Mammal life history strategies are strongly associated with environmental realms

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Summary

Mammalian investments in survival, development, and reproduction are constrained by physiological and evolutionary factors[1], so their life history strategies can be characterized by a few axes of variation[2–4]. These axes conform a space in which species are positioned according to which life history strategies are favoured in the environment they exploit[1,5,6]. Yet, a global synthesis quantifying the realized mammalian life history diversity is lacking and exploring how the environment shapes mammalian life history strategies is missing. Here, we used six life history traits to build a global life history space and explored how major environmental realms (land, air, water) influence mammalian life history strategies. We demonstrate that realms are tightly linked to distinct life history strategies. Predominantly, aquatic and aerial species adhere to slower life history strategies, while terrestrial species tend to exhibit faster life histories. Highly encephalized terrestrial species,

like monkeys, are a notable exception to these patterns. In addition, species transitioning between the terrestrial and aquatic realms, such as seals and otters, show intermediate life history strategies. Furthermore, time since evolutionary divergence from land is a strong predictor of aquatic life history strategies. Our results provide compelling evidence linking environmental realms to the diversity of life history strategies among mammals, potentially informing assessments of species viability.

Main:

The diversity of mammalian adaptation, ranging from the fast and semelparous life histories of antechinus[7] to the slow and long life of bowhead whales[8], have allowed mammals to occupy all land[9,10], exploit air[11–13], and even return to the sea[14]. Despite this wide ecological radiation[10], evolutionary history and energetic constrains limit the set of life history strategies (*i.e.*, combinations of life history traits) that are viable in nature[1,5,6]. Mammalian investments in survival, growth, and reproduction are summarised along two major axes of life history trait variation[3,4,15,16]. A first dimension generally relates to the time scale of live (*i.e.*, fast-slow continuum[1–4,15,17]). In contrast, the second dimension generally reflects the timing and intensity of species' reproductive investment[2,3,18] (but see Healy et al., 2019). While these two dimensions are consistent across empirical studies considering different subsets of species and traits[2,3,17], species organization within the life history space remain largely unknown, preventing the disentanglement of the drivers of mammalian life history diversity.

Environmental conditions profoundly influence species' life history strategies[5,6]. Variable environments, for instance, affect the pace of life of species[19] selecting for delayed life cycles and longer lives compared to constant and stable environments[5,19]. Thus, similar life history strategies are selected by similar environmental pressures[5,6], resulting in a redundant

occupation of the life history space regardless of taxonomic affiliation[15,20,21]. However, mammal's widespread distribution across major environmental realms (*i.e.*, land, water, air), begs the question of whether their life history strategies are equally represented across these three major realms. Indeed, distinct physical dimensions and environmental requirements expose species to realm-specific pressures[22]. For instance, real-specific selection pressures have led to slower-paced lives in aerial species[3,11] or more fecund life histories in the aquatic realm[3,17]. Consequently, species inhabiting different environmental realms may possess distinct life history strategies.

Time is a currency necessary to accumulate evolutionary adaptations needed to transgress realms[23–26]. Consequently, time since evolutionary divergence to a new realm should reflect the degree to which a species' life history strategies are adapted to the environment. For instance, mammal lineages that later diverged from land back to the aquatic realm, like seals or otters, generally have a lower degree of aquatic specialization[8,14,27] and higher genetic similarities with terrestrial sister taxa[28]. Accordingly, mammalian species with early return back to water may display a higher degree of life history specialization to the aquatic realm[14]. Yet, the association between time since evolutionary divergence to a different realm and species' life history strategies remains unexplored.

Here, we use six life history traits representing investments in survival, growth, and reproduction for 3,438 mammalian species[29] to examine the influence of major environmental realms on mammalian life history strategies. In agreement with previous research[2,3], 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 mammalian life history strategies (Fig. 1a). Based on this finding as a springboard, we then test three hypotheses: (H1) Species' position in the life history space will associate with the environmental realm

they occupy, as a consequence of different environmental pressures acting among major realms[5,19,22]. Specifically, we expect aerial species to exhibit slower life history strategies compared to terrestrial species, and aquatic species to occupy areas corresponding to faster[3] and more fecund strategies[17]. (H2) Species transitioning between aquatic and terrestrial realms (*i.e.*, semi-aquatic species) will display intermediate life history strategies, given that they experience selective pressures from both realms[8,27]. (H3) Aquatic history strategies will be associated with the time since evolutionary divergence from land. Specifically, we expect that mammalian species that have evolved for longer time in the aquatic realm will display more distinct life history strategies (*i.e.*, faster pace in this case[3]) compared to species that transgressed from land to water more recently[8,14,23,28].

Global life history strategies are constrained and profoundly divergent

Mammalian life history traits vary mostly along a two-dimensional space, which suggests a strong trait covariation limiting viable life history strategies. We gathered trait data related to survival, development, and reproduction from the AMNIOTE database[29] for 4,953 mammal species. We excluded species without information for body mass and used a phylogenetically-informed imputation to fill missing data for the other traits data[15,30], resulting in a total of 3,438 species (see Supplementary Methods 1 for the accuracy of the imputation procedure). Residuals from a linear regression of each trait against body mass were then used as body-size corrected trait values for further analyses [2,3,31] (Extended Data Fig. 1b). Finally, we conducted a principal component analysis (PCA) to discern the primary dimensions of mammalian trait variation (Supplementary Methods 2 and Extended Data Fig. 2 for results about the robustness of the life history space).

The first two principal components (PC) of the PCA account for 75.1% of life history variation, conforming a life history space characterised by two primary trade-offs: litter size

vs. gestation length, and number of litters per year *vs.* age at female maturity and weaning length (Figure 1a). The configuration of this space is line with previous studies on smaller sets of species (267 species in Bielby et al., 2007; 80 species in Gaillard et al., 1989). The first dimension of this space (PC1) captures the fast-slow continuum[1], 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) reflects lifetime reproductive effort, illustrating the trade-off between litter size and frequency, as well as offspring quality (*i.e.,* altricial *vs.* precocial), and reproductive frequency (*i.e.,* semelparity *vs.* iteroparity). Species' positioning and life history trait correlations in the life history space remain consistent after accounting for evolutionary history ($r = 0.95$; $p < 0.001$ for species; $r = 0.85$, $p < 0.001$ for traits; see Supplementary methods 2), suggesting that this two-dimensional life history strategy space applies to all mammals, independent of shared ancestry (Extended Data Fig. 3).

Mammalian species exhibit a remarkably uneven, concentrated distribution within the life history space. Comparing global mammal occupation patterns along this space to null models representing bivariate normal distributions with identical mean and covariance[30], the occupied space is smaller than expected by chance (Extended data Fig. 4a). For example, at the 99% quantile of species probability distribution, observed functional richness (*i.e.*, amount of space occupied by species) is 32% smaller than the simulated counterpart ($SES_{Fric99\%} = -11.79$, $p < 0.001$, $n = 999$ iterations). Additionally, species' distribution is much more divergent than the simulated ($SES_{Fdiv} = 18.79$, $p < 0.001$; $n = 999$ iterations; Extended data Fig.4b), primarily due to species clustering in two hotspots at opposite ends of the fast-slow continuum. Our findings reveal a dichotomy in successful investments to survival, development, and reproduction of global mammals: species investing on quantity of reproductive investment contrast with those prioritizing quality[1,5,6]. Species in the "fast

hotspot" (Fig. 1), such as mice and rabbits, optimize fast turnover and high reproductive output, enabling them to propagate their genes in unpredictable and unfavourable environments[5,6]. Conversely, "slow hotspot" species (Fig. 1a), including primates, cetaceans and bats, typically make costly parental investments to equip their few offspring with advantageous adaptations for long-term persistence and environmental exploitation[5,6,32]. This bimodal pattern mirrors that of plant traits[30,33], suggesting that, across the Tree of Life, species tend to cluster around a few contrasting syndromes that lead to successful strategies[34].

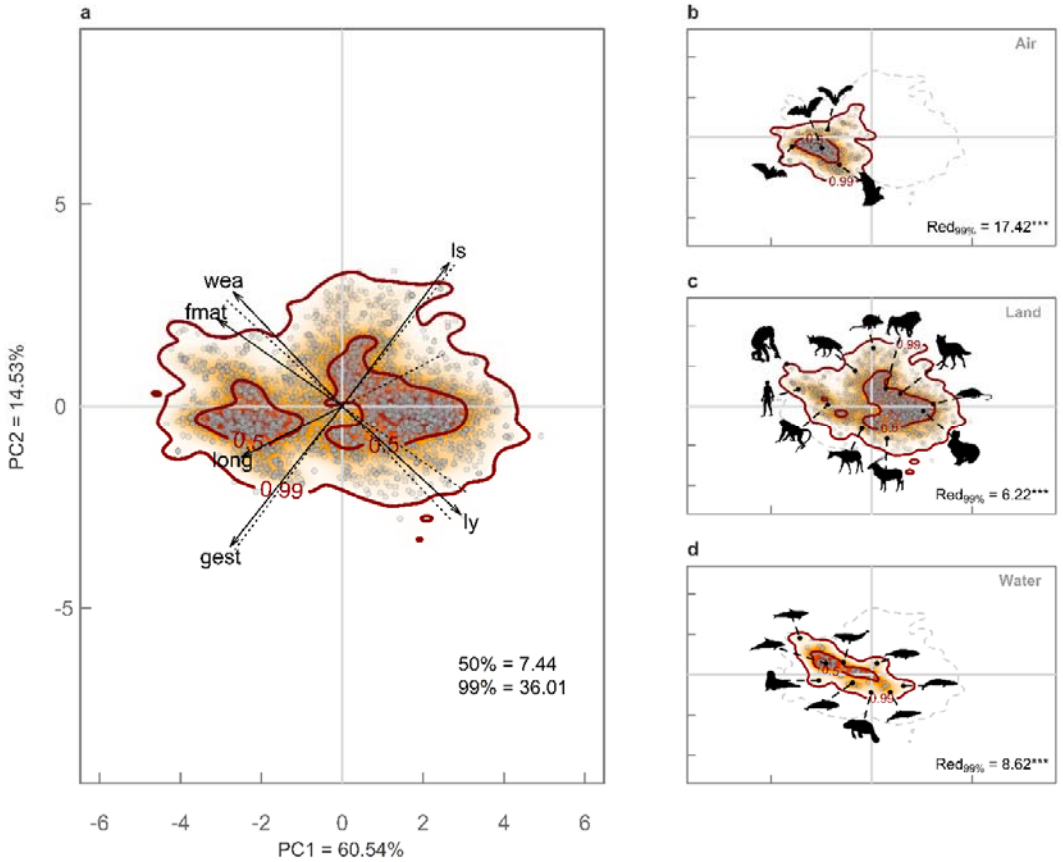

Fig. 1 | Bimodal global mammal space occupation stems from differences among environmental realms. a, Probabilistic species distributions in the space defined by the two first principal components (PC1 and PC2) of PCA considering life history traits for all mammals. Arrows indicate the loadings of each 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 (SES). 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/).

Divergent life history strategies correspond to different environmental realms

Major environmental realms select for distinct and highly redundant life history strategies (Fig. 1b-d; Fig. 2). This finding is confirmed by a PERMANOVA analysis, which attributes 35% of variation in life history traits to differences among realms. The marked differences in life history strategies among realms are further demonstrated by the dissimilarities between pairs of realms ($D_{land\text{-}water}$ = 69%, $D_{land\text{-}air}$ = 86%, $D_{air\text{-}water}$ = 86%; $p < 0.001$ in all cases, n = 999 iterations, Fig. 2; Extended data Table 2), as well as by the high levels of species redundancy within individual realms (*i.e.*, species within an environmental realm tend to have similar trait values; $R_{air} = 17.42$; $R_{land} = 6.22$, $R_{air} = 17.42$, $R_{water} = 8.62$; $p < 0.001$ in all cases, n = 999 iterations; Extended data Table 2). Terrestrial species disproportionally occupy the "fast hotspot" (Fig. 1c), including representatives of marsupials as well as the Carnivora, Lagomorpha, Rodentia, and Eulipotyphla orders (Extended data Fig. 5). Primates and Perissodactyla are the only exceptions to this pattern since they cluster in the slowest portion of the life history space. On the contrary, aerial (Fig. 1a) and aquatic species (Fig. 1d) are confined to the slow end of the spectrum. Despite the similar pace of life of aquatic and aerial species, their reproductive strategies differ substantially. Aerial species exhibit long gestation

times, while aquatic species display late female maturity and extended weaning (Fig. 1a). The predominance of slow strategies in aquatic species contrasts with previous observations mainly based on baleen whales[3], which are among the longest-lived aquatic species (Fig. 1d). Our study, however, includes dolphins, displaying a more complete picture. Dolphins and baleen whales exhibit distinct migratory, dietary, and social habits[8], influencing resource perception and gathering within realms and affecting life history variation[35–37].

Despite marked differences and redundancy among realms, characteristic strategies of a given environmental realm can be observed in others. This shared set of life history strategies is particularly evident in the case of the aquatic realm, fully contained within the life history space occupied by terrestrial species ($\text{Nestedness}_{\text{land-water}} = 1$, Fig. 2b). The aerial realm is also highly overlapping with the terrestrial one ($\text{Nestedness}_{\text{land-air}} = 0.89$; Fig. 2a); primates, a small subset of terrestrial species, are the main reason for such an overlap. For example, apes (including humans), and dolphins have essentially the same life history traits, whereas terrestrial Lemuriformes and Tarsius species are located in the part of the life history space occupied by bats (Figure 1; Extended Data Fig. 5). The arboreal behaviour of lemurs[38] allows them to escape from unfavourable situations, decreasing extrinsic mortality, extending longevity, and selecting for slow lives[11,39]. Similar occupation of life history space between higher primates and dolphins (Fig. 2a, Fig. 1) might be linked with complex social structures and high encephalization in both groups[8,40,41]. The development of high encephalisation and social behaviours requires vast parental investments[32,42] but, in turn, enables species to exploit the environment in a plastic way, avoiding hazards and stressful situations[37,42]. Consequently, high encephalization, which generally relates with both social and behavioural facets[32,43], may enable terrestrial species to adopt strategies that would be otherwise unfavourable. We tested this hypothesis by modelling the brain-mass ratio of terrestrial mammalian species (*i.e.* the ratio between brain dimension and body mass[41,44]) as a function

of species' position in the life history space (Supplementary methods 4). We found a robust association between larger brain-mass ratios and slow life histories ($R^2 = 0.53$, Extended data Fig. 6), suggesting that larger brain size may significantly influence the diversity of terrestrial life history strategies. Consequently, while the environmental realm in which species live seems to drive life history strategies, behavioural, and ecological characteristics of species (*e.g.*, sociality, plastic thinking, arboreality) may allow them to successfully exploit parts of the life history space that would otherwise not be viable in their specific realms[21].

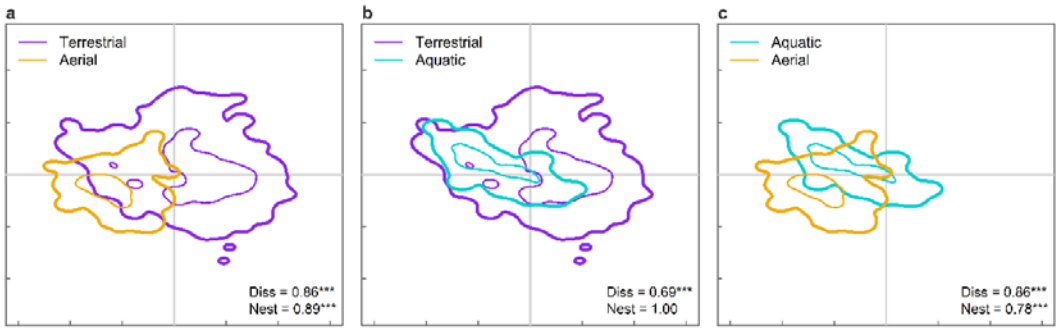

Fig. 2 | Environmental realms select for distinct yet nested life history strategies. Overlap-based dissimilarities between terrestrial (purple), aerial (light orange), and aquatic (light blue) species distributions in the life history space. Specifically: **a,** dissimilarity between terrestrial and aerial structures; **b,** dissimilarity between terrestrial and aquatic structures; **c,** dissimilarity between aerial and aquatic structures. Each system is highlighted at 50% (dashed line) and 99% (full line) 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).

Species transitioning between realms have intermediate life history strategies

The life history strategies of semi-aquatic species provide further evidence for the profound influence on life history variation by environment realms. We examined 58 semi-aquatic

mammal species that engage in activities such as feeding, mating, and offspring weaning in aquatic environments, but are not exclusively aquatic like dolphins or whales (Supplementary Methods 3). To understand how the life history strategies of these species differ from strictly terrestrial and strictly aquatic species, we analysed their dissimilarity patterns. Semi-aquatic species exhibit intermediate life history strategies, slower than terrestrial species but faster than fully aquatic ones (Fig. 3). This pattern holds within semi-aquatic mammals, whereby species occupy different regions of the life history space depending on their degree of water-dependence. For example, species with greater aquatic involvement, such as seals and walruses[8,14], occupy portions of the life history space similar to fully aquatic species like manatees, beluga, or sperm whales. Conversely, species with lesser water-dependence, like rodents and otters[8,14,27], are located in the hotspot typical of terrestrial mammals (Fig. 3).

The reported intermediate life history strategy location of semi-aquatic mammals is independent of taxonomic order. This robustness confirms the association between environmental realms and life history strategies even among closely related species. For example, terrestrial and semi-aquatic carnivores separate in the life history space following the same patterns seen in the global dataset with terrestrial carnivores being faster than their semi-aquatic counterparts (Extended data Fig. 7a-c). Moreover, the sea otter (*Enhydra lutris*), the only fully aquatic carnivore, exhibits a markedly different life history strategy compared to semi-aquatic otters (Extended data Fig. 7). Among Cetartiodactyla, aquatic (dolphins, whales) and semi-aquatic (hippos) species have slower life history strategies than terrestrial species (giraffe, bison, gazelles; Extended data Fig. 7d-f). Altogether, these findings suggest that species transitioning between aquatic and terrestrial realms possess intermediate life history strategies.

Time since divergence to aquatic realm associates with species life history strategies

The amount of time a mammal has evolved in the aquatic realm is associated with its life history strategy. For the 143 aquatic-related species (*i.e.*, aquatic, and semi-aquatic) in our dataset that transgressed realms, back from the terrestrial to the aquatic realm, we extracted from the literature their time since divergence (in m.y.) from their last terrestrial ancestor. There is a significant association between the time since divergence to aquatic realms and the position of mammals in the life history space (R^2 = 0.34 in semi-aquatic species, Figure 3d; R^2 = 0.40 in water-related species, Figure 3e; Extended data Table 2). With the notable exception of the platypus, semi-aquatic species with longer evolution in the aquatic realm, like seals and hippos, overlap in the life history space with cetacean and sirenians, that transgress realms at earlier times (Fig. 3d-e). Conversely, species with shorter evolutionary history in water, like mustelids and otters[8,14,27], are clustered towards the regions dominated by terrestrial species (Figure 3 d-e). Accordingly, a longer evolution under aquatic selection pressures may foster the accumulation of necessary for aquatic specialization[14,23,28]. This process could cause early diverging semi-aquatic species to gradually align with the trait space occupied by fully aquatic ones. Our findings indicate a link between the evolutionary separation from a shared aquatic-terrestrial ancestor and the life history strategies of species, underscoring the role of time in shaping realm-specific adaptations.

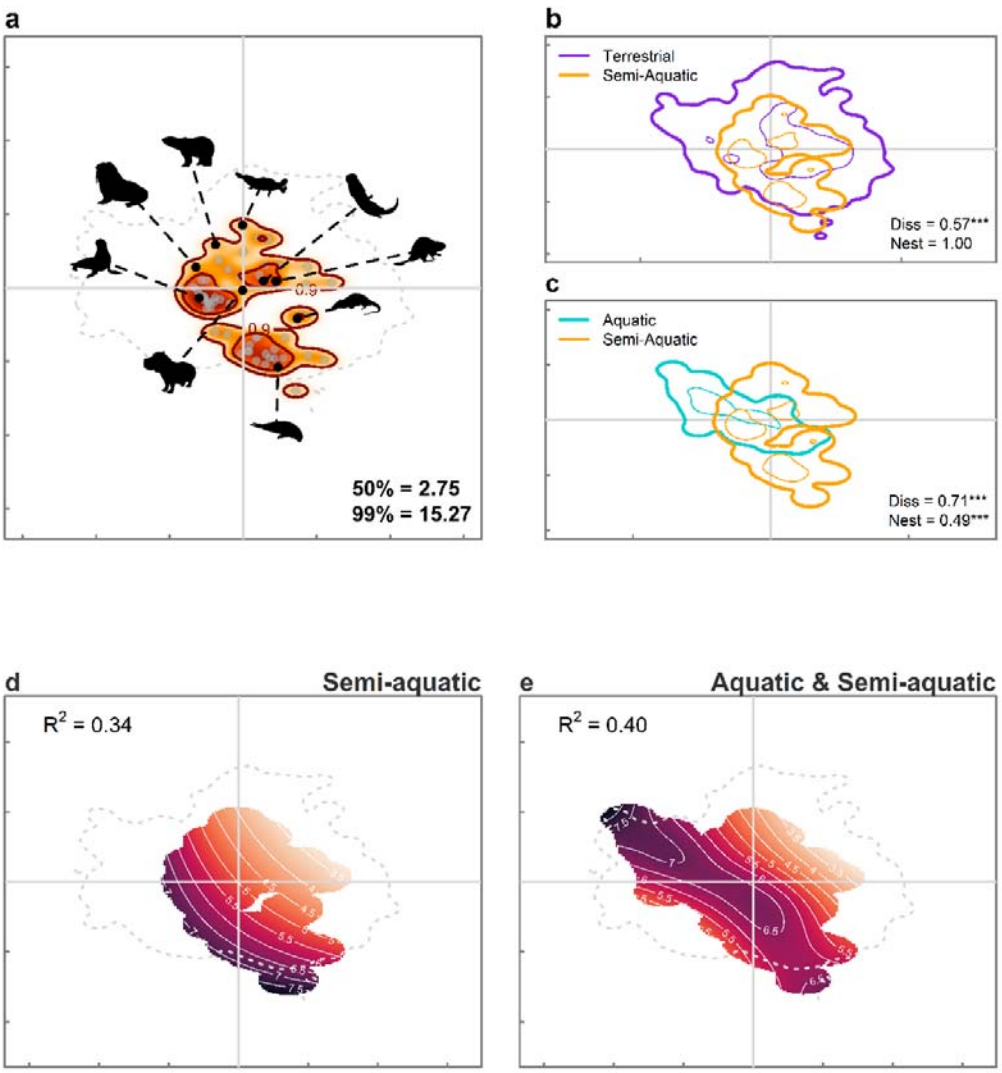

Fig. 3 | Semi-aquatic species transition between aquatic and terrestrial life histories depending on the evolutionary time they spent in water. **a,** Occupation of transitional mammals in the life history space. The colour gradient (red, orange, and white) depicts different density of species in the 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. 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. **d-e,** time since divergence from terrestrial ancestor mapped in the life history space. **d**; time since divergence modelled as a function of the position of semi-aquatic species in the life history space. **e**; time since divergence modelled as a function of the position of aquatic-related species in the life history space. Adjusted r-squared of each generalized additive models (GAMs) are reported in the upper part of the panels. Darker tones represent long time since divergence and lighter tones represent short time since divergence. White contour lines represent the thresholds of different time since divergence.

Conclusion

Our analyses of over 3,000 mammal species reveal that major environmental realm is a strong predictor of mammalian life history strategies. Aerial[3,11] and aquatic[14,45,46] realms require specific adaptations, such as flight-capable skeletal structures[12,13] or enhanced thermoregulatory abilities for aquatic life[8,14]. These adaptations slow down and prolong lifespans in ways seemingly unexploited in the terrestrial realm by mammals[11]. However, despite each realm's unique set of life history strategies, all of them overlapped within the life history space due to species' adaptations that enable the exploitation of otherwise unsuccessful strategies in each realm. Empirical research has shown that adaptations in social[37], migratory[36], dietary characteristics[35], and cerebral[32,47] can influence species' life histories. Consequently, variations in these behavioural and ecological characteristics modulate species' responses to environmental pressures[5] and expand the spectrum of life history strategies available for exploitation within a realm, as observed for activity patterns[21]. For instance, differences in migratory, dietary, and social habits among baleen whales and dolphins[8] may facilitate distinct life history strategies in aquatic environments, accounting for the rapid pace of life we observed in baleen whales. Similarly, the high sociality and

encephalization of primates[48] may allow these terrestrial mammals to exploit the slower end of the life history spectrum. The strong relationship we uncovered between brain dimension and the position of terrestrial species within the life history space (Extended data Fig. 4) supports this hypothesis. Accordingly, we advocate for future research to investigate the influence of ecological and behavioural adaptations on life history variation among terrestrial and aquatic mammals.

The time elapsed since an extant aquatic mammal diverged from its last terrestrial ancestor influences its life history strategy. The environmental pressures of a particular realm enable species to develop the necessary adaptations for success in that environment[5,6]. Accordingly, if the realm determines the type and magnitude of the environmental pressure acting on species, the duration these pressures are experienced can be pivotal in accumulating the evolutionary adaptations required for realm-specific specialization[23–26,28]. Our finding of a correlation between the life history strategies of aquatic-related species and the duration of aquatic-related evolution (Figure 3d-e) supports this hypothesis, suggesting a combined impact of environmental pressures and exposure duration on realized mammalian life history diversity. However, more research is needed to fully understand the process driving the evolution of mammalian life history strategies under different environmental constraints.

Our study provides a comprehensive assessment of global mammalian life history strategies, revealing the fundamental role of environmental realm in shaping these patterns. Remarkably, these relations persist even among closely related species, highlighting the profound 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[9,10]. Simultaneously, this foundation improves our understanding of the drivers and consequences of ongoing global

changes[15,49] and future biodiversity patterns[15,20,50]. 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.

Methods

Data collection and trait imputation

To characterise the mammals life history strategies, we downloaded the data from Amniote database which comprises information for ca. 18.300 species of mammals, reptiles and birds[29]. 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 1000 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).

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 synthetic trait spaces that are the result of combining different correlated traits space (see Carmona, Tamme et al., 2021 and Carmona, Bueno et al., 2021 for examples). Further, recent simulations have shown that studying the patterns of occupation of the synthetic space considering the imputed species yields results that are much closer to the real patterns of occupation of the space than those reached when only those species for which there is full trait information are considered[51]. Because accounting for

evolutionary relationships improves the accuracy of the imputation[52], we downloaded mammalian phylogenies from Vertlife database[53]. 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[54]. 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[55]. Species that were missing in the life history traits database were pruned using *drop.tip* function of *'phyltools'* R package.

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. 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[56]. After the imputation, we estimated the reliability of the imputation procedure (Supplementary methods 1). The imputation procedure efficiently retrieved the real position of a species, with an error of around 2.8% of the range for the first component and 1.7% for the second component. The final procedure resulted in a dataset of 3,438 mammalian species (53.7% of currently recognized living mammals[9]) from 29 orders in which 37.6% of traits information (1,293 species) derived from empirical measurement and 62.4% (2,145 species) were imputed.

Ascribing species to environmental realms

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[57] and IUCN[58] databases using the R packages *'worms'*[59] and *'redlist'*[60], 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 on the classification of "fully" aquatic species (*i.e.*, species that spent the entire life in water, *e.g.*, dolphins, whales, dugongs[8]), there is not a strict classification of semi-aquatic species[27]. Due to this, the Worms and IUCN databases classification did not match for many species. For instance, *Macaca mulatta* is classified as semi-aquatic according to the Worms database, while IUCN classifies it as terrestrial. 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 database. 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 to summarize the amount of time spent in water during fundamental phases of species life histories (*e.g.*, birth, mating; Supplementary methods 3). The AD Index was used to refine aquatic classification by relabelling species scoring zero in 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 (Supplementary methods 3). 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% of the total), 85 species were classified as aquatic (2.5% of the total), and 58 species were classified as semi-aquatic (*i.e.,* transitional species, 1.7% of the total).

All previously mentioned taxonomies (*i.e.*, life history traits, phylogeny, Worms and IUCN databases) were standardized using *gnr_resolve* function of the *'taxize'* R package[61] resolving for the Global Biodiversity Information Facility (GBIF) Backbone Taxonomy.

Construction of the global life history traits space

Body mass is a strong allometric constraint that affects the values of many other life history traits[2,31,62]. Mammals' body mass can span from the few grams of shrews, to the tons for whales, and the aquatic realm strongly selects for bigger sizes compared to the terrestrial realm[45]. 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 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[62,63]. Body mass–corrected residuals were further centred, scaled, and used as size-corrected life history traits (Extended data Fig. 1).

Mapping species position in multidimensional spaces based on trait information allows the identification of major axis of trait variation[64,65], as well as summarizing species' ecological strategies. We constructed mammalian life history space by performing 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. 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 three other spaces: one built considering only complete set of records (*i.e.,* non-imputed data; N = 1,293; Extended data Fig. 2); one built considering the imputed dataset without body mass correction (N = 3,438); and one built considering the same body mass–corrected residuals used to build the life history space (N = 3,438) but accounting for the phylogenetic history of species (Extended data Fig. 3; Extended data Table 1). In all abovementioned 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 2).

Exploring patterns within the global life history space

We derived life history structure (*i.e.*, the patterns of organization of species in the life history space) using the trait probability density framework (TPD)[66], 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[66,67], and with a standard deviation computed using the unconstrained bandwidth selectors from the *'Hpi'* function in the *'ks'* package[68,69]. To estimate the life history structure of the whole set of mammals, all species' kernels were weighted and aggregated to form a single continuous trait probability density (TPD) function across the whole mammalian life history space. The value of the TPD function in any given point of the life history space reflects the density of species in that particular area of the life history space[66,67]. 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. We used the *'TPD'* R package[67,70].

We used mammalian global structure to test whether mammals distribute in the life history space following a random assembly of life history traits (*i.e.*, life history strategies are randomly selected) or whether certain life history strategies are more prevalent than others[6,30,64]. First, we computed functional richness (the amount of functional space occupied[66,71]) at increasing probability thresholds (*i.e.*, from 0.1% to 99.9% of the TPD function, using 0.1% increments). In this way, we estimated a "profile" of the probabilistic distribution of species, reflecting what proportion of the life history space is occupied at different probability thresholds. We compared the observed functional richness profile with a

null model (999 repetitions) considering a bivariate normal distribution of species with the same mean and variance as the observed data (see Carmona, Bueno et al., 2021).[30] This analysis was performed by sampling 3,438 simulated species *(i.e.,* complete set of mammals) from a bivariate normal distribution with the same mean and covariance of observed data calculated using the '*rmvnorm'* function of the R package '*tmvtnorm'*[72]. In the same way as done for the observed data, for each repetition of the null model we computed life history structure and measured functional richness at increasing probability thresholds. We then compared the observed and null functional richness profiles; functional richness values lower than expected under the null model would suggest that the global set of mammals occupy a smaller portion of the life history space than expected under a normal distribution and vice-versa.

Then, using the same null model, we tested whether the portions of life history space that are mainly exploited by mammalian species are closer or farther than expected from the centre of the distribution. For this, we estimated functional divergence (*i.e.,* degree to which species' density is skewed towards the extremes of the life history space) considering 99% of the total species' probability[66,71] for both observed and simulated data. High functional divergence would reveal that species are segregated towards the edges of the life history space, whereas low divergence would indicate that species are clustered in the centre of the life history space[30].

We estimated the standardized effect size (SES) of both the functional profiles (at each probability threshold) and the functional divergence measures as: SES = (observed value – mean (simulated values))/standard deviation (simulated values). SES values express the number of SD units by which the observed value deviates from the mean of the simulated ones. A SES value lower than 0 indicates that the observed metric is smaller than the average of the simulated values and vice versa. Finally, we tested the statistical significance of

observed and simulated differences by estimating two-sided p-values computed by confronting the SES values with a cumulative normal distribution with mean = 0 and standard deviation = 1[30].

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 by highlighting the contours containing 50% and 99% of the total probabilistic distribution of species order (Extended data Fig. 5).

Exploring environmental realms' patterns in the life history space

We produced environmental 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. Similarly, to the complete mammalian life history structure, we represented graphically the TPD for each realm and highlighted contours containing 50% and 99% of the total probability.

We compared several aspects of the structure of each of the environmental realms (*i.e.*, air, land, water and transitional). First, we compared them in terms of the amount of life history space that they occupy (*i.e.*, their functional richness). Because functional richness is known to be positively related to the number of species present in a group, we built a null model (999 repetitions) randomizing species assignment[30]. 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 SES as explained above. Under this null model, negative SES values would indicate that the species present in the realm are more clustered in the life history 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[30], suggesting that the realms exert a strong selection on life history strategies. This procedure allows to compare functional richness among realms with very different number of species (Extended data 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'*[73]). 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[30].

We estimated pairwise dissimilarities in life history structures between pairs of realms (*i.e.*, air, land, water, and transitional). 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[15,50,74]. 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 (*i.e.*, turnover) and another reflecting how differently the two realms occupy the shared parts of the life history space (*i.e.*, nestedness[67]).

We tested whether the observed dissimilarities between environmental realms were significantly higher than expected by chance by means of null models[75,76]. 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 (Extended Data Table 2b).

Then, we explored whether high encephalization[32,42,43,77] allows to exploit portion of the life history space otherwise not successful for the terrestrial realm (Supplementary methods 4). The final procedure resulted in generalized additive models (GAM) mapping species encephalization (expressed as brain-mass ratio[41,44]; brain mass information were extracted from Combine database[78]) in response to the species position in the life history space (Extended data Fig. 6).

Lastly, we explored whether dissimilarities between environmental realms were maintained also in closely related species. To do this, we computed TPD functions for orders having species inhabiting in different realms. Because all aerial species belong to the Chiroptera order, we decided to focus on orders having both terrestrial and aquatic species. We extracted 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 a life history structure for terrestrial species and one for aquatic species. We represented graphically structures highlighting 50 and 99% of the total probability and we computed pairwise dissimilarities between the terrestrial and aquatic life history structure of each order (Extended data Fig. 7).

Evolutionary time in the environmental realms and species life histories

While the aerial realm consists in the single Chiroptera order that diverged from a common terrestrial ancestor and diversified to all its modern form[79], aquatic-related (*i.e.*, aquatic and semi-aquatic) species have returned to water in multiple independent occasions across different lineages[8,80]. Consequently, we decided to focus on the subset of aquatic-related species and to test whether the length of evolution in relation to water is related to species life history strategies. For this, we performed a literature search to compile a database of time since divergence from the last terrestrial ancestor for the full set of aquatic and semi-aquatic species (N =143). It worth to mention that lineages diversified from a last common terrestrial ancestor, like seals or cetaceans[80,81], shared the same time since divergence.

We mapped squared root-transformed time since divergence from last terrestrial ancestor of the full set of aquatic-related species as a response to species positions in the life history space following Carmona, Tamme, et al., 2021. We used generalized additive models (GAM), where time was used as response variable, and the species coordinates in the life history space were used as explanatory variables. The latter was computed using 5 basis functions (k) of thin plate regression splines basis type, considering both main effect of each PCs composing the life history space as well as the interaction between them. As smoothing parameter estimation, we used the REML method, and we used a gamma family distribution (Figure 3e; Extended Data Table 3). Additionally, to test whether the findings were consistent also within semi-aquatic species, we performed another GAM model considering only the semi-aquatic species and using the same parameters reported above (Figure 3d; Extended Data Table 3). Both GAMs were computed using the r package *'mgcv'*[82].

All statistical analyses were performed using R version 4.0.3[83].

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Author Contributions

P.C.L., R.S-G., and C.P.C. conceived the core ideas behind this paper, all authors provided fundamental inputs for its final development. E.B collected all data and performed the literature search needed to sort species in environmental realms. E.B performed the literature search needed to collect data on evolutionary divergence, assisted by R.S-G. E.B. analysed the data with fundamental inputs from C.P.C., P.C.L, and R.G-S. All authors contributed to interpretation of the results. E.B. and C.P.C. led the writing of the manuscript which was edited by all authors.