

1 **Aquatic and terrestrial organisms display contrasting life**
2 **history strategies as a result of environmental adaptations**

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15

16 **Abstract**

17 Aims: Aquatic and terrestrial realms display stark differences in key
18 environmental factors and phylogenetic composition. Despite such differences,
19 their consequences for the evolution of species' life history strategies remain
20 poorly understood. Here, we examine whether and how life history strategies
21 vary between terrestrial and aquatic species.

22 Location: Global.

23 Time period: Variable, the earliest year being in 1906 and the most recent in
24 2015.

25 Major taxa studies: Macroscopic animals and plants species.

26 Methods: We use demographic information for 638 terrestrial and 117 aquatic
27 animal and plant species, to derive key life history traits capturing their
28 population turnover, and investments in survival, development, and
29 reproduction. We use phylogenetically corrected least squares regression to
30 explore the differences in the trade-offs between life history traits in both
31 realms. We then quantify the life history strategies of aquatic and terrestrial
32 species using a phylogenetically corrected principal component analysis.

33 Results: We find that the same trade-offs structure terrestrial and aquatic life
34 histories, resulting in two dominant axes of variation describing species' pace-
35 of-life and reproductive spread through time. Life history strategies differ
36 between aquatic and terrestrial environments, with phylogenetic relationships
37 playing a minor role. We show that adaptations of plants and animals to
38 terrestrial environments have resulted in different life history strategies,
39 particularly with their reproductive mode and longevity. Terrestrial plants display

40 a great diversity of life history strategies, including the species with the longest
41 lifespans. Aquatic animals, on the contrary, exhibit higher reproductive
42 frequency than terrestrial animals, likely due to reproductive adaptations (i.e.
43 internal fecundation) of the later to land.

44 Main conclusions: Our findings show that aquatic and terrestrial species are
45 ruled by the same life history principles, but have evolved different strategies
46 due to distinct selection pressures. Such contrasting life history strategies have
47 important consequences for the conservation and management of aquatic and
48 terrestrial species.

49 *Keywords:* Aquatic–terrestrial comparisons, comparative demography, fast-slow
50 continuum, life history trait, matrix population model, phylogenetic inertia

51

52 Introduction

53 The rich diversity of life history strategies worldwide stem from three
54 fundamental demographic building blocks: survival, development, and
55 reproduction (Stearns, 1992). The life histories that emerge from the
56 combination of these three processes determine the viability of populations
57 (Salguero-Gómez *et al.*, 2016b; McDonald *et al.*, 2017) and guide the
58 effectiveness of conservation plans (Paniw *et al.*, 2019). However, despite the
59 growing body of literature in life history theory (Lande *et al.*, 2017), few studies
60 have explicitly contrasted their validity across terrestrial and aquatic organisms
61 (Webb, 2012).

62 Life history theory predicts that any strategy is shaped by two counter-
63 acting forces: environmental filtering and phylogenetic inertia (Stearns, 1992).
64 Regarding the former, existing environmental differences between aquatic and
65 terrestrial realms (e.g., water density and viscosity) could have produced
66 divergences in their respective life history strategies (Dawson & Hamner, 2008;
67 Webb, 2012; Gearty *et al.*, 2018). Under phylogenetic inertia (Freckleton, 2000;
68 Blomberg & Garland, 2002), life history strategies are expected to be more
69 similar, irrespective of environment, amongst closely related lineages

70 Life history theory is rooted upon the concept of trade-offs as an unifying
71 principle across the tree of life and realms (Stearns, 1992). This body of
72 literature predicts that, due to limitations in available energy and physiological
73 constraints, compromises among survival, development, and reproduction are
74 inescapable (Stearns, 1992). Such constraints are expected to result in a finite
75 set of viable demographic schedules. Indeed, comparative demographic studies
76 have successfully identified and organised them into a few major axes of trait

77 co-variation (Gaillard *et al.*, 1989; Salguero-Gómez *et al.*, 2016b). A seminal
78 concept in organising such a trait co-variation is the “fast-slow continuum”
79 (Stearns, 1992). In it, species are organised along two extremes: at the fast-
80 living extreme, species develop fast, become highly reproductive, but die young
81 (e.g. *Bromus tectorum* [cheatgrass], Griffith, 2010; planktonic species,
82 Reynolds, 2006); while at the slow extreme, species develop slowly, live long,
83 and reproduce rarely and late in life (e.g. *Somniosus microcephalus*, the
84 Greenland shark, Nielsen *et al.*, 2016; *Pinus longaeva*, the Bristlecone pine,
85 Peñuelas & Munné-Bosch, 2010). However, an explicit comparison of the fast-
86 slow continuum between aquatic and terrestrial species remains, to our
87 knowledge, untested.

88 Based on the strong environmental and phylogenetic differences
89 between aquatic and terrestrial realms, life history strategies should differ
90 between both realms. Life was originated on the sea, and the land colonisation
91 resulted in a great divergence of the biodiversity patterns observed in both
92 realms (Grosberg *et al.*, 2012; Costello & Chaudhary, 2017). There is a higher
93 richness of species on land (~80%), while aquatic biota are more diverse at the
94 phylum level (~34) than the terrestrial realm (~15) (Costello & Chaudhary,
95 2017). Also, land colonisation required adaptations to: the effects of gravity on
96 body structures, avoid desiccation, the elimination of waste products, together
97 with other processes (see reviews in Grosberg *et al.*, 2012; Webb, 2012). For
98 example, early life stages can feed and develop during dispersal in aquatic
99 environments (Burgess *et al.*, 2016; Bush *et al.*, 2016; Vermeij & Grosberg,
100 2017), but terrestrial species had to evolve reproductive systems independent

101 to environmental water, such as internal fecundity or seeds (Grosberg *et al.*,
102 2012; Bush *et al.*, 2016; Steele *et al.*, 2019).

103 The colonisation of land likely resulted in the evolution of life histories to
104 deal with higher temporal environmental variability (Dawson & Hamner, 2008;
105 Ruokolainen *et al.*, 2009). On land environmental variation is more random and
106 less auto-correlated than in aquatic environments (Ruokolainen *et al.*, 2009).
107 Classical life history theory predicts the evolution of longevity in constant
108 environments (Lande *et al.*, 2017). However, there is recent evidence that
109 longevity can be an strategy to deal with environmental variation (Morris *et al.*,
110 2008; McDonald *et al.*, 2017). On the other hand, fast life histories, are
111 expected to show increasing fluctuations in population sizes with increasing
112 environmental variation (Morris *et al.*, 2008; McDonald *et al.*, 2017). For that
113 reason, some authors have argued that the colonization of land resulted in the
114 evolution of longer lifespans to smooth out the short-term but large-amplitude
115 terrestrial environmental fluctuations (*sensu* Steele *et al.*, 2019).

116 Here, we test the hypothesis that (i) trade-offs are universal both in
117 aquatic and terrestrial systems, and (ii) that terrestrial species have evolved
118 different life history strategies compared to aquatic ones. We use high-
119 resolution demographic data from 117 aquatic and 638 terrestrial species
120 across the globe from the COMPADRE and COMADRE databases (Salguero-
121 Gómez *et al.*, 2015, 2016a). We estimate key life history traits capturing
122 population turnover, and investments in survival, development, and
123 reproduction of those species. To test these hypotheses, we first determine
124 whether correlations between life history traits differ across realms as a way to
125 examine whether trade-offs diverge between terrestrial vs. aquatic species.

126 Second, we explore the main axes of life history variability shaping aquatic and
127 terrestrial species. The presence of different life history axes of variation and/or
128 a distinct positioning of aquatic species compared to terrestrial ones within
129 those axes would suggest dissimilar selection pressures occurring above and
130 below water. Given the scarcity of trans-realm comparative studies and the lack
131 of demographic information for many aquatic species, elucidating these
132 questions is a key step forward towards understanding the evolution of life
133 histories across realms.

134 **Material and Methods**

135 *Demographic data and life history traits*

136 We calculated species' life history strategies using demographic data describing
137 information across the full life cycle of each species. This high-quality
138 demographic information was obtained from the COMPADRE Plant Matrix
139 Database (v. 5.0.1; Salguero-Gómez *et al.*, 2015) and COMADRE Animal
140 Matrix Database (v. 3.0.1; Salguero-Gómez *et al.*, 2016a). In them, the
141 demographic data is archived into matrix population models (MPMs, hereafter)
142 for over 700 plant and 400 animal species, respectively. MPMs are summaries
143 of organisms' demographic processes (*i.e.*, vital rates) that together determine
144 their life history strategies and resulting population dynamics (Caswell, 2001).
145 For this reason, MPMs provide the ideal means to compare the vast array of life
146 history strategies (Franco & Silvertown, 2004; McDonald *et al.*, 2017).

147 To compare life history traits across aquatic and terrestrial species, we
148 imposed a series of selection criteria to the available demographic data (see
149 details in Appendix S2: Data selection in Supporting information). These criteria

150 resulted in 638 terrestrial species and 117 aquatic species used in this study
151 (Appendix S1). We also classified aquatic vs terrestrial species according to the
152 information provided in the World's Register of Marine Species
153 (www.marinespecies.org) and the Catalogue of Life
154 (<http://www.catalogueoflife.org>). The number of species studied here
155 represented a similar taxonomic coverage relative to the known biodiversity of
156 the aquatic (~0.05%) and terrestrial realm (~0.01%; Table S1 in Appendix S2).

157 Quantifying a species' life history strategy requires detailed information
158 regarding the timing, intensity, frequency, and duration of key demographic
159 processes across its life cycle (Stearns, 1992). To quantify species' life history
160 strategies, we calculated several life history traits from each MPM that are *a*
161 *priori* not correlated using well-established methods (Salguero-Gómez *et al.*,
162 2016b). We selected seven life history traits commonly used in comparative
163 demography (Stearns, 1992; Gaillard *et al.*, 2005; Bielby *et al.*, 2007; Salguero-
164 Gómez *et al.*, 2016). These traits include: generation time (T), age at sexual
165 maturity (L_a), rate of senescence (H), mean vital rate of progressive
166 development (γ), the mean vital rate of sexual reproduction (ϕ) and degree of
167 iteroparity (S) (Table S2). Such traits provide insights of the species' population
168 turnover, as well as of survival, developmental, and reproductive strategies
169 (detailed in Table S2 in Appendix S2).

170 *Phylogenetic analyses and trait comparisons*

171 We accounted for and estimated the phylogenetic influence on the differences
172 in life history trait values within species and between aquatic vs. terrestrial
173 realms. To do so, we constructed a species-level phylogenetic tree (Figure S2
174 in Appendix S3) with data from Open Tree of Life (OTL,

175 <https://tree.opentreeoflife.org>. Hinchliff *et al.*, 2015). OTL combines publicly
176 available taxonomic and phylogenetic information across the tree of life
177 (Hinchliff *et al.*, 2015). Briefly, we built separate trees for our species of algae,
178 plant, and animals, using the *rotl* R package (Michonneau *et al.*, 2016), which
179 were assembled in a supertree using the function *bind.tree* in the *phytools*
180 package (Revell, 2012). To account for the phylogenetic relatedness of species
181 we computed the branch lengths and resolved polytomies (Revell, 2012). We
182 also tested the sensitivity of our results to the choice of a particular set of
183 branch lengths, by repeating our analyses setting all the branch lengths to one
184 and using Pagel's branch length (Tables S4-S7 in Appendix S3) using the
185 software Mesquite 1.05 (Maddison & Maddison, 2001) and its PDAP module
186 1.06 (Midford *et al.*, 2005). For further details on the construction of the tree see
187 Appendix S3.

188 To test whether life history trait trade-offs are congruent between aquatic
189 vs. terrestrial species, we carried out a series of Phylogenetic General Least
190 Square (PGLS) analyses (Revell, 2010). This approach allows us to
191 accommodate residual errors according to a variance-covariance matrix that
192 includes ancestral relationships between any pair of species from our
193 phylogenetic tree (Revell, 2010, 2012). We implemented our set of PGLSs in R
194 using the correlation structures provided by the package *ape* (Paradis *et al.*,
195 2004). We used a Brownian motion model of evolution (BM), combined with the
196 *pgls* function from the *nlme* package (Pinheiro *et al.*, 2014). Separate PGLSs
197 were fitted using Ornstein Uhlenbeck (OU) model of evolution, which describes
198 Brownian model under the influence of friction (Uhlenbeck & Ornstein, 1930).
199 Both models were compared using Akaike Information Criterion (Akaike,

200 1974); the BM generally outperformed the OU model, but both showed similar
201 results. Therefore, we only report the PGLS results from the Brownian motion
202 model.

203 *Exploring dominant axes of life history strategies*

204 To explore the patterns of association among life history traits for aquatic vs.
205 terrestrial species, we performed a series of principal components analyses
206 (PCA). PCA is a multivariate analysis that reduces a set of correlated variables
207 into linearly uncorrelated measurements, the so-called principal components
208 (PCs). Life history trait data were log- and z-transformed (mean=0, SD=1) to
209 fulfil normality assumptions of PCAs (Legendre & Legendre, 2012). Finally, we
210 identified and excluded outliers for each life history trait as those located outside
211 of the 2.5th-97.5th percentile range of the distribution. However, we note that the
212 exclusion of outliers did not alter our main findings (see Tables S8-S11 in
213 Appendix S4).

214 To account for shared ancestry while exploring differences in aquatic vs.
215 terrestrial life history strategies, we used a phylogenetically informed PCA
216 (pPCA Revell, 2009). The pPCA considers the correlation matrix of species'
217 traits while accounting for phylogenetic relationships and simultaneously
218 estimating Pagel's λ with maximum likelihood methods. Pagel's λ quantifies the
219 strength of the phylogenetic relationships on trait (co-)evolution under a BM
220 (Freckleton, 2000; Blomberg & Garland, 2002). This metric varies between 0
221 when the observed patterns are not due to phylogenetic relationships, and 1
222 when the observed patterns can be explained by the employed phylogeny
223 (Blomberg & Garland, 2002; Revell, 2010). The pPCA was estimated using the

224 phyl.pca function from the R package *phytools* (Revell, 2012), assuming a BM
225 (Revell, 2010).

226 A full dataset (*i.e.*, no missing values) is necessary to run the pPCA
227 analyses. However, estimating life history traits for species' MPMs was not
228 always possible (see *Missing data* in Appendix S2: Extended methods). For
229 example, we could not calculate the rate of senescence for *Fucus vesiculosus*.
230 The rate of senescence (Keyfitz's entropy) can only be calculated for life tables
231 that have not reached stationary equilibrium before the 95% of a cohort are
232 dead (Caswell, 2001; Jones *et al.*, 2014), which was not the case for this
233 species. In these cases, we imputed the missing data using function *amelia*
234 from the *Amelia* package (Honaker *et al.*, 2011). This function uses a bootstrap
235 EM algorithm to impute missing data. We then created 10 imputed datasets and
236 ran analyses on each separately. In addition, we tested the sensitivity of our
237 results to missing traits in the dataset using pPCA in two ways. First, we ran a
238 pPCA only with species without any missing data (62 aquatic species, 477
239 terrestrial species, Tables S10 and S11 in Appendix S4), and with missing
240 species trait values filled using imputation methods (see Tables S8, S9, S12
241 and S13 in Appendix S4). The results from the multiple imputations were
242 presented as their respective mean values with their standard deviation. To test
243 the differences between the distributions of pPCA scores between realms, we
244 used the mean position resulting from the multiple imputations.

245 We also examined the consistency of our results and explored the
246 differences between realms by performing the pPCA analyses on different
247 subsets of data. These subsets included comparisons between mobile vs.
248 sessile organisms, Animalia vs. Plantae/Chromista kingdoms, and aquatic vs.

249 terrestrial realms. We considered sessile species as those that do not have
250 active locomotion during the adult stages of their life cycle (e.g. corals, sponges,
251 plants) and those species with limited adult locomotion (e.g. clams, worms,
252 snails). This distinction was made because key traits (e.g. reproduction,
253 development, energetic requirements) can differ between sessile and mobile
254 organisms (Bush *et al.*, 2016; Vermeij & Grosberg, 2017). We also performed a
255 series of pPCA analyses sub-setting species into Animalia kingdom, and
256 Plantae and Chromista (brown algae). This distinction was also made because
257 animals and plants/algae differ in key physiological, trophic and development
258 traits (Grosberg *et al.*, 2012; Burgess *et al.*, 2016). Such ecological differences
259 between sessile/mobile and taxonomic kingdoms, could have a potential impact
260 on our hypothesis about the different evolution of life history strategies in
261 aquatic and terrestrial species.

262 **Results**

263 *Trade-offs are pervasive across realms*

264 Life history traits are shaped by the same trade-offs below water as on land
265 (Figure 1). Our PGLS analyses reveal a similar magnitude and the same
266 direction of pair-wise correlations between traits for aquatic and for terrestrial
267 species (Figure 1 and Tables S9, S11 and S13 in Appendix S4). Regardless of
268 the realm, producing many recruits (high ϕ ; Table S2 in Appendix S2) results in
269 fast population turnover (low T). Likewise, species that postpone their first
270 reproductive event (high L_a) have low senescence rates (high H) (Figure 1).
271 Species with fast development (high γ) achieve reproductive maturity early (low
272 L_a) at the cost of high senesce rates (low H). Also, those species high

273 reproductive output (high φ) and frequent reproduction (high S), have low
274 senescence rates (high H) (Figure 1).

275 *Aquatic species are faster than terrestrial ones*

276 Together, the first two axes of our phylogenetically corrected principal
277 component analysis (pPCA; Table 1) explain over 60% of the examined
278 variation in life history traits (Figure 2, Table 1). Principal component axis 1
279 (PC1) explains $47.42 \pm 0.34\%$ (Mean \pm S.E.) of the variation and represents the
280 fast-slow continuum. Indeed, PC1 portrays a trade-off between species with fast
281 development and short lifespans, and slow development, high investment in
282 survival (low senescence rates), and postponement of maturity (Figure 2). PC2
283 explains $21.02 \pm 0.11\%$ of the variation in life history traits related to reproductive
284 strategies. In PC2, those species characterised by high reproductive rate and
285 high iteroparity are located at the top vs. species with fewer reproductive events
286 across their lifetimes, located at the bottom of Figure 2. These patterns are
287 robust within different life modes (Figure 3a,b and Table S14 in Appendix S4),
288 kingdoms (Figure 3c,d and Table S15 in Appendix S4), and realms (Table S16
289 in Appendix S4).

290 Aquatic life history strategies are displaced towards the fast extreme of
291 the fast-slow continuum ($t_{197,49} = -6.22$, $P < 0.01$; Figure 2). On land, the studied
292 species occupy fast paces of life, such as *Solidago mollis* (soft goldenrod),
293 *Setophaga cerulean* (cerulean warbler), as well as slow ones, such as
294 *Pseudomitrocereus fulviceps* (the giant cardon). In the aquatic realm, in
295 contrast, the resulting paces of life are constrained to faster values compared to
296 terrestrial species (PC1, Figure 2). In contrast, aquatic organisms are not
297 displaced towards any of the extremes of the PC2. Both aquatic and terrestrial

298 species show a wide range of reproductive strategies, with highly reproductive
299 species such as such as *Lantana camara* (big-sage) or *Gracilaria gracilis* (red
300 seaweed), and species less reproductive species, such as *Mirounga leonina*
301 (southern elephant seal) and *Gorilla beringei* (eastern gorilla). There are no
302 significant differences between the realms in the PC2 ($t_{215.04}= 0.18$, $P=0.86$;
303 Figure 2).

304 *Mode-of-life and kingdom drive key life history differences across realms*

305 The main axes of life history variation remain unaltered across realms, modes-
306 of-life (whether species are mobile or sessile during their adulthood) or
307 taxonomic affiliation. The first and second axes of life history trait variation
308 correspond to the fast-slow continuum and reproductive strategies in both
309 sessile and mobile species (Figure 3a,b and Table S14 in Appendix S4), in
310 Animalia and Plantae/Chromista kingdoms (Figure 3c,d and Table S15 in
311 Appendix S4), in terrestrial species and aquatic species (Table S16 in Appendix
312 S4).

313 Aquatic and terrestrial sessile species display significant differences in
314 their position across first axes of life history variation. Aquatic sessile species
315 are displaced towards the fast end (*i.e.*, low PC1 scores) of the fast-slow
316 continuum ($t_{64.91}=-53.32$, $P<0.01$; Figure 3a). Aquatic sessile species do not
317 show significant differences in their reproductive strategies compared to
318 terrestrial ones ($t_{59.22}=1.95$, $P=0.06$; Figure 3a). In contrast, mobile aquatic
319 species are not displaced towards any end of the fast-slow continuum when
320 compared to terrestrial mobile species ($t_{96.34}=0.55$, $P=0.58$; Figure 3b), neither
321 in the reproductive axis ($t_{118.88}=1.84$, $P=0.07$; Figure 3b).

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

329 *Ancestry does not shape cross-realm life history strategies*

330 Overall, phylogenetic ancestry (*i.e.*, phylogenetic inertia) plays a minor role in
331 constraining life history strategies between realms. The estimates of Pagel's λ
332 in our pPCA are indeed low (0.26 ± 0.00). Such values of the phylogenetic signal
333 remain low across sessile ($\lambda=0.18\pm 0.01$; Table S14 in Appendix S4), mobile
334 species ($\lambda=0.36\pm 0.01$; Table S14 in Appendix S4), plants and algae
335 ($\lambda=0.18\pm 0.01$; Table S15 in Appendix S4) and animals ($\lambda=0.31\pm 0.02$; Table S15
336 in Appendix S4). In addition, the phylogenetic signal is similar between
337 terrestrial ($\lambda=0.24\pm 0.01$; Table S16 in Appendix S4) and aquatic species
338 ($\lambda=0.19\pm 0.02$; Table S16 in Appendix S4).

339 For both aquatic and terrestrial species, reproductive traits (\square and S in
340 Table S2) are systematically more labile (*i.e.*, lower phylogenetic signal) than
341 traits associated to survival (H , L_a), development (γ) or turnover (T). Generation
342 time (T) and age at reproductive maturity (L_a) are strongly phylogenetically
343 associated with the number of recruits produced (\square) and the degree of
344 iteroparity (S)(Fig.1). The traits with the highest loading on the fast-slow
345 continuum (T , H and L_a) are strongly phylogenetically linked to two leading traits
346 of the reproductive-strategies axis (\square and S). Equally, the variation on age at

347 maturity (L_a) is largely explained by its phylogenetic association with
348 developmental rates (γ) (Figure 1).

349 **Discussion**

350 Our comparison of 117 aquatic and 638 terrestrial species demonstrates that
351 life history strategies are organised along the same dominant axes of variation
352 and constrained by the same trade-offs, regardless of realm. The sampled
353 aquatic species have not evolved the high longevities attained by some of our
354 studied terrestrial species, but those aquatic animals are more reproductive
355 than the terrestrial ones. The relatively weak phylogenetic signal in our analyses
356 suggest that these key life history differences are not explained by the
357 differential taxonomic composition of both realms (Freckleton, 2000; Blomberg
358 & Garland, 2002). Overall, we suggest that the contrasting environmental
359 conditions between aquatic and terrestrial realms may play a major role in the
360 observed life history patterns and differences.

361 We show greater diversity of life history strategies on land compared to
362 aquatic environments. This finding is congruent with the higher species richness
363 (Costello & Chaudhary, 2017) and larger range of species biomass housed in
364 the terrestrial realm (Bar-On *et al.*, 2018). The colonisation of land established a
365 period of unparalleled innovations in the evolution of plants and animals, driven
366 by challenges in water retention, mobility, and dispersal (Steele *et al.*, 2019).
367 Adaptations like plant vascularity, and animal terrestrial mobility were key for
368 the proliferation of populations and species diversification (Steele *et al.*, 2019).
369 These innovations allowed the exploitation of novel ecological niches, ultimately
370 resulting in a six-fold increase in speciation rate (Costello & Chaudhary, 2017).

371 We argue that such adaptations are reflected in the vast diversity of life histories
372 observed in the terrestrial realm relative to that in the aquatic realm in our study.

373 Nevertheless, plants and animals evolved different sets of adaptations to
374 terrestrial and aquatic environments (Burgess *et al.*, 2016; Steele *et al.*, 2019),
375 resulting in distinct life history strategies too. Terrestrial plants account for most
376 of the diversity of life histories observed in our study, but they show slower
377 strategies than aquatic species. Slow life history strategies can buffer
378 environmental variation compensating the uncertainties of reproductive success
379 through high adult survival (Morris *et al.*, 2008; McDonald *et al.*, 2017), and
380 have been suggested as an adaptation of plants to terrestrial environments
381 (Steele *et al.*, 2019). Such a pattern, however, is not shared with terrestrial
382 animals, which do not show any displacement towards any extreme of the fast-
383 slow continuum, compared to aquatic animals. In contrast, terrestrial animals
384 could have compensated environmental uncertainties through the evolution of
385 complex behaviours (e.g. societies, nesting) and physiological adaptations (e.g.
386 thermoregulation, internal fecundation) (Grosberg *et al.*, 2012; Steele *et al.*,
387 2019).

388 A major challenge for land colonisation is reproducing in a non-aquatic
389 environment (Grosberg *et al.*, 2012; Burgess *et al.*, 2016), influencing the
390 evolution of divergent life history strategies. External fertilisation is the
391 predominant reproductive strategy in aquatic environments (Bush *et al.*, 2016).
392 Aquatic colonisers to land environments had to evolve strategies to protect early
393 stages (e.g. to desiccation) and enable their development in non-aquatic
394 environments (Strathmann, 1990; Burgess *et al.*, 2016; Steele *et al.*, 2019).
395 Plants, like many benthic aquatic species, have a sessile adulthood, so their

396 dispersal is in early developmental stages only. This life-mode promoted the
397 evolution of flowers, pollination and seeds (Kenrick & Crane, 1997), resulting in
398 the observed high reproductive outputs and frequencies in plants, despite the
399 fact that they can also reach high longevities (e.g. Salguero-Gómez *et al.*,
400 2016b; McDonald *et al.*, 2017).

401 On the other hand, the colonisation of land constrained animal
402 reproduction to internal fertilisation, with a consequent decrease in reproductive
403 outputs and frequency. Again, we argue that this finding is likely linked to the
404 prevalence of external fertilisation in the ocean compared to the terrestrial realm
405 (Bush *et al.*, 2016). Both viscosity and nutrient concentration are higher in
406 seawater than in air (Dawson & Hamner, 2008), allowing propagules to remain
407 suspended for long periods of time (Strathmann, 1990; Burgess *et al.*, 2016).
408 The release of progeny in the water column comes with a high early predation
409 risk and low establishment probability and high early mortality (Strathmann,
410 1990; Burgess *et al.*, 2016). To compensate such early mortality, aquatic
411 species release high numbers of propagules and frequently, resulting in highly
412 reproductive life histories. In contrast, most terrestrial animals retain female
413 gametes on or in their bodies, and fertilisation and early development are
414 usually internal (Bush *et al.*, 2016; Steele *et al.*, 2019), resulting in less
415 reproductive strategies. Still, there are aquatic species that have internal
416 fecundity, such as some sharks or marine mammals (Steele *et al.*, 2019),
417 explaining the range of reproductive strategies observed in our study.

418 Although the volume of data used in our study has a similar ratio to that
419 of the biodiversity held in aquatic vs. terrestrial realms (~0.01%; Table S1 in
420 Appendix S1), it still represents a limited fraction of the known diversity

421 (Grosberg *et al.*, 2012; Costello & Chaudhary, 2017). Importantly, here we have
422 focused mostly on macroscopic organisms, for which full demographic
423 information is more readily available than for small species (Salguero-Gómez *et al.*,
424 2015, 2016a). Organisms like insects, but also microscopic organisms, such
425 as plankton or bacteria, are challenging subjects for demographic studies, so
426 their data are very scarce (Salguero-Gómez *et al.*, 2016a; Conde *et al.*, 2019).
427 In addition, recently discovered extremely long-lived marine species (e.g.
428 *Somniosus microcephalus*, Nielsen *et al.*, 2016; *Monorhaphis chuni*, Jochum *et al.*,
429 2012) are likely examples of slow strategies for which we do not yet have
430 complete demographic data. Thus, the increase of studies quantifying the
431 demographic processes of the full life cycle of species will likely shed more light
432 on the differences between aquatic and terrestrial life histories.

433 In this study, we used demography as the common currency to quantify
434 the life history strategies of species. Species life history strategies are highly
435 determined by the demographic processes of survival, development and
436 reproduction (Stearns, 1992; Caswell, 2001). Researchers quantifying life
437 history strategies have used different approaches to compare species (e.g.
438 fishes in Winemiller & Rose, 1992; plants in Westoby, 1998; Grime & Pierce,
439 2012). These approaches have significantly contributed to improve our current
440 understanding of life history strategies both in terrestrial and aquatic realms
441 (Grime & Pierce, 2012). However, in some cases, these approaches use taxon-
442 specific traits (such as the leaf–height–seed strategy scheme by Westoby,
443 1998), which would not allow us to compare across different taxonomic groups,
444 such as animals and plants. For that reason, demographic data quantifying
445 important moments of the life cycle of species (Salguero-Gómez *et al.*, 2016b),

446 provides the ideal means to compare strategies across very different and
447 distant taxonomic groups. Importantly, we also demonstrate that considering
448 incomplete demographic information (e.g. only survival investments) can lead to
449 the inaccurate characterisation of the life history strategy of a given species.
450 Information on the pace-of-life explains the life history variation of about 52.52%
451 of aquatic and 49.05% of terrestrial species. Typically lacking reproductive
452 information, which is much more challenging to collect than to estimate survival,
453 prevents us from improving our understanding by 21.61% and 21.35%, of
454 aquatic and terrestrial species respectively.

455 Overall, our study provides a promising entry-point to trans-realm
456 comparative biology. Our findings evidence the existence of strong differences
457 between the life history strategies of aquatic and terrestrial systems as a
458 consequence of the colonization of land environments. Such contrasting life
459 history strategies are probably linked to the distinct responses to climate
460 change (Pinsky *et al.*, 2019), exploitation (McCauley *et al.*, 2015) or extinction
461 rates (Webb & Mindel, 2015) observed in aquatic and terrestrial systems.
462 Understanding how the contrasting patterns of life histories translate into
463 differences in their response to disturbances will be crucial to improve
464 management decisions and predict future biodiversity trends.

465

466

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639 *Data accessibility statement:* Matrix population models are available at
640 www.compadre-db.org.

641

642 **Table 1. Life history traits used in the comparative analyses of 638**
 643 **terrestrial and 117 aquatic species to examine differences in strategies**
 644 **between both realms, together with their loadings on the first two**
 645 **principal component axes, grouped by their attribution to turnover,**
 646 **survival, development, or reproduction.** Pagel's λ (and its associated P -
 647 value) describes the strength of phylogenetic inertia, ranging between 1, when
 648 life history trait differences are entirely due to the phylogenetic structure of the
 649 data under Brownian motion, and 0, meaning no phylogenetic structuring in the
 650 pattern. The mean loading values of each life history trait are visually depicted
 651 in Figure 2A. SE values were calculated via 10 imputations (See Methods). Bold
 652 numbers indicate traits loadings above 55% for each PC.

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

653 **Figure 1. Trade-offs among life history traits are congruent between**
654 **aquatic and terrestrial environments.** Pair-wise correlations between seven
655 life history traits (Table S4) for 117 aquatic (blue) and 638 terrestrial (brown)
656 species. Arrows indicate the direction of each pair-wise correlation using
657 phylogenetic generalised least squares: positive (arrow-up), negative (arrow-
658 down) or not-significant correlation (horizontal bar; $P>0.05$). The mean
659 phylogenetic signal (Pagel's λ) of each pair-wise correlation, displayed in the
660 lower-triangle, ranges from weak (white, ~ 0.1) to strong (dark green, ~ 0.9).

661 **Figure 2. Aquatic and terrestrial life history strategies are organised in two**
662 **main axes of variation, the fast-slow continuum and the reproductive**
663 **strategies.** Phylogenetically-corrected principal component analysis (pPCA) for
664 the first two axes (percentage of variance absorbed in brackets) for seven key
665 life history traits from 117 aquatic (blue) and 638 terrestrial species (brown).
666 Arrow lengths indicate mean loading of each life history trait, and colour
667 indicates associations with population turn-over (black), survival (green),
668 development (dark blue), and reproduction (red). Each point represents the
669 mean position of a species on this two-dimensional space for 10 imputed data
670 sets (see Methods). Violin plots (top and right) depict the distribution of species
671 along each PC axis; white dot: mean; black thick line: 25th-75th quantile; black
672 thin line: SD; ns: not-significant; *: $P<0.01$; **: $P<0.005$. The silhouettes, starting
673 at the top left, and counter-clock-wise, correspond to: *Lantana camara*,
674 *Clinostomus funduloides*, *Solidago mollis*, *Setophaga cerulea*, *Mazzaella*
675 *splendens*, *Mirounga leonina*, *Gorilla beringei*, *Paramuricea clavata*,
676 *Pseudomitrocereus fulviceps*, *Chlorocardium rodiei*, *Orcinus orca*, *Cypripedium*
677 *calceolus* and *Gracilaria gracilis*.

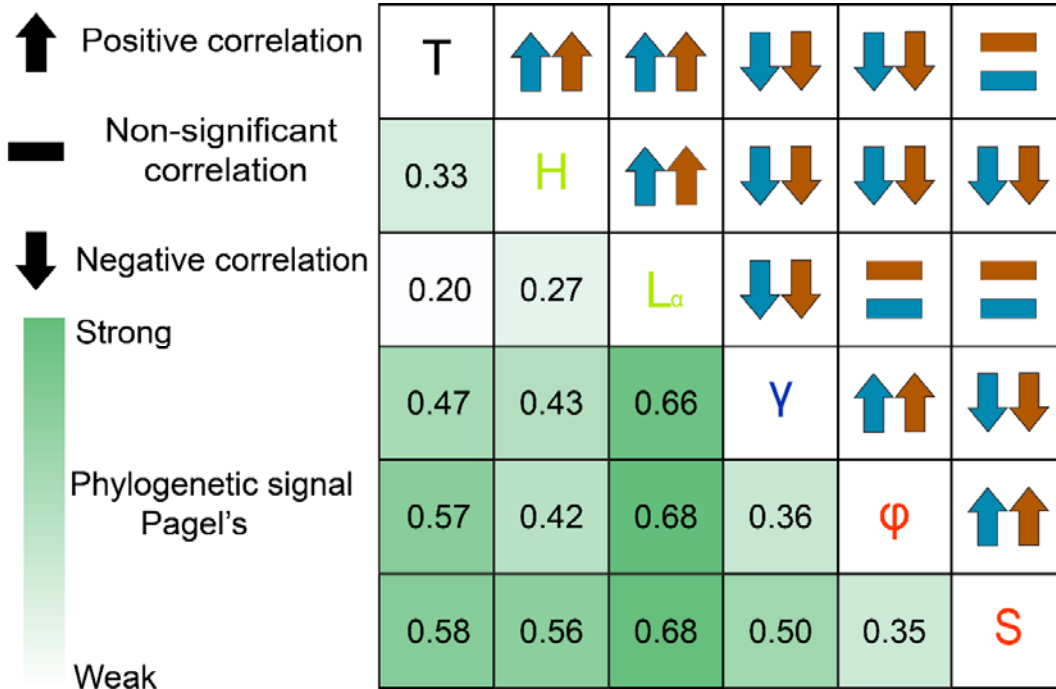
678 **Figure 3. The main axes of life history variation remain constant,**
679 **regardless of the degree mobility/sessility or taxonomic kingdom.**

680 Phylogenetically-corrected principal component analysis of seven life history
681 traits across 683 species. Trait definition in Figure 2 and Table S4. Note that the
682 fast-slow continuum remains the dominant axis of variation, explaining 40-45%
683 of the variation, followed by an axis of reproductive strategies, which explains
684 20-22% of the variation in life history traits. ns: not-significant; *: $P < 0.05$; **:
685 $P < 0.01$. (a) Sessile organisms, with silhouettes (not to scale; starting at the top
686 left, and counter-clock-wise) representing: *Lantana camara*, *Mya arenaria*,
687 *Mazzalena splendens*, *Paramuricea clavata*, *Chlorocardium rodiei* and
688 *Cypridium calceolus*. (b) Mobile organisms: *Clinostomus funduloides*,
689 *Setophaga cerulea*, *Chelydra serpentine*, *Elephas maximus* and *Isurus*
690 *oxyrinchus* (c) Kingdoms Plantae and Chromista: *L. camara*, *Pterygophora*
691 *caliphornica*, *M. splendens* *C. rodiei* and *C. calceolus*. (d) Kingdom Animalia: *M.*
692 *arenaria*, *C. funduloides*, *S. cerulea*, *Gorilla beringei*, *P. clavata* and *E.*
693 *maximus*.

694

695 **Figure 1**

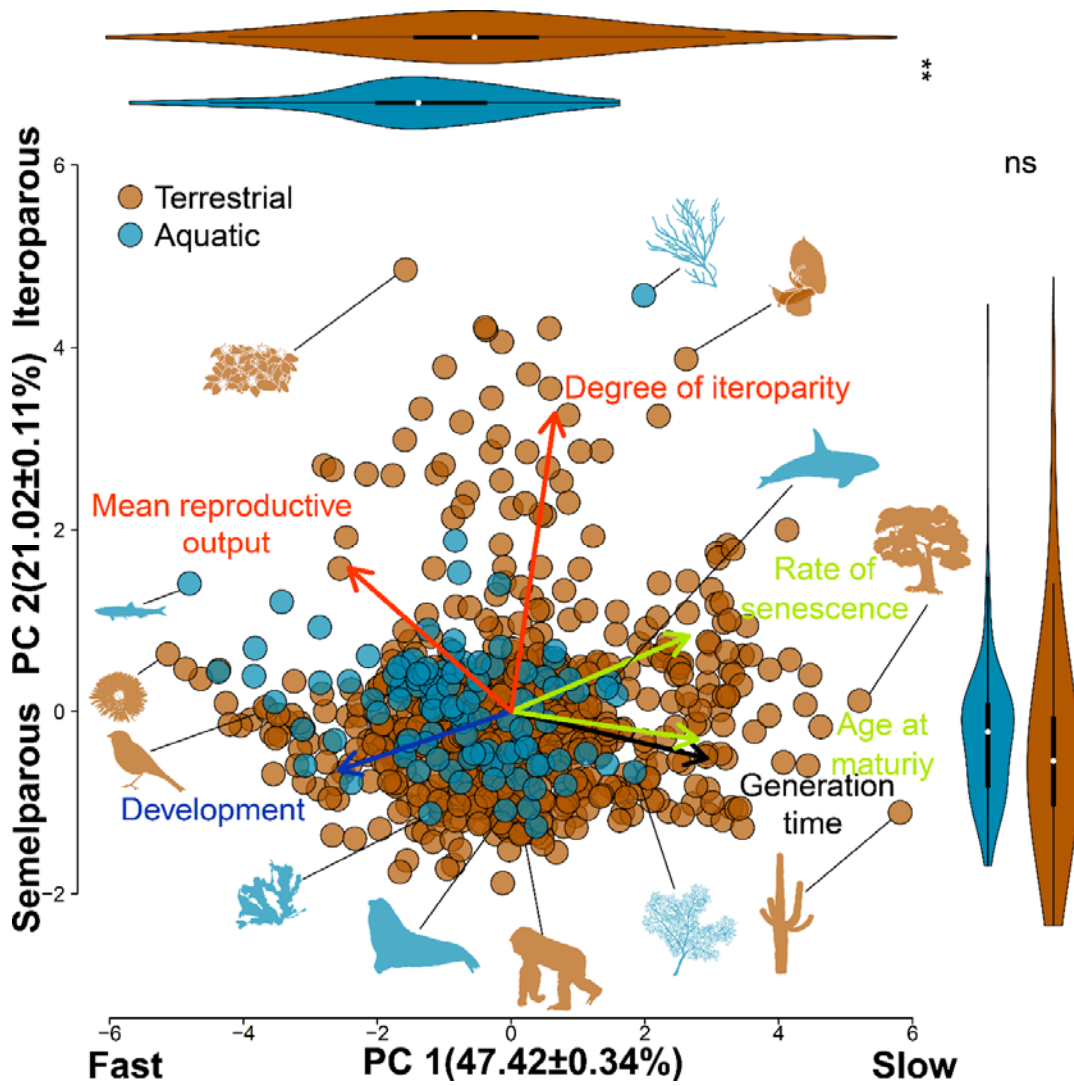
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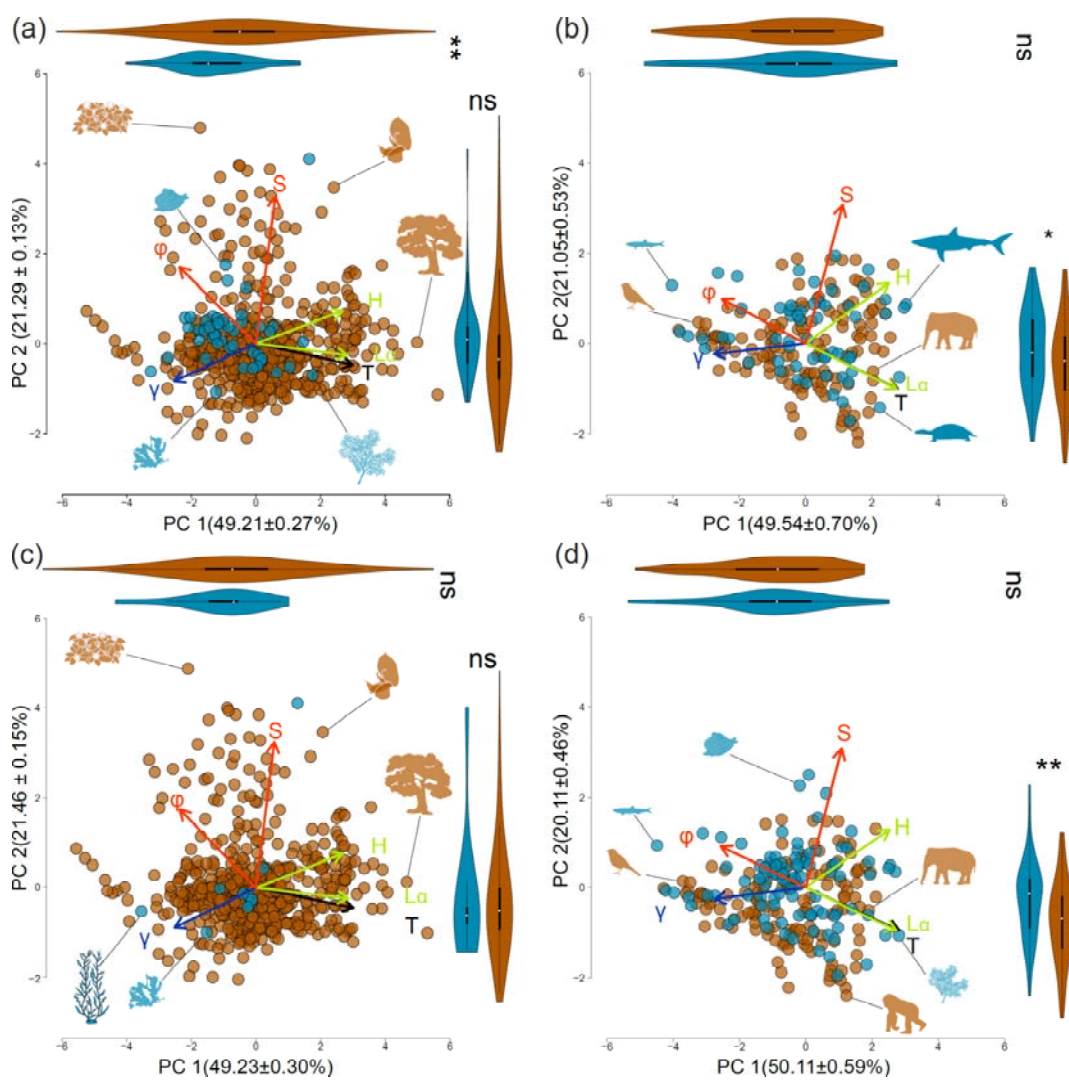
699 **Figure 2**



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701

702 **Figure 3**



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