Worldwide diversity in mammalian life histories: environmental realms and evolutionary adaptations

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Abstract

Mammalian life history strategies can be characterized by a few axes of variation, conforming a space where species are positioned based on the life history strategies favoured in the environment they exploit. Yet, we still lack global descriptions of the diversity of realized mammalian life history and how this diversity is shaped by the environment. We used six life history traits to build a life history space covering worldwide mammalian adaptation, and we explored how environmental realms (land, air, water) influence mammalian life history strategies. We demonstrate that realms are tightly linked to distinct life history strategies. Aquatic and aerial species predominantly adhere to slower life history strategies, while terrestrial species exhibit faster life histories. Highly encephalized terrestrial species are a notable exception to these patterns. Further, we show that different mode of life may play a significant role in expanding the set of strategies exploitable in the terrestrial realm. Additionally, species transitioning between terrestrial and aquatic realms, such as seals, exhibit intermediate life history strategies. Our results provide compelling evidence of the link between environmental realms and the life history diversity of mammals, highlighting the importance of differences in mode of life to expand life history diversity.

Introduction

The diversity of mammalian adaptations, ranging from the fast and semelparous (reproducing only once in a lifetime; Stearns 1992) life history of antechinus to the slow and long lives of bowhead whales (Perrin *et al.* 2009) has allowed mammals to occupy all the land (Burgin *et al.* 2018; Grossnickle *et al.* 2019), exploit air (Babich Morrow *et al.* 2021; Maina 2000), and even inhabit the sea (Davis 2019). Despite this wide ecological radiation (Grossnickle *et al.* 2019), evolutionary history and energetic constraints limit the set of life history strategies (*i.e.*, combinations of life history traits) that are viable in nature (Grime & Pierce 2012; Stearns 1992). These limits restrict mammalian investments in survival, growth, and reproduction to two major dimensions of life history trait variation (Carmona *et al.* 2021b; Gaillard *et al.* 1989; Healy *et al.* 2019; Oli 2004). The first dimension generally encompasses the time scale of life, referred to as the fast-slow continuum (Bielby *et al.* 2007; Capdevila *et al.* 2020; Gaillard *et al.* 1989; Healy *et al.* 2019; Stearns 1992). In contrast, the second dimension depends more on the subset of species and traits considered, but generally reflects the timing and intensity of a species' reproductive investment (Bielby *et al.* 2007; Capdevila *et al.* 2020; Gaillard *et al.* 1989; Healy *et al.* 2019). While these two life history dimensions are consistently observed across studies with various species and trait subsets (Bielby *et al.* 2007; Capdevila *et al.* 2020; Gaillard *et al.* 1989), we still lack a comprehensive understanding of how mammals are organized within this broad life history space. This gap hampers exploring and quantifying realized mammalian life history diversity, preventing a thorough comprehension of similarities and differences among mammalian species (Carmona *et al.* 2021b; Pinsky *et al.* 2022).

Environmental conditions profoundly influence species' life history strategies (Grime & Pierce 2012; Southwood 1988). Variable environments, for instance, affect the pace of life of species (Tuljapurkar *et al.* 2009), selecting for delayed life cycles and longer lives compared to constant and stable environments (Grime & Pierce 2012; Tuljapurkar *et al.* 2009). Accordingly, because similar life history strategies are selected by similar environmental pressures (Grime & Pierce 2012; Southwood 1988), it is reasonable to expect a highly redundant occupation of the life history space regardless of taxonomic affiliation (Carmona *et al.* 2021b). Yet, mammals' widespread distribution across major environmental realms (*i.e.*, land, water, air) begs the question of whether mammalian life history strategies are equally represented across these three realms.

Environmental realms are characterized by distinct physical dimensions, structural properties, and environmental requirements (Pinsky *et al.* 2022; Steele 1985). Consequently, species inhabiting each specific environmental realm are under unique eco-physiological constraints not experienced by species from other realms (Pinsky *et al.* 2019; Webb 2012) that may favour different life history strategies. For instance, the energetically expensive nature of the aquatic realm imposes stringent physiological constraints on its dwellers, entailing significant investments in offspring size and specialization compared to terrestrial life (Perrin *et al.* 2009). Indeed, across different taxonomies, aquatic species pay the cost of producing precocial offspring capable of thermoregulating in water by giving birth to single individuals (Davis 2019; Perrin *et al.* 2009). Similarly, the high longevity associated to the ability of flight demands specialized structures and size, which extend gestation length and mother dependence, compared to terrestrial representatives (Babich Morrow *et al.* 2021; Barclay 1994; Maina 2000). Thus, adaptations needed to cope with realm-specific pressures seem to constraint the set of life history strategies available in a realm, while simultaneously selecting for realm-specific life history strategies.

Yet, diversity within a specific environmental realm may well be similar to the one found at the global scale (Reich *et al.* 2003; Toussaint *et al.* 2021). Evolutionary adaptations may enable species to expand ecological opportunities, mitigating the constraints of environmental realms, and thus influencing the diversity of life history strategies realized in a realm (Cox *et al.* 2021; Grime & Pierce 2012; Southwood 1988). Capacities like climbing trees or burrowing on the ground provide partial escape routes from the environmental constraints unique to terrestrial living, selecting for generally longer lifespans akin to those in flying species (Bels & Russell 2023; Healy *et al.* 2014, 2019; Mincer & Russo 2020). Similarly, larger brains typically allow species to avoid hazardous situations, selecting for slower lives compared to other terrestrial representatives (Benson-Amram *et al.* 2016; González-Lagos *et al.* 2010; Seyfarth & Cheney 2002). Therefore, adaptations facilitating the navigation of realms-specific pressures can expand the diversity of species' life history strategies present in the realm, leading to convergence across realms.

Quantifying the patterns of realized diversity across various environmental realms is crucial for revealing and understanding the complexity of mammalian life history strategies. However, identifying the ecological, environmental, and evolutionary drivers that shape mammalian diversity is challenging without a clear picture of which investments in survival, growth, and reproduction are feasible, shared, and commonly observed across realms. Without this understanding, we lack the necessary foundations to relate environmental conditions and functional adaptations to the life histories of species (Laughlin 2014; Mouillot *et al.* 2021), and we remain ill-equipped to disentangle emergent patterns in response of species to global change across different environmental realms (Pinsky *et al.* 2019).

Here, we use six life history traits representing investments in survival, growth, and reproduction for 3,438 mammalian species (53.7% of currently recognized living mammals, Burgin *et al.* 2018) to examine the influence of major environmental realms on mammalian life history strategies. In agreement with previous research (Bielby *et al.* 2007; Gaillard *et al.* 1989), we first show that two axes of variation relating to the fast-slow continuum and the reproductive strategies continuum are sufficient to explain a large proportion of mammalian life history strategies (Fig. 1a). Using this plane as a springboard, we proceed to test three hypotheses: (H1) species' position in the life history space will associate with the environmental realm they occupy, consequence of the different eco-physiological pressures acting within each major realm (Grime & Pierce 2012; Pinsky *et al.* 2022; Tuljapurkar *et al.* 2009; Webb 2012). Specifically, we expect aerial and aquatic species to be close in the life history space, with aerial species occupying portion of the life history space defined by longevous lives while aquatic species will display higher iteroparity (*i.e.*, spreading reproductive effort during a lifetime; Capdevila *et al.* 2020; Gaillard *et al.* 1989). Accordingly, given the partial adscription of semi-aquatic species to both the terrestrial and aquatic realms, (H2) species transitioning between water and land experience a blend of aquatic and terrestrial selective pressures, showing intermediate life history strategies between these two realms (Hood 2020; Perrin *et al.* 2009). Additionally, (H3) within the terrestrial realm, different mode of life will smooth terrestrial constraints, expanding the diversity in terrestrial life history strategies available on land. Specifically, species with arboreal, semi-arboreal, and fossorial mode of life will display slower life history strategies than species confined on land, overlapping with aerial species in the life history space.

Methods

Data collection and trait imputation

To characterise the mammals' life history strategies, we used the Amniote database which comprises information for ca. 18,300 species of mammals, reptiles, and birds (Myhrvold *et al.* 2015). We extracted mammalian species (N = 4,953) and selected the life history traits with the most complete information *(i.e.,* traits with records for at least 1,000 species): litter size (ls, number of offspring per reproductive event), litter per year (ly, number of litters per year), age at female maturity (fmat, time needed for female individuals to reach maturity in days), weaning length (wea, time needed to wean the offspring in days), gestation length (gest, time passing between conception and birth in days), longevity (long, individual lifespan in years) and adult body mass (bm, in grams). For finer definitions and information on traits' measurements, please refer to Myhrvold et al. (2015).

Because no trait was fully informed for all species, we imputed missing life history trait values. Recent studies have shown that imputation of individual traits allows to accurately characterize the position of species in trait spaces that are the result of combining different correlated traits (see Carmona, Tamme, et al. 2021; Carmona, Bueno, et al. 2021 for examples). Additionally, recent simulations indicate that examining patterns in space occupation built considering imputed species produces results much closer to real patterns in space occupation compared to considering only species with complete trait information (Stewart et al. 2023). Because accounting for evolutionary relationships improves the accuracy of the imputation (Penone *et al.* 2014), we downloaded mammalian phylogenies from Vertlife database (Upham *et al.* 2019). We selected the complete fossil-based set of 10,000 phylogenies and computed a single maximum clade credibility tree (MCC tree) using the *maxCladeCred* function of *'phangorn'* R package (Schliep 2011). The 135 species absent in the phylogeny but with life history information were added at the genus' root using *add.species.to.genus* function of *'phytools'* R package (Revell 2012). Species that were missing in the life history traits database were pruned.

For the imputation procedure, we selected mammalian species with information for body size and at least one of the other considered life history traits (*i.e.*, ls, ly, fmat, wea, gest, long), resulting in a subset of 3,438 species. Within this subset, 1,293 species had complete trait measurements (c.a. 37.6% of the total). Then, following Carmona, Tamme, et al. 2021, we included phylogenetic information in the imputation procedure using the first 10 phylogenetic eigenvectors derived from the MCC tree. For the imputation, we used the *missForest* function from the *'missForest'* R package (Stekhoven 2022). After the imputation, we estimated the reliability of the imputation procedure using a procedure where artificial gaps in trait data are created in species with complete information (Supplementary Methods 1). The imputation procedure accurately retrieved the real position of a species, with an average error of 2.8% of the total range for the first component and 1.7% for the second component of the functional space (see "Construction of the mammalian life history space" below). Imputations errors were consistent across orders with different level of data completeness and coverage. Previous studies have demonstrated the high reliability of estimating functional structure on datasets with significantly higher proportions of imputed data (Stewart et al. 2023).

The final procedure resulted in a dataset of 3,438 mammalian species (53.7% of currently recognized living mammals, Burgin *et al.* 2018) from 29 orders.

Ascribing species to environmental realms and mode of life

In order to have information on species adscription to the terrestrial, aerial, and aquatic realms, we downloaded information on the environment exploited by each mammal from the Worms (WoRMS Editorial Board 2020) and IUCN (IUCN 2017) databases using the R packages *'worms'*(Holstein 2018) and *'redlist'* (Chamberlain 2020), respectively. We classified mammalian species as "terrestrial" (*i.e.*, land realm) in case of unambiguous classification from both databases, whereas we limited "aerial" category (air) to powered flight species (*i.e.,* Chiroptera order). Although there is no doubt about the classification of "fully" aquatic species (*i.e.*, species that spent their entire life in water, *e.g.,* dolphins, Perrin *et al.* 2009), there is not a strict classification of semi-aquatic species (Hood 2020). Due to this, the Worms and IUCN databases classification did not match for many species. To solve this problem, we performed a finer classification of aquatic species by summarizing species' dependency on water. First, we selected all species classified as freshwater and marine in at least one of the IUCN and Worms databases. Then, we created an Aquatic Dependency Index (AD Index) to classify species as "fully" aquatic, "fully" terrestrial, or semi-aquatic. We built the AD Index answering a series of binary questions capable of summarizing the amount of time spent in water during fundamental phases of species life histories (*e.g.,* birth, mating; Supplementary methods 2). The AD Index was used to refine aquatic classification by relabelling species scoring zero in the AD Index (*i.e.,* no important parts of life are strictly constrained by water presence) as terrestrial species. Then, we classified as aquatic (hereafter aquatic) all species scoring 5 out of a maximum of 5 on the AD Index (*i.e.,* species that spent their whole life in water, like dolphins), while we classified as semi-aquatic all species scoring between 1 and 4. Out of the 3,438 mammalian species considered in our analyses, 2,634 species were classified as terrestrial (76.6% of total set of species), 661 species were classified as aerial (19.2%), 85 species were classified as aquatic (2.5%), and 58 species were classified as semi-aquatic (*i.e.,* transitional species, 1.7%).

We further classified terrestrial species according to their arboreal, semiarboreal, and fossorial mode of life by using the same classification applied in Santini, *et al.* 2022. We manually added missing information throughout a literature review (Bels & Russell 2023; IUCN 2017; UMich 2022). Out of the 2,634 species classified as terrestrial, 595 species were classified as arboreal (22.6% of terrestrial species), 175 species were classified as semiarboreal (6.6%), 117 species were classified as fossorial (4.4%), and 1,747 species were classified as ‘fully’ terrestrial (*i.e.*, confined on land, 66.3%).

Species taxonomies across all previously mentioned data tables (*i.e.*, life history traits, phylogeny, Worms, IUCN, and mode of life databases) were standardized using *gnr_resolve* function of the *‘taxize’* R package (Chamberlain & Szöcs 2013) resolving for the Global Biodiversity Information Facility (GBIF) Backbone Taxonomy.

Construction of the mammalian life history space

Body mass is a strong allometric constraint that affects the values of many other life history traits (Bielby *et al.* 2007; Jeschke & Kokko 2009; Sibly & Brown 2007). Mammals’ body mass can span from the few grams of shrews to tons for whales, and the aquatic realm strongly selects for bigger sizes compared to the terrestrial realm (Gearty *et al.* 2018). Therefore, to address life history strategies without confounding effects from different orders of magnitude, we accounted for the effect of body mass before computing the mammalian life history space. For this, we performed a series of ordinary linear regressions between single log-transformed life history traits and log-transformed species' adult body mass. Then, we extracted body mass–corrected residuals for each species from each regression (Bielby *et al.* 2007; Jeschke & Kokko 2009). Body mass–corrected residuals were further centred and scaled to homogenize their variance and residuals’ contribution to meet the requirement for subsequent analyses (Legendre & Legendre 2012). Finally, we used body mass–corrected residuals as size-corrected life history traits. The use of residuals in this context has been criticized because of the potential bias generated when different traits are related to body size; however, we found no evidence of such potential bias in our dataset (see Supplementary Methods 3; Supplementary Fig. 1).

Mapping species' position in multidimensional spaces based on trait information allows the identification of major axes of trait variation (Bueno *et al.* 2023; Díaz *et al.* 2016), as well as summarizing species' ecological strategies. We constructed the mammalian life history space by performing a principal component analysis (PCA) on the complete set of mammalian species. We retained the first two axes which together account for 75.1% of variance in mammalian life history traits (Supplementary Table 1a).

Then, we estimated the reliability of our methodological choices by comparing this life history space (*i.e.*, the scores of species in the selected number of principal components) with two other spaces: one built considering only complete set of records (*i.e.*, non-imputed data; N = 1,293; Supplementary Fig. 2); and one built considering the imputed dataset without body mass correction (N = 3,438). In both cases, the comparisons revealed strong correspondence between spaces, demonstrating that our methodological choices do not influence the inferred relationships between life history traits (Supplementary Methods 3).

Exploring patterns within mammalian life history space

We derived the life history structure (*i.e.*, the patterns of organization of species in the life history space) using the trait probability density (TPD) framework (Carmona *et al.* 2016), which computes species' probabilistic distribution in the life history space using multivariate kernel density estimation. The kernel density estimation for each species was estimated as a multivariate normal distribution centred at the species' coordinates in the PCA space (Carmona *et al.* 2016, 2019). Standard deviation was computed using the unconstrained bandwidth selectors from the '*Hpi*' function in the '*ks*' package (Duong 2007, 2022). To estimate the life history structure of the whole set of mammals, all species' kernels were weighted and aggregated to form a single continuous TPD function across the whole mammalian life history space. The value of the TPD function at any given point of the life history space reflects the density of species in that particular area of the life history space (Carmona *et al.* 2016, 2019). We graphically represented the so-built mammalian life history structure by highlighting the contours containing 50% and 99% of the total probabilistic distribution of species (Fig. 1a). We used the *'TPD'* R package (Carmona 2019; Carmona *et al.* 2019).

We further investigated the extent to which the distribution of mammals in the life history space deviates from what would be expected from a random assembly of traits (Carmona et al. 2021a; Díaz et al. 2016; Southwood 1988). For that, we calculated functional richness (*i.e.*, the amount of functional space occupied by species, Carmona *et al.* 2016, 2024) at increasing probability thresholds (*i.e.*, from 0.1% to 99.9% of the TPD function) and functional divergence (*i.e.*, degree to which species' density is skewed towards the extremes of the life history space; Carmona *et al.* 2016; Mason *et al.* 2005). We compared the observed values of functional richness and divergence to a null model that assumes a bivariate normal distribution of species within the space (Carmona *et al.* 2021a; Supplementary Methods 4, Supplementary Fig. 4).

Lastly, to have a clearer picture of how different species are positioned in the life history space, we computed TPD functions for each mammalian order with at least 6 species (total of 18 orders). We graphically represented the mammalian life history structure of each order (Supplementary Fig. 5).

Exploring environmental realms' patterns in the life history space

We produced realm-specific TPD functions by aggregating the species that are characteristic of each realm. We followed the same procedure explained above for the global set of mammalian species. In the same way as done with the complete mammalian life history structure, we represented graphically the TPD for each realm (Fig. 1b-d).

We compared the structure of each of the environmental realms (*i.e.*, air, land, water, and transitional) considering multiple aspects. First, we compared realms in terms of functional richness. Because functional richness is known to positively correlate with the number of species present in a group, we built a null model (999 repetitions) randomizing species assignment. This approach enable us to compare functional richness among realms with different number of species (Carmona *et al.* 2021a). For each realm, we randomly extracted the same number of observed species from the complete mammalian database and computed TPD functions of the random community. We computed functional richness at the 99% of total probability for both observed and randomized structures and calculated standardized effect size (SES) as: SES = (observed value – mean (simulated values))/standard deviation (simulated values). Negative SES values would indicate that the species present in the realm are more clustered in the space (*i.e.,* occupy a smaller portion of the life history space, and therefore species are redundant in their life history strategy) than expected given the same number of randomly selected species and vice versa. A highly clustered realm would indicate high redundancy of life history strategies (Carmona *et al.* 2021a), suggesting that the prevalent conditions in that realm exert a strong selection on life history strategies. For each realm, we estimated two-sided p-values computed by confronting the SES values with a cumulative normal distribution with mean = 0 and standard deviation = 1 (Supplementary Table 2a).

Then, we statistically tested whether dissimilarities in species positioning were a product of a realm-driven selection of life history strategies. We estimated how much of the total variation in the position of the species on life history space was explained by difference in realms. For this, we first calculated the dissimilarities (using Euclidean distances) between all pairs of species in the life history space. Then, we performed a PERMANOVA analysis considering the three major environmental realms (*i.e.,* air, land, and water) as the explanatory variable (R package *‘vegan‘;* Oksanen *et al.* 2020). If the realm explains a large portion of life history variation, it means that life history variability is mainly related to differences between realms rather than differences among species within the realm (Carmona *et al.* 2021a).

We estimated pairwise dissimilarities in life history structures between pairs of realms (*i.e.*, air, land, water, and transitional, Fig. 2). Dissimilarities were calculated as 1 - overlap of the corresponding TPD functions producing measures varying between 1, indicating a complete overlap between the considered TPD functions, and 0, when the two functions are completely disjoint. TPD-based dissimilarities consider both differences in the boundaries and differences in the density of the occupation of the life history space (Carmona *et al.* 2021b; Germain *et al.* 2023; Toussaint *et al.* 2021). These dissimilarities can be further decomposed into two complementary components: one quantifying up to what point the life history differences between realms are related to the occupation of exclusive regions of the space (turnover) and another reflecting how differently the two realms occupy the shared parts of the life history space (nestedness; Carmona *et al.* 2019).

We tested whether the observed dissimilarities between environmental realms were significant by means of a null model (Micó *et al.* 2020; Traba *et al.* 2015). In this null model, for each pair of realms, we considered only the set of species belonging to both realms and we randomized the realm classification. We maintained the same number of species observed in each considered realm and avoided species assignment to multiple realms. For each repetition of the null model (n = 999), we estimated the TPD functions of each realm and estimated their dissimilarity, as well as its nestedness and turnover components. Finally, we computed SES values for all mentioned metrics as described above (Supplementary Table 2b).

Then, we explored whether dissimilarities between environmental realms were maintained among closely related species. Because all aerial species belong to the Chiroptera order, we excluded them from the analysis. Within each order, we estimated the centroid in the functional space for each environmental realm exploited by species in the order. We statistically tested for differences in the centroid positions between environmental realms by means of linear mixed effect models using the R package *'lmerTest'* (Kuznetsova *et al.* 2017). We performed two models, one for each principal component, using the mean score of the order along the PCs as response variable, environmental realm as fixed effect, and mammalian orders as random intercept (Supplementary Table 3, Fig. 4). Furthermore, we computed TPD functions for orders that had at least six species in both the aquatic (in this case identified by both aquatic and semi-aquatic species) and terrestrial realms. For each of these orders, we calculated TPD functions for terrestrial species and for aquatic species. We represented graphically these TPD functions and computed pairwise dissimilarities between the terrestrial and aquatic life history structure of each order (Supplementary Fig. 6).

Extracting differences in terrestrial mode of life and species life histories

For the terrestrial realm, we further produced specific TPD functions for each of the considered modes of life (*i.e.*, arboreal, semiarboreal, fossorial, and confined on land) following the same procedure as mentioned above. We represented graphically the TPD for each mode of life highlighting different probability contours (Supplementary Fig. 7). We applied the same procedure used for environmental realms to compute functional richness and pairwise dissimilarities among modes of life and realms (Supplementary Table 5).

Then, we tested whether, within taxonomically related species, exploiting the environmental realm with different mode of life allows for distinct set of life history strategy than species confined on land. For that, we selected all mammalian orders showing arboreal, semiarboreal, or fossorial species and species confined on land. Within each order, we extracted the centroid of the functional structure of the species confined on land and of the mode of life exploited in the order (Fig. 4). Then, we produced three datasets (one for arboreality, one for semi-arboreality, and one for fossoriality), containing the centroids of the mode of life together with the ones of species confined on land for each of the considered orders. We used these datasets to statistically test for differences between species confined on land and species showing different modes of life through a series of linear mixed effect models using the R package '*lmerTest* ' (Kuznetsova *et al.* 2017) and the same model setup as above (Supplementary Table 6).

Similarly to arboreal, semiarboreal, and fossorial mode of life, species with high encephalisation are capable to exploit the environment in a plastic way, avoiding hazards and stressful situations (González-Lagos *et al.* 2010; Zhu *et al.* 2023). Consequently, we further explored whether high encephalization (Barton & Capellini 2011; González-Lagos *et al.* 2010) allows to exploit portions of the life history space otherwise not successful for the terrestrial realm (Supplementary Methods 5). The final procedure resulted in two generalized additive models (GAMs) mapping species observed brain mass (Barton & Capellini 2011; Benson-Amram *et al.* 2016) as a function of the species position in the life history space (Carmona *et al.* 2021b; Supplementary Fig. 9).

Life history patterns and species evolutionary non-independence

Considering that both environmental filtering and evolutionary history influence current traits correlations (Revell & Harmon 2022; Stearns 1992; Westoby *et al.* 2023), a convergence in life history strategies among species within an environmental realm may be exclusively a result of the shared ancestry of species occupying the realm, rather than a combined effect of shared ancestry and realm-driven selection on life history traits (de Bello *et al.* 2015;

Westoby *et al.* 2023). Thus, we explored whether life history patterns remained consistent after accounting for non-independence of species by examining: 1) traits correlation structure defining the life history space; and 2) the relationships between species' life history strategies, environmental realms, and mode of life.

To determine the influence of phylogenetic non-independence of species on traits covariations in the life history space, we created a phylogenetically informed space (hereafter Phyl-space) using the same size-corrected life history traits employed in the observed life history space. We performed phylogenetically informed PCA (PPCA; Revell 2009), which considers species' phylogenetic non-independence by estimating a traits correlation matrix reflecting the ancestral relationships across the phylogenetic tree (Revell 2009; Revell & Harmon 2022). Unlike PCA, PPCA does not produce major axes of trait variation, but rather major axes of evolutionary independent variation, ensuring that phylogenetic correlations between PPC axes scores is zero (Revell 2009; Revell & Harmon 2022). PPCA was performed using the *phyl.pca* function from '*phytools'* R package (Revell 2012). We defined the Phyl-space by extracting the first three PPCs, together accounting for 67.46% of phylogenetically independent variance (Supplementary Table 1d; Supplementary Fig. 3). Then, we compared trait correlations defining the Phyl-space with those defining the life history space built without considering species' phylogenetic relatedness. This involved testing for correlations among angles between all pairs of trait loadings in both the original life history space and the Phyl-space (see Bueno *et al.* 2023; Supplementary Table 1d). High correlations would suggest that the inferred relationships between pairs of traits are similar across spaces.

To explore the relationships between species' life history strategies, environmental realms, and mode of life, we performed a series of Phylogenetic Generalized Least Square regressions (PGLS, Revell & Harmon 2022; Symonds & Blomberg 2014). Two models were applied, one for each axis of the life history space, with species position as the response variable and environmental realms as predictors. PGLS adjust for the phylogenetic signal in the response variable by modulating traits correlations based on the variance-covariance matrix derived from species' phylogenetic relationships, thus 'down-weighting' these correlations (Symonds & Blomberg 2014). Given that approximately 20% of the mammals considered are aerial species (*i.e.* bats), which simultaneously diverged from their last common terrestrial ancestor more than 60 million years ago (Upham *et al.* 2019), we excluded aerial species from the model.

Similarly, we performed two more PGLS models on the subset of terrestrial species, using species position as the response variable and mode of life as the predictor. All models were performed using the *gls* function from *'nlme' R* package (Pinheiro *et al.* 2023), and employed a Brownian motion correlation structure, extracted using the *corBrownian* function from '*ape*' R package (Paradis & Schliep 2019). For each model, a Tukey's HSD test to identify difference among groups, using *the glht* function of the *'multcomp'* package (Hothorn *et al.* 2008), respectively (Supplementary Table 4,7).

All statistical analyses were performed using R version 4.0.3 (R Core Team 2020).

Results & Discussion

Worldwide life history strategies are constrained and profoundly divergent

Mammalian life history traits vary mostly along a two-dimensional space that accounts for 75.1% of the total life history variation. This space is characterized by two primary trade-offs: litter size *vs.* gestation length, and number of litters per year *vs.* age at female maturity and weaning length (Fig. 1a). The first dimension (PC1) captures the fast-slow continuum (Stearns 1992), distinguishing fast species with short lives, gestation and weaning, early maturity, and frequent litters, from slow species with fewer and infrequent litters, longer lives, and later maturity (Fig. 1a). The second dimension (PC2) captures the trade-off between litter size and frequency, reflecting lifetime reproductive effort thought offspring quality (*i.e.,* altricial *vs.* precocial, with species born in an underdeveloped state *vs* mature and mobile individual from birth) and reproductive frequency (*i.e.,* semelparity *vs.* iteroparity). This configuration not only aligns with findings from earlier studies on smaller subsets of species (267 species in Bielby et al., 2007; 80 species in Gaillard et al., 1989), but also underscores the pervasive nature of life history trade-offs across a broad range of mammalian adaptations. From the poles to deserts, mammals pay the costs associated with longevity and investments in offspring survival by decreasing either the frequency or the magnitude of their reproductive output, depending on whether they favour either pre- (*i.e.,* longer gestation) and postnatal (*i.e.,* longer weaning) investment (Stearns 1992). Remarkably, the trade-offs defining mammalian life history space remain consistent in a phylogenetically informed space (angles correlation r = 0.85, p < 0.001; Supplementary Fig. 3, Table 1d). This consistency stresses the universal nature of the trade-offs defining mammalian life history variation, independent on species taxonomical affiliation.

Mammalian species exhibit a remarkably uneven and concentrated distribution within the life history space. Mammalian patterns in space occupation significantly deviate from what is expected under a normal distribution of species in the space, with species occupying 32% less space and being 49% more divergent than bivariate normal distributions with the same number of species (Supplementary Fig. 4). Rather than dispersing evenly across the life history space, species aggregate in two hotspots at opposite ends of the fast-slow continuum: those investing in the quantity of reproductive investment *vs.* those prioritizing quality

(Grime & Pierce 2012; Stearns 1992). “Fast hotspot” species (Fig. 1), like mice and rabbits, focus on rapid reproduction for gene propagation (Grime & Pierce 2012). In contrast, “slow hotspot” species, such as primates, cetaceans, and bats, invest in extensive parental care, preparing offspring for survival (Barton & Capellini 2011; Grime & Pierce 2012). Despite the diversity in mammalian adaptations, life history strategies are dichotomized: either capitalizing on rapid gene propagation thought short-term reproductive opportunities or enhancing offspring survival though long-term distribution of reproductive effort. This bimodal pattern echoes observations in plant strategies for aboveground resource allocation (Carmona *et al.* 2021a; Díaz *et al.* 2016), showing a tendency for species to congregate around few contrasting syndromes that lead to successful strategies (Junker *et al.* 2022).

Divergent life history strategies correspond to different environmental realms

Major environmental realms select for distinct and highly redundant life history strategies (Fig. 1-2). PERMANOVA analysis attributed 35% of variation in life history traits to differences among realms, as highlighted by high dissimilarities between environmental realms ($D_{\text{land-water}} = 69\%$, $D_{\text{land-air}} = 86\%$, $D_{\text{air-water}} = 86\%$; $p < 0.001$ in all cases; Fig. 2; Supplementary Table 2). This is further evidenced by high levels of species redundancy within realms, indicating realm-specific convergence around similar trait values ($R_{\text{land}} = 7.99$, $R_{\text{air}} = 9.25$, $R_{\text{water}} = 4.38$, $p < 0.001$; Supplementary Table 2). Terrestrial species disproportionately occupy the “fast hotspot”, while aerial and aquatic species are confined to the slow end of the spectrum (Fig. 1). These differences between terrestrial and aquatic species along the fast-low continuum were consistent after accounting for species relatedness (Supplementary Table 4), confirming the realm-driven selection on mammalian life histories. To access aerial and aquatic realms, species require costly morpho-physiological specializations that necessitate increased parental investment in offspring, ensuring that they are well-equipped to meet the physical demands of their respective realms (Barclay & Fleming 2020; Perrin *et al.* 2009). The strong energetic demands of water on both mother and offspring compel the rationing of resources through delays in offspring maturity and the mother's successive births (Davis 2019; Perrin et al. 2009). Conversely, although the morpho-mechanical investments for flight extend weaning and gestation length, the aerial realm imposes lower energetic constraints on mothers, slowing the pace of life of species but potentially facilitating more frequent reproduction (Fig. 1, Barclay 1994; Barclay & Fleming 2020).

Despite marked differences among environmental realms, characteristic strategies of one realm can be observed in others. This is notably seen in the aquatic realm, whose strategies are fully encompassed by those of terrestrial species ($\text{Nestedness}_{\text{land-water}} = 1$, Fig. 2), with apes (including humans), sharing similar life history traits as dolphins. The aerial realm also significantly overlaps with the terrestrial ($\text{Nestedness}_{\text{land-air}} = 0.89$), largely due to Lemuriformes and Tarsius (Supplementary Fig. 5). Although the energetic requirements of aerial and aquatic adaptations seem to drive a distinction toward a highly constrained set of life history strategies not as favoured on land, their strong overlap prompts questions about the driver behind this – less favoured – convergence. Dietary, migratory, and social habits might affect resource utilization and thus life history variation (Famoso *et al.* 2018; Soriano-Redondo *et al.* 2020; Zhu *et al.* 2023), suggesting that ecological strategies could enable species to adopt otherwise less favoured life history strategies in their realms. For instance, baleen whales' greater similarity to some rodents than dolphins (Supplementary Fig. 5) may stem from unique migratory (long distance of baleen whales *vs.* short distances of dolphins), dietary (filter feeding vs hunting), and social behaviours (low vs high sociality) affecting baleen whales energetic needs, thus adaptation to aquatic life (Perrin *et al.* 2009).

Accordingly, the interplay of ecological adaptation with realms' constraints may be the fundamental driver of life history diversity within realms: realm constraints delineate physically possible life history strategies, while ecological adaptations may act to mitigate these constraints, expanding the diversity of life history strategies within realms (Cox *et al.* 2021).

It is important to note that while incorporating phylogenetic relationships into the imputation procedure is fundamental for ensuring accuracy (Penone et al. 2014; Stewart et al. 2023), it may reduce the observed dissimilarities among closely related species. Although we cannot dismiss this possibility, it's essential to recognize that this potential effect would primarily work towards narrowing the gaps among environmental realms, thereby rendering our results conservative estimates of these dissimilarities. Moreover, this effect is likely to be minimal, as indicated by our tests of imputation accuracy, which involve creating artificial gaps in trait information and demonstrate a very high level of accuracy (Supplementary Methods 1).

Species transitioning between realms have intermediate life history strategies

The life history strategies of semi-aquatic species provide further evidence for the profound influence of environment realms on life history variation. Semi-aquatic species exhibit intermediate life history strategies, slower than terrestrial species but faster than fully aquatic ones, in a way that seems associated to species' water-dependence (Fig. 3-4a). For instance, species with greater aquatic involvement, such as seals and walruses (Davis 2019; Perrin *et al.* 2009), occupy portions of the life history space similar to fully aquatic species like manatees or beluga, while rodents and otters (Hood 2020; Perrin *et al.* 2009) are located in the hotspot typical of terrestrial mammals (Fig. 3). A stronger dependence on water comes with morpho-physiological adaptations required to compensate aquatic constrains (Farina *et al.* 2023; Hood 2020; Perrin *et al.* 2009), associating with life history strategies similar to the ones observed in the aquatic realm (Fig. 3-4a).

The lack of significant deviations of semiaquatic mammals from what is expected under a random assignment of species ($R_{\text{semi-aquatic}} = -0.89$; $p = 0.27$) further underscores the absence of strong directional selection pressure (such as that observed across realms) in shaping the life history diversity of transitional species. While species with significant aquatic involvement face energetic constraints imposed by water, potentially favouring aquatic-like strategies (Davis 2019; Hood 2020; Perrin *et al.* 2009), those only partially subjected to aquatic constraints have access to ecological opportunities that may steer them towards different life history trajectories, more dependent on the environmental pressures encountered on land. Indeed, excluding Carnivora and Cetartiodactyla —where seals and hippos form a continuum between terrestrial and aquatic species— semi-aquatic representatives (*e.g.,* rodents, Eulipotyphla) show diverse patterns in the deviation from the average life history strategies observed among their terrestrial counterparts (Figure 4a; Supplementary Fig. 6). Nevertheless, differences among semi-aquatic and both terrestrial and aquatic strategies remained consistent regardless of the shared ancestry of species (Supplementary Table 4). This suggests a combined effect of the degree of aquatic dependency and terrestrial environmental and ecological pressures, rather than shared ancestry alone, in guiding the differentiation of transitional species. However, we advocate for future research investigating the evolution of aquatic and semi-aquatic adaptations to shed light on the drivers shaping life history selection of transitional species (Farina *et al.* 2023).

Slow life history strategies in arboreal and fossorial species

The arboreal, semiarboreal, and fossorial modes of life are associated with distinct life history strategies compared to species confined on land. Land-confined species mainly clustered in the “fast hotspot” of the life history space, whereas arboreal, semiarboreal, and fossorial species tend to cluster towards the slow (arboreal) and intermediate (fossorial and semiarboreal) portions of the life history space (Supplementary Fig. 7). These discrepancies are confirmed by pairwise comparison dissimilarities ($D_{\text{land-arboreal}} = 61\%$, $D_{\text{land-semiarboreal}} = 47\%$, $D_{\text{land-fossorial}} = 53\%$; $p < 0.001$ in all cases) and remain consistent regardless of the shared ancestry of species (Supplementary Table 6-7). With varying extents, the arboreal, semiarboreal, and fossorial modes of life enable species to evade mortality risks and access new ecological opportunities (Bels & Russell 2023; Scheffers *et al.* 2017; Stroud & Losos 2016). This reduction in mortality resulting from the vertical exploitation of land (Healy *et al.* 2019; Shattuck & Williams 2010), allows to modify pressures acting on species, thereby expanding the life history diversity of the terrestrial realm (as observed for diel niche, Cox *et al.* 2021). Emphasizing the consistency of these patterns, arboreal and fossorial species are significantly skewed towards the slower end of the life history space, even when compared to taxonomically related, land-confined counterparts (Fig. 4). Interestingly, the presence of order-dependent patterns in the deviation of semiarboreal species from their land-confined counterparts (Fig. 4) as well as the lack of significant deviation from what is expected under a random assignment of species in semi-arboreal structure ($R_{\text{semi-arboreal}} = 1.01$; $p = 0.24$), mirrors what is observed for semiaquatic species. These results suggest a joint effect of a transition between arboreal advantages and terrestrial pressures in the diversification of semi-arboreal strategies, although future insights are necessary to test the role of transitional species in life history diversification. Yet, life on land appears to directionally favour a maximization of reproductive output at the expense of investment in offspring survival. Nevertheless, the capability for vertical movement smoothing risks of land (Healy *et al.* 2019; Shattuck &

Williams 2010) associate to investments devoted to maximizing offspring care, thus survival (Stearns 1992), through a reduction of reproductive output per reproductive event (Supplementary Fig. 7; Fig 4).

Life history strategies common to terrestrial, aerial, and aquatic realms coincide with those observed in arboreal, semiarboreal, and fossorial modes of life. Nestedness between terrestrial and aerial species decreased by 55% (thus increasing the dissimilarity between the realms by 10%) when only land-confined terrestrial species are considered, although these species constitute 66.3% of all terrestrial species (Supplementary Fig. 8, Supplementary Table 5). Moreover, the dissimilarity between aquatic and land-confined species increased by 15% compared to the dissimilarity computed across the entire spectrum of terrestrial adaptations. Arboreality is the main reason for these overlaps in the life history space (Supplementary Fig. 8), especially in the case of the aquatic realm. Arboreal and aquatic species share more similar life history strategies than arboreal and land-constrained species ($D_{\text{water-arboreal}} = 55\%$, $D_{\text{land-arboreal}} = 61\%$, $p < 0.001$), with a completely overlap in the portion of space occupied by arboreal primates and dolphins (Fig. 1-2). This convergence in life history strategies may be driven by the distinct pressures of aquatic and arboreal adaptations, leading to parallel investments in response to drivers acting on different life history components of species, such as maternal investment in water (Perrin *et al.* 2009) and decreased mortality in primates (Healy *et al.* 2019; Shattuck & Williams 2010).

Yet, other ecological drivers influencing the convergence in life history strategies may remain hidden. Both primates and dolphins show complex social structures and high encephalization (Perrin *et al.* 2009; Ridgway *et al.* 2017; Worthy & Hickie 1986). Similarly to arboreal, semiarboreal, and fossorial mode of life, high encephalization, generally relating to both social and behavioural facets (Barton & Capellini 2011; Pérez-Barbería *et al.* 2007), allows species to exploit the environment in a plastic way, avoiding hazards (González-Lagos *et al.* 2010; Zhu *et al.* 2023). We tested whether high encephalization may play a role in selecting terrestrial strategies, by modelling the brain-mass ratio of terrestrial mammalian species (*i.e.,* the ratio between brain dimension and body mass (Benson-Amram *et al.* 2016; Worthy & Hickie 1986) as a function of species' position in the life history space. We found a robust association between larger brain mass and slow life histories (R^2 = 0.48, Supplementary Fig. 9), suggesting that larger brain size may play a role in influencing the diversity of terrestrial life history strategies. Consequently, while the environmental realm in which species live seems to drive life history strategies, behavioural characteristics of species seem to play a role in expanding the set of life history strategies exploitable in the terrestrial realm (Cox *et al.* 2021; Zhu *et al.* 2023). Specifically, we suggest that vertical movements (*e.g.,* arboreality, fossoriality) along with other ecological (diet, migratory habits, diel niche) or behavioural adaptations that influence life history variation (Cox *et al.* 2021; Famoso *et al.* 2018; Soriano-Redondo *et al.* 2020; Zhu *et al.* 2023) may modify the environmental pressures perceived under specific constraints, while simultaneously providing access to new ecological opportunities (Grime & Pierce 2012; Southwood 1988). These factors may play a fundamental role in defining the range of life history strategies available under similar environmental conditions. Future insight should focus on disentangling the role of ecological and behavioural characteristics in influencing species life history diversity, particularly under a macroecological perspective (Keith *et al.* 2023).

Conclusion

Our analyses of over 3,400 mammal species reveal that major environmental realms are strong predictors of mammalian life history strategies. The unique adaptations required for life in aerial and aquatic realms, such as flight-capable skeletal structures or enhanced thermoregulatory abilities, not only delineate distinct life history strategies but also slow down and prolong lifespans in ways not commonly seen in terrestrial mammals. However, despite each realm's unique set of life history strategies, all of them overlapped to some degree within the life history space due to species' adaptations that enable the exploitation of otherwise unsuccessful strategies in each realm. On land, arboreal, semi-arboreal, and fossorial modes of life crucially expand the diversity of life history strategies available, enabling terrestrial species to parallel strategies predominantly seen in aquatic species, regardless of taxonomic relatedness. Similarly, the strong relationship we uncovered between brain dimension and the position of terrestrial species within the life history space suggest a role of sociality and encephalization in allowing terrestrial mammals to exploit the slower end of the life history spectrum.

Our comprehensive assessment of worldwide mammalian life history strategies underscores the pivotal role of environmental realm in shaping life history diversity. Notably, trade-offs and patterns in life history diversity persist among closely related species, emphasizing the pervasive relation between environmental realms and life history evolution. Our findings not only provide empirical insights into mammalian adaptation, but also establish a foundation for further exploration of ecological and evolutionary processes. In addition, this foundation may allow to improve our understanding of the drivers and consequences of ongoing global changes and future biodiversity patterns. As we confront these challenges, our study emphasises the importance of understanding the intricate interplay between environment, ecology, and evolution to disentangle, anticipate, and mitigate the impacts on mammalian life history diversity.

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Competing interests

All authors declare no competing interests.

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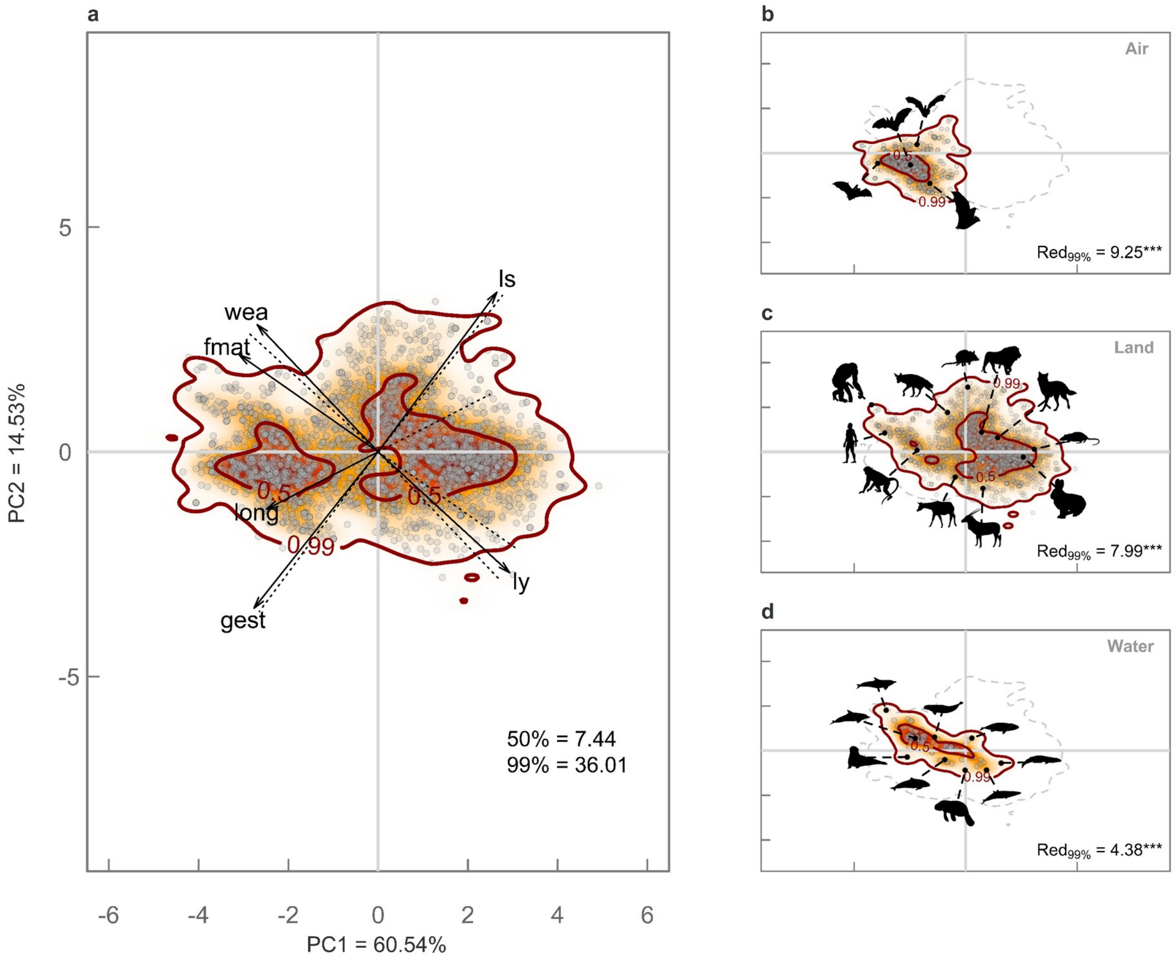

Fig. 1 | Bimodal global mammal space occupation stems from differences among environmental realms. a, Probabilistic species distributions in the space defined by the two first principal components (PC1 and PC2) of PCA considering life history traits for all mammals. Arrows indicate the loadings of each trait in the PCA. The legend shows the amount of functional space (i.e., functional richness) occupied at 50% and 99% probabilities (indicated by thick contour lines). The red regions falling within the limits of 50% probability correspond to the hotspots mentioned in the text. wea, weaning length; fmat, time to reach female maturity; ls, size of litter; gest, gestation length; long, longevity; ly, number of litters yearly. **b – d,** Patterns in space occupation of aerial (**b**), terrestrial (**c**), and aquatic (**d**) mammals. Legends show functional redundancy of the realm calculated as absolute values of the Standardized Effect Size (Red$_{99\%}$). SES was calculated considering the amount of functional space occupied by observed and randomized realm at 99% probability. * is SES p-value < 0.05; ** SES p-value < 0.01; *** SES p-value < 0.001. In all panels, the colour gradient (red, orange, and white) depicts different density of species in the space (red areas have higher density of species). Silhouettes of characteristic species from each realm were downloaded from PhyloPic (http://www.phylopic.org/).

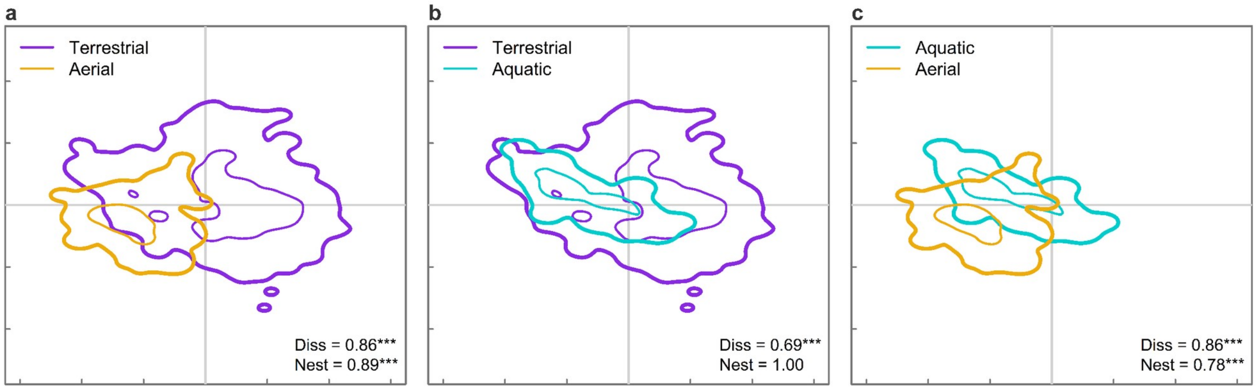

Fig. 2 | Environmental realms select for distinct yet nested life history strategies. Overlap-based dissimilarities between terrestrial (purple), aerial (light orange), and aquatic (light blue) species distributions in the life history space. Specifically: **a,** dissimilarity between terrestrial and aerial realms; **b,** dissimilarity between terrestrial and aquatic realms; **c,** dissimilarity between aerial and aquatic realms. Each realm is highlighted at 50% (fine lines) and 99% (thick lines) of total probability. SES of dissimilarity and nestedness values for each pairwise comparisons are reported in the legend together with SES p-values (* SES p-value < 0.05; ** SES p-value < 0.01; *** SES p-value < 0.001).

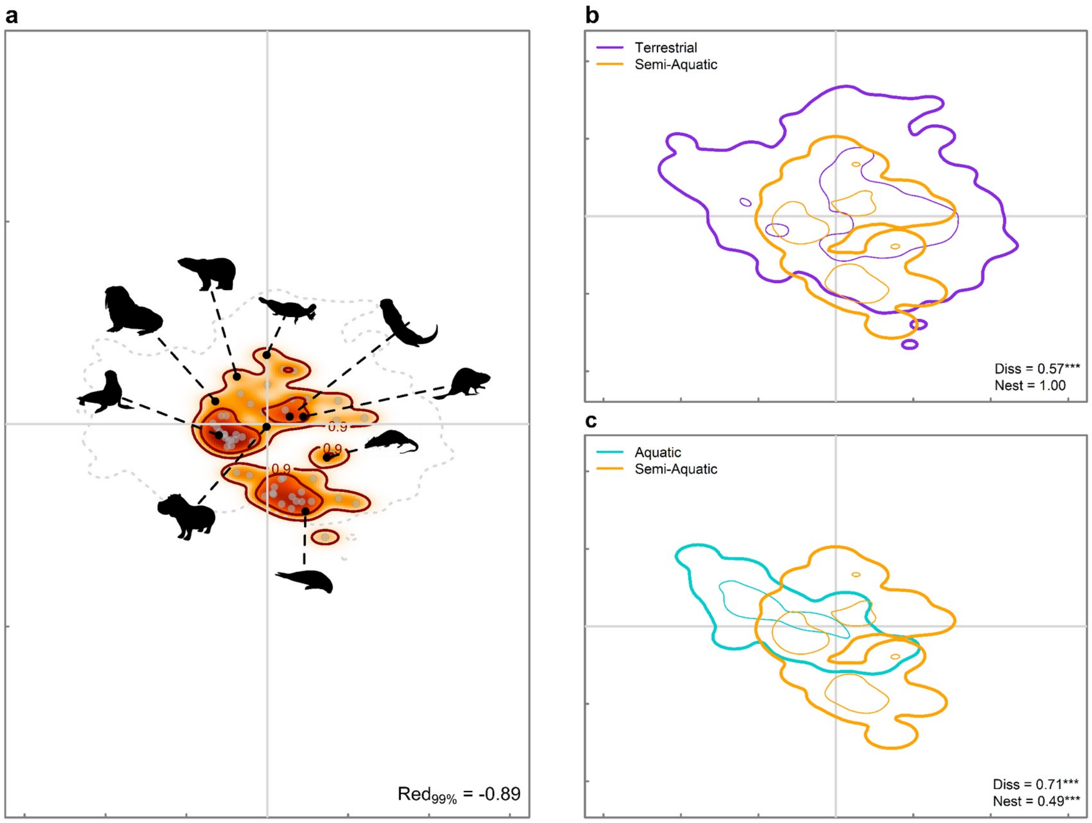

Fig. 3 | Semi-aquatic species transition between aquatic and terrestrial life histories depending on the evolutionary time they spent in water. **A,** Occupation of transitional mammals in the life history space. The colour gradient (red, orange, and white) depicts different density of species in the space (red areas have higher density of species). The legend shows the amount of functional space (*i.e.*, functional richness) occupied at 50% and 99% probabilities (indicated by thick contour lines). Dashed grey line show the portion of space occupied by global mammals. Legend show functional redundancy of transitional species calculated as absolute values of the Standardized Effect Size (Red$_{99\%}$). SES was calculated considering the amount of functional space occupied by observed and randomized realm at 99% probability. Silhouettes of characteristic semi-aquatic species were downloaded from PhyloPic (http://www.phylopic.org/). **B-c,** pairwise overlap-based dissimilarities between semi-aquatic (SA) and both terrestrial (**b**) and fully aquatic (**c**) mammals. In both panels, contours at 50% (fine lines) and 99% (thick lines) are highlighted for terrestrial (purple), aquatic (light blue), and semi-aquatic (orange) species. Legends show observed dissimilarities between realms and semi-aquatic species (Diss) and value of nestedness (Nest). P-values for the standardized effect size (SES) of dissimilarity and nestedness are present only for significant SES. ***: SES p-value < 0.001. All panels show the probabilistic species distributions in the spaces defined by the two first principal components (PC1 and PC2) of PCA considering life history traits for all mammals.

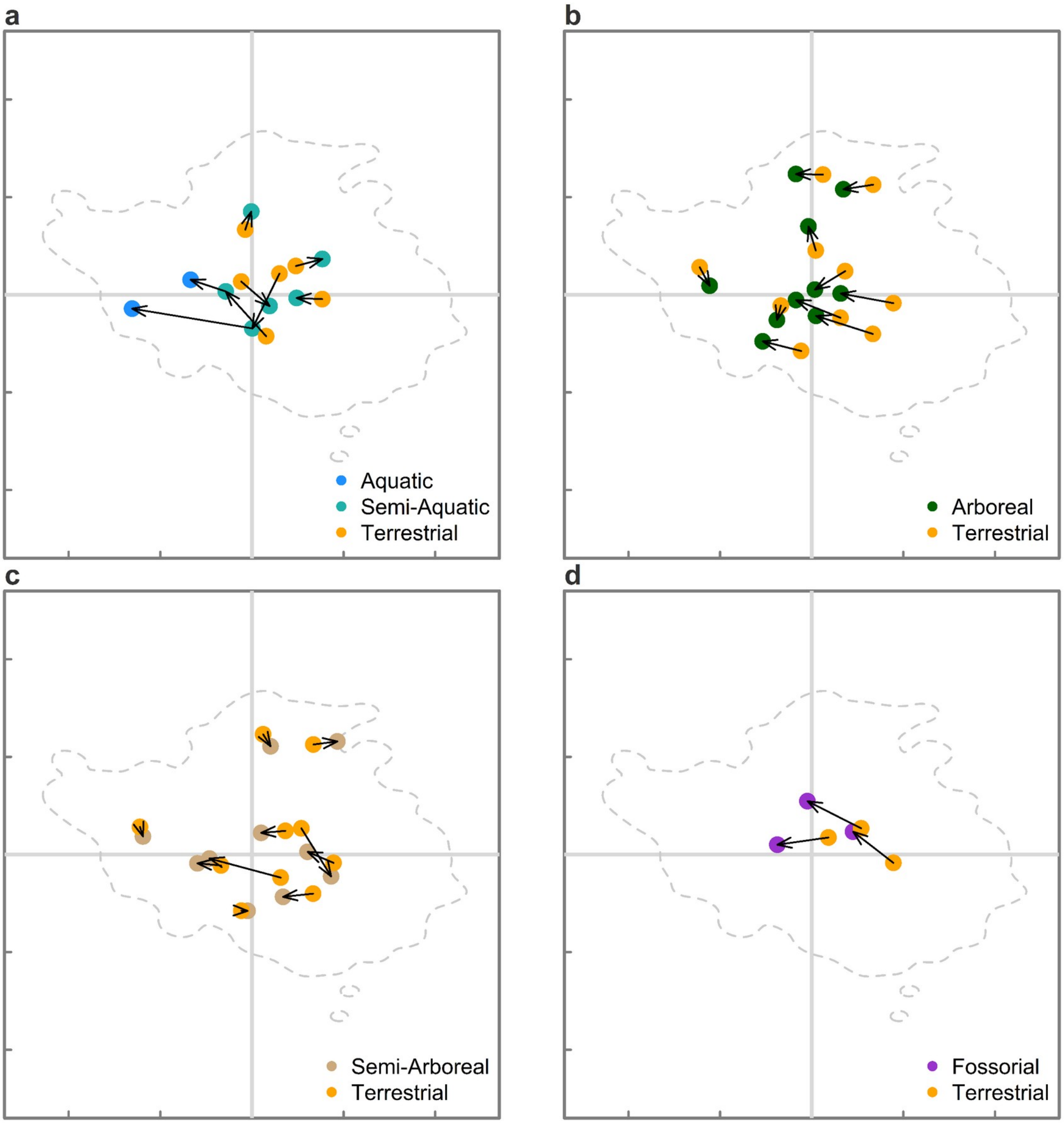

Fig. 4 | Aquatic realms and mode of life associate with slower life histories in taxonomically related species. Differences in the centroid among life history structures of species within the same order **(a)** across aquatic, semi-aquatic, and terrestrial realms, and **(b-d)** among different modes of life on land. **(a)** ach point represents the average life history strategy of terrestrial (orange), semi-aquatic (sea-green), and aquatic (blue) representatives within an order. Arrows connect the centroids of terrestrial to either semi-aquatic or aquatic structures within the same order. Aquatic adaptations are observed in two orders (i.e., Carnivora and Cetartiodactyla), resulting in only two points being shown. The other panels illustrate the centroid differences among life history structures of species confined to land and **(b)** arboreal, **(c)** semiarboreal, and **(d)** fossorial species of the same order. Each point represents the average life history strategy of land-constrained (orange), arboreal (green), semi-arboreal (brown), and fossorial (purple) representatives within the terrestrial realm. Arrows connect centroids of the land-constrained structure and the specific mode of life structure identified within the same order.