Research

Global patterns of fragmentation and connectivity of mammalian carnivore habitat

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Although mammalian carnivores are vulnerable to habitat fragmentation and require landscape connectivity, their global patterns of fragmentation and connectivity have not been examined. We use recently developed high-resolution habitat suitability models to conduct comparative analyses and to identify global hotspots of fragmentation and connectivity for the world's terrestrial carnivores. Species with less fragmentation (i.e. more interior high-quality habitat) had larger geographical ranges, a greater proportion of habitat within their range, greater habitat connectivity and a lower risk of extinction. Species with higher connectivity (i.e. less habitat isolation) also had a greater proportion of high-quality habitat, but had smaller, not larger, ranges, probably reflecting shorter distances between habitat patches for species with restricted distributions; such species were also more threatened, as would be expected given the negative relationship between range size and extinction risk. Fragmentation and connectivity did not differ among Carnivora families, and body mass was associated with connectivity but not fragmentation. On average, only 54.3 per cent of a species' geographical range comprised high-quality habitat, and more troubling, only 5.2 per cent of the range comprised such habitat within protected areas. Identification of global hotspots of fragmentation and connectivity will help guide strategic priorities for carnivore conservation.

Keywords: mammalian carnivore; habitat fragmentation; connectivity; habitat models; conservation

1. INTRODUCTION

The loss and degradation of habitat have been identified as the primary threat to the world's mammals, affecting 40 per cent of species in a recent assessment of International Union for Conservation of Nature (IUCN) Red List data [1], a result consistent with prior evidence identifying habitat destruction as the principal cause of the loss of biodiversity worldwide [2,3]. As habitat is destroyed, concurrent fragmentation often partitions the remaining natural areas into progressively smaller, more isolated patches immersed within a human-modified matrix. This isolation of habitat patches can restrict connectivity, which is the movement of organisms or ecological processes across landscapes [4]. Conserving landscape connectivity is a vital component of biodiversity conservation [5–8]. For example, connectivity is essential for the natural ranging behaviour of animals among foraging or breeding sites and for dispersal

from their natal ranges, thus allowing for the exchange of genetic material among otherwise isolated populations. At broad spatial and temporal scales, conserving landscape connectivity is also necessary to maintain the continuity of ecological processes and to allow natural range shifts in response to long-term environmental transitions, including ecological adaptation to global climate change [9]. Because of the documented impacts of habitat fragmentation, connectivity conservation lends strength to efforts to protect natural populations in fragmenting landscapes and is increasingly becoming incorporated into land-management plans worldwide [7].

Mammalian carnivores are particularly vulnerable to habitat loss and fragmentation owing to intrinsic biological traits, such as large body sizes, large area requirements, low densities and slow population growth rates, as well as external anthropogenic threats, including hunting and other forms of direct persecution [10–14]. Consequently, carnivores may not be able to persist in landscapes dominated by humans, particularly those not connected by functional linkages or a permeable matrix between natural areas. Further, apex predators

can exert important top-down effects in ecological communities, and their decline or disappearance can generate cascades with system-level impacts [15–18]. Because carnivores are ecologically pivotal organisms whose status can be indicative of the connectedness of landscapes, they can be effective focal species to evaluate the degree of both fragmentation and connectivity across large landscapes [7].

Although the destruction and fragmentation of habitat is accelerating globally and such processes are clearly impacting a diversity of mammals, including carnivores, global patterns of habitat fragmentation and connectivity have not yet been examined. Herein, we use recently developed high-resolution distribution and habitat suitability models of the world's mammals to compare how fragmentation and connectivity interact with life-history characteristics to affect the conservation status of terrestrial mammalian carnivores and to identify their global hotspots of fragmentation and connectivity.

2. METHODS

(a) Habitat suitability models

Using baseline data from the 2009 IUCN Red List of Threatened Species, Rondinini *et al.* [19] recently developed habitat suitability models for the world's extant terrestrial mammals ($n = 5027$ species). These habitat preference models were developed at 300 m resolution and limited to occur within the known geographical range of the species to avoid extrapolating beyond their distribution limits. In our analyses, we examined habitat suitability models for all species of terrestrial mammalian carnivores for which there were adequate data, which included 13 families and 246 species. Habitat suitability models were not developed for domestic cats (*Felis catus*) and dogs (*Canis familiaris*, including dingo) and they were thus not included in our analyses.

As detailed by Rondinini *et al.* [19], three environmental variables formed the basis of the models: elevation, type of land cover and hydrological features. The elevational map was produced by resampling to 300 m the Shuttle Radar Topography Mission (SRTM) elevation [20] at 1 arcsecond resolution (*ca* 90 m at the equator). The type of land cover was mapped using Globcover v. 2.1 [21], a 300 m resolution global map with 63 classes based on the standard UN Land Cover Classification System [22]. The map of hydrological features was produced by merging polygonal water bodies (lakes and large rivers) from Globcover with linear water bodies from Vmap0 [23].

Elevational range where a species is found, when known and recorded in the IUCN Red List, was incorporated into the habitat models [19]. Expert information on other habitat affinities, including preferred types of land cover, tolerance to human impact and relationship to water bodies, are in the form of a textual description within the IUCN database. For incorporation into the habitat models, such textual descriptions were extracted in several steps. First, each species was assigned to one or more broad habitat types (forest, shrubland, grassland, bare, artificial). This information was then intersected with the suitability of flooded

habitat and the level of tolerance to human-modified (degraded or mosaic) natural habitat types. For each species, this then generated an automated classification of the classes of the land-cover map. If necessary, where detailed expert knowledge on habitat preference was available, suitability of individual classes in the land-cover map was then modified manually, including specifying if the distribution of a species should be restricted near water bodies.

Three levels of suitability of land cover were defined in the habitat models: (i) high—corresponding to preferred habitat (i.e. where the species can persist), (ii) medium—where a species can be found, but cannot persist in the absence of nearby primary habitat, and (iii) unsuitable—where a species is expected to be seldom or never found [19]. All cells in the model within the elevation range of the species retained the suitability score assigned to the land cover class, while cells outside the elevation range were classified as unsuitable. For species restricted near water bodies, all cells further than 1 km from water were classified as unsuitable. Additionally, habitat was classified as to whether or not it occurred within known protected areas based on the World Database on Protected Areas [24]. To calculate areas accurately, models were developed in a Mollweide equal area projection using the free-software GRASS GIS [25].

(b) Fragmentation and connectivity

These habitat suitability models served as the basis for our analyses of fragmentation and connectivity of global carnivore habitat. We focused on high-quality habitat, given that such habitat is by definition the most essential for species persistence. When delineating high-quality patches in the geographical range, we eliminated small patches (less than four adjacent cells at 300 m resolution) created by artefacts contained in the land use/cover map. This reduced the influence of spurious, isolated patches and improved computational efficiency of our fragmentation and connectivity analyses. We then defined high-quality habitat patches to be formed by neighbouring cells (eight nearest neighbours) using ArcGIS v. 9.3 (ESRI, Redlands, CA, USA).

We described the degree of fragmentation of high-quality habitat for each species with the GISfrag metric [26]. This index measures the average Euclidean distance of all cells within a high-quality habitat patch to the nearest edge of the patch. Because the metric is based on distance into interior habitat, low values represent less interior habitat and thus higher degrees of fragmentation, whereas high values represent more interior habitat and lower levels of fragmentation. The index thus is positively related to the amount of 'interior' or 'core' high-quality habitat for each species. There are many possible landscape metrics to evaluate fragmentation and connectivity, and ultimately a sensitivity analysis would be required to evaluate if results are consistent across indices [27]. We selected GISfrag because it is a relatively simple, robust and parsimonious metric, related to the 'Core Area' metric [28,29] but with the advantage that it does not require specification of an arbitrary depth-of-edge distance from the patch perimeter to define a core area within a patch. GISfrag also works well for

both convoluted and insular fragmentation patterns and at both the patch and landscape levels, and is comparable across landscapes of different extents [30–32]. In addition, it provides stable, readily interpretable information because it explicitly accounts for the proportion of a landscape occupied by habitat; Neel *et al.* [33] concluded that in order to best interpret a metric, it should have known and consistent behaviour as a function of habitat area.

We also evaluated the degree of connectivity of high-quality habitat for each species, adopting a similar distance-based approach as the GISfrag metric but instead focusing on the isolation of high-quality habitat cells by the intervening matrix of medium- and low-quality habitats. Specifically, we calculated the average cost-weighted distance between high-quality habitat cells, with cost weights assigned based on habitat suitability scores. High-quality habitat was assigned a baseline cost weight of 1, assuming that such habitat is permeable and does not restrict movement. Medium-quality habitat was assigned an intermediate cost weight of 2, assuming that such habitat somewhat restricts movement between high-quality habitat patches. Unsuitable habitat was assigned a high cost weight of 10, assuming infrequent or no movement through such landscapes. Because this metric is based on cost-weighted distance between high-quality habitat, low values represent shorter distances and thus more connectivity among habitat patches, whereas high values represent longer distances and thus less connectivity among patches. Therefore, the index is positively related to the degree of isolation of high-quality habitat.

We consider our connectivity metric to be similar to those that evaluate potential connectivity [34]. Unlike actual connectivity, which directly measures functional connectivity by empirically quantifying the movement of individuals through the landscape, potential connectivity metrics estimate functional connectivity by incorporating basic, indirect knowledge of the potential of organisms to move among habitat patches. In our analyses, this potential is incorporated through modelling the suitability of habitat in the intervening matrix among patches for each focal species. We also note that our metrics are similar to most other fragmentation and connectivity metrics in that they describe characteristics of individual habitat patches and their adjacent neighbours, rather than more complex ecological processes within and among patches [35,36]. For example, our metrics do not assess landscape arrangement and position, which often require a more complex, and computationally intensive, graph theory approach [37–39].

For species with disjunct geographical ranges as delineated in the IUCN database, connectivity was evaluated within each range segment but not between disjunct segments, in part because the habitat models were limited to within the current geographical range of a species [19]. Additionally, the IUCN Red List guidelines suggest delineation of disjunct ranges only when major discontinuities are present [40], so such gaps are highly unlikely to be crossed by focal species. Range boundaries in the IUCN database reflect modern geographical range and not historical distribution, and thus probably include more disjunct

distributions than existed before widespread anthropogenic impacts; future advances should consider evaluating historical versus current geographical range and resulting range fragmentation and loss of connectivity. In addition, connectivity analyses excluded the Marine Otter (*Lontra felina*) and Sea Otter (*Enhydra lutris*) because their current ranges, composed of disjunct segments along coastal areas, entirely comprised high-quality habitat and thus cost-distance between high-quality cells could not be calculated.

(c) Data analyses

We conducted comparative analyses to examine the relationship between the fragmentation and connectivity metrics across carnivore species, and also to describe the relationship of these metrics to various species characteristics, including the size of the current geographical range, the proportion of high-quality habitat within the geographical range, body mass, taxonomic family and IUCN Red List status. We first used Pagel's λ [41] to determine the strength of the phylogenetic signal in these covariates. Because of the spatially explicit nature of our data, we used the spatially corrected version of λ (λ') introduced by Freckleton & Jetz [42] to correct for the influence of spatial dependence in our continuous variables. We found that phylogenetic signal varied among our covariates; we obtained high values for taxonomic family ($\lambda = 0.98$) and body mass ($\lambda' = 0.99$), but low values for fragmentation ($\lambda' = 0.07$), connectivity ($\lambda' = 0.03$), the proportion of high-quality habitat within the geographical range ($\lambda' = 0.03$), geographical range ($\lambda' = 0.01$) and IUCN status ($\lambda < 0.01$). Because of this range of values, we corrected for phylogenetic signal in our analyses, using generalized least-squares regression for continuous covariates [43,44] and generalized estimating equations for our categorical covariates depicting IUCN status and taxonomic family [44,45]. For our generalized least-squares regressions, we assumed that the continuous covariates evolved randomly [46], so we used a Brownian-motion model to define the structure of the correlation among species. We used the extant mammalian phylogeny developed by Bininda-Emonds *et al.* [47], pruned to only include the Carnivora, for all our phylogenetic analyses. Because of recent taxonomic revisions, this carnivore phylogeny included 227 of the 246 carnivore species in the IUCN database, so we conducted our phylogenetic analyses on this subset of species. All phylogenetic analyses were conducted in the R statistical package (v. 2.10.1, R Foundation for Statistical Computing, Vienna, Austria) using the APE [44] and GEIGER [48] packages.

Body mass of each species was extracted from the PanTHERIA database [49]. For carnivore species in the IUCN database with no body mass values listed in PanTHERIA, typically owing to recent taxonomic revisions, we used the midpoint of the body mass range presented in Nowak [50] for that species; if Nowak [50] did not list body mass values for that species, we instead used PanTHERIA body mass values for the closest relative as indicated by Wilson & Reeder [51]. For all statistical analyses, we log-transformed the fragmentation and connectivity metrics, range size and body mass, and arcsine square-root transformed

the proportion of high-quality habitat within the geographical range.

For the taxonomic family analyses, we used generalized estimating equations to test for differences in the fragmentation and connectivity metrics among 10 families of Carnivora, including Canidae (dogs, wolves, coyotes, jackals and foxes; $n = 33$ for phylogenetic analyses), Eupleridae (fossa and other Malagasy carnivores; $n = 8$), Felidae (cats; $n = 34$), Herpestidae (mongooses; $n = 30$), Hyaenidae (aardwolf and hyenas; $n = 4$), Mephitidae (skunks; $n = 10$), Mustelidae (weasels; $n = 54$), Procyonidae (raccoons and relatives; $n = 14$), Ursidae (bears; $n = 8$) and Viverridae (civets, genets, linsangs and relatives; $n = 28$). For categorical variables, generalized estimating equations compare each category in relation to a reference category that we identified as Canidae, which have relatively generalized habitat requirements and are the most widely distributed family of the Carnivora, occurring from hot, arid deserts (Fennec Fox, *Vulpes zerda*) to arctic ice fields (Arctic Fox, *Alopex lagopus*) [50]. Because of small sample sizes, we excluded two monotypic families from the phylogenetic analyses— Ailuridae (Red Panda, *Ailurus fulgens*) and Nandiniidae (African Palm Civet, *Nandinia binotata*), and one family with only two species—Prionodontidae (Banded Linsang, *Prionodon linsang*; Spotted Linsang, *P. pardicolor*).

We also used generalized estimating equations to test for differences in the fragmentation and connectivity metrics among IUCN status categories. Data-Deficient species ($n = 14$) were excluded from the phylogenetic analyses, and Endangered and Critically Endangered were combined into one category ('Endangered') owing to the relatively small sample size ($n = 5$) of Critically Endangered carnivore species. We therefore compared among four status categories, including Least Concern ($n = 135$ for phylogenetic analyses), Near Threatened ($n = 23$), Vulnerable ($n = 32$) and Endangered ($n = 23$). We identified Least Concern as the reference category to which the other categories were compared in the generalized estimating equations. A species is classified by the IUCN as Least Concern when it is widespread and abundant and does not qualify for listing in other categories, and as Near Threatened when it does not qualify for a threatened category now, but is likely to do so in the near future [52]. A species is classified as Vulnerable when the best available evidence indicates that it faces a high risk of extinction in the wild. A species is classified as Endangered and Critically Endangered when it is considered to be facing a very high or extremely high risk of extinction in the wild, respectively.

Our methodology also allowed us to identify global hotspots of fragmentation and connectivity of high-quality habitat for the world's carnivores. Fragmentation and connectivity hotspots were identified by summing the values at each 300×300 m cell for fragmentation and connectivity metrics, respectively, for all carnivore species worldwide. This process therefore generated global maps depicting the degree of habitat fragmentation and connectivity for the world's carnivores.

Because we summed metrics for all species within a given area, these hotspots in part reflect global patterns of species distribution and richness. To evaluate the potential influence of carnivore diversity on hotspot locations, we also generated a species richness map for the order Carnivora by summing the number of carnivore species with high-quality habitat (as depicted with our GISfrag metric) for each 300×300 m cell globally. We note that these estimates of species richness are based not on the total extent of the geographical ranges of carnivores, but rather on the extent of suitable habitat within their ranges; these fine-resolution distribution data predict known species occurrences better than geographical ranges [19]. To further explore the effects of species richness on fragmentation hotspots, we divided our fragmentation metric within each cell globally by the number of species with suitable habitat within that cell. This process generated an average fragmentation index that was standardized by species richness. We then mapped this standardized fragmentation index globally for the order Carnivora and compared it with our fragmentation hotspot map. While beyond the scope of this study, further analyses of the influence of species distributions on hotspot locations could incorporate more complex macroecological approaches, such as null models of species range placement [53–55].

3. RESULTS AND DISCUSSION
(a) *Comparative analyses*
(i) *Fragmentation*
Mammalian carnivores differed considerably in their degree of habitat fragmentation. Carnivore species with less fragmentation (i.e. higher distance into interior habitat) had larger geographical ranges ($\beta \pm$ s.e. $= 0.193 \pm 0.028$, $t = 6.867$, $p < 0.001$), a greater proportion of high-quality habitat within their range ($\beta \pm$ s.e. $= 1.215 \pm 0.060$, $t = 20.100$, $p < 0.001$) and greater connectivity (i.e. lower cost-weighted distances) among high-quality habitat ($\beta \pm$ s.e. $= -0.308 \pm 0.039$, $t = -7.927$, $p < 0.001$). Fragmentation was not correlated to body size ($\beta \pm$ s.e. $= 0.069 \pm 0.129$, $t = 0.534$, $p < 0.594$), and it did not differ among families of Carnivora (all $p > 0.294$ in relation to Canidae).

Species with higher degrees of habitat fragmentation are at greater risk of extinction. Fragmentation of high-quality habitat significantly differed among IUCN status categories Least Concern, Near Threatened, Vulnerable and Endangered. Specifically, species classified as Least Concern had lower levels of fragmentation compared with species classified as Vulnerable ($\beta \pm$ s.e. $= -0.357 \pm 0.036$, $t = -9.802$, $p < 0.001$) and Endangered ($\beta \pm$ s.e. $= -0.476 \pm 0.029$, $t = -16.152$, $p < 0.001$); fragmentation did not significantly differ between Least Concern and Near Threatened ($\beta \pm$ s.e. $= -0.019 \pm 0.030$, $t = -0.636$, $p = 0.529$). Concordant with the negative relationship we documented between fragmentation and range size, and consistent with prior findings [13,56–59], carnivores with smaller geographical ranges also had higher risk of extinction. Specifically, carnivores classified as Least Concern had significantly larger ranges than those classified as Near Threatened ($\beta \pm$ s.e. $= -1.044 \pm 0.058$, $t = -17.897$, $p < 0.001$), Vulnerable ($\beta \pm$ s.e. $= -1.287 \pm 0.071$, $t = -18.179$,

$p < 0.001$) and Endangered ($\beta \pm$ s.e. $= -2.534 \pm 0.057$, $t = -44.205$, $p < 0.001$). Although the causal mechanisms underlying the correlational patterns between habitat fragmentation, range size and extinction risk warrant further investigation, a broad geographical distribution may buffer against the effects of habitat loss [57,58], and our results suggest that greater habitat fragmentation in species with smaller ranges may contribute to their elevated extinction risk. Large-range species also tend to be habitat generalists [60] and, as our results demonstrate, have a higher proportion of suitable habitat, less fragmentation and more connectivity within their range.

(ii) *Connectivity*

Mammalian carnivores also differed considerably in their degree of connectivity of high-quality habitat. As with fragmentation patterns, carnivore species with greater habitat connectivity (i.e. lower cost-weighted distance between high-quality habitat) had a greater proportion of suitable habitat within their geographical range ($\beta \pm$ s.e. $= -2.071 \pm 0.091$, $t = -22.697$, $p < 0.001$). However, in contrast to patterns observed with fragmentation, species with more habitat connectivity had smaller, not larger, geographical ranges ($\beta \pm$ s.e. $= 0.171 \pm 0.043$, $t = 3.945$, $p < 0.001$, $n = 225$), probably reflecting shorter distances between habitat patches for species with more restricted distributions. Habitat connectivity was correlated with body size ($\beta \pm$ s.e. $= 0.374 \pm 0.187$, $t = 2.001$, $p = 0.050$), with smaller-bodied species tending to have more connectivity. As with fragmentation, connectivity did not differ among Carnivora families (all $p > 0.544$ in relation to Canidae).

Species classified as Least Concern had less habitat connectivity than species classified as Near Threatened ($\beta \pm$ s.e. $= -0.437 \pm 0.046$, $t = -9.437$, $p < 0.001$) and Endangered ($\beta \pm$ s.e. $= -0.261 \pm 0.046$, $t = -5.672$, $p < 0.001$), but greater habitat connectivity than species classified as Vulnerable ($\beta \pm$ s.e. $= 0.132 \pm 0.056$, $t = 2.348$, $p = 0.025$). Although it is counterintuitive that endangered species had higher habitat connectivity, this pattern is probably due, in part, to the strong influence of geographical range size. That is, our results indicate that species with more habitat connectivity had smaller geographical ranges, and also that species with smaller ranges have higher extinction risk. The negative association between extinction risk and range size is near-ubiquitous across numerous studies and taxa [57], and our results again suggest the importance of range size in predicting threat status.

(b) *Global hotspots*
(i) *Fragmentation*
Summing the fragmentation metric across all species ($n = 246$) reveals global patterns of core habitat and fragmentation for the world's terrestrial carnivores (figure 1). Primary hotspots of high-quality core habitat include much of the Amazon Basin in South America and sub-Saharan Africa, as well as portions of western North America and southeastern and northern Asia. Such locations therefore represent
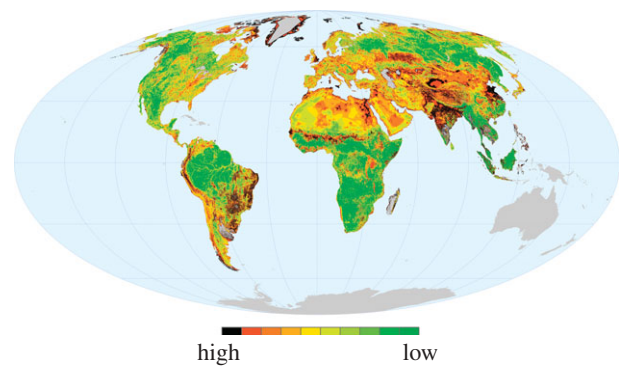
Figure 1. Global hotspots of fragmentation and core habitat for the world's terrestrial mammalian carnivores ($n = 246$). Green denotes sites with low fragmentation, where the most carnivore species have the most intact high-quality core habitat. Black denotes sites with high fragmentation, where relatively few carnivore species occur and these species have relatively little core habitat.
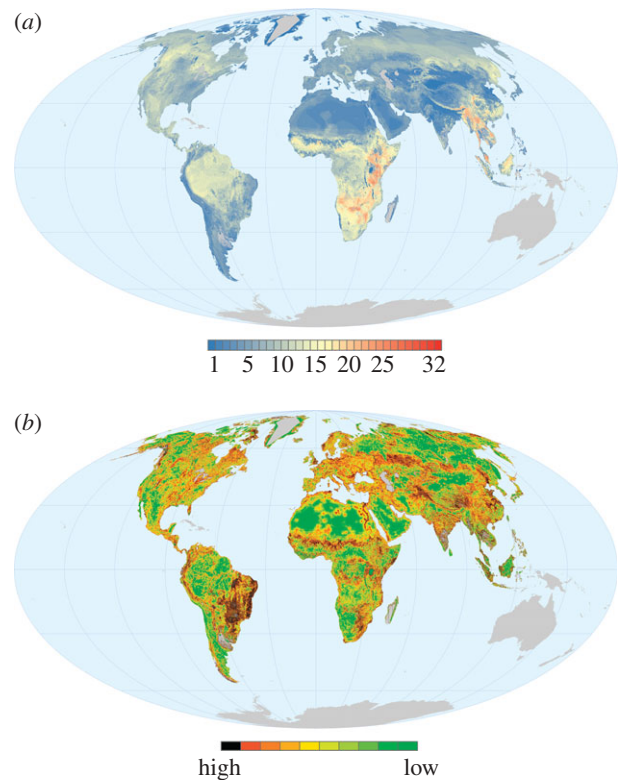

Figure 2. (*a*) Species richness of the world's terrestrial mammalian carnivores ($n = 246$) based on the extent of suitable habitat. Blue denotes sites with few carnivore species, and red denotes sites with the highest species richness. (*b*) Global hotspots of fragmentation and core habitat, standardized by species richness. Green denotes sites with low fragmentation, where carnivores, averaged across species with suitable habitat at a site, have the most intact high-quality core habitat. Black denotes sites with high fragmentation, where carnivore species on average have relatively little core habitat.

areas with the highest richness of carnivore species (figure 2*a*) that on average have the most interior high-quality habitat (figure 2*b*). At a global scale, conservation actions focused towards these sites, including efforts to protect core carnivore habitat, therefore have the potential to disproportionately benefit the world's carnivores.
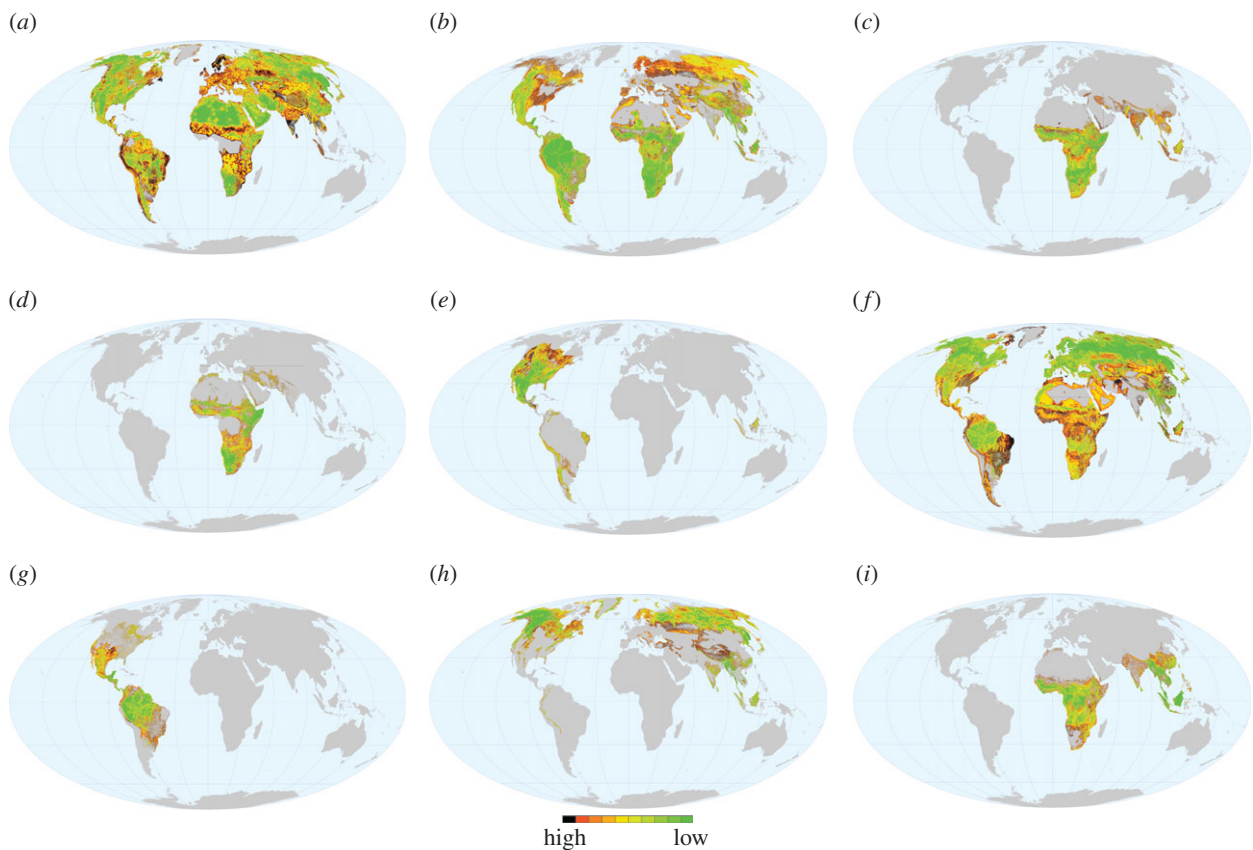
Figure 3. Global hotspots of fragmentation and core habitat for the world's terrestrial mammalian carnivores by family, including (*a*) Canidae, (*b*) Felidae, (*c*) Herpestidae, (*d*) Hyaenidae, (*e*) Mephitidae, (*f*) Mustelidae, (*g*) Procyonidae, (*h*) Ursidae and (*i*) Viverridae. Green denotes sites with low fragmentation, where the most carnivore species have the most intact high-quality core habitat. Black denotes sites with high fragmentation, where relatively few carnivore species occur and these species have relatively little core habitat.

Conversely, fragmentation hotspots represent regions with relatively low interior distances within high-quality habitat, summed across all species present in an area. Such regions include much of South America outside the Amazon Basin, southern and central Asia, as well as portions of eastern North America, Europe, northern Africa and southwestern Asia. The most severe of these fragmentation hotspots identify regions where relatively few carnivore species occur (figure 2*a*) and those species have relatively little core habitat (figure 2*b*). Note that some locales (most notably desert regions of northern Africa and central and southwestern Asia, and parts of the southern Andes of South America) do have, on average, relatively extensive core habitat (figure 2*b*) for the few species that occur there (figure 2*a*). Carnivore diversity, however, is sufficiently low in these regions that they do not appear as global hotspots of core habitat (figure 1). Native terrestrial mammalian carnivores are absent from Greenland, Antarctica and Australia (figure 2*a*).

Families of Carnivora exhibited regional heterogeneity in locations of hotspots of high-quality core habitat (figure 3). At the family level, hotspots of core habitat for Canidae generally included much of North America, desert regions of Africa and southwestern Asia, and portions of northern and eastern Asia. Felidae core habitat is evident in much of South America, including the Amazon Basin, in sub-Saharan Africa, and in portions of western North America and southeastern Asia. Mustelidae core habitat includes expanses of northern forests

of North America and Eurasia, as well as the Amazon Basin and portions of Europe, southeastern Asia, and central and southern North America. Core habitat is concentrated in central and southern North America for Mephitidae, and in the Amazon Basin and small patches of Central America and southern North America for Procyonidae. Core habitat is generally limited to portions of sub-Saharan Africa for Herpestidae and Hyaenidae, and to sub-Saharan Africa and portions of southeastern Asia for Viverridae. Ursidae core habitat is concentrated in northwestern North America and portions of northern Asia. Eupleridae, not mapped here, is endemic to Madagascar.

(ii) *Connectivity*

Likewise, summing the connectivity metric among all species ($n = 244$) reveals global patterns of isolation and connectivity of high-quality habitat for the world's terrestrial carnivores (figure 4). Primary hotspots of isolation of carnivore habitat include much of southern and southeastern Asia and sub-Saharan Africa, as well as portions of eastern South America and Central America. Such regions therefore represent areas with the highest richness of carnivore species (figure 2*a*) that have the least connectivity (i.e. highest cost-weighted distance) among high-quality habitat within their current geographical range. Consequently, efforts to restore broad-scale landscape connectivity in
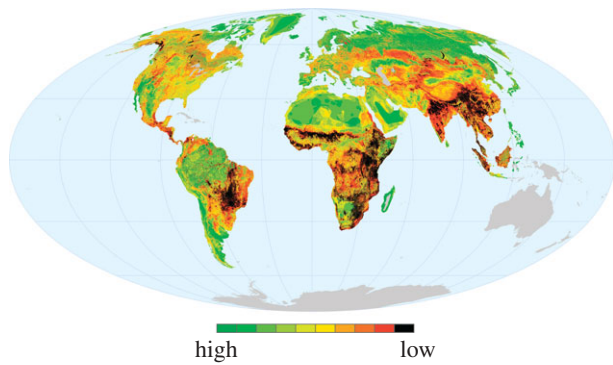
high   low

Figure 4. Global hotspots of habitat connectivity and isolation for the world's terrestrial mammalian carnivores ($n = 244$). Black denotes sites of low connectivity, with the highest richness of carnivore species that have the least connectivity (most isolation) among high-quality habitat within their current geographical range. Green denotes sites of high connectivity, where relatively few carnivore species have highly isolated high-quality habitat patches.

these hotspots may be particularly beneficial for global carnivore conservation.

Conversely, regions with low cost-weighted distances among high-quality habitat, summed across species present in an area, include much of northern Eurasia, northern Africa, and portions of northeastern and southwestern North America, western and southern South America, and southwestern Asia. Such regions tend to support relatively few carnivore species (figure 2a), thus contributing to lower cumulative cost-weighted distances among patches when pooling across species. The Amazon Basin, however, also has relatively low cumulative cost-weighted distances, even though it supports many species (figure 2a), indicating relatively high habitat connectivity for the species that occur there.

As with fragmentation, families of Carnivora differed in locations of hotspots of isolation of high-quality habitat (figure 5). Generally, Canidae had relatively connected habitat throughout much of their distributions, with notable exceptions in southern and central Asia, as well as portions of eastern Africa, eastern South America and northern North America. Habitat connectivity for Felidae was similar to patterns seen for the entire Carnivora, with hotspots of habitat isolation in eastern South America, Central America, eastern Africa, and southern and southeastern Asia. Habitat isolation for Mustelidae was most pronounced across much of central Eurasia and southeastern Asia, as well as portions of western and northern North America and sub-Saharan Africa. Habitat connectivity was most constricted in Central America and small patches of western North America for Mephitidae, in Central America and eastern South America for Procyonidae, in sub-Saharan Africa for Herpestidae, in eastern Africa for Hyaenidae, and in southeastern Asia for Ursidae and Viverridae.

4. CONCLUSIONS

On average, across all 246 species of terrestrial mammalian carnivores, only 54.3 per cent (range: 3.7–100%; s.e. = 0.016) of a species' current geographical range comprised high-quality habitat. More troubling, only 5.2 per cent (range: 0–88.2%; s.e. = 0.005) of the average range comprised high-suitability habitat located within known protected areas, a trend of considerable concern for the conservation of the world's carnivores and one consistent with prior findings of the inadequacy of the current global network of protected areas to conserve terrestrial vertebrate diversity [61]. Further, our results demonstrate that carnivores with less suitable habitat also experience higher habitat fragmentation and less habitat connectivity, with smaller and more isolated patches of remaining high-quality habitat within their range. Moreover, species with less interior habitat and thus higher levels of fragmentation are at a greater risk of extinction.

Of additional concern is that habitat loss is especially prevalent in many of the global hotspots of carnivore habitat identified in our models, particularly tropical regions in the Americas, Africa and Asia that experience high deforestation [1]. For example, much of the tropical forest in the Amazon Basin, which our analyses repeatedly designated as a critical global hotspot of carnivore habitat across multiple Carnivora families, is predicted to be degraded or destroyed by projected agricultural expansion and development schemes [14,62–64].

Although the locations of these hotspots are generally congruent with patterns of species richness, they advance our knowledge in two important ways. First, they narrow the focus of mammal distribution to include only those species-rich regions that specifically support high-quality habitat for many carnivore species. This focus is particularly critical given that on average only about half of the geographical range of terrestrial carnivores comprises high-quality habitat. Indeed, although prior efforts based solely on geographical ranges have provided valuable insights on global conservation priorities of mammals [57,65], such analyses have been critiqued because species are not homogeneously distributed across their range [66]. Further, prior global studies of mammal distribution have been at low resolution, between 10 000 and 20 000 km^2 [1,65], and this lack of detailed large-scale information has hindered conservation efforts [19]. With a resolution of 0.09 km^2, the habitat models developed by Rondinini *et al.* [19] and used here help address this limitation.

Second, our fragmentation and connectivity models extend other efforts by evaluating not only global patterns of species richness based on suitable habitat [19], but in addition modelling how such high-quality habitat is distributed into patches with relatively more interior habitat within patches and greater connectivity among them. We feel evaluation of such patterns of fragmentation and connectivity is an important step in prioritizing global mammal conservation efforts, in that fragmentation is the primary threat to the world's mammals [1] and connectivity conservation is thus a critical need [7]. Perhaps the greatest utility of our models will be at the local scale, which is the scale of conservation action [67]. The unprecedented 300 m resolution of the global habitat models allows for more detailed analyses of fragmentation and connectivity patterns at fine scales particularly useful for conservation planning. Consequently, a valuable next step will be to more thoroughly examine fine-scale
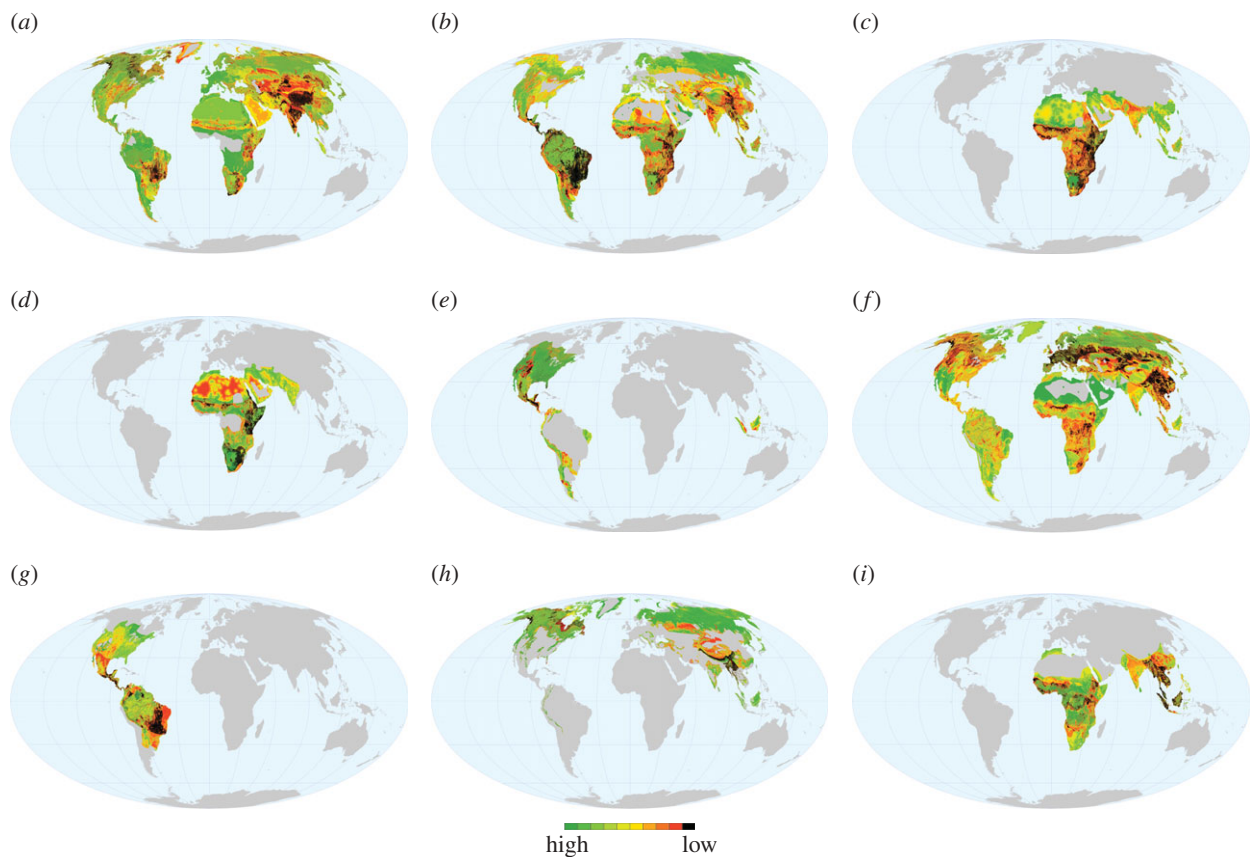
Figure 5. Global hotspots of habitat connectivity and isolation for the world's terrestrial mammalian carnivores by Family, including (*a*) Canidae, (*b*) Felidae, (*c*) Herpestidae, (*d*) Hyaenidae, (*e*) Mephitidae, (*f*) Mustelidae, (*g*) Procyonidae, (*h*) Ursidae and (*i*) Viverridae. Black denotes sites of low connectivity, with the highest richness of carnivore species that have the least connectivity (most isolation) among high-quality habitat within their current geographical range. Green denotes sites of high connectivity, where relatively few carnivore species have highly isolated high-quality habitat patches.

patterns of fragmentation and connectivity within families of Carnivora and for individual species of particular conservation concern, including identifying specific locations of core habitat patches and connectivity among them, in order to guide local conservation efforts.

Overall, our models represent the first explicitly macroecological analyses of global patterns of habitat fragmentation and connectivity in mammalian carnivores, species particularly sensitive to such impacts. Indeed, to our knowledge, this represents the first such analysis for any mammalian taxon. Our comparative analyses revealed that carnivores differed in the degree of habitat fragmentation and connectivity and these differences predicted extinction risk. Further, our approach allowed the identification of global hotspots of core carnivore habitat and isolation of high-quality habitat patches. Future work will explore how the extent and geographical distribution of these global hotspots are congruent with those identified when considering only species of highest extinction risk, particularly given that hotspots of species richness and extinction threat may not overlap [68,69]. Similarly, further efforts should examine hotspot congruence when considering carnivore habitat within and outside known protected areas [61], which our results indicate only represent a small proportion of high-quality carnivore habitat worldwide. Ultimately, we anticipate that efforts to identify global hotspots of fragmentation and connectivity, in conjunction and collaboration with other prioritization schemes [70], will provide valuable tools for developing more effective strategies for conserving the world's carnivores.

REFERENCES

1 Schipper, J. *et al.* 2008 The status of the world's land and marine mammals: diversity, threat, and knowledge. *Science* **322**, 225–230. (doi:10.1126/science.1165115)
2 Wilcove, D. S., Rothstein, D., Dubow, J., Phillips, A. & Losos, E. 1998 Quantifying threats to imperiled species in the United States. *Bioscience* **48**, 607–615. (doi:10.2307/1313420)
3 IUCN. 2004 *IUCN Red List of threatened species*. Gland, Switzerland: IUCN.
4 Taylor, P. D., Fahrig, L., Henein, K. & Merriam, G. 1993 Connectivity is a vital element of landscape structure. *Oikos* **68**, 571–573. (doi:10.2307/3544927)
5 Beier, P. & Noss, R. F. 1998 Do habitat corridors provide connectivity? *Conserv. Biol.* **12**, 1241–1252. (doi:10.1046/j.1523-1739.1998.98036.x)

6 Bennett, A. F. 1999 *Linkages in the landscape: the role of corridors and connectivity in wildlife conservation.* Gland, Switzerland: IUCN.

7 Crooks, K. R. & Sanjayan, M. 2006 *Connectivity conservation.* Cambridge, UK: Cambridge University Press.

8 Hilty, J. A., Lidicker, W. Z. & Merenlender, A. M. 2006 *Corridor ecology: the science and practice of linking landscapes for biodiversity conservation.* Washington, DC, USA: Island Press.

9 Heller, N. E. & Zavalenta, E. S. 2009 Biodiversity management in the face of climate change: a review of 22 years of recommendations. *Biol. Conserv.* **142**, 14–32. (doi:10.1016/j.biocon.2008.10.006)

10 Noss, R. F., Quigley, H. B., Hornocker, M. G., Merrill, T. & Paquet, P. C. 1996 Conservation biology and carnivore conservation in the Rocky Mountains. *Conserv. Biol.* **10**, 949–963. (doi:10.1046/j.1523-1739.1996.10040949.x)

11 Woodroffe, R. & Ginsberg, J. R. 1998 Edge effects and the extinction of populations inside protected areas. *Science* **280**, 2126–2128. (doi:10.1126/science.280.5372.2126)

12 Crooks, K. R. 2002 Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conserv. Biol.* **16**, 488–502. (doi:10.1046/j.1523-1739.2002.00386.x)

13 Cardillo, M., Purvis, A., Sechrest, W., Gittleman, J. L., Bielby, J. & Mace, G. M. 2004 Human population density and extinction risk in the world's carnivores. *PLoS Biol.* **2**, 909–914. (doi:10.1371/journal.pbio.0020197)

14 Cardillo, M., Mace, G. M., Jones, K. E., Bielby, J., Bininda-Emonds, O. R. P., Sechrest, W., Orme, C. D. L. & Purvis, A. 2005 Multiple causes of high extinction risk in large mammal species. *Science* **309**, 1239–1241. (doi:10.1126/science.1116030)

15 Terborgh, J. *et al.* 2001 Ecological meltdown in predator-free forest fragments. *Science* **294**, 1923–1926. (doi:10.1126/science.1064397)

16 Johnson, C. N., Isaac, J. L. & Fisher, D. O. 2007 Rarity of a top predator triggers continent-wide collapse of mammal prey: dingoes and marsupials in Australia. *Proc. R. Soc. B* **274**, 341–346. (doi:10.1098/rspb.2006.3711)

17 Letnic, M., Kock, F., Gordon, C., Crowther, M. S. & Dickman, C. R. 2009 Keystone effects of an alien top-predator stem extinctions of native mammals. *Proc. R. Soc. B* **276**, 3249–3256. (doi:10.1098/rspb.2009.0574)

18 Terborgh, J. & Estes, J. A. 2010 *Trophic cascades: predators, prey, and the changing dynamics of nature.* Washington, DC, USA: Island Press.

19 Rondinini, C. *et al.* 2011 Global habitat suitability models of terrestrial mammals. *Phil. Trans. R. Soc. B* **366**, 2633–2641. (doi:10.1098/rstb.2011.0113)

20 United States Geological Survey. 2006 Shuttle Radar Topography Mission version 2.0 (3 arc second). See http://www.landcover.org/data/srtm (accessed 26 February 2010).

21 IONIA. 2009 Globcover Land Cover. See http://ionia1.esrin.esa.int (accessed 28 February 2010).

22 Di Gregorio, A. & Jansen, L. J. M. 2000 Land Cover Classification System: classification concepts and user manual. See http://www.fao.org/DOCREP/003/X0596E/X0596e00.htm (accessed 28 February 2010).

23 National Imagery and Mapping Agency. 1997 World Miscellaneous Water Lines (VMAP0). See https://www.1.columbia.edu/sec/acis/eds/dgate/studies/C1301/data/World_MiscWaterLines_LINES.zip (accessed 26 February 2010).

24 IUCN & UNEP. 2009 *The World Database on Protected Areas* (*WDPA*). Cambridge, UK: UNEP-WCMC.

25 GRASS Development Team. 2010 Geographic Resources Analysis Support System (GRASS) Software, Version 6.4.0. Open Source Geospatial Foundation. See http://grass.osgeo.org (accessed 15 October 2010).

26 Ripple, W. J., Bradshaw, G. A. & Spies, T. A. 1991 Measuring forest landscape patterns in the Cascade Range of Oregon, USA. *Biol. Conserv.* **57**, 73–88. (doi:10.1016/0006-3207(91)90108-L)

27 Saura, S. & Pascual-Hortal, L. 2007 A new habitat availability index to integrate connectivity in landscape conservation planning: comparison with existing indices and application to a case study. *Landscape Urban Plann.* **83**, 91–103. (doi:10.1016/j.landurbplan.2007.03.005)

28 McGarigal, K., Cushman, S. A., Neel, M. C. & Ene, E. 2002 *FRAGSTATS: spatial pattern analysis program for categorical maps.* Amherst, MA, USA: University of Massachusetts. See http://www.umass.edu/landeco/research/fragstats/fragstats.html.

29 Leitão, A. B., Miller, J., Ahern, J. & McGarigal, K. 2006 *Measuring landscapes: a planners handbook.* Washington, DC: Island Press.

30 Gustafson, E. J. 1998 Quantifying landscape spatial pattern: what is the state of the art? *Ecosystems* **1**, 143–156. (doi:10.1007/s100219900011)

31 Gustafson, E. J., Knutson, M. G., Niemi, G. J. & Friberg, M. 2002 Evaluation of spatial models to predict vulnerability of forest birds to brood parasitism by cowbirds. *Ecol. Appl.* **12**, 412–426. (doi:10.1890/1051-0761(2002)012[0412:EOSMTP]2.0.CO;2)

32 Gustafson, E. J. & Loehle, C. 2006 Effects of parcelization and land divestiture on forest sustainability in simulated forest landscapes. *Forest Ecol. Manage.* **236**, 305–314. (doi:10.1016/j.foreco.2006.09.015)

33 Neel, M. C., McGarigal, K. & Cushman, S. A. 2004 Behavior of class-level landscape metrics across gradients of class aggregation and area. *Landscape Ecol.* **19**, 435–455. (doi:10.1023/B:LAND.0000030521.19856.cb)

34 Fagan, W. F. & Calabrese, J. M. 2006 Quantifying connectivity: balancing metric performance with data requirements. In *Connectivity conservation* (eds K. R. Crooks & M. Sanjayan), pp. 297–317. Cambridge, UK: Cambridge University Press.

35 Girvetz, E. H., Jaeger, J. A. G. & Thorne, J. H. 2007 Comment on 'Roadless space use of the Conterminous United States'. *Science* **318**, 1240. (doi:10.1126/science.1145349)

36 Girvetz, E. H., Thorne, J. H., Berry, A. M. & Jaeger, J. A. G. 2008 Integration of landscape fragmentation analysis into regional planning: a statewide multi-scale case study from California, USA. *Landscape Urban Plann.* **86**, 205–218. (doi:10.1016/j.landurbplan.2008.02.007)

37 Urban, D. L. & Keitt, T. H. 2001 Landscape connectedness: a graph theoretic perspective. *Ecology* **82**, 1205–1218. (doi:10.1890/0012-9658(2001)082[1205:LCAGTP]2.0.CO;2)

38 Theobald, D. M. 2006 Exploring the functional connectivity of landscapes using landscape networks. In *Connectivity conservation* (eds K. R. Crooks & M. Sanjayan), pp. 416–443. Cambridge, UK: Cambridge University Press.

39 Saura, S., Estreguil, C., Mouton, C. & Rodriguez-Freire, M. 2011 Network analysis to assess landscape connectivity trends: application to European forests (1990–2000). *Ecol. Indicators* **11**, 407–416. (doi:10.1016/j.ecolind.2010.06.011)

40 IUCN Standards and Petitions Subcommittee. 2010 Guidelines for using the IUCN Red List categories and criteria. Version 8.1. Prepared by the Standards and Petitions Subcommittee in March 2010. See http://intranet.iucn.org/webfiles/doc/SSC/RedList/RedListGuidelines.pdf.//intranet.iucn.org/webfiles/doc/SSC/RedList/RedListGuidelines.pdf.

41 Pagel, M. 1999 Inferring the historical pattern of biological evolution. *Nature* **401**, 877–884. (doi:10.1038/44766)

42 Freckleton, R. P. & Jetz, W. 2009 Space versus phylogeny: disentangling phylogenetic and spatial signals in comparative data. *Proc. R. Soc. B* **276**, 21–30. (doi:10.1098/rspb.2008.0905)

43 Grafen, A. 1989 The phylogenetic regression. *Phil. Trans. R. Soc. Lond. B* **326**, 119–157. (doi:10.1098/rstb.1989.0106)

44 Paradis, E. 2006 *Analysis of phylogenetics and evolution with R.* New York, USA: Springer.

45 Paradis, E. & Claude, J. 2002 Analysis of comparative data using generalized estimating equations. *J. Theor. Biol.* **218**, 175–185. (doi:10.1006/jtbi.2002.3066)

46 Felsenstein, J. 1985 Phylogenies and the comparative method. *Am. Nat.* **125**, 1–15. (doi:10.1086/284325)

47 Bininda-Emonds, O. R. P. *et al.* 2007 The delayed rise of present-day mammals. *Nature* **446**, 507–512. (doi:10.1038/nature05634)

48 Harmon, L. J., Weir, J. T., Brock, C. D., Glor, R. E. & Challenger, W. 2008 GEIGER: investigating evolutionary radiations. *Bioinformatics* **24**, 129–131. (doi:10.1093/bioinformatics/btm538)

49 Jones, K. E. *et al.* 2009 PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* **90**, 2648. (doi:10.1890/08-1494.1)

50 Nowak, R. M. 2005 *Walker's carnivores of the world.* Baltimore, MD, USA: The Johns Hopkins University Press.

51 Wilson, D. E. & Reeder, D. M. 2005 *Mammal species of the world: a taxonomic and geographic reference*, 3rd edn. Baltimore, MD, USA: The Johns Hopkins University Press.

52 IUCN. 2001 *IUCN Red List categories and criteria*, Version 3.1. Gland, Switzerland: IUCN.

53 Gotelli, N. J. 2001 Research frontiers in null model analysis. *Glob. Ecol. Biogeogr.* **10**, 337–343. (doi:10.1046/j.1466-822X.2001.00249.x)

54 Colwell, R. K., Rahbek, C. & Gotelli, N. J. 2004 The mid-domain effect and species richness patterns: what have we learned so far? *Am. Nat.* **163**, E1–E23. (doi:10.1086/382056)

55 Rahbek, C., Gotelli, N. J., Colwell, R. K., Entsminger, G. L., Rangel, T. F. L. V. B. & Graves, G. R. 2007 Predicting continental-scale patterns of bird species richness with spatially explicit models. *Proc. R. Soc. B* **274**, 165–174. (doi:10.1098/rspb.2006.3700)

56 Purvis, A., Gittleman, J. L., Cowlishaw, G. & Mace, G. M. 2000 Predicting extinction risk in declining species. *Proc. R. Soc. Lond. B* **267**, 1947–1952. (doi:10.1098/rspb.2000.1234)

57 Cardillo, M., Mace, G. M., Gittleman, J. L., Jones, K. E., Bielby, J. & Purvis, A. 2008 The predictability of extinction: biological and external correlates of decline in mammals. *Proc. R. Soc. B* **275**, 1441–1448. (doi:10.1098/rspb.2008.0179)

58 Fritz, S. A., Bininda-Emonds, O. R. P. & Purvis, A. 2009 Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. *Ecol. Lett.* **12**, 538–549. (doi:10.1111/j.1461-0248.2009.01307.x)

59 Gaston, K. J. & Fuller, R. A. 2009 The sizes of species' geographic ranges. *J. Appl. Ecol.* **46**, 1–9. (doi:10.1111/j.1365-2664.2008.01596.x)

60 Brown, J. H. 1984 On the relationship between abundance and distribution of species. *Am. Nat.* **124**, 255–279. (doi:10.1086/284267)

61 Rodrigues, A. S. L. *et al.* 2004 Effectiveness of the global protected area network in representing species diversity. *Nature* **428**, 640–643. (doi:10.1038/nature02422)

62 Laurance, W. F., Cochrane, M. A., Bergen, S., Fearnside, P. M., Delamonica, P., Barber, C., D'Angelo, S. & Fernandes, T. 2001 The future of the Brazilian Amazon. *Science* **291**, 438–439. (doi:10.1126/science.291.5503.438)

63 Soares-Filho, B. S. *et al.* 2006 Modelling conservation in the Amazon basin. *Nature* **440**, 520–523. (doi:10.1038/nature04389)

64 Visconti, P. *et al.* 2011 Future hotspots of terrestrial mammal loss. *Phil. Trans. R. Soc. B* **366**, 2693–2702. (doi:10.1098/rstb.2011.0105)

65 Ceballos, G., Ehrlich, P. R., Soberon, J., Salazar, I. & Fay, J. P. 2005 Global mammal conservation: what must we manage? *Science* **309**, 603–607. (doi:10.1126/science.1114015)

66 Rondinini, C., Wilson, K. A., Boitani, L., Grantham, H. & Possingham, H. P. 2006 Tradeoffs of different types of species occurrence data for use in systematic conservation planning. *Ecol. Lett.* **9**, 1136–1145. (doi:10.1111/j.1461-0248.2006.00970.x)

67 Smith, R. J., Verissimo, D., Leader-Williams, N., Cowling, R. M. & Knight, A. T. 2009 Let the locals lead. *Nature* **462**, 280–281. (doi:10.1038/462280a)

68 Orme, C. D. L. *et al.* 2005 Global hotspots of species richness are not congruent with endemism or threat. *Nature* **436**, 1016–1019. (doi:10.1038/nature03850)

69 Ceballos, G. & Erlich, P. R. 2006 Global mammal distribution, biodiversity hotspots, and conservation. *Proc. Natl Acad. Sci. USA* **103**, 19 374–19 379. (doi:10.1073/pnas.0609334103)

70 Rondinini, C. *et al.* 2011 Reconciling global mammal prioritization schemes into a strategy. *Phil. Trans. R. Soc. B* **366**, 2722–2728. (doi:10.1098/rstb.2011.0112)