Longevity, body dimension and reproductive mode drive differences in aquatic versus terrestrial life history strategies

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Abstract

1. Aquatic and terrestrial environments display stark differences in key environmental factors and phylogenetic composition but their consequences for the evolution of species' life history strategies remain poorly understood.
2. Here, we examine whether and how life history strategies vary between terrestrial and aquatic species. We use demographic information for 685 terrestrial and 122 aquatic animal and plant species to estimate key life history traits. We then use phylogenetically corrected least squares regression to explore potential differences in trade-offs between life history traits between both environments. We contrast life history strategies of aquatic *vs.* terrestrial species in a principal component analysis while accounting for body dimensions and phylogenetic relationships.
3. Our results show that the same trade-offs structure terrestrial and aquatic life histories, resulting in two dominant axes of variation that describe species' pace-of-life and reproductive strategies. Terrestrial plants display a large diversity of strategies, including the longest-lived species in this study. Aquatic animals exhibit higher reproductive frequency than terrestrial animals. When correcting for body size, mobile and sessile terrestrial organisms show slower paces of life than aquatic ones.
4. Aquatic and terrestrial species are ruled by the same life history trade-offs, but have evolved different strategies, likely due to distinct environmental selective pressures. Such contrasting life history strategies have important consequences for the conservation and management of aquatic and terrestrial species.

Keywords: Aquatic–terrestrial comparisons, comparative demography, fast-slow continuum, life history trait, matrix population model, phylogenetic analyses.

Translated Abstract

1. Los ambientes acuáticos y terrestres presentan diferencias notables en distintos factores ambientales y en su composición filogenética. Sin embargo, las consecuencias de estas diferencias para la evolución de las estrategias de vida de las especies siguen siendo desconocidas.

2. En este estudio examinamos si y cómo las estrategias de vida varían entre especies terrestres y acuáticas. Utilizamos datos demográficos de 685 especies de plantas y animales terrestres y 122 acuáticos para estimar rasgos de la historia de vida de dichas especies. Luego, utilizamos regresiones de mínimos cuadrados corregidas filogenéticamente para explorar las posibles diferencias en los "trade-offs" entre los rasgos de la historia de vida de las especies en ambos ambientes. Contrastamos las estrategias de vida de las especies acuáticas frente a las terrestres utilizando un análisis de componentes principales, corrigiendo por la dimensión del cuerpo y las relaciones filogenéticas.

3. Nuestros resultados muestran que los mismos "trade-offs" estructuran las estrategias de vida terrestres y acuáticas, lo que resulta en dos ejes dominantes de variación que describen el ritmo de vida de las especies y las estrategias reproductivas. Las plantas terrestres muestran una gran diversidad de estrategias, incluyendo las especies más longevas en este estudio. Los animales acuáticos exhiben mayor frecuencia reproductiva que los animales terrestres. Al corregir el tamaño del cuerpo, los

organismos terrestres móviles y sésiles muestran ritmos de vida más lentos que los acuáticos.

4. A pesar de que las especies acuáticas y terrestres se rigen por los mismos "trade-offs" han desarrollado diferentes estrategias en ambos ambientes, probablemente debido a distintas presiones selectivas. Tales diferencias en las estrategias de vida tienen consecuencias importantes para la conservación y la gestión de las especies acuáticas y terrestres.

Introduction

The rich diversity of life history strategies worldwide stem from three fundamental demographic building blocks: survival, development, and reproduction (Stearns, 1992). Importantly, these life histories determine the viability of populations (Paniw, Ozgul, & Salguero-Gómez, 2018), rates of speciation (Venditti, Meade, & Pagel, 2010), and guide the effectiveness of conservation plans (Carr et al., 2003; Veličković et al., 2016). Despite the advanced development of life history theory (Lande, Engen, & Sæther, 2017), few studies have contrasted the validity of life history principles across terrestrial and aquatic organisms (Webb, 2012).

Life history theory is rooted upon the concept of trade-offs as a unifying principle across the tree of life (Stearns, 1992). Given the limitations in available energy and physiological constraints, compromises among survival, development, and reproduction are inescapable for any organism, whether aquatic or terrestrial (Stearns, 1992). Such constraints should result in a finite set of viable life history strategies. The evolution of a life history strategy in a given environment is then determined by two counteracting processes: environmental filtering and evolutionary history (Stearns, 1992). Environmental filtering stems from extrinsic factors favouring certain strategies over others. For example, aquatic environments enable the evolution of sessile animals due to the suspended nutrients and organic material in the water column. Such a strategy is not possible for terrestrial animals (Webb, 2012). On the other hand, evolutionary history represents the influence of phylogenetic relationships in determining the potential adaptations of a given species (Blomberg & Garland, 2002; Freckleton, 2000). Life history strategies are then expected to be more similar, irrespective of environment, amongst closely related lineages.

According to life history theory, the same trade-offs should be experienced by aquatic and terrestrial organisms. Comparative demographic studies have successfully identified and organised trade-offs into a few major axes of trait co-variation (Gaillard et al., 1989; Salguero-Gómez, Jones, Jongejans, et al., 2016). A seminal concept in organising such trait co-variation is the "*fast-slow* continuum" (Stearns, 1992). In it, species are placed along a continuous axis bounded by two extremes: at the fast-living extreme, species develop quickly, are highly reproductive, but have short lifespans; while at the slow extreme, species have high survival rates, develop slowly, and live long. However, an explicit comparison of the fast-slow continuum between aquatic and terrestrial species remains, to our knowledge, untested.

If trade-offs are universal, the strong environmental and phylogenetic dissimilarities between aquatic and terrestrial environments should result in different life history strategies. For example, aquatic and terrestrial habitats impose differing selective pressures on body size. Indeed, aquatic endotherms have larger body sizes than terrestrial ones, due to the strict energetic demands of the aquatic environments (Gearty, McClain, & Payne, 2018). Such constrains must have consequences for aquatic life history strategies, given that a large body size co-varies positively with a slow pace of life (Jean-Michel Gaillard et al., 1989; Healy et al., 2014). On the other hand, aquatic environments allow early life stages to feed and develop during the dispersal phase, promoting external reproduction (Burgess, Baskett, Grosberg, Morgan, & Strathmann, 2016; Bush, Hunt, & Bambach, 2016; Vermeij & Grosberg, 2017). Terrestrial species had to evolve reproductive systems independent of environmental water, such as internal fecundity or seeds (Bush et al., 2016; Grosberg, Vermeij, & Wainwright, 2012; Steele, Brink, & Scott, 2019). In the case of aquatic species, strategies should have evolved to counteract the uncertainty of recruitment success derived from external reproduction (Charnov & Schaffer 1973; Tuljapurkar et al. 2009).

The colonisation of land likely resulted in the evolution of life history strategies to deal with higher temporal environmental variation (Dawson & Hamner, 2008; Ruokolainen, Lindén, Kaitala, & Fowler, 2009). On land, environmental variation is more stochastic and less temporally auto-correlated than in aquatic environments (Dawson & Hamner, 2008). Classical life history theory predicts the evolution of longevity in constant environments (Lande et al., 2017). However, longevity can also be a strategy to deal with environmental variation (McDonald et al., 2017; Morris et al., 2008). For example, by spreading their reproductive output across several years, long-lived species are able to exploit favourable conditions in a stochastic environment, compensating for unfavourable years (McDonald et al., 2017). Instead, fast life histories are expected to show increasing fluctuations in population sizes with increasing environmental variation. For that reason, some authors have argued that the colonisation of land resulted in the evolution of longer lifespans to smooth out the large environmental fluctuations in terrestrial environments (*sensu* Steele et al., 2019).

Here, we test the hypotheses that (i) life history trade-offs are universal across aquatic and terrestrial systems, and that (ii) terrestrial species have evolved distinct life history strategies compared to aquatic ones. We use high-resolution demographic data from 122 aquatic and 685 terrestrial species across the globe from the COMPADRE and COMADRE databases (Salguero-Gómez, Jones, Archer, et al., 2016; Salguero-Gómez et al., 2015). We estimate key life history traits that reflect various moments of population turnover, as well as investments in survival, development, and reproduction of each species. To test these hypotheses, we first determine whether correlations between life history traits differ across environments as a way to examine whether trade-offs diverge between terrestrial *vs*. aquatic species. Second, we explore the main axes of life history variability shaping aquatic and terrestrial species. The presence of different life history axes of variation and/or a distinct positioning of aquatic species compared to terrestrial ones within those axes would suggest dissimilar selection pressures occurring in terrestrial and aquatic environments. Given the scarcity of comparative studies and the lack of demographic information for many aquatic species, elucidating these questions is a key step towards understanding the evolution of life histories across environments.

Material and Methods

Demographic data and life history traits

We calculated species' life history strategies using demographic data describing the full life cycle of each species. This high-quality demographic information was obtained from the COMPADRE Plant Matrix Database (v. 5.0.1; Salguero-Gómez et al., 2015) and COMADRE Animal Matrix Database (v. 3.0.1; Salguero-Gómez, Jones, Archer, et al., 2016). These repositories archive demographic data as matrix population models (MPMs, hereafter) for over 700 plant and 400 animal species, respectively. MPMs are summaries of organisms' demographic processes (*i.e.,* vital rates such as survival, development and reproduction) that together determine their life history strategies and resulting population dynamics (Caswell, 2001). For this reason, MPMs provide the ideal means to compare the vast array of life history strategies (Franco & Silvertown, 2004; McDonald et al., 2017).

To compare life history traits across aquatic and terrestrial species, we imposed a series of selection criteria to the available demographic data (see details in Appendix S2: Data selection in Supporting Information). These criteria resulted in 685 terrestrial species and 122 aquatic species used in this study (Appendix S1). To determine the marine, freshwater or terrestrial origin of species we used the primary habitat reported in the World's Register of Marine Species (WORMS, www.marinespecies.org) and the Catalogue of Life (CL, http://www.catalogueoflife.org) databases. We estimated the total number of species in terrestrial, freshwater and marine environments based on estimates provided in Grosberg et al., (2012), together with information provided in WORMS and CL. The number of species studied here represented a similar taxonomic coverage relative to the known biodiversity of the aquatic (~0.04-0.03%) and terrestrial environment (~0.01%; Table S1 in Appendix S2).

Quantifying a species' life history strategy requires detailed information regarding the timing, intensity, frequency, and duration of key demographic processes across its life cycle (Capdevila & Salguero-Gómez, 2019; Stearns, 1992). To quantify species' life history strategies, we calculated several life history traits from each MPM using well-established methods (Salguero-Gómez, Jones, Jongejans, et al., 2016). We selected six life history traits commonly used in comparative demography (Bielby et al., 2007; Gaillard et al., 2005; Salguero-Gómez, Jones, Jongejans, et al., 2016; Stearns, 1992). These traits include: generation time (T), age at sexual maturity (L_α), rate of senescence (H), mean vital rate of progressive development (γ), the mean vital rate of sexual reproduction (φ) and degree of iteroparity (S) (Table 1). Such traits provide insights into a species' population turnover, as well as of survival, developmental, and reproductive strategies (detailed in Table 1).

For every species, we decomposed the MPM, $\boldsymbol{A}$, into two sub-components (equation 1): the $\boldsymbol{U}$ matrix, which represents the survival-dependent vital rates (e.g. development, shrinkage, fission, etc); and the $\boldsymbol{F}$ matrix, containing the stage-specific per-capita reproduction rates (Caswell, 2001; W. Morris & Doak, 2002). Those species showing clonality were removed from the analyses, in order to avoid potential over estimation of survival rates. This decomposition facilitates the estimation of key life history traits such as the time elapsed since, or to, a given demographic event (e.g., age at maturity, mean life expectancy; see Table 1).

$$\boldsymbol{A} = \boldsymbol{U} + \boldsymbol{F} \qquad \text{equation 1}$$

The traits T, L_α and R_0 were calculated using stage-from-age demographic decompositions (Caswell, 2001; p. 124-127; see Table 1), where the beginning of life was *a priori* defined as the first non-propagule stage in the life cycle of the organism (Burns et al., 2010). This approach avoids uncertainties associated with the longevity of spores and seeds (Burns et al., 2010; Caswell, 2001; Salguero-Gómez, Jones, Jongejans, et al., 2016; Silvertown & Franco, 1993) and assures the comparability with species without such life cycle stages. To calculate S and H (Demetrius, 1974; Keyfitz, 1977), we first obtained the age-specific survivorship curve (l_x), and the age-specific fertility trajectory (m_x) following Caswell (2001; p. 118-121), and implemented the formulae described in Table 1. The traits progressive development (γ) and sexual reproduction (φ) summarise investments into development and reproduction annually for all stages across the life cycle weighted by the relative representation of stages under stationary conditions (Table 1).

Phylogenetic analyses and trait comparisons

We accounted for and estimated the phylogenetic influence on the differences in life history trait values within species and between aquatic *vs.* terrestrial environments. To do so, we constructed a species-level phylogenetic tree (Figure S4 in Appendix S3) with data from Open Tree of Life (OTL, https://tree.opentreeoflife.org, (Hinchliff et al., 2015)). OTL combines publicly available taxonomic and phylogenetic information across the tree of life (Hinchliff et al., 2015). Briefly, we built separate trees for our species of algae, plants, and animals, using the *rotl* R package (Michonneau, Brown, & Winter, 2016). These trees were assembled in a supertree using the function *bind.tree* in the *phytools* package (Revell, 2012). To account for the phylogenetic relatedness of species we computed the branch lengths and resolved polytomies (Revell, 2012). We also tested the sensitivity of our results to the choice of a particular set of branch lengths, by repeating our analyses setting all the branch lengths to one and using Pagel's branch length (Tables S5-S8 in Appendix S3). We did so using the software Mesquite 1.05 (Maddison & Maddison, 2001) and its PDAP module 1.06 (Midford, Garland Jr, & Maddison, 2005), for further details on the construction of the tree see Appendix S3.

To test whether life history trait trade-offs are congruent between aquatic *vs.* terrestrial species, we carried out a series of Phylogenetic General Least Square (PGLS) analyses (Revell, 2010). This approach allows us to accommodate residual errors according to a variance-covariance matrix that includes ancestral relationships between any pair of species from our phylogenetic tree (Revell, 2010; Revell, 2012). The variance-covariance matrix represents the expected covariance between species' trait values, given a phylogenetic tree and under a specific model of evolution (see below) (Revell, 2009). The expected covariance between species' trait values is directly proportional to the distance between the species and their most recent common ancestor, what is measured as the branch length of the phylogeny (Revell, 2009).

We implemented our set of PGLSs in R using the correlation structures provided by the package *ape* (Paradis, Claude, & Strimmer, 2004). We used a Brownian motion model of evolution, combined with the *pgls* function from the *nlme* package (Pinheiro, Bates, Debroy, Sarkar D, & R Core Team, 2014). Separate PGLSs were fitted using Ornstein Uhlenbeck model of evolution, which describes a Brownian model under the influence of friction (Uhlenbeck & Ornstein, 1930). Both models were compared using Akaike Information Criterion (Akaike, 1974); the Brownian motion model generally outperformed the Ornstein Uhlenbeck model, but both showed similar results. Therefore, we only report the PGLS results from the Brownian motion model.

Exploring dominant axes of life history strategies

To explore the patterns of association among life history traits for aquatic *vs*. terrestrial species, we performed a series of principal components analyses (PCA). PCA is a multivariate analysis that reduces a set of correlated variables into linearly uncorrelated measurements, the so-called principal components (PCs). Life history trait data were log- and z-transformed (mean=0, SD=1) to fulfil normality assumptions of PCAs (Legendre & Legendre, 2012). Finally, for each life history trait we identified outliers for each life history trait as those located outside of the 2.5th-97.5th percentile range of the distribution, and excluded them.

PCA is a method based on correlation and variance–covariance matrices, as it is very sensitive to the presence of outliers (Legendre & Legendre, 2012), we ran the PCA with and without the outliers. We note that the exclusion of outliers did not alter our main findings (see Tables S9-S12 in Appendix S4).

To account for shared ancestry while exploring differences in aquatic *vs.* terrestrial life history strategies, we used a phylogenetically informed PCA (pPCA; Revell, 2009). The pPCA considers the correlation matrix of species' traits while accounting for phylogenetic relationships and simultaneously estimating Pagel's λ with maximum likelihood methods. Pagel's λ quantifies the strength of the phylogenetic relationships on trait evolution under a Brownian motion model (Blomberg & Garland, 2002; Freckleton, 2000). This metric varies between 0, when the observed patterns are not due to phylogenetic relationships, and 1 when the observed patterns can be explained by the employed phylogeny (Blomberg & Garland, 2002; Revell, 2010). The pPCA was estimated using the *phyl.pca* function from the R package *phytools* (Revell, 2012), assuming a Brownian motion model of evolution (Revell, 2010).

A complete dataset (*i.e.*, no missing values) is necessary to run the pPCA analyses. However, estimating life history traits for species' MPMs was not always possible (see *Missing data* in Appendix S2: Extended methods). For example, we could not calculate the rate of senescence for *Fucus vesiculosus*. Indeed, in general, the rate of senescence (Keyfitz' entropy) can only be reliably calculated for life tables that have not reached stationary equilibrium before 95% of a cohort are dead (see Caswell, 2001; Jones et al., 2014), which was not the case for this species. In these cases, we imputed the missing data using the function *amelia* from the *Amelia* package (Honaker, King, & Blackwell, 2011).

This function uses a bootstrap expectation-maximisation algorithm to impute missing data (Honaker, King, & Blackwell, 2011). We then created 10 imputed datasets and ran analyses on each separately.

Body dimension pPCA correction

Body weight and size are highly correlated with many life history traits. Life history studies typically correct for body dimension (e.g. size or weight) explicitly to unmask potential correlations in life history traits once the effect of body dimension has been taken into account (e.g. Bielby et al., 2007; Gaillard et al., 1989). There are multiple ways to account for body dimension in life history analyses (Jeschke & Kokko, 2009). Here, we used the residuals of the linear models between each life history trait of interest and the body dimension of each species in the pPCA (Revell, 2009). Note that we present both non-corrected and corrected weight/size pPCA results (Figures 3 and 4, respectively).

We performed body dimension-corrected pPCA separately for mobile and sessile species. For sessile species, such as plants, algae, corals or sponges, body size measurements are more frequently used than body weight, with the opposite applying to mobile species such as mammals, birds or reptiles. Therefore, we collected adult body mass (g) data from Myhrvold et al., (2015) for mammals birds, reptiles and amphibians, and from FishBase (Base et al., 2007) for teleost and elasmobranch fishes. For terrestrial plants, we utilised maximum height (m) reported per species in TRY database (Kattge et al., 2011), complemented with information from the Botanical Information and Ecology Network (BIEN; http://bien.nceas.ucsb.edu/bien/). For corals we used the Coral Traits Database (Madin et al., 2016). For the rest of the species, we extracted size information from the Animal Diversity Web (https://animaldiversity.org) and the WORMS (http://www.marinespecies.org). Not all our species had body dimension information available, reducing our initial sample size. The number of species decreased from 74 to 50 aquatic and from 127 to 115 terrestrial mobile species, and from 48 to 40 aquatic and from 558 to 258 terrestrial sessile species (see Tables S2 and S3, Appendix S2).

Analysis validation

We examined the consistency of our results and explored the differences between environments, modes of life, and taxonomic groups by performing the pPCA analyses on different subsets of data. These subsets included comparisons between mobile *vs.* sessile organisms, Animalia *vs.* Plantae/Chromista kingdoms, and aquatic *vs.* terrestrial environments. We considered sessile species as those that do not have active locomotion during the adult stages of their life cycle (e.g. corals, sponges, plants) as well as species with limited adult locomotion (e.g. clams, worms, snails). This distinction was made because key traits (e.g. reproduction, development, energetic requirements) can differ between sessile and mobile organisms (Bush et al., 2016; Vermeij & Grosberg, 2017). We also performed a series of pPCA analyses sub-setting species into Animalia kingdom, and Plantae and Chromista (brown algae). This distinction was made because animals and plants/algae differ in key physiological, trophic, and developmental traits (Burgess et al., 2016; Grosberg et al., 2012). Such ecological differences between sessile/mobile and taxonomic kingdoms could have a potential impact on our hypothesis about how the evolution of life history strategies differ in aquatic and terrestrial species.

We tested the sensitivity of our results to missing traits in the dataset using pPCAs in two ways. First, we ran a pPCA only with the species with complete data (62 aquatic species, 477 terrestrial species, Tables S13 and S14, Appendix S4). Then, we ran another pPCA with all species, we were able to include species with missing data by imputing the necessary missing data (see details in Tables S9, S10, S13 and S14, Appendix S4). The results from the multiple imputations were presented as their respective mean values with their standard deviation. To test the differences between the distributions of pPCA scores between environments, we used a Welch's t-test on the mean position of species resulting from the multiple imputations. The Welch's t-test is an adaptation of the Student's t-test, but with more flexibility when the two samples have unequal variances and/or unequal sample sizes, such as between aquatic and terrestrial species.

We evaluated the performance of the imputation method utilised in our study using the diagnostic tools available in the R package *Amelia* (Honaker et al., 2011). We used the function *compare.density* to compare the distribution of the imputed values against the distribution of the observed values (Figures S2 and S3, Appendix S2). We used the function *overimpute* as a cross-validation method to assess the predictive ability of the imputation (Nguyen, Carlin, & Lee, 2017) (see *Imputation validation* in Appendix S2). Overall, the performance of the imputation model was good, although it lost predictive power at the extreme values, particularly in terrestrial species (Figures S2 and S3, Appendix S2).

Results

Trade-offs are pervasive across environments

Life history traits are shaped by the same trade-offs for terrestrial and aquatic organisms (Figure 1). Our PGLS analyses reveal a similar magnitude and the same direction of pair-wise correlations between traits for aquatic and for terrestrial species (Figure 1 and Tables S10, S12 and S14, Appendix S4).

Regardless of the environment, producing many recruits (high φ; Table 1) results in fast population turnover (low T). Species that postpone their first reproductive event (high L_α) have low senescence rates (high H; Figure 1). Species with fast development (high γ) achieve reproductive maturity early (low L_α) at the cost of high senesce rates (low H). Also, those species with high mean reproductive output (high φ) and frequent reproduction (high S), have low senescence rates (high H; Figure 1).

Longevity is more prevalent in terrestrial environments

Together, the first two axes of our phylogenetically corrected principal component analysis (pPCA; Table 1) explain ~68% of the examined variation in life history traits (Figure 2, Table 1). Principal component axis 1 (PC1) explains 47.42±0.34% (S.E.) of the variation and represents the fast-slow continuum. Indeed, PC1 portrays a trade-off between species with fast development and short lifespans, and species with slow development, high investment in survival (low senescence rates), and postponement of maturity (Figure 2). PC2 explains 21.02±0.11% of the variation in life history traits related to reproductive strategies. In PC2, those species characterised by high reproductive rate and high iteroparity are located at the top of the PC2 axis *vs.* species with fewer reproductive events across their lifetimes, located at the bottom. These patterns are robust within different life modes (Figure 3a,b and Table S15 in Appendix S4), kingdoms (Figure 3c,d and Table S16 in Appendix S4), and environments (Table S17, Appendix S4).

The sampled aquatic life history strategies in our study are displaced towards the fast extreme of the fast-slow continuum ($t_{197.49}$=-6.22, P<0.01; Figure 2). On land, the studied species tend to occupy fast pace of life regions, such as the *Setophaga cerulean* (cerulean warbler), as well as slow ones, such as

Pseudomitrocereus fulviceps (the giant cardon). In the aquatic environment, the resulting pace of life values are constrained to faster values compared to terrestrial species (PC1; Figure 2). In contrast, aquatic organisms are not displaced towards any of the extremes of the PC2. Both aquatic and terrestrial species show a wide range of reproductive strategies, with no significant difference in their positioning along PC2 ($t_{215.04}$= 0.18, P=0.86; Figure 2). Some species are highly reproductive, such as *Lantana camara* (big-sage) or *Gracilaria gracilis* (red seaweed) while others have low reproductive outputs, such as *Mirounga leonina* (southern elephant seal) and *Gorilla beringei* (eastern gorilla).

Mode-of-life, kingdom, and body dimension drive key life history differences across environments

The main axes of life history variation remain unaltered across environments, modes-of-life (*i.e.,* whether species are mobile or sessile during their adulthood), taxonomic affiliation, and when correcting for body dimension. The first and second axes of life history trait variation correspond to the fast-slow continuum and reproductive strategies in both sessile and mobile species (Figure 3a,b and Table S15 in Appendix S4), in Animalia and Plantae/Chromista kingdoms (Figure 3c,d and Table S16 in Appendix S4), and in terrestrial and aquatic species (Table S17, Appendix S4). These patterns remain the same after correcting for body weight in mobile species and body size in sessile species for both aquatic and terrestrial organisms (Table S18, Appendix S4).

Aquatic and terrestrial sessile species display significant differences in their position across the first axis of life history variation. Aquatic sessile species are displaced towards the fast end (*i.e.,* low PC1 scores) of the fast-slow continuum ($t_{64.91}$=-53.32, P<0.01; Figure 3a). Aquatic sessile species do not show significant differences in their reproductive strategies compared to terrestrial ones ($t_{59.22}$=1.95, P=0.06; Figure 3a). Mobile aquatic species are not displaced towards any end of the fast-slow continuum when compared to terrestrial mobile species ($t_{96.34}$=0.55, P=0.58; Figure 3b), this is also true for the reproductive axis ($t_{118.88}$=1.84, P=0.07; Figure 3b).

Terrestrial plants have a wide range of life history strategies with no significant displacement in the fast-slow axis ($t_{9.52}$=-1.16, P=0.27; Figure 3c) neither or reproductive axis ($t_{9.16}$=0.25, P=0.81; Figure 3c), compared to aquatic plants. Terrestrial animals do not show any significant displacement within the fast-slow continuum ($t_{199.08}$=0.74, P=0.46; Figure 3d). However, aquatic animals are significantly displaced towards the upper end of the reproductive axis compared to their terrestrial counterparts ($t_{208.60}$= 4.27, P<0.01; Figure 3d).

When correcting for body dimension, the same patterns arise for sessile and mobile organisms (Figure 4). Terrestrial species are displaced towards the slow end of the fast-slow continuum when compared to aquatic ones, both for sessile ($t_{53.80}$=-3.64, P<0.01; Figure 4a) and mobile organisms ($\mathrm{t}_{108.91}$=-3.56, P<0.01; Figure 4b). However, neither sessile ($t_{84.51}$=0.22, P=0.83; Figure 4a) nor mobile species ($t_{128.5}$ = -0.28, P=0.78; Figure 4b) show significant differences in their reproductive strategies between aquatic and terrestrial environments.

Ancestry does not shape cross-environmental life history strategies

Overall, phylogenetic ancestry (*i.e.* phylogenetic inertia) plays a minor role in constraining life history strategies between environments. The estimates of Pagel's λ in our pPCA are indeed weak (0.26±0.00). Such values of the phylogenetic signal remain weak across sessile species (λ=0.18±0.01; Table S15, Appendix S4), mobile species (λ=0.36±0.01; Table S15, Appendix S4), plants and algae (λ=0.18±0.01; Table S16, Appendix S4) and animals (λ=0.31±0.02; Table S16, Appendix S4). In addition, the phylogenetic signal is similar between terrestrial (λ=0.24±0.01; Table S17 in Appendix S4) and aquatic species (λ=0.19±0.02; Table S17 in Appendix S4).

The traits with the highest loading on the fast-slow continuum (T, H and L_α) are strongly phylogenetically linked to two leading traits of the reproductive-strategies axis (ϕ and S). Equally, the variation in age at maturity (L_α) is largely explained by its phylogenetic association with developmental rates (γ; Figure 1). For both aquatic and terrestrial species, reproductive traits (ϕ and S in Table 1) are systematically more labile (*i.e.*, lower phylogenetic signal) than traits associated to survival (H, L_α), development (γ) or turnover (T). Generation time (T) and age at reproductive maturity (L_α) are strongly phylogenetically associated with the number of recruits produced (ϕ) and the degree of iteroparity (S; Figure 1).

Discussion

Our results show that life history strategies of terrestrial and aquatic organisms are organised along the same dominant axes of variation and are constrained by the same trade-offs, regardless of the environment. The aquatic species we have examined here have not evolved the high longevities attained by some of the terrestrial species. However, we have found that aquatic animals are more reproductive than terrestrial ones. The relatively weak phylogenetic signal in our analyses suggest that these key life history differences are not primarily explained by the differential taxonomic composition of both environments (Blomberg & Garland, 2002; Freckleton, 2000). Overall, we suggest that the contrasting environmental conditions between aquatic and terrestrial environments may play a major role in the observed life history patterns and differences.

Terrestrial plants and mobile animals show slower paces of life than aquatic ones

Our analyses reveal a greater diversity of life history strategies in terrestrial compared to aquatic environments, for our studied species. This finding is congruent with the higher species richness (Costello & Chaudhary, 2017) and larger range of species biomass housed in the terrestrial environment (Bar-On, Phillips, & Milo, 2018). The colonisation of land established a period of unparalleled innovations in the evolution of plants and animals, driven by challenges in water retention, mobility, and dispersal (reviewed in Steele et al., 2019). Adaptations like plant vascularity, and animal terrestrial mobility were key for the proliferation of populations and species diversification (Steele et al., 2019; Wiens, 2015). These innovations allowed the exploitation of novel ecological niches, ultimately resulting in a six-fold increase in speciation rate (Costello & Chaudhary, 2017; Wiens, 2015). We argue that such adaptations are reflected in the vast diversity of life histories observed in the terrestrial environment relative to that in the aquatic environment in our study.

Plants and animals evolved different sets of adaptations to terrestrial and aquatic environments (Burgess et al., 2016; Steele et al., 2019), resulting in distinct life history strategies too. Terrestrial plants account for most of the diversity of life histories observed in our study, but they show slower life history strategies than aquatic species. Slow life history strategies can buffer environmental variation, compensating the uncertainties of reproductive success through high adult survival (McDonald et al., 2017; Morris et al., 2008). Indeed, slow life histories have been suggested as an adaptation of plants to terrestrial environments (Steele et al., 2019).

Correcting for body dimension allowed us to reveal a slower pace of life in terrestrial animals compared to aquatic ones. Terrestrial animals have been suggested to compensate for environmental uncertainties through the evolution of complex behaviours (e.g. sociality, nesting) and physiological adaptations (e.g. thermoregulation, internal fecundation) (Grosberg et al., 2012; Steele et al., 2019). Such traits would explain the lack of significant differences in the fast-slow continuum between terrestrial and aquatic species. However, our results also show that, when correcting for body weight, aquatic animals have a faster pace of life than terrestrial ones. Water-dwelling endotherms have larger body mass than their terrestrial counterparts (Gearty et al., 2018). Hence, given the correlation of body dimension and the fast-slow continuum (Gaillard et al., 1989; Healy et al., 2014), for a given size, aquatic mobile animals are faster-lived than terrestrial ones.

Aquatic animals are more reproductive than terrestrial ones

Terrestrial and aquatic environments also differ in the repertoire of reproductive strategies. Aquatic colonisers of terrestrial environments had to evolve strategies to protect early developmental stages (e.g. to desiccation) and enable their development in non-aquatic environments (Burgess et al., 2016; Steele et al., 2019; Strathmann, 1990). Plants, like many benthic aquatic species, have a sessile adulthood, so their dispersal relies on early developmental stages only. This mode-of-life promoted the evolution of flowers, pollination, and seeds (Kenrick & Crane, 1997). Sessile mode-of-life resulted in the observed high reproductive outputs and frequencies in plants, despite the fact that they can also reach high longevities (e.g. McDonald et al., 2017; Salguero-Gómez, Jones, Jongejans, et al., 2016).

Aquatic animals show higher reproductive outputs and frequencies than terrestrial animals. This pattern is likely linked to the prevalence of external fertilisation in aquatic environments, while internal fertilisation is more common in terrestrial ones (Bush et al., 2016). Both viscosity and nutrient concentration are higher in seawater than in air (Dawson & Hamner, 2008), allowing propagules to remain suspended for long periods of time (Burgess et al., 2016; Strathmann, 1990). The release of progeny in the water column comes with a high early predation risk and mortality, and low establishment probability (Burgess et al., 2016; Strathmann, 1990). To compensate for such early mortality, aquatic species release high numbers of propagules frequently, resulting in highly reproductive life histories. Differently, most terrestrial animals retain female gametes on or in their bodies, with fertilisation and early development being also internal (Bush et al., 2016; Steele et al., 2019), resulting in less reproductive strategies. Still, some aquatic species exist with internal fertilisation, such as sharks or marine mammals (Steele et al., 2019), partly explaining the range of reproductive strategies observed in our study.

Data limitations

Although the volume of data used in our study has a similar ratio to that of the biodiversity held in aquatic *vs.* terrestrial environments (Table S1, Appendix S1), it still represents a limited fraction of the known diversity (Costello & Chaudhary, 2017; Grosberg et al., 2012). Importantly, here, we have focused mostly on macroscopic organisms, for which full demographic information is more readily available than for smaller species (Salguero-Gómez, Jones, Archer, et al., 2016;

Salguero-Gómez et al., 2015). Organisms like insects, but also microscopic organisms, such as plankton or bacteria, are challenging subjects for demographic studies, so their data are scarce (Conde et al., 2019; Salguero-Gómez, Jones, Archer, et al., 2016). In addition, recently discovered extremely long-lived marine species (e.g. *Somniosus microcephalus*, Nielsen et al., 2016; *Monorhaphis chuni*, Jochum, Wang, Vennemann, Sinha, & Müller, 2012) are likely examples of slow strategies for which we do not have complete demographic data yet. Thus, the increase of studies quantifying the demographic processes of the full life cycle of species will likely shed more light on the differences between aquatic and terrestrial life histories.

In this study, we used demographic schedules as the common currency to quantify the life history strategies of species. Species life history strategies are highly determined by the demographic processes of survival, development, and reproduction (Caswell, 2001; Stearns, 1992). Researchers quantifying life history strategies have used different approaches to compare species (e.g. fishes in Winemiller & Rose, 1992; plants in Grime & Pierce, 2012; Westoby, 1998). These approaches have significantly contributed to improve our current understanding of life history strategies both in terrestrial and aquatic environments (Grime & Pierce, 2012). However, in some cases, these approaches use taxon-specific traits (such as the leaf–height–seed strategy scheme by Westoby, 1998), which would not allow us to compare across different taxonomic groups, such as animals and plants. For that reason, quantifying important moments of the life cycle of species with demographic data (Salguero-Gómez, Jones, Jongejans, et al., 2016) provides the ideal means to compare strategies across very different and distant taxonomic groups. We also demonstrate that considering incomplete demographic information (e.g., only investments in survival) can lead to the inaccurate characterisation of the life history strategy of a given species. Information on the fast-slow continuum explains 49.29% and 47.69% of the life history variation in aquatic and terrestrial species, respectively (Table S17 in Appendix S4). Demographic studies typically miss reproductive information because it is more challenging to collect and estimate. We show here that the current lack of data on reproductive rates prevents us from improving our understanding of life history strategies by over 20% across environments (Table S17 in Appendix S4).

Conclusions

Our study provides an entry-point to comparative life history studies between aquatic and terrestrial environments. Our findings evidence the existence of strong differences between the life history strategies of aquatic and terrestrial species as a consequence of the colonization of terrestrial environments. Such contrasting life history strategies are probably linked to the distinct responses to climate change (Pinsky, Eikeset, McCauley, Payne, & Sunday, 2019), exploitation (McCauley et al., 2015), or extinction rates (Webb & Mindel, 2015) observed in aquatic and terrestrial systems. Understanding how patterns of life histories translate into differences in their response to disturbances will be crucial to improve management decisions and predict future biodiversity trends.

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Table 1. Formulation of the life history traits used to explore the variation in life history strategies in the 685 terrestrial and 122 aquatic species studied. λ is the deterministic population growth rate, which corresponds to the dominant eigenvalue of the matrix ***A*** (Caswell, 2001); l_x and m_x are the age-specific survival and fertility schedules, respectively; ***U*** and ***F*** are the sub-matrices of survival- and fertility-dependent processes, respectively (equation 1); ***U'*** is the survival-independent matrix of transition probabilities (equation 2); ***w*** is the stable stage distribution of the matrix ***A***, and *i* and *j* are the row and column entries of the matrix population model, respectively.

Life history trait			Definition	Calculation
Turnover	Generation time	T	Number of years required for an average individual in the population to replace itself.	$T = \frac{\sum x \times (l_x \times m_x)}{\sum (l_x \times m_x)}$
Survival	Rate of senescence	H	Shape of the age-specific survivorship curve l_x as quantified by Keyfitz' entropy (H). H >1, = 1, <1 correspond to species whose mortality hazards decrease, stay constant, or increase with age, respectively.	$H = \frac{-\log(l_x) l_x}{\sum l_x}$
	Age at maturity	L_α	Average amount of time from birth to reproduction.	Caswell 2001, p. 124

Development	Mean vital rate of progressive growth (γ)	γ	Mean probability of transitioning forward to a larger/more developed stage in the life cycle of the species, weighted by the stable stage distribution, ***w***.	$\gamma = \sum_{1}^{m} \overline{U'}_{i,j}\bar{w}_j \big\rvert_{i<j}$
Reproduction	Mean vital rate of sexual reproduction	φ	Mean per-capita number of sexual recruits across stages in the life cycle of the species, weighted by ***w***.	$\phi = \sum_{1}^{m} \bar{F}_j \bar{w}_j$
	Degree of iteroparity	S	Temporal spread of reproduction throughout lifespan as quantified by Demetrius' (1974) entropy (*S*). High/low *S* values correspond to iteroparous/semelparous populations.	$S = -e^{-log\lambda} l_x m_x log\left(e^{-log\lambda} l_x m_x\right)$

Table 2. Life history traits used in the comparative analyses of 685 terrestrial and 122 aquatic species to examine differences in life history strategies between both environments, together with their loadings on the first two principal component axes. Pagel's *λ* (and its associated *P*-value) describes the strength of phylogenetic inertia ranging between 1, when life history trait differences are entirely due to the phylogenetic structure of the data under Brownian motion, and 0 meaning no phylogenetic structuring in the pattern. The mean loading values of each life history trait are visually depicted in Figure 2A. S.E. values were calculated via 10 imputations (See Methods). Bold numbers indicate traits loadings above 50% for each principal component.

Life history traits		Phylogenetic signal		PC 1	PC 2
		Pagel's *λ*	*P*-value	47.42±0.34%	21.02±0.11%
Generation time	T	0.57	<0.01	**0.83±0.00**	-0.08±0.01
Rate of senescence	H	0.48	<0.01	**0.72±0.01**	0.24±0.01
Age at maturity	L_α	0.52	<0.01	**0.80±0.00**	-0.11±0.01
Development	γ	0.71	<0.01	**-0.73±0.00**	-0.11±0.01
Mean sexual reproduction	Φ	0.32	<0.01	**-0.69±0.01**	**0.51±0.01**
Degree of iteroparity	S	0.11	<0.01	0.18±0.02	**0.92±0.00**

Figure 1. Trade-offs among life history traits are congruent between aquatic and terrestrial environments. Pair-wise correlations between six life history traits (Table S5) for 122 aquatic (blue) and 685 terrestrial (brown) species. Arrows indicate the direction of each pair-wise correlation using phylogenetic generalised least squares: positive (arrow-up), negative (arrow-down) or not-significant correlation (horizontal bar; $P>0.05$). The mean phylogenetic signal (Pagel's λ) of each pair-wise correlation, displayed in the lower-triangle, ranges from weak (white, ~0.00) to strong (dark green, ~1.00).

Figure 2. Aquatic and terrestrial life history strategies are organised in two main axes of variation, the fast-slow continuum and the reproductive strategies. Trait definitions are in Table 1. Phylogenetically-corrected principal component analysis (pPCA) for the first two axes (percentage of variance absorbed in brackets ± S.E.) for six key life history traits from 122 aquatic (blue) and 685 terrestrial species (brown). Arrow lengths indicate mean loading of each life history trait, and colour indicates associations with population turn-over (black), survival (green), development (dark blue), and reproduction (red). Each point represents the mean position of a species on this two-dimensional space for 10 imputed data sets (see Methods). Violin plots (top and right) depict the distribution of species along each principal component axis; white dot: mean; black thick line: 25th-75th quantile; black thin line: S.D.; ns: not-significant; *: $P<0.01$; **: $P<0.005$. The silhouettes, starting at the top left and moving counter-clock-wise, correspond to: *Lantana camara*, *Clinostomus funduloides*, *Setophaga cerulea*, *Pterygophora californica*, *Mirounga leonina*, *Gorilla beringei*, *Paramuricea clavata*, *Pseudomitrocereus fulviceps*, *Cypripedium calceolus*, and *Gracilaria gracilis.*

Figure 3. The main axes of life history variation remain constant, regardless of the degree of mobility/sessility or taxonomic kingdom. Phylogenetically-corrected principal component analysis of six life history traits across 683 species. Trait definitions are shown in Table 1. Note that the fast-slow continuum remains the dominant axis of variation across all partitions, explaining 49-50% of the variation, followed by an axis of reproductive strategies, which explains ~21% of the variation in life history traits. ns: non-significant; *: *P*<0.05; **: *P*<0.01. (a) Sessile organisms, with silhouettes (starting at the top left and moving counter-clock-wise) representing: *Lantana camara*, *Paramuricea clavata, Pseudomitrocereus fulviceps,* and *Gracilaria gracilis*. (b) Mobile organisms: *Clinostomus funduloides*, *Setophaga cerulea*, *Elephas maximus,* and *Isurus oxyrinchus* (c) Kingdoms Plantae and Chromista: *L. camara*, *Pterygophora californica*, *P. fulviceps, C. calceolus*, and *G. gracilis*. (d) Kingdom Animalia: *Mya arenaria*, *C. funduloides, S. cerulea*, *Gorilla beringei, P. clavata*, and *E. maximus*.

Figure 4. The main axes of life history variation remain constant in sessile (a) and mobile (b) species when correcting by maximum body size (m) and adult body mass (g), respectively. Phylogenetically and size-corrected principal component analysis of six life history traits across 464 species. Trait definitions are in Table 1. Note that the fast-slow continuum remains the dominant axis of variation, explaining ~51% of the variation, followed by an axis of reproductive strategies, which explains 18-19% of the variation in life history traits. ns: non-significant; *: *P*<0.05; **: *P*<0.01. (a) Sessile organisms, with silhouettes (starting at the top left and moving counter-clock-wise) representing: *Gracilaria gracilis, Lantana camara*, *Pinus ponderosa* and *Paramuricea clavata*.

(b) Mobile organisms: *Enhydra lutris, Gorilla beringei*, *Isurus oxyrinchus*, and *Presbytis thomasi*.