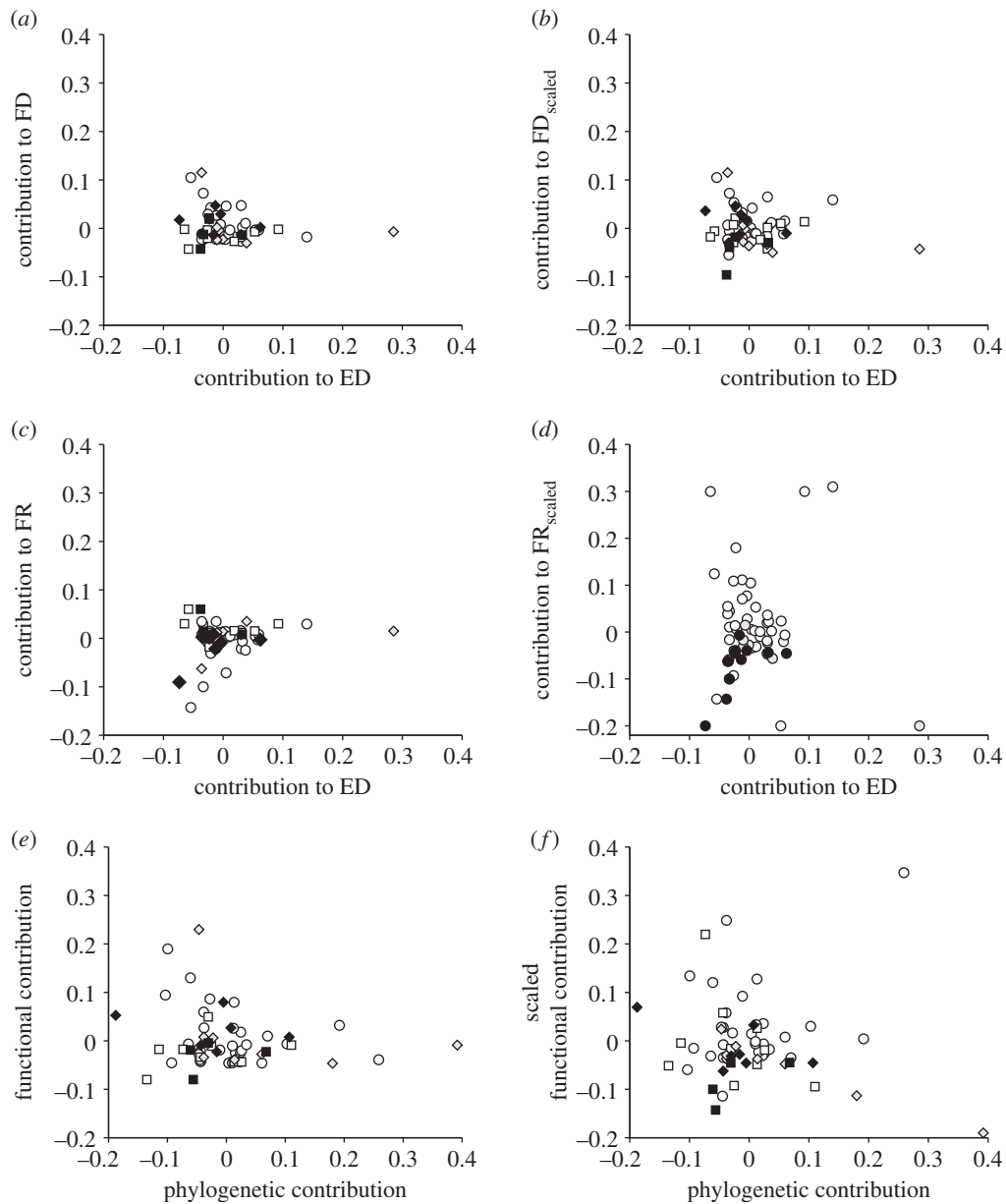


**Figure 2.** Relationships between contributions of large carnivore species (greater than 10 kg) to evolutionary distinctiveness (ED) and functional diversity (FD; raw (a); geographically scaled (b)), ED and functional redundancy (FR; raw (c); geographically scaled (d)), and unique phylogenetic (PC) and functional (FC; raw (e), geographically scaled (f)) contributions within the global assemblage. Data represent residual contributions of each species after the value corresponding to equal contribution from all species has been removed. Each species has been coded by their global IUCN status (circle, least concern; open square, near threatened; open diamond, vulnerable; filled diamond, endangered; filled square, critically endangered).

[21] suggested that one global conservation priority should be to protect and reconstruct as functionally complete assemblages as possible. Results from the present study accentuate this recommendation, because species-rich assemblages of large carnivores also seem to harbour a large amount of phylogenetic history as well as high FR. Such redundancy has been closely linked to ecological resilience and may hence aid in buffering ecosystems from the ecological effects of environmental perturbations [42].

Previous studies on bat and avian assemblages have shown lower FD within local assemblages than expected by chance [41,43]. This study does not uniformly support these results on a continental scale for large carnivores. Petchey *et al.* [41] suggested that environmental filtering, i.e. local environmental conditions promoting species with similar adaptations to these conditions to coexist, could potentially cause the lower than expected local FD, and highlighted that their patterns likely occurred within regional scales. Three continental

assemblages of large carnivores, including the two most species-rich ones (Asia and Africa), showed lower FD than expected by chance, whereas the assemblages in North and South America did not deviate from random expectations. These results indicate that regional processes do not necessarily cause large carnivore species to be more similar than expected by chance, and also suggest that different processes may have shaped the community structure of large carnivores across the different continents. One possible explanation for the contradictory results among continents could be that the heavy species depletions in North and South America since the Late Pleistocene [21] have diluted their species pool so that species on average have become less similar compared with continents with more intact assemblages, i.e. the species that have gone extinct have been more similar to extant species than expected by chance. Such non-random extinction patterns could for instance have occurred if extinct species were ecologically similar, but less competitive than their extant counterparts. There



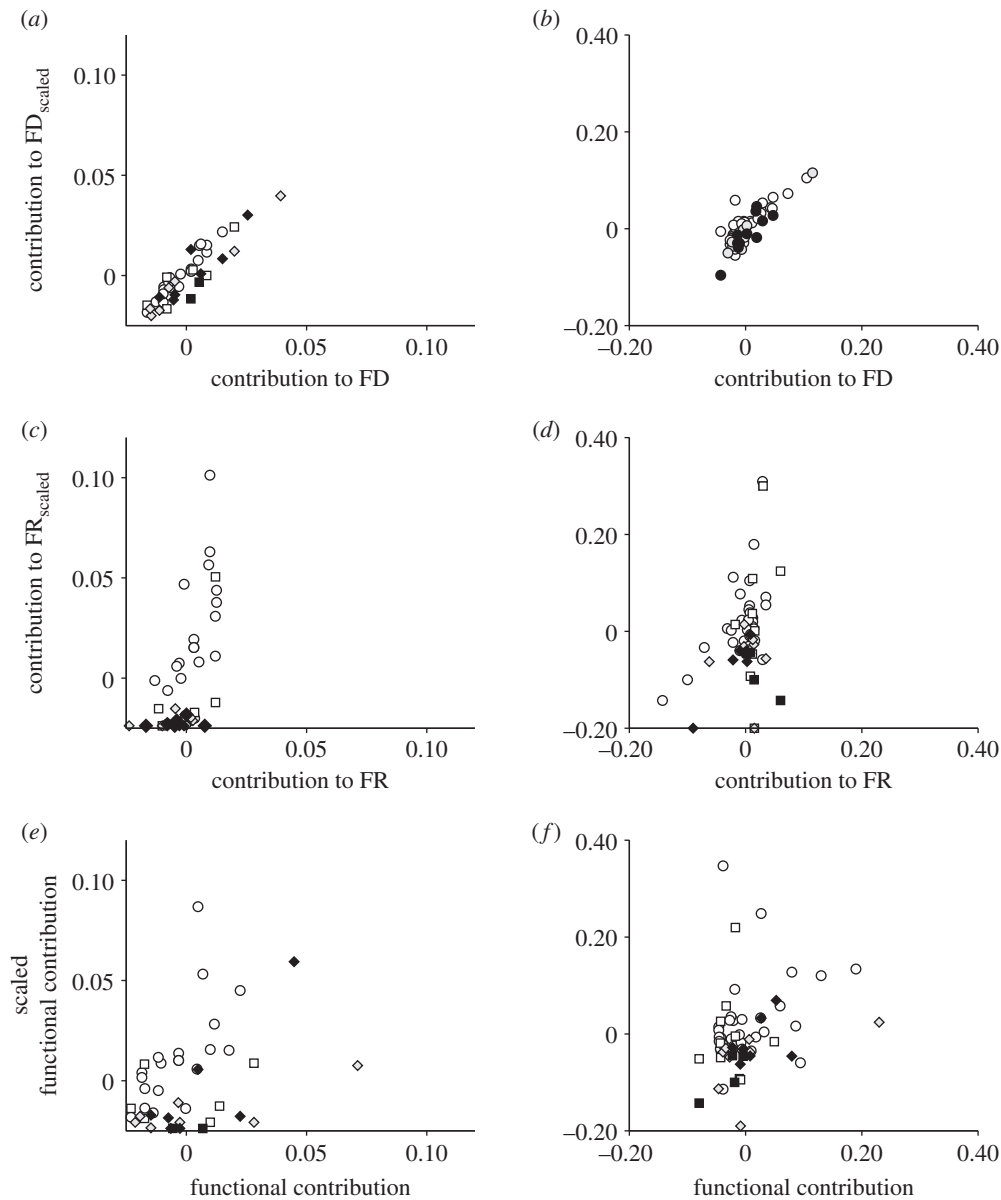
**Figure 3.** Relationships between contributions of large carnivore species (greater than 10 kg) to evolutionary distinctiveness (ED) and functional diversity (FD; raw (a); geographically scaled (b)), ED and functional redundancy (FR; raw (c); geographically scaled (d)), and unique phylogenetic (PC) and functional (FC; raw (e), geographically scaled (f)) contributions within the continental assemblages. Data represent residual contributions of each species after the value corresponding to equal contribution from all species has been removed. Each species has been coded by their global IUCN status (circle, least concern; open square, near threatened; open diamond, vulnerable; filled diamond, endangered; filled square, critically endangered).

appears to be little deviation from random expectations with regards to PD distributed across continents, as well as the FR contained within each continental assemblage.

Although it seems possible to reconcile simultaneous optimization of PD and FD when prioritizing between carnivore assemblages, the same does not appear to hold for prioritizations between species within assemblages. The analyses do not support that individual species of large carnivores simultaneously provide high contributions to phylogenetic and functional components of diversity. Contrarily, globally there appears to be a direct cost of prioritizing one diversity component over another, indicated by the negative correlation between contributions to phylogenetic and functional components. For instance, the two species that provided the largest contribution to ED to the global assemblage, the giant panda (*Ailuropoda melanoleuca*) and the aardwolf (*Proteles cristata*) both had low contributions to

FD. Similarly, the lion had by far the highest contribution to FD in the global assemblage, but was ranked as a low contributor to both ED and unique PC. Therefore, conservation decisions prioritizing large carnivore species may face an ecological future discount problem analogous to economic cost–benefit analyses, where contemporary functional benefits have to be weighted against evolutionary potential for maintaining future ecosystem function [44].

Several large species, such as the lion, the grey wolf and the tiger (*Panthera tigris*) either had large unique contributions to FD, or clustered together into groups with large contributions. Some of these species are among the most recognized and used conservation flagship species in the world [17]. The results from this study provide ecological justification for this attention, and highlight that a conservation focus on large apex predators may have large contemporary ecological benefits. Unfortunately, many of these species are



**Figure 4.** Relationships between the contribution of large carnivore species (greater than 10 kg) to raw and geographically scaled FD within the global (a) and (b) continental assemblages, to raw and geographically scaled FR in the global (c) and continental (d) assemblages, and between raw and geographically scaled unique functional contributions to the global (e) and continental (f) assemblages. Data represent residual contributions of each species after the value corresponding to equal contribution from all species within a given assemblage had been removed. Each species has been coded by their continental IUCN status (circle, least concern; open square, near threatened; open diamond, vulnerable; filled diamond, endangered; filled square, critically endangered).

also exceptionally conflict prone, as they are often accused of causing real or perceived financial losses and other types of suffering for local human societies. Management and conservation of these types of species is, therefore, politically complex [45], a complexity that is accentuated by their possession of biological traits which often lead to elevated local, regional or global extinction risks [19].

The substantial declines in FD and FR of assemblages after scaling species contributions by geographical range sizes suggest that habitat alteration and loss is reducing the ecosystem services provided by higher trophic levels [46]. Weak correlations between raw and geographically scaled FD, FR and FC of assemblages further points to a large influence of range contraction on large carnivore ecosystem function across continental scales. Similarly, weak correlations between geographically scaled metrics and species richness and phylogenetic components of diversity highlight that spatial distribution of species may be critical for determining how

well species richness and phylogenetic components of diversity capture carnivore ecosystem function across assemblages. However, geographical range sizes did not seem to alter relative species contributions to FD within assemblages.

The results from studies like these are dependent on the reliability of the quantifications of phylogenetic and functional relationships. Although the phylogenetic tree used in this study is over a decade old [22], it is still the most complete phylogeny presented for the extant Carnivora. It was based on consensus information at the time of its publication, and must be regarded as a reliable hypothesis for the phylogenetic relationships among carnivore species. The number and the nature of traits selected to depict functional relationships, as well as the methods used to quantify them, are highly influential on FD [9,24,47]. Although dendrogram-based measures of FD have been criticized [48], their similarity to phylogenetic analyses provides a congruent framework for simultaneous evaluations of PD and FD. In addition, if used in a relative

context, as has been done in this study, they provide an unbiased quantification of relative FD among assemblages [8].

To conclude, this study suggests that prioritizing species-rich assemblages of large carnivores will simultaneously capture high PD, FD, and FR. However, a lack of positive correlations between species contributions to phylogenetic and functional components of diversity suggests that conservation prioritizations of large carnivore species may face trade-offs between selecting species that will optimize contemporary ecosystem function versus the evolutionary

potential for future ecosystem performance. The results provide some ecological justification for large apex carnivores as a focus for conservation action, and moreover suggests that range contraction is a likely cause of diminishing carnivore ecosystem function.

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