Ecomorphological disparity of small carnivore guilds

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Running title: ECOMORPHOLOGICAL DISPARITY OF SMALL CARNIVORE GUILDS

Summary

Mammalian species composition might change in relation to biotic or abiotic factors depending on the scale of investigation. Ecomorphology is one of the tools that can be employed to understand how species composition changes through space and time. Here, the morphological diversity of small carnivore guilds (defined as a pool of carnivoran species whose body mass is <7 kg) is explored using 2D geometric morphometrics of mandibles belonging to 61 species. A strong taxonomic signal emerges by looking at mandibular morphospace so that separation of carnivoran families is apparent. Mustelids are the most distinct, being characterised by a short and curved corpus mandibulae, while felids exhibit a typical hypercarnivore mandible with no crushing molar area. Overlap occurs between canids, viverrids and herpestids possibly in relation to their generalized feeding habits and killing behaviours. When species are grouped according to their presence/absence into six carnivoran species-rich ecosystems, an ecogeographical pattern occurs. Guilds from higher latitudes such as Yellowstone (USA) and Krokonose (Europe) together with the Kruger (South Africa) assemblage are highly depleted of mandibular morphotypes. In contrast, guilds from tropical areas (Gunung Lensung, Indonesia; Yasuni, Ecuador and La Amistad, Panama) exhibit high diversity of mandibular shapes corresponding to higher values of morphological disparity. This latter parameter correlates positively with precipitation variables, supporting a strong influence of climate on historical community assembly of small carnivore guilds. Clearly, small carnivores can play a key role in ecosystem functioning and more theoretical work is needed to better identify this at multiple spatial and temporal scales.

Key Words: climate, community assemblage, geometric morphometrics, mandible shape, morphospace, Mustelidae

Introduction

Ecological differences between animal species provide compelling evidences in understanding their distribution through space and time (Rosenzweig, 1995). If on one side abiotic factors influence species ecology and distribution, on the other side biotic interactions act as a balancing ecological force that might generate unpredictable patterns. In this regard, mammals of the order Carnivora received considerable attention because they are generally secondary consumers and apex predators in many trophic chains and they include species with a high degree of ecological interactions (Gittleman, 1985; Donadio & Burskik, 2006; Davies *et al.*, 2007). Such interactions are significantly documented by direct or indirect competition between taxa due to overlap in trophic niche or spatial selection (Palomares & Caro, 1999).

On a evolutionary time scale, the interplay of abiotic and biotic factors is considered the main driving force of carnivoran morphological diversification (Van Valkenburgh, 1999; Wesley-Hunt, 2005; Goswami, 2010), supporting a direct link between carnivorans' ecology and morphology. The term ecomorphology well describes this link (Wainwright, 1994): species are functional units within ecosystems and their function is determined by their organismal structures (Polly, 2010; Polly *et al.*, 2011). This innovative ecological concept allows species-specific phenotypes to be re-interpreted into a wider context of community analyses. By looking at functional morphology and how it varies across species, it is possible to predict the potential impact of abiotic and biotic factors on animal communities.

Distribution of carnivoran ecomorphologies can change across the continents (Werdelin & Wesley-Hunt, 2010) although it appears to be unchanged over time when only large taxa are considered (Van Valkenburgh, 1985, 1988, 1995; Meloro, 2011a). Here, I investigate ecomorphologies of small carnivorans (hereafter small carnivores) across different ecosystems in order to identify abiotic or biotic factors responsible for their current assemblage within communities.

The small carnivores

Defining small carnivores can be a challenge due to the broad ecological and biological diversity. The suffix “large” or “small” relates to how humans perceive animal species. The grey wolf, *Canis lupus*, the tiger, *Panthera tigris*, the lion, *Panthera leo*, or the spotted hyena, *Crocuta crocuta*, are generally associated with large fierce beasts, but smaller forms such as the omnivorous red fox, *Vulpes vulpes*, become difficult to categorize.

The concept of guild (Root, 1967) can help to clarify such an issue because it groups all species capable of exploiting the same resource in a similar way. Simberloff & Dayan (1991) provided a broad overview of the use and misuse of guilds, especially in the carnivoran literature, and there is no right or wrong guild definition. Van Valkenburgh (1985, 1988, 1989) pioneered the use of the term “large” carnivores as group of Carnivora that includes all species whose average body weight is >7 kg. On the other hand, Carbone *et al.* (1999) identified an eco-physiological threshold in carnivoran species bigger than 21.5 kg that are generally apex predators with a strong functional role within an ecosystem. Are there any thresholds to define small carnivore guilds? Friscia *et al.* (2006) studied “small” carnivoran ecomorphologies including all species weighing <10 kg, while Roemer *et al.* (2009) recently grouped small carnivores as “mesopredators” whose body mass is <15 kg.

Defining the “small” threshold might be problematic, and here I have considered 7 kg as a valid ecomorphological threshold. Due to the main focus on the carnivoran mandible shape, this value is highly appropriate because all taxa above or below this threshold show distinct mandibular morphologies irrespective of their phylogenetic relatedness (Meloro & O’Higgins, 2011). Such a definition is operationally useful as it provides a direct link with previous studies on carnivoran morphological diversity over space and time (Van Valkenburgh, 1985, 1988, 1989; Meloro, 2011a). Consequently, small carnivores are defined here as all members of the order Carnivora whose average body weight is <7 kg, including taxa from the tiny least weasel, *Mustela nivalis*, that weigh a few hundred grams to the relatively large northern raccoon, *Procyon lotor* (6.4 kg; Gittleman, 1985).

Mandibular shape in Carnivora

The mandible has a dual function in the mammalian skeleton: 1. it provides support to the developing dentition; 2. it provides attachment to the main masticatory muscles (temporalis, masseter and zygomaticomandibularis) (Herring, 1980, 1993). Both these functions are integrated parts of the complex feeding system and can be used to predict feeding adaptations from skeletal morphology only. Early anatomical investigations by Herring & Herring (1974), Greaves (1983, 1985) and Radinsky (1981a,b, 1982) identified a significant association between mandibular morphology and diet in mammals in general and Carnivora in particular. Interestingly, such association did not emerge directly from mandibular metric data that are better descriptors of species' taxonomic affiliation (Crusafont-Pairó & Truyols-Santonja, 1957).

In spite of the significant progresses made in the quantification of complex biological shapes (Adams *et al.*, 2004, 2013; Lawing & Polly, 2009), ecomorphological patterns within Carnivora are still remarkably unchanged: taxonomic differences always emerge when describing mandibular (and skull) morphology, while shape differences between dietary groups are subtle especially after phylogenetic relatedness is taken into account (Meloro *et al.*, 2008, 2011; Figueirido *et al.*, 2010, 2011, 2013; Meloro & O'Higgins, 2011; Prevosti *et al.*, 2012). This is due to the strong interplay between carnivoran feeding adaptations and clade differentiation (Crusafont-Pairó & Truyols-Santonja, 1956, 1957, 1958; Meloro & Raia, 2010): many feeding ecologies can be specific to certain taxonomic groups (e.g. all felids show hypercarnivorous craniodental morphologies related to their strictly meat-eating diet). In particular, the expansion or reduction of molar crushing vs. slicing area (Van Valkenburgh, 1989) drives such patterns of dietary differentiation in Carnivora and it significantly describes differences in mandibular morphologies across species (both small and large, see Popowics, 2003; Friscia *et al.*, 2006; Meloro, 2011b; Asahara, 2013).

Ecomorphological disparity

Since mandible shape is made up of a complex suite of traits, it requires high dimensional data (e.g. a suite of multiple measurements or functional ratios) to be described in detail. Multivariate techniques such as Principal Component Analysis reduce such data into orthogonal vectors that generally describe what is called a “morphospace”. Species within the morphospace are dots whose distribution can possibly be influenced by multiple factors.

Foote (1992, 1993) introduced disparity as a way to measure and describe species distributions in a morphospace. Disparity quantifies the morphospace volume occupied by a specific set of taxa. This metric was generally employed to investigate macroevolutionary patterns such as the relative expansion or contraction of some particular clades relative to others. For Carnivora, Van Valkenburgh (1999) identified a stasis in ecomorphological disparity through time, while Holliday & Steppan (2004) supported a smaller morphospace occupation by hypercarnivorous (strictly meat-eating) species relative to other ecomorphological groups. A recent study by Werdelin & Wesley-Hunt (2010) confirmed such findings although they identified less ecomorphological disparity for canids compared to other clades. Similar disparity values occurred for carnivoran species from different continents. Accordingly, disparity is here computed as a measure of the small carnivore guild distributions across different continents in the mandibular morphospace. Ecogeographical patterns are expected to occur because previous studies showed that disparity of geographically distinct mammalian assemblages changes with latitude (Shepherd, 1998).

Methods

Mandibles belonging to 61 species of Carnivora were photographed in lateral view and subsequently analysed using the software tpsDig2 (Rohlf, 2010a). This is a subset of data collected by Meloro & O'Higgins (2011) and includes wild-captured adult specimens representative of small (<7 kg) taxa housed at the Natural History Museum of London. Species selection was drawn from lists of six carnivoran species-rich terrestrial ecosystems (Bio Inventory, source: http://www.ice.ucdavis.edu/bioinventory/bioinventory.html): Krokonose, Czech Republic (*n* = 12); Yellowstone, USA (*n* = 8); Gunung Lensung, Indonesia (*n* = 18); Kruger National Park, South Africa (*n* = 12); Yasuni, Ecuador (*n* = 10) and La Amistad, Panama (*n* = 12) (Table 5.1). Intraspecific variation was not explored here according to other ecomorphological studies that looked at macroevolutionary (i.e. above species level) patterns within Carnivora (e.g. Van Valkenburgh, 1985, 1988, 1989; Christiansen & Adolfssen, 2005; Evans *et al.*, 2007; Polly & MacLeod, 2008; Meloro & O'Higgins, 2011; Meloro, 2011a,c).

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Two-dimensional (2D) coordinates of 14 landmarks (lnd) were recorded on each mandibular photograph using tpsDig2 (Rohlf, 2015; Figure 5.1). The landmarks functionally describe anatomical features including canine (lnd 1–2), premolar row (lnd 3–4), molar slicing (lnd 4–5) and crushing (lnd 5–6) area, coronoid (lnd 7), condyle (lnd 8–9), and angular process (10–11), as well as mandibular corpus depth (lnd 12–14). Meloro (2011b) and Meloro & O'Higgins (2011) consistently proved the existence of an association between this shape configuration and feeding adaptations in extant and fossil Carnivora.

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Generalized Procrustes Analysis (Rohlf & Slice, 1990) was employed to translate, rotate and scale the 2D landmark coordinates to a unit centroid size (i.e. the square root of the sum of the squared distances of a set of landmarks from the configuration centroid; Bookstein, 1989). The new registered coordinates (i.e. procrustes coordinates) were projected into thin plate spline function, and a weight matrix of affine (Uniform) and non-affine (Partial Warps) components was generated. Relative Warp Analysis (RWA) was subsequently employed using tpsRelw (Rohlf, 2015) to identify orthogonal vectors (Principal Components, here named Relative Warps) that summarise shape variation described by the elements of the weight matrix. Such a procedure detects main shape differences (quantifiable also as procrustes distances) within the morphospace via thin plate spline: deformation grids applied at the onset of each RW extreme score summarize shape deformations from the un-deformed score positioned at the origin of each RW axis (the consensus configuration).

Specimens were labelled according to taxonomic affiliation and geographical guild membership (see Meloro, 2011a) to scrutinize patterns of morphospace occupation by small carnivores. Multiple analysis of variance (MANOVA) was employed to test whether taxonomic groups differ significantly in mandible shape using Relative Warp scores as dependent and family as factor (Meloro *et al.*, 2008). The morphological disparity (Foote, 1992, 1993) was computed to quantify morphospace volume occupied by each geographical guild. In geometric morphometrics, disparity is obtained as the sum of squared procrustes distances from each species to the grand group mean divided by the number of group members minus 1 (Zelditch *et al.,* 2003, 2004). This is exactly equivalent to the sum of variances obtained from Relative Warp scores for each identifiable group (in this case the geographic guilds). By using the software IMP (Zelditch *et al.*, 2004), a series of 999 permutations was computed each time to identify 95% confidence intervals around the morphological disparity values. A two-group permutation test was also employed to detect whether differences in disparity values between groups were larger or smaller than expected by chance.

For each geographical guild, factors such as bioclimatic variables and number of species within taxonomic groups potentially predated by small carnivores (Rodentia, Lagomorpha and Marsupialia; Ewer, 1973) were also quantified using WorldClim database from DIVA GIS (Hijmans *et al.*, 2005) and species lists drawn from the Bio Inventory. Those factors are expected to possibly influence morphospace occupation and volume of small carnivore guilds (see Meloro, 2011a for the case of large carnivores). Due to the small number of guilds analysed, a Spearman's rank correlation test was employed to explore any possible association between morphological disparity and climatic or biotic factors (i.e. number of prey species identified in each guild; Meloro, 2011).

Results

Relative Warp Analysis extracted 24 orthogonal axes with the first nine explaining altogether ~95% of the shape variance. The first two Relative Warps explained 34.39% and 22.49% shape variances, respectively (Figure 5.2). These axes describe clear partitioning of broad taxonomic groups: all mustelids occupy positive RW1 scores and negative RW2 scores, felids show intermediate RW1 scores and highly positive RW2 scores, while canids, herpestids and viverrids are distinguished for their generally negative RW1 scores; procyonids occupy all areas of the morphospace. MANOVA confirmed such a significant partitioning of RW1/2 morphospace areas by family groups (Wilk's lambda = 0.1326, F = 18.86, df = 10, 108, $p < 0.0001$) with mustelids and felids being the most different groups of all the other taxonomic combinations (Table 5.2).

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RW1 describes (from negative to positive scores) the relative shortening of the corpus due to a smaller premolar row and a curved corpus profile detectable in mustelids. The ramus mandibulae is tall and slender in this group, while it becomes enlarged horizontally and short vertically in small feliform carnivorans such as herpestids and viverrids at the negative RW1 scores. RW2 correlates with changes in the main position of landmark 5 that separates the molar slicing from the crushing area, thus determining the unique condition of hypercarnivorous felids that occupy extreme positive scores on this axis. The ramus mandibulae is also projected more posteriorly in species at positive RW2, evidencing an almost straight profile for the corpus that is more curved posteriorly in species at the negative end of this axis (Figure 5.2).

When species are labelled according to their guild affiliation, distinct patterns in morphospace occupations occur: the guild of Yellowstone is highly depleted in morphotypes together with that of Kruger (Figure 5.3). Morphologically richer small carnivore guilds are from tropical areas such as La Amistad and Gunung Lensung that exhibit also the higher number of taxa.

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Morphological disparity analysis partially confirmed this trend with Kruger and Yellowstone showing the smallest values and La Amistad and Gunung Lensung the highest (Figure 5.4). The 95% confidence intervals are broad and therefore no significant differences were detected in disparity values except between Gunung Lensung and Yellowstone, whose disparity difference is higher than expected by chance 95% of the times (Table 5.3). A non-parametric Spearman’ rank correlation identified a significantly positive correlation between disparity and climatic precipitation variables, while a strong negative correlation was found with numbers of lagomorph species recorded in each of the analysed ecosystems (Table 5.4, Figure 5.4).

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Discussion

Mandible shape of small carnivores exhibits an evident taxonomic signal and this pattern is no exception in carnivoran datasets. Previous morphometric studies identified a similar degree of morphospace segregation by family both on large extant and fossil Carnivora (Meloro *et al.*, 2008; Figueirido *et al.*, 2010, 2011, 2013; Meloro, 2011a,b, 2012) and all extant Carnivora *sensu lato* (Meloro & O'Higgins, 2011). The most distinct groups of small carnivores are the hypercarnivorous felids and the mustelids (Figure 5.2): on one side, small predatory cats show more reduced molar crushing area than the rest of small carnivoran clades while mustelids are distinguished by a more posteriorly curved corpus mandibulae. Such main feature of mandibular shape variation is in agreement with earlier investigations on carnivoran skulls (see Radinsky, 1981a,b, 1982) that especially highlighted the unique mustelid condition of masticatory muscles arrangement: the posterior temporalis is generally more developed in this group, thus imposing an almost straight and anteriorly curved configuration in the shape of the ramus mandibulae (Ewer, 1973). This configuration influences to some extent also the glenoid fossa – a structure that provides articulation between the cranium and the mandibular condyle to allow more efficient masticatory loading during the carnassial (lower m1 and upper P4) shear bite. The m1 slicing area is also enlarged as typical of highly carnivorous, predaceous forms (e.g. weasels) but not in such an extreme way as in the felids.

On the opposite area of the mandibular morphospace, small canids, herpestids and viverrids show considerable overlap. This pattern was already highlighted by Meloro & O'Higgins (2011) and it appears to be the result of more generalized omnivorous feeding adaptations. Small canids, here represented by fox-like morphotypes (e.g. *Vulpes vulpes* in Figure 5.2), are mostly distinguished by the negative RW2 scores. On the other hand, the hypercarnivorous bush dog, *Speothos venaticus*, together with the bat-eared fox, *Otocyon megalotis*, occupy more positive RW2 scores towards felids' morphospace (Figure 5.2). The bush dog scores close to the origin of RW1 axis due to its highly developed molar slicing area (Van Valkenburgh, 1991), while the bat-eared fox occupies a more negative RW1 score due to its longer molar row with undifferentiated m1 as a result of its insectivorous feeding habit (Ewer, 1973).

Viverrids and herpestids also occupy negative RW1 scores and they show a degree of morphospace partitioning. Wesley-Hunt *et al.* (2010) identified an overlap in ecomorphologies of these two families although this pattern is not detected here, with viverrids being characterised by a much thinner mandibular corpus especially below the molars (extreme negative RW1 scores and slightly negative RW2), while herpestids have a thicker corpus below the enlarged molar crushing area (less negative RW1 and more negative RW2). A thick corpus is correlated with hard food consumption in Carnivora although this is mostly based on studies about large bone cracker carnivorans (Werdelin, 1989; Raia, 2004; Meloro *et al.*, 2008; Figueirido *et al.*, 2013). The diet of omnivorous and insectivorous mongooses might also include crabs (e.g. the marsh mangoose, *Atilax paludinosus*) or other relatively hard dietary items such as insect exoskeletons (Ray, 1997) that require longer and more rapid masticatory cycles. These cycles impose higher masticatory loadings when compared to more predatory viverrids that mostly focus their diet on small mammals and other vertebrates (Ewer, 1973).

Another mandibular feature that distinguishes viverrids from herpestids is the much longer angular process in the former group (Figure 5.2). A long angular process suggests more-developed superficial masseter fibres whose action includes a forward pulling component: this could be linked to the killing behaviour of genets that use a series of rapid but imprecise bites in contrast to the use of a single precise bite in mongooses (Ewer, 1973).

Procyonids also show an interesting pattern in morphospace occupation with both omnivorous coatis, *Nasua* spp., clustering within viverrids' morphospace (the two white circles that occupy negative RW1 scores and positive RW2 scores; Figure 5.2). The northern raccoon is very close to the consensus configuration (i.e. the origin of RW1/2 axes), while the frugivorous kinkajou, *Potos flavus*, plots near the tayra, *Eira barbara*, a South American mustelid (Figure 5.2). Procyonids exhibit a very high polymorphism in the mandible shape as a possible result of their broad dietary niche differentiation through time. Early members of Procyonidae had a generalized dentition that allowed them to evolve distinct morphologies in relation to a more plant-dominant food consumption (Koepfli *et al.*, 2007). The frugivorous *Potos flavus* has always been considered a peculiar form (Figueirido *et al.*, 2010) that here occupies extreme positive scores of RW1 due to its musteloid corpus curvature and expansion of molar crushing area.

Even if taxonomy and (to some extent) diet are recognised as some of the main factors explaining species distribution within the small carnivore mandibular morphospace, no geographic patterns become apparent. Both viverrids and herpestids are evidently absent in guilds from Europe and North America (Figure 5.3) that exhibit a higher number of mustelid morphotypes. The Yellowstone guild lacks small felid morphotypes possibly due to the generalized niches of the ‘large’ bobcat, *Lynx rufus*, and the Canadian lynx, *Lynx canadensis*, whose diet can focus mainly on lagomorphs and small rodents. The South African guild shows an opposite trend with a community highly depleted of mustelid morphotypes but enriched with viverrids and herpestids, while Asiatic, Central and South American morphospaces show a homogenous species distribution in all areas of the morphospace (Figure 5.3). Ewer (1973) and Hunt (1996) already highlighted the mustelid/viverrid–herpestid pattern observed in the Old World and the mandibular morphospace confirms how long-term evolutionary processes generated the species distribution we observe today. This pattern has little influence on morphological disparity which is generally low in European, North American and African guilds (Figure 5.4). The most morphologically diverse communities are detected across the tropics. This observation partially confirms previous findings by Shepherd (1998) who performed a latitudinal survey of morphological disparity in mammalian communities from North America. She concluded that at higher latitudes species have lower shape diversity than in the tropics. This trend is independent of species number, so that no correlation occurs between species richness and morphological disparity (Foote, 1992, 1993).

No association between small carnivore guild disparity and latitude or longitude was detected; however the inclusion of bioclimatic variables supports a very strong positive influence of precipitation variables. The relative impact of climate on ecomorphologies of carnivoran communities was highlighted by Polly (2010) in a survey on locomotory skeletal traits across North American species. Ecogeographical patterns are also broadly evident in the majority of mammalian groups, including small carnivores (e.g. mustelids; Meiri *et al.*, 2007). In theory, climate might influence morphological variability of small carnivore species assemblages indirectly via diversification of their potential prey (e.g. rodents). This is clearly not the case: the number of rodent species, and other small mammalian prey are not significantly correlated to small carnivore morphological disparity (Table 5.4). Only number of lagomorph species shows a negative association with disparity. Different explanations can be here considered for such a counter-intuitive pattern:

1. Number of prey species might not be a good predictor of small carnivore morphological disparity simply because it is the wrong metric to consider. Prey biomass is expected to influence more directly small predator populations and eventually their species composition via competitive exclusion (Powell & Zielinski, 1983; Norrdall & Korpimacki, 1995; St Pierre *et al.*, 2006).
2. Although lagomorphs are the focal prey species for only a small fraction of small carnivores, their abundance and diversity can strongly impact feeding behaviour of

different species within this guild. For instance, Carvalho & Gomez (2004) studied niche partitioning among four sympatric small carnivores and observed niche convergence between the red fox and the wildcat, *Felis silvestris*, during periods of abundance of wild rabbits, *Oryctolagus cuniculus*, thus facilitating their co-existence. This pattern, on a broader and longer evolutionary time scale, might have generated the negative trend we observe today: lagormorph-rich communities might support a higher richness of small carnivores (generally mustelids with higher bite forces; Christiansen & Wroe, 2007) with more similar morphotypes (hence lower disparity values).

The strong negative correlation between the number of lagomorphs and precipitation variables (with bio18, r_s = -0.99; with bio13 and bio16, r_s = -0.94) indicates variable interaction enforcing the strong impact of climate on small carnivore guilds. High precipitation in tropical areas guarantees food availability in all seasons, facilitating small carnivore to diversify in functional morphotypes (including meat eaters, frugivores, insectivores). Additionally, small carnivores include a high number of arboreal secondary consumers, whose diversity correlates strongly with tree cover (Louys *et al.*, 2011) and precipitation (Polly, 2010).

The mandibular shape morphospace provides a clear starting point to further explore patterns and processes that influence small carnivore species assemblages. If long-term evolutionary processes characterize their assembly rules, then climatic changes might be a key influence of their morphological diversity. Future studies should combine such interspecific approach with finer-scale patterns of geographical variation. More ecomorphological approaches are also needed to better identify the degree of interaction and the functional guilds within small carnivores.

Acknowledgements

I am grateful to the staff of the Natural History Museum, London for their invaluable help during the course of my research visits. In particular P. Jenkins, L. Tomsett, R. Portela-Miguez, A. Salvador, and D. Hills kindly supported me through the years. A big thank you to P. Raia, A. Loy and P. O'Higgins who introduced me to morphometrics and the world of small carnivores. E. Do Linh San kindly invited me to participate to this book, while M. Asahara, J.J. Sato, and L. Werdelin strongly improved the quality and style of this manuscript.

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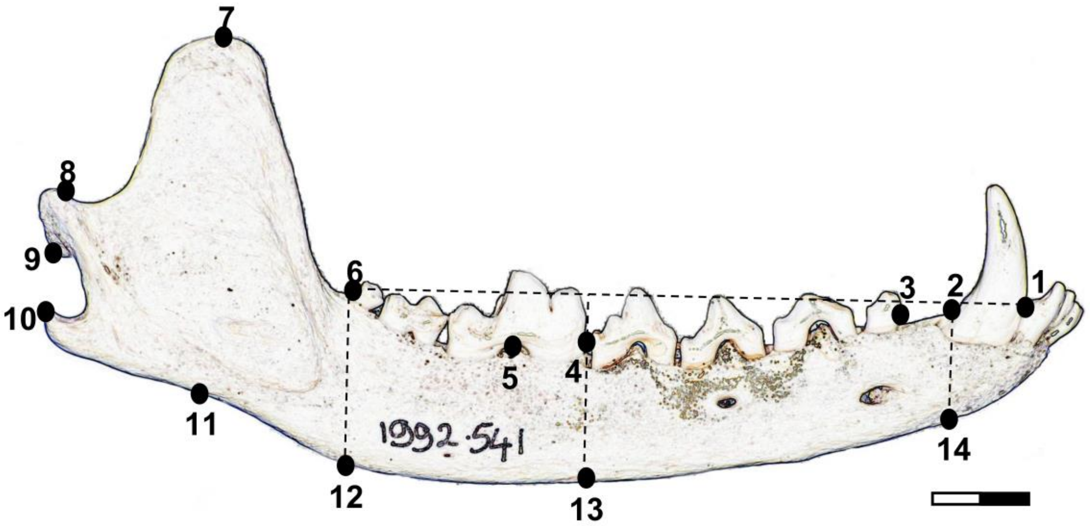

Figure 5.1 The position of landmarks on a mandible outline of red fox, *Vulpes vulpes* (NHM 1992.541). 1–2: anteroposterior diameter of c1; 2–3: diastema length; 3–4: length of the premolar row; 4–6: length of the molar row; 5: projection of the protocone cusp on the m1 baseline; 2–14: thickness of the mandibular corpus under the canine; 4–13 and 6–12: thickness of the mandibular corpus under molar row; 7: tip of the coronoid process; 8–9: maximum depth of the condylar process (Processus condylaris); 10: most lateral extreme point of angular process; 11: the ventral extreme of angular process. Total scale bar equals 1.0 cm.

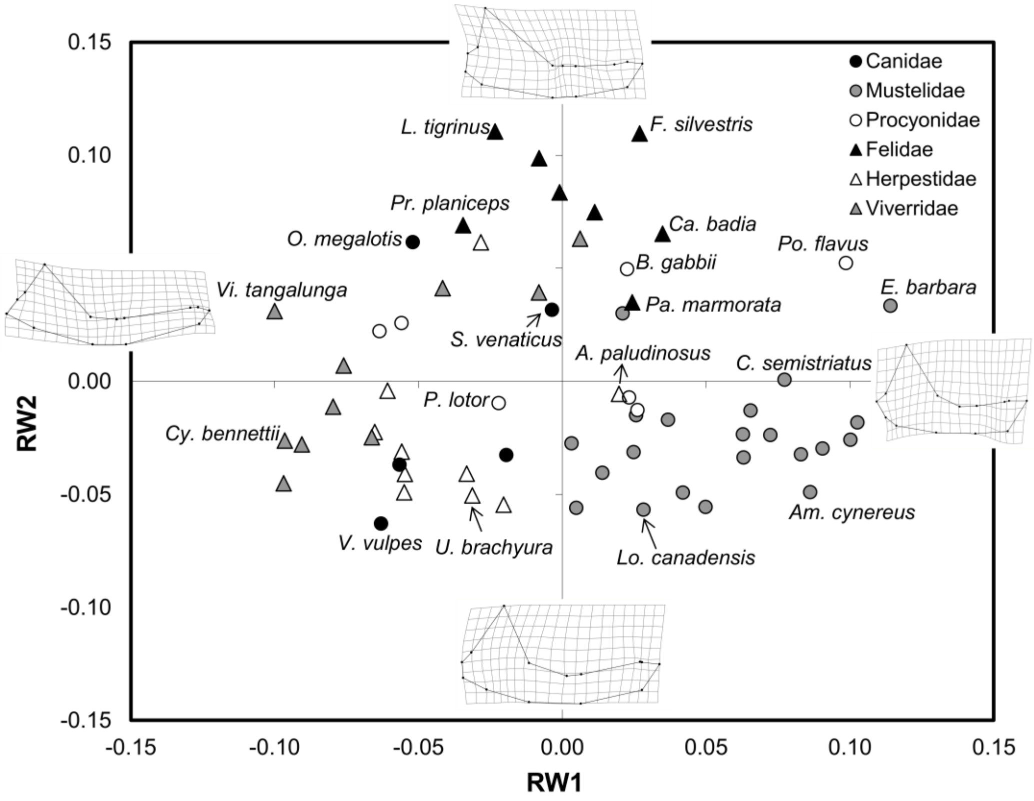

Figure 5.2 Scatter plot of RW1 vs. RW2 for a sample of mandibles belonging to 61 small carnivore species (labelled according to family). Transformation grids visualize shape deformation relative to the mean (regular grid, not shown) at the positive and negative extremes of Relative Warp (RW) axes.

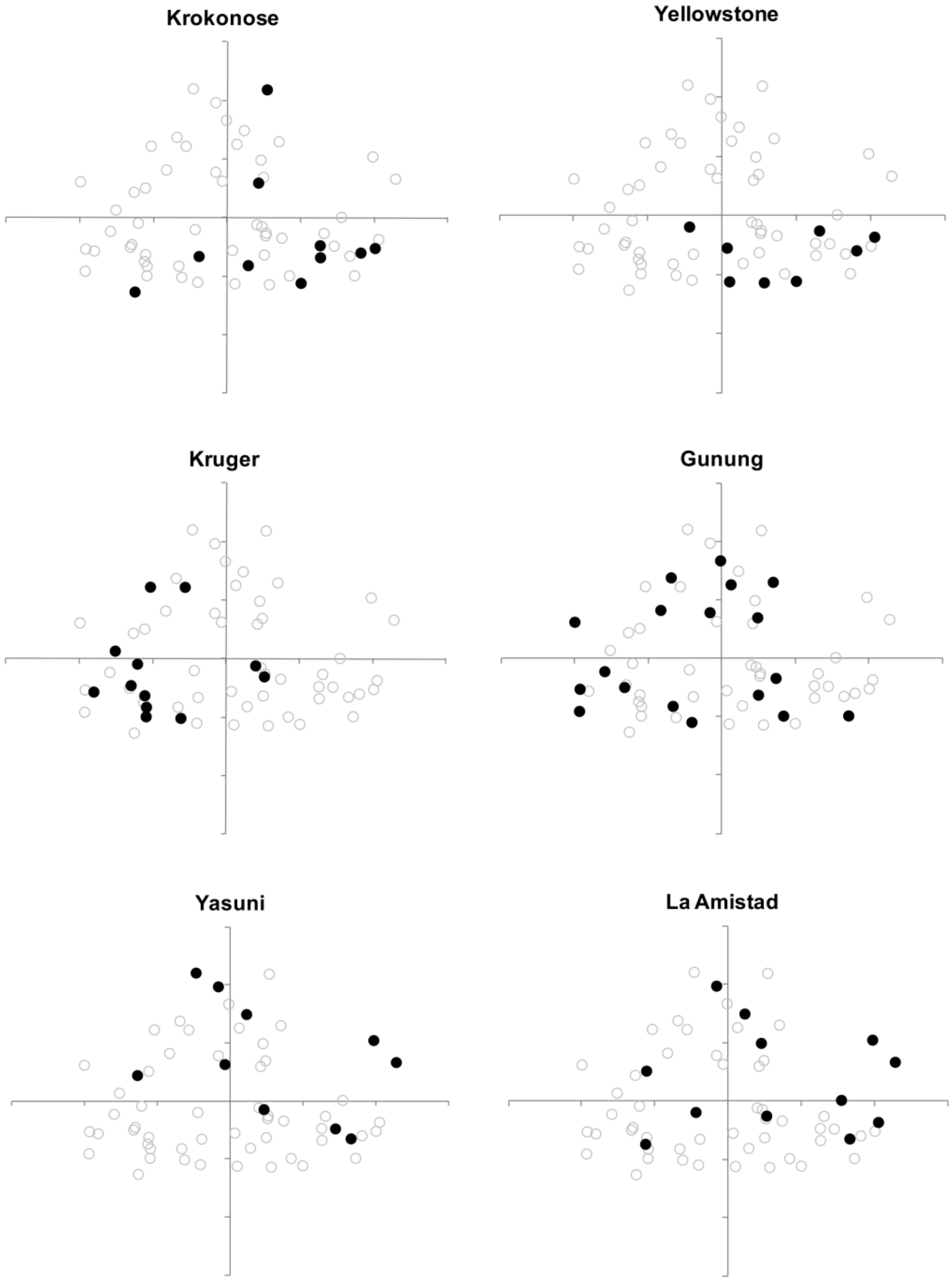

Figure 5.3 Scatter plots of RW1 (x-axis, scale -0.15 / +0.15) vs. RW2 (y-axis, scale -0.15 / +0.15) showing each extant small carnivore guild highlighted by closed circles: Krokonose, Czech Republic (*n* = 12); Yellowstone, USA (*n* = 8); Kruger National Park, South Africa (*n* = 12); Gunung Lensung, Indonesia (*n* = 18); Yasuni, Ecuador (*n* = 10); and La Amistad, Panama (*n* = 12).

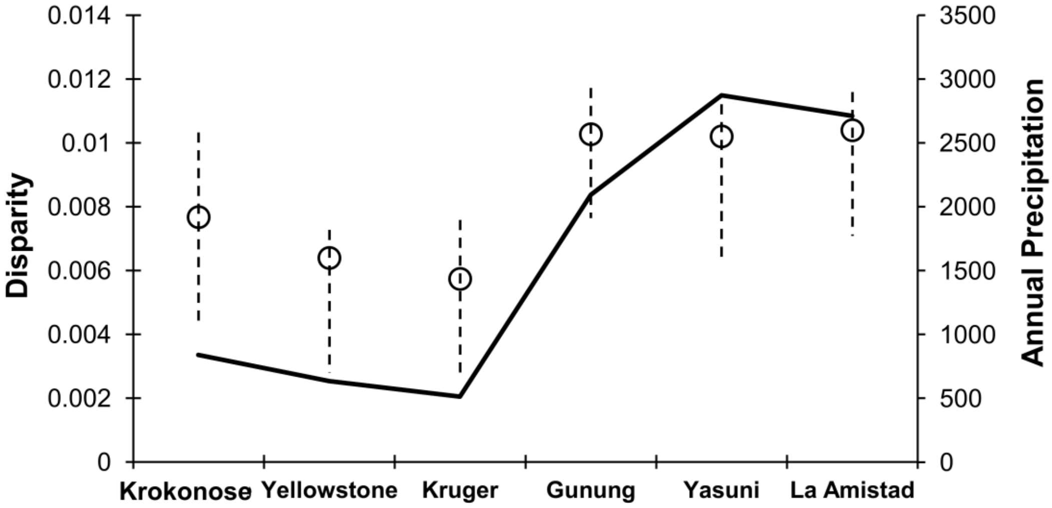

Figure 5.4 Disparity values (circles) computed for morphospace of each extant small carnivore guild superimposed on annual precipitation values (in mm/year). The vertical dotted bars correspond to 95% confidence intervals around morphological disparity values after 999 randomizations. The solid line shows precipitation values from different localities.

Table 5.1 List of small carnivore species guilds geographically partitioned.

Krokonose	Yellowstone	Kruger	Gunung Lensung	Yasuni	La Amistad
Felis silvestris	*Lontra canadensis*	*Atilax paludinosus*	*Amblonyx cinereus*	*Eira Barbara*	*Bassaricyon gabbii*
Martes foina	*Martes americana*	*Galerella sanguinea*	*Arctogalidia trivirgata*	*Galictis vittata*	*Bassariscus sumichrasti*
Martes martes	*Martes pennanti*	*Genetta genetta*	*Catopuma badia*	*Herpailurus yaguarondi*	*Conepatus semistriatus*
Mustela erminea	*Mephitis mephitis*	*Genetta tigrina*	*Cynogale bennettii*	*Leopardus tigrinus*	*Eira barbara*
Mustela eversmannii	*Mustela erminea*	*Helogale parvula*	*Hemigalus derbyanus*	*Leopardus wiedii*	*Galictis vittata*
Mustela nivalis	*Mustela frenata*	*Herpestes ichneumon*	*Lutra sumatrana*	*Mustela africana*	*Herpailurus yaguaroundi*
Mustela putorius	*Neovison vison*	*Ichneumia albicauda*	*Martes flavigula*	*Nasua nasua*	*Leopardus wiedii*
Neovison vison	*Procyon lotor*	*Ictonyx striatus*	*Mustela nudipes*	*Potos flavus*	*Mustela frenata*
Nyctereutes procyonoides		*Mungos mungo*	*Paguma larvata*	*Procyon cancrivorus*	*Nasua narica*
Vulpes vulpes		*Otocyon megalotis*	*Paradoxurus hermaphroditus*	*Speothos venaticus*	*Potos flavus*
		Paracynictis selousi	*Pardofelis marmorata*		*Procyon lotor*
		Rhynchogale melleri	*Prionailurus bengalensis*		*Urocyon cinereoargenteus*
			Prionailurus planiceps		
			Prionodon linsang		
			Urva brachyura		
			Urva semitorquata		
			Viverra tangalunga		
			Viverricula indica		

Table 5.2 Probability values for pairwise Hotelling's t square comparisons performed using the first two RWs are shown below the diagonal. The *p*-values with Bonferroni correction are shown above the diagonal. Significant differences ($p < 0.05$) are indicated in bold.

	Canidae	**Felidae**	**Herpestidae**	**Mustelidae**	**Procyonidae**	**Viverridae**
Canidae	-	**0.04**	1.00	**<0.0001**	1.00	1.00
Felidae	**<0.001**	-	**<0.0001**	**<0.0001**	0.11	**<0.001**
Herpestidae	0.65	**<0.0001**	-	**<0.0001**	0.43	0.36
Mustelidae	**<0.0001**	**<0.0001**	**<0.0001**	-	**<0.001**	**<0.0001**
Procyonidae	0.17	**0.01**	**0.03**	**<0.0001**	-	0.09
Viverridae	0.26	**<0.0001**	**0.02**	**<0.0001**	**0.01**	-

Table 5.3 Two-group permutation tests for differences in disparity values between small carnivore guilds. Below the diagonal are differences in disparity in absolute values. Above the diagonal are *p*-values after 999 permutations. Gunung Lensung is here abbreviated as "Gunung".

	Krokonose	**Yellowstone**	**Kruger**	**Gunung**	**Yasuni**	**La Amistad**
Krokonose	-	0.95	0.93	0.41	0.93	0.90
Yellowstone	0.0013	-	1.00	**0.05**	0.93	0.82
Kruger	0.0019	0.0007	-	0.24	0.85	0.60
Gunung	0.0026	0.0039	0.0045	-	1.00	1.00
Yasuni	0.0025	0.0038	0.0045	0.0001	-	1.00
La Amistad	0.0027	0.0040	0.0047	0.0001	0.0002	-

Table 5.4 Non-parametric Spearman's rank correlation coefficients (r_s) and p-values between potential prey or bioclimatic variables and morphological disparities of six small carnivore guilds.

Variables	r_s	p
Number of Insectivora	-0.72	0.12
Number of Rodentia	0.77	0.10
Number Lagomorpha	**-0.88**	**0.05**
Total number of prey	0.66	0.14
Total number of marsupials	0.60	0.18
bio1 = Annual mean temperature	0.14	0.71
bio2 = Mean diurnal range (mean of monthly [max. temp - min. temp])	-0.43	0.36
bio3 = Isothermality (bio2/bio7)(× 100)	0.54	0.24
bio4 = Temperature seasonality (standard deviation × 100)	-0.66	0.14
bio5 = Max. temperature of warmest month	-0.26	0.56
bio6 = Min. temperature of coldest month	0.55	0.27
bio7 = Temperature annual range (bio5 - bio6)	-0.60	0.18
bio8 = Mean temperature of wettest quarter	-0.03	1.00
bio9 = Mean temperature of driest quarter	0.37	0.42
bio10 = Mean temperature of warmest quarter	-0.03	1.00
bio11 = Mean temperature of coldest quarter	0.43	0.36
bio12 = Annual precipitation	**0.83**	**0.03**
bio13 = Precipitation of wettest month	**0.89**	**0.02**
bio14 = Precipitation of driest month	**0.83**	**0.03**
bio15 = Precipitation seasonality (coefficient of variation)	0.09	0.80
bio16 = Precipitation of wettest quarter	**0.89**	**0.02**
bio17 = Precipitation of driest quarter	**0.83**	**0.03**
bio18 = Precipitation of warmest quarter	**0.94**	**0.01**
bio19 = Precipitation of coldest quarter	0.77	0.10