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Research

Chameleon biogeographic dispersal is associated with extreme life history strategies

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Understanding the role of traits in dispersal is necessary to improve our knowledge of historical biogeography, community assembly processes and predictions of species' future movements. Here we aimed to determine the relationship between three traits (coastal distribution, body size, position on the fast/slow life history continuum) and past dispersal probability on an evolutionary timescale in chameleons (Chamaeleonidae). Using species' distribution data we identified the nine most important biogeographic regions for all included chameleons (181/217 species). We compiled life history trait data and used phylogenetic factor analysis to infer independent body size and fast/slow life history trait axes. Finally, we tested whether traits and trait combinations related to biogeographic dispersal success in the past, using trait-dependent biogeographic models. All three traits were associated with past biogeographical movements. Lineages having coastal distributions and those with large bodies had higher dispersal probabilities. Interestingly, chameleons with either a very fast or very slow life history were more successful dispersers than species with an intermediate strategy. Together, the three traits – coastal, large-bodied and extreme life history – form a dispersal syndrome. Traits have played an important role in the biogeographic history of chameleons. While only fast traits have been linked to present-day invasion success in reptiles, both extremes of the life history spectrum were likely advantageous for dispersal and establishment during past biogeographic movements. Fast-living species may be less susceptible to stochastic extinction in the first phases of a colonization (due to rapid population growth), and slow-living species may be less vulnerable to environmental stochasticity (due to low demographic variability). Our results call for broader analyses testing the general influence of life history strategy in biogeographic dispersal success, which would help explain species distribution patterns on Earth.

Keywords: biogeography, Chamaeleonidae, dispersal, life history continuum, species' traits, trait-dependent biogeography

Introduction

Species' traits can impact biogeographic processes such as dispersal, extinction and cladogenesis and likely play a part in shaping the distribution of life on Earth (Ronce and Clobert 2012, Zamudio et al. 2016, Chichorro et al. 2019). While associations between traits and short-distance dispersal at the level of individuals and populations have been studied extensively (Whitmee and Orme 2013), the role of traits in broad-scale historical biogeographic dispersal outcomes at the species level is only just beginning to be formally investigated (Sukumaran and Knowles 2018, Klaus and Matzke 2020). Integrating dispersal events and species' trait evolution on evolutionary timescales offers potential insight into the role of traits in species' biogeographic movements. This will advance our understanding of processes in historical biogeography and community assembly, which may enable better predictions of species' movements in the future (Lowe and McPeek 2014, Estrada et al. 2016).

To colonize a distant location, species must succeed at three sequential stages of dispersal: emigration, movement (or 'passage' if referring to passive dispersal) and establishment (Nathan 2001). Different types of traits might be linked to successfully overcoming each stage (Estrada et al. 2016). The emigration stage in biogeographic dispersal is strongly influenced by species' geographic distributions; coastal species, for example, are more likely to be moved from their native range by storms and cyclones than species living far away from the coast (Blom et al. 2019). In the movement and establishment stages, larger animals might have a survival advantage since their relative metabolic rate (relative to body size) is lower than that of smaller species (Andrews and Pough 1985, White et al. 2019), which improves their resistance to stress (including long periods of food and water shortage; Van Bocxlaer et al. 2010). On the other hand, transoceanic, cyclone-driven rafting dispersal of small organisms has long been reported (Ozgo et al. 2016, Lindo 2020). Establishment at a new location depends first and foremost upon the arrival of a reproductively viable founding population, which is determined by population size and species' life history traits (Safriel and Ritte 1980). While some traits are likely linked to specific stages of the dispersal process (e.g. coastal distribution to emigration), other traits may be related to several dispersal stages at the same time (such as body size). In addition, traits may have multiplicative effects, i.e. a species holding several dispersal traits may have a much higher probability of dispersal success than could be expected based on estimations from the individual traits. It is therefore important to consider combinations of traits that might form a successful disperser phenotype (Van Bocxlaer et al. 2010).

Further clues to understanding how traits influenced biogeographic movements in the past can be found in today's biological invasions. In some groups, invasive species belong to lineages with particularly frequent historical biogeographical movements (e.g. in pines: Gallien et al. 2016; and in Australian acacias and eucalypts: Gallien et al. 2019). Furthermore, in both processes taxon-specific barriers need to be overcome for a successful range expansion (e.g. large water bodies). While some barriers may be very different in the two processes (e.g. those related to emigration), others may be comparable (e.g. those related to establishment) and the traits associated with overcoming them may be similar.

In today's biological invasions, a species' position on the fast/slow life history continuum has been linked to its invasion success (Sol et al. 2012, Capellini et al. 2015, Allen et al. 2017). The fast/slow life history continuum (Dobson and Oli 2007, Jeschke and Kokko 2009) is a descriptive analogue of the mechanistic r/K selection theory of life history evolution (MacArthur and Wilson 1967, Pianka 1970). Life history traits of fast species can be equated to those of r-strategists (e.g. early reproduction, big litters/clutches), and life history traits of slow species to those of K-strategists (e.g. low fecundity, long lifespan). Birds with traits associated with slow life history and bet-hedging strategies, such as large brains and iteroparous reproduction, are more successful invaders (Sol et al. 2012). Slow and bet-hedging species may have the resources (and lifespans) to wait for favourable environmental conditions to produce offspring (Cáceres 1997), and they exhibit less demographic variability over the years, which buffers the effects of environmental stochasticity (Sæther and Bakke 2000, Jeppsson and Forslund 2012). On the other hand, in mammals, amphibians and (non-avian) reptiles, the opposite pattern has been found: species with fast life histories are more successful throughout the invasion pathway than slow species (Capellini et al. 2015, Allen et al. 2017). Fast species are able to quickly establish sizable populations, hence they may be able to quickly overcome the period in which founder populations are particularly vulnerable to stochastic extinction (Caswell et al. 2003, Blackburn et al. 2015). The relationship between life history strategy and present-day biological invasions and species' movements has inspired us to investigate the role these strategies have played as drivers of global biogeography in the past.

Here, we use recently developed trait-dependent biogeographic models (Klaus and Matzke 2020) to test the effect of three binary traits (coastal distribution, body size and life history strategy) and their combination in dispersal outcomes on an evolutionary timescale. We investigate these traits in the family of chameleons (Chamaeleonidae) which comprises 217 species in 12 genera (according to <www.reptile-database.org>, accessed 20 May 2021). Most species occur in Madagascar and Africa, but some species can be found in southern Europe, the Middle East, India and Indian Ocean islands (IUCN 2019). Chameleons are situated within the squamate clade of Acrodonta, and are hypothesized to have diverged from their sister clade Agamidae ca 90 million years ago (Mya) (Townsend et al. 2011, Tolley et al. 2013). Chameleon phylobiogeography suggests an African origin with multiple oceanic dispersal events to Madagascar, the Comoros Islands, Arabia, the Seychelles, India and Europe (Raxworthy et al. 2002, Townsend et al. 2011, Tolley et al. 2013), which makes the group well-suited for investigating how traits relate to dispersal patterns.

First, we analysed whether chameleon distributions (coastal versus non-coastal) and body size (and associated life history trait covariation) are related to past dispersal outcomes, two traits identified as affecting historical dispersal in other reptile clades (Blom et al. 2019, Nicolaï and Matzke 2019). Body size is known to evolve under different selective pressures from life history (e.g. temperature; Tinkle et al. 1970), but through allometric constraints selection pressures on body size can indirectly influence traits that are related to the fast/slow life history spectrum (Bauwens and Díaz-Uriarte 1997, Bakewell et al. 2020, Meiri et al. 2021). We therefore placed species on a body size-independent fast/slow life history continuum using phylogenetic factor analysis. We then evaluated the relationship between this body size-independent life history strategy and past dispersal outcomes, which has not been done in the context of historical biogeographic dispersal before. Finally, we combined all three traits (coastal distribution, body size and life history strategy) and investigated the possibility of a successful dispersal syndrome. We used trait-dependent biogeographic models to test the following hypotheses:

1) Coastal lineages and large-bodied lineages were better dispersers than non-coastal and small-bodied lineages, respectively, in the past, as demonstrated in other reptile clades.
2) Chameleon lineages with fast life histories were better biogeographic dispersers than lineages with slow traits in the past, following patterns in invasive reptiles.
3) Chameleon lineages holding all traits hypothesized to favour dispersal (coastal distribution, large body and fast life history strategy) were better dispersers than lineages holding only one of these traits.

Material and methods

To assess whether, and how, three traits (coastal distribution, body size and body size-independent life history strategy) have influenced past dispersal success of chameleons we built and compared trait-independent and trait-dependent biogeographical models (Fig. 1). Biogeographical models estimate ancestral ranges of species based on species' extant distributions and allow us to estimate past movements between discrete
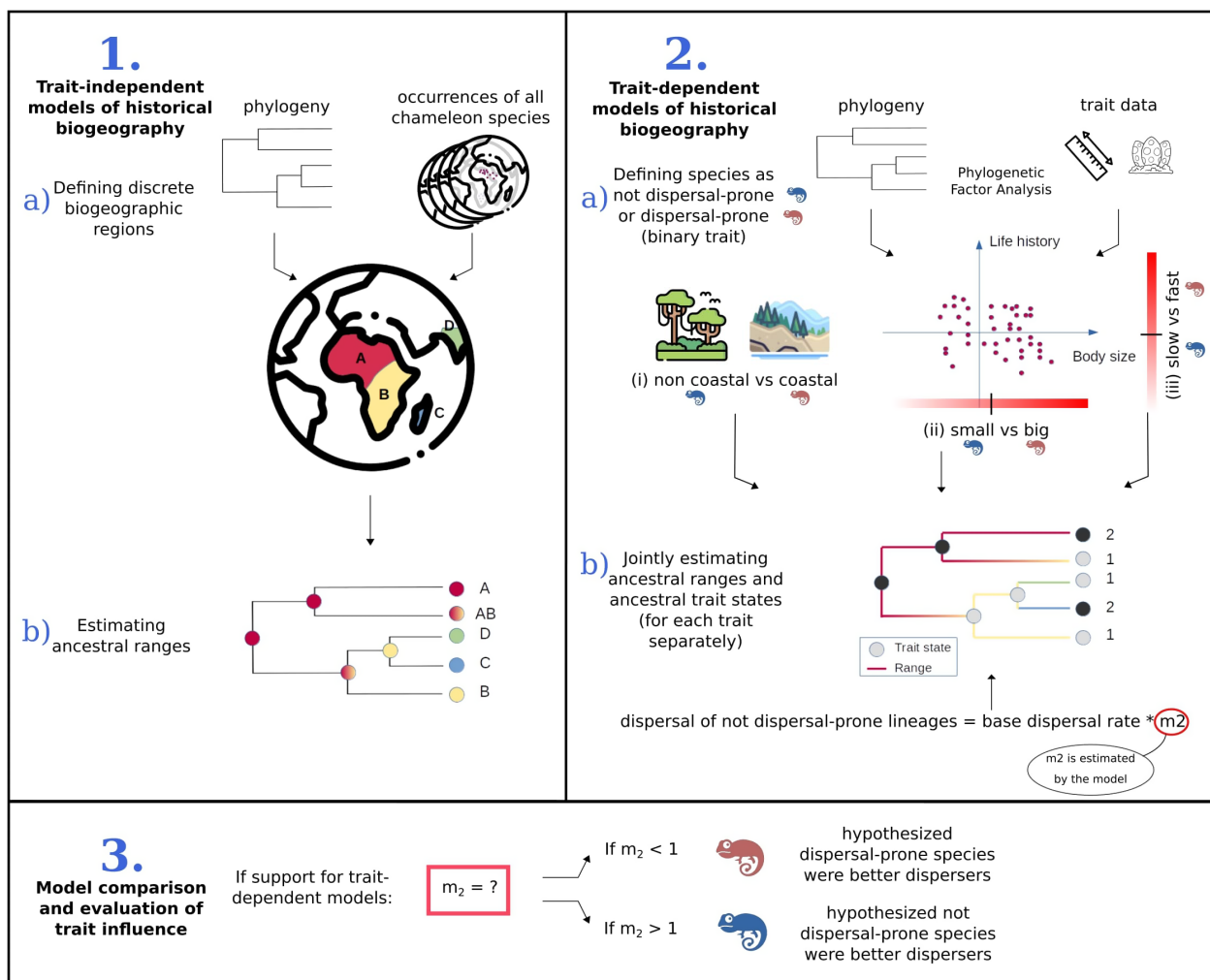

Figure 1. Schematic presentation of analysis workflow. Icons: <www.flaticon.com>.

biogeographic regions (see 'Chamaeleonidae biogeographic regions' section for details on the definition of these regions). In trait-dependent biogeographical models, a binary trait can influence dispersal rates of lineages. To define this binary trait and classify species according to body size and body size-independent life history strategy we used phylogenetic factor analysis (see 'Trait data and phylogenetic factor analysis' section for details). Comparison between trait-dependent and trait-independent models reveals whether a given trait had an influence on dispersal success in the past. If this is the case, the direction of the relationship between a given trait and dispersal success will be investigated (with the estimated parameter m2; see 'Trait-dependent dispersal: 'BioGeoBEARS'' section for details). All analyses were performed using R ver. 3.6.3 (<www.r-project.org>) unless otherwise specified.

Chamaeleonidae phylogeny and distribution

We focused only on chameleon species for which genetic data were available (181/217 species, ca 83%), using a subset of the Tonini et al. (2017) squamate consensus tree. To quantify the effect of phylogenetic uncertainty in results we repeated the analyses on a set of 100 uniformly sampled trees from a sample of the posterior distribution of Tonini et al. (2017) (Supporting information). Species' distribution data were obtained from IUCN (2019). We kept records where presence was defined as extant and origin as native. We transformed the data into rasters in cylindrical equal area projection (Behrmann with standard parallels at 30° to avoid distortion of area at higher latitudes, which allows for a better comparison between different raster cells at different latitudes) with a resolution of ca 93 × 93 km.

Chamaeleonidae biogeographic regions

To estimate species' movements in the past, the first step is to identify the most important biogeographic regions specific to chameleon species. We did so with a data-driven approach using extant species' distribution data. After evaluating alternative bioregionalization methods (Supporting information) we chose to use a clustering algorithm (unweighted pair group with arithmetic mean, Kreft and Jetz 2010) on between-site phylogenetic distances (modified Simpson's phylogenetic beta-diversity index (Lennon et al. 2001 after Simpson 1943); Eq. 1). This method calculates the phylogenetic distance between raster cells based on extant species' distribution data and their phylogenetic relationships, and then groups raster cells together according to the amount of evolutionary history they share. Hence, this method identifies barriers that have acted as actual barriers to gene flow over evolutionary time, and dispersal that is estimated between regions can be considered biogeographic dispersal (Kreft and Jetz 2010) (Eq. 1):

$$\text{Simpson} = \frac{\min(b,c)}{\min(b,c)+a} \qquad (1)$$

where a = length of shared branches on the phylogenetic tree between two different raster cells, and b and c = length of unique branches in two different raster cells.

The phylogenetic beta-diversity matrix was weighted by a geographical distance matrix (great-circle distances on latitude/longitude coordinates). Non-contiguous regions were separated manually. In this way, we identified nine biogeographic regions: North Africa and Arabia, Central Africa, Southeast Africa, Southwest Africa, India, Socotra, Madagascar, the Comoros Islands and the Seychelles (Fig. 2). Extant species occupy three biogeographical regions at maximum. We therefore allowed ancestral distributions to extend to a maximum of three regions (Supporting information).

Trait data and phylogenetic factor analysis

Trait-dependent biogeographic models can presently only take binary traits into account (see 'Trait-dependent dispersal: 'BioGeoBEARS'' section). We hence defined four binary trait datasets, based on three focal traits and their combination: 1) coastal distribution: coastal species (species living within 10 km of the coast) versus non-coastal species; 2) body size and associated life history trait covariation: large-bodied species versus small-bodied species; 3) body size-independent life history: fast versus slow life history; and 4) dispersal syndrome: species holding all three hypothesized dispersal traits (coastal distribution + large bodied + fast life history) versus species that do not have all three traits.

We identified species as coastal if they lived less than 10 km away from the sea (74 coastal species, ca 41%) using QGIS (QGIS Development Team 2020) and a global terrain model for ocean and land (GEBCO Bathymetric Compilation Group 2021). To assess sensitivity to the 10 km threshold, we analysed three additional classifications where we defined species as coastal if they lived less than 2, 15 or 25 km away from the sea. To rank species according to body sizes and life history strategies, we compiled a dataset of life history traits and identified the main axes of variation with a phylogenetic factor analysis (PFA, Tolkoff et al. 2018). The trait data included: snout–vent length (SVL, 100% coverage) as a proxy for body size, clutch size (67% coverage), number of clutches per year (24% coverage), age at sexual maturity (29% coverage), gestation time (28% coverage) and reproductive lifespan (18% coverage; Nečas 1999, Glaw and Vences 2007, Tilbury 2010, Allen et al. 2017, Meiri 2018, Hughes and Blackburn 2020).

We performed PFA using the Julia package PhylogeneticFactorAnalysis.jl ver. 0.1.4 (Hassler et al. 2022) which relies on a development version of BEAST (Suchard et al. 2018) to be released with BEAST ver. 1.10.5. Missing data were handled in PFA through integrating out missing values in likelihood calculations, allowing inclusion of species with incomplete trait data, while avoiding biases associated with data imputation (Supporting information). To identify a size-specific fast/slow continuum (cf. Jeschke and Kokko 2009) independent from allometric constraints,
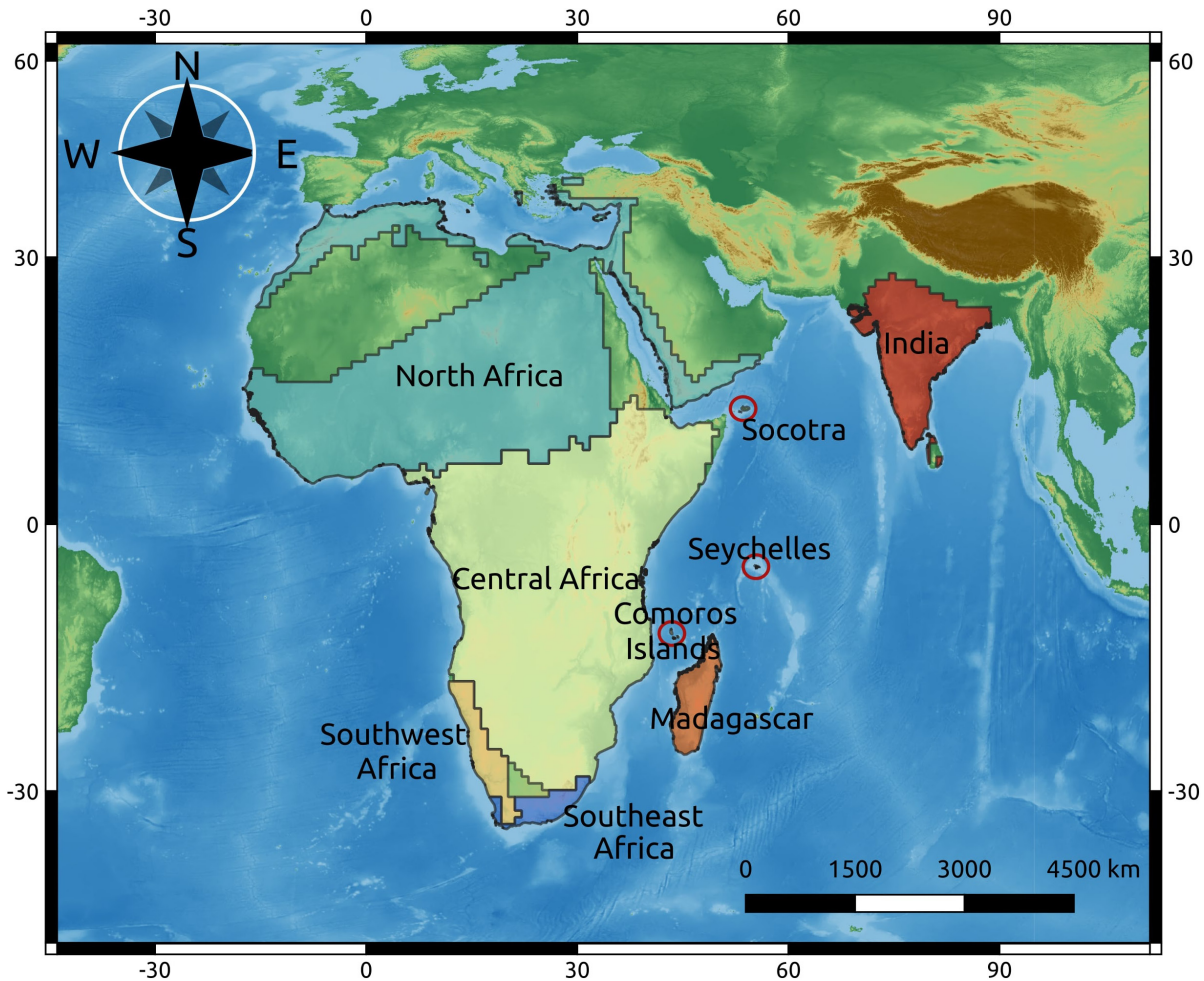
Figure 2. The nine biogeographic regions for Chamaeleonidae, identified through unweighted pair group with arithmetic mean (UPGMA) clustering on a modified Simpson's phylogenetic beta-diversity distance matrix. (Global terrain model of oceans and land taken from GEBCO Compilation Group (2021).)

we structured the PFA so that body size (as captured by SVL) loaded only onto the first factor while all other traits loaded onto all factors. This forced life history trait variation associated with body size onto the first factor with any additional factors capturing size-independent patterns of life history covariation (Supporting information). The first factor capturing size-dependent relationships was defined by positive loadings on SVL and clutch size (Fig. 3). The second factor was associated with size-independent fast/slow strategies and defined by gestation time and sexual maturity, with fast species of early sexual maturity and short gestation time on one side, and species with opposing traits on the other. Altogether, 32% of trait variance was attributable to the first factor and 16% to the second.

We used the first factor of the PFA to assess the role of body size and associated allometric relationships by median-splitting the species along this factor (i.e. using the median to assign species as small or large). We used the second factor as a representation of the fast/slow spectrum and median-split species along this factor to differentiate fast from slow species and obtain the life history trait dataset. We further

tested alternative splitting thresholds (Supporting information): 1) the fastest 25% of species versus the rest; 2) the fastest 75% versus the rest; and 3) the fastest 25% and slowest 25% ('extreme' life history) versus the rest. According to the results of these splits our definition of the dispersal syndrome changed. Finally, we assessed the sensitivity of our main results to the binarization of the continuous traits by moving the cutoff 10% in either direction.

Trait-dependent dispersal: 'BioGeoBEARS'

To assess the effect of traits on dispersal outcomes in the biogeographic history of chameleons, we used three biogeographic models that estimate ancestral ranges implemented in the R package 'BioGeoBEARS' ver. 1.1.2 (Matzke 2013, 2014): 1) dispersal–extinction–cladogenesis (DEC; Ree et al. 2005, Ree and Smith 2008); 2) DIVA-like (a likelihood implementation of DIVA; Ronquist 1997); and 3) BAYAREA-like (a likelihood implementation of BayArea; Landis et al. 2013). In the 'BioGeoBEARS' implementation of these models, biogeographical movements (i.e. anagenetic and cladogenetic
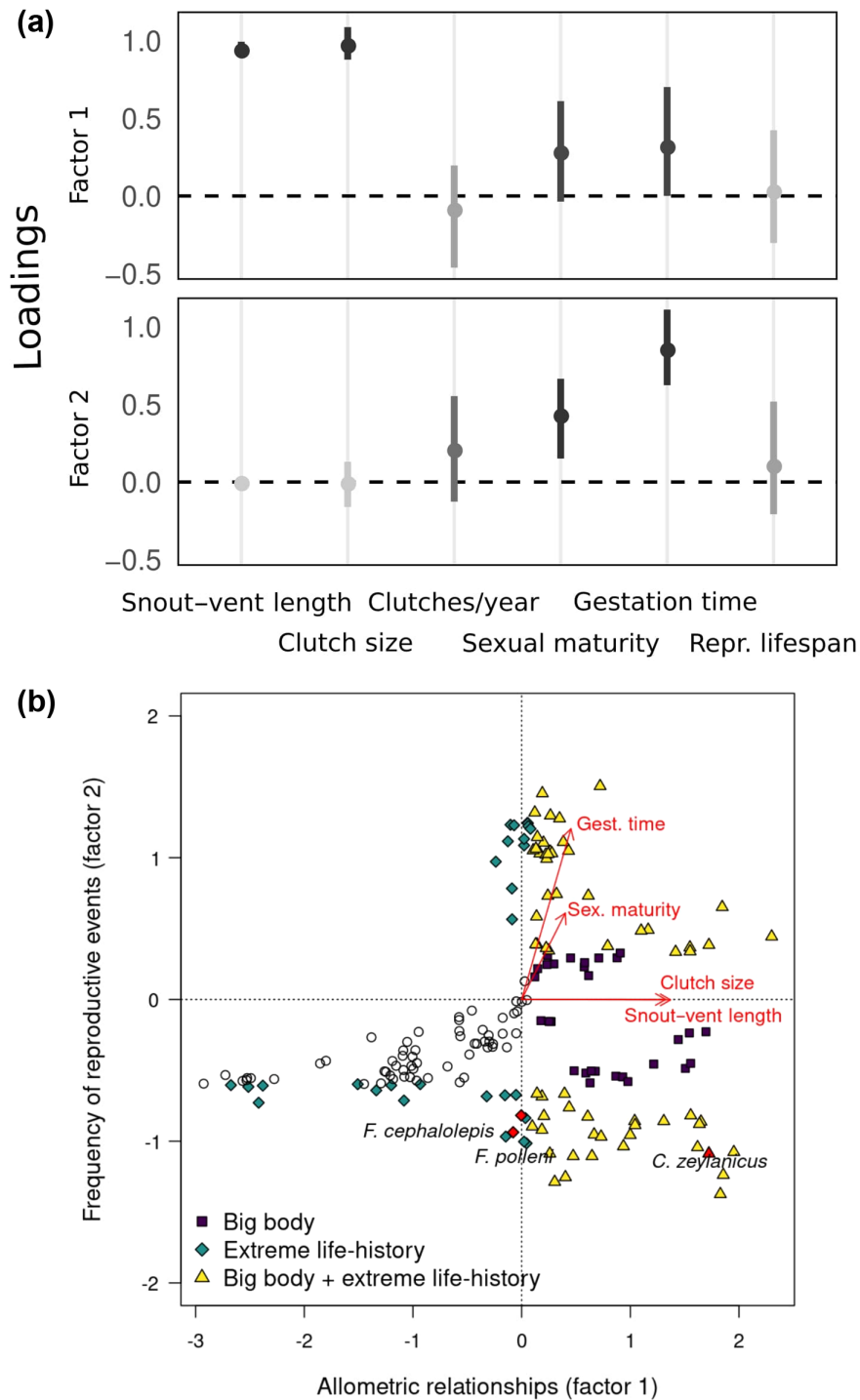
Figure 3. Results of the phylogenetic factor analysis. The estimates for the loadings of the body size and life history variables onto the two identified factors are given in (a). Points represent the posterior mean while error bars represent the 95% highest posterior density interval. Shading indicates the posterior probability p that loadings are of the same sign as their posterior means. The light end of the spectrum corresponds to p = 0.5 (i.e. the loadings value has equal probability of being positive or negative), while the dark end corresponds to p = 1 (i.e. the parameter's sign is certain). In (b), chameleon species are plotted in the factor space with different symbols depending on whether the species were classified as large-bodied (square), having an extreme life history strategy (diamond) or as being both large-bodied and having an extreme life history strategy (triangle). Small-bodied species with an intermediate life history strategy are indicated by simple dots. The original variables that loaded most strongly on the two identified factors are represented by red arrows. The three species that are associated with recent oceanic dispersal are labelled and indicated by red symbols.

dispersal rates) can be influenced by lineages' trait values. These models go beyond investigating correlations between traits and species' distributions to allow quantitative estimations of the importance of traits in dispersal processes at large temporal and spatial scales (Sukumaran and Knowles 2018, Klaus and Matzke 2020). At present the trait can take only two states (i.e. it is a binary trait) and it is itself evolving on the phylogeny, i.e. ancestral trait states and ranges are jointly estimated on the phylogeny. All models are implemented in a common likelihood framework which allows for model comparison.

The influence of trait states on dispersal rates is implemented via dispersal multipliers m1 and m2. If a lineage is in trait state 1 (e.g. large body size), the base dispersal rate d is multiplied by m1, and if a lineage is in trait state 2 (e.g. small body size), d is multiplied by m2 (Klaus and Matzke 2020 and <http://phylo.wikidot.com/biogeobears>). In practice, m1 is fixed to 1, and only m2 is inferred: m2 > 1 indicates that lineages in trait state 2 (e.g. small-bodied) were more successful dispersers than lineages in trait state 1, and m2 < 1 indicates the inverse. The transition rates from one trait state to the other, t12 and t21, are inferred as well. To compare trait-independent models to trait-dependent '+m2' models, the log-likelihood from the independent trait evolution on the tree is combined with the log-likelihood from the independent geographic data. Therefore, we ran just the trait data under binary discrete character models as implemented in the 'BioGeoBEARS' package to independently estimate the parameters t12 and t21 (Klaus and Matzke 2020). The log-likelihood of the trait-independent models was then the sum of the log-likelihood of these independent trait data and the log-likelihood of the geographic data (i.e. log-likelihood from 'BioGeoBEARS' runs without parameters m2, t12 and t21). The log-likelihood reflects whether incorporating the trait (e.g. body size) improves model fit and m2 indicates which trait state the dispersal is associated with (e.g. large body size).

Plate tectonics and island uplift influenced species' past movements between biogeographic regions. We therefore implemented a time-stratified analysis and defined manual dispersal multiplier matrices (MDMMs) to account for islands uplifts and differences in the ease of continental versus oceanic-with-currents versus oceanic-against-currents dispersal (Supporting information). We also took changing geography into account by modifying dispersal probabilities between any two areas depending on the distance between them (+x model variant). Based on GPlates (Müller et al. 2018) and the global plate and rotation model of Matthews et al. (2016), we accounted for changing distances between regions by recalculating the distances for every time slice (Supporting information). We further introduced a root constraint in Central Africa to reflect findings from the literature (Tolley et al. 2013, Supporting information).

In summary, we first evaluated 30 trait-independent models: three types of biogeographical models (DEC, DIVA and BAYAREA) × two types of influence of geographic distances (base model and +x-variant) × five different MDMMs. We compared these 30 models with the corrected Akaike information criterion (AICc), and identified the best base model:

DEC with MDMM distinguishing continental versus oceanic barriers and paleo-current directions (Supporting information). Second, for each of the traits (coastal distribution, body size, four life history strategies, dispersal syndrome) we ran the two trait-dependent biogeographic models (+m2 and +m2x) using the previously selected best base model. Third, for each trait, we used AICc to compare the four final models (two trait-independent models: base, base + x and two trait-dependent models: base + m2, base + m2x). In addition, we ran founder event models (+j) for two traits (body size and extreme life history strategy) but, since they did not affect the m2 parameter estimates significantly (Supporting information) and a critique of Ree and Sanmartín (2018) highlighted conceptual problems, we did not pursue this avenue further to reduce computation time.

To assess phylogenetic uncertainty, we reran the trait-dependent model for every trait (coastal distribution, body size, life history strategy and dispersal syndrome) for every tree across the set of 100 trees from the posterior. Each new run included a new phylogenetic factor analysis to reclassify species as large versus small, to reclassify the life history strategies and to recalculate the dispersal phenotype (Supporting information).

All 'BioGeoBEARS' analyses were performed on R ver. 3.6.2 (<www.r-project.org>) using the GRICAD infrastructure (<https://gricad.univ-grenoble-alpes.fr>). The biogeographical analyses amounted to more than 44 600 h × cores of computation time.

Results

Trait-dependent biogeographic models

Coastal distribution and body size
Non-coastal lineages did not disperse at all and large chameleons had a higher dispersal probability than lineages with small body sizes in the past. The trait-dependent models were selected as best models by the AICc-based model comparison for coastal distribution and body size (Table 1; Supporting information), split between just trait-dependent (coastal distribution: 63%, body size: 74%) and distance-and-trait-dependent models (coastal distribution: 37%, body size: 26%; Supporting information). The multiplier of the non-dispersal-prone forms (m2) was 0 for both traits. Phylogenetic uncertainty had little effect on dispersal multiplier estimates in the coastal distribution and body size analyses (Fig. 4). Using different distances to the sea (2, 15, 25 km) to classify species as coastal did not change interpretation of our results (Supporting information). Neither did moving the cutoff during binarization of body size 10% in either direction, i.e. considering the first 40% and 60% of species as large, respectively (Supporting information).

Life history strategy
Initial results suggested that fast lineages had generally higher dispersal probabilities than slow lineages: m2 of the

Table 1. Best models per trait as selected by model comparison with AICc. Only models with an AICc weight greater than 1% are included. m2: dispersal multiplier of species in the non-dispersal-prone form: non-coastal distribution, small bodied, intermediate life history (m2 > 1 indicates that species with non-dispersal-prone traits were more successful dispersers than species in trait state 1, and m2 < 1 indicates the inverse); x: dispersal multiplier of geographic distance.

Trait set	Best models	LnL	AICc weight (%)	m2	x
Coastal distribution	DECm2	−272	63	0	0
	DECm2x	−271	37	0	−0.11
Body size	DECm2	−253	74	0.0028	0
	DECm2x	−253	26	0.0028	-10^{-6}
Extreme life history	DECm2	−248	74	0.15	0
	DECm2x	−248	26	0.15	-10^{-6}
Dispersal syndrome	DECm2	−234	74	0.02	0
	DECm2x	−234	26	0.02	-10^{-6}

median-split classification of life history strategies was 0.84, trait-dependent models accruing an AICc weight of 27% (Supporting information), and m2 was 0.22 when comparing the fastest 25% of all species against the rest, trait-dependent models accruing an AICc weight of 93% (Supporting information). However, when comparing the fastest 75% against the rest, m2 of the best model was 2.19 (AICc weight of trait-dependent models = 68%; Supporting information), indicating that the slowest 25% of all species had a higher dispersal probability than the fastest 75%, contrary to the initial results. We therefore developed an ad hoc hypothesis and tested whether the extremes of the life history spectrum may be advantageous to dispersal. When comparing the fastest 25% and slowest 25% of species jointly against the rest, m2 was 0.15 and trait-dependent models accrued an AICc weight of 100% (Table 1, Supporting information), indicating that

species with an extreme life history strategy had an 85% higher dispersal probability than species with an intermediate one. Phylogenetic uncertainty influenced the extreme life history result more than coastal distribution and body size, with the median m2 being at 0.33 ± 0.07. Moving the cutoff during binarization 10% in either direction, i.e. hypothesizing the extreme 40% and 60% of species to be dispersal-prone, respectively, did not change our results (Supporting information).

Dispersal syndrome
According to the life history results, our prediction for the dispersal syndrome changed to expecting that chameleons dispersed more when they were at the same time coastal, large-bodied and with extreme life history strategy (instead of only a fast one). We identified 34 species (ca 19%) as having such a dispersal syndrome, significantly more than could have been expected by chance (Supporting information). Species that did not hold this combination of traits had a 98% lower probability of dispersal (m1 was fixed to 1, m2 estimated as 0.02; Fig. 4), and trait-dependent models accrued an AICc weight of 100% (Table 1, Supporting information). When running the trait-dependent model on a set of trees, m2 values varied around 0.03 ± 0.14 but a small number of trees (3%) generated low log-likelihood models with m2 parameters close to 1 (Supporting information).

Biogeographic history of chameleons and trait evolution

Trait-dependent models were consistently better supported by AICc comparison than trait-independent models. Notably, two nodes were estimated identically in all trait-dependent models but differently in the trait-independent
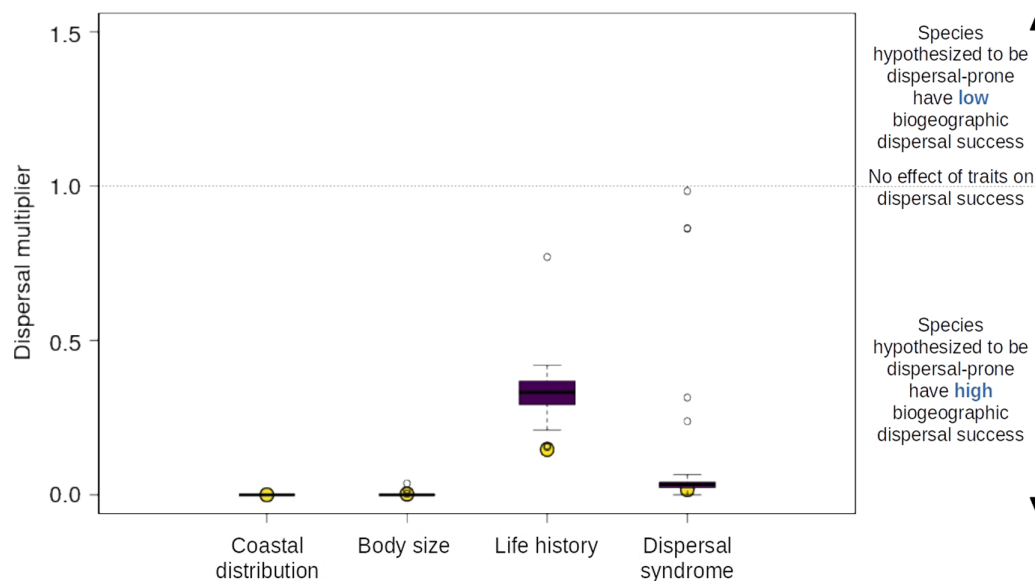

Figure 4. Values of the dispersal multiplier parameters as estimated by trait-dependent DEC models (DEC+m2). m1 (multiplier of the dispersal-prone forms) was fixed to 1. All multipliers presented here are estimations of m2, the multiplier for the non-dispersal-prone forms. The yellow points indicate the m2 parameter estimation from the consensus tree; the boxplots reflect the uncertainty in m2 parameter estimates due to phylogenetic uncertainty: the models were run on a set of 100 trees from the posterior.

model (Supporting information). All trait-dependent models agreed on the most recent common ancestor (MRCA) of *Bradypodion pumilum* and *B. damaranum* occupying Southeast and Southwest Africa (Supporting information). The trait-independent model, however, inferred this node to be restricted to Southeast Africa which then led to the inference of two independent range expansions by *B. pumilum* and *B. damaranum* to Southwest Africa (Supporting information). Similarly, the trait-dependent models estimated a more widespread ancestor for part of *Trioceros* than the trait-independent model (Supporting information).

Despite all trait-dependent models being better supported than trait-independent models, there were also differences in estimations of ancestral ranges within trait-dependent models. Shortly after the split of Brookesiinae and Chamaeleoninae, the ancestor of the Chamaeleoninae developed a dispersal-prone form and expanded its range to the Seychelles and Madagascar, but the order of events is unclear (coastal distribution and life history models inferred that Madagascar was colonized first; body size and dispersal syndrome models inferred that the Seychelles were colonized first; Supporting information).

The biogeographic history of the genus *Chamaeleo* was well supported by all models, except for the timing of the colonization of Socotra and North Africa and Arabia. The coastal distribution and dispersal syndrome models agreed on an ancestor occupying Central Africa, North Africa and Arabia, and Socotra ca 20 Mya. In other models this same ancestor was restricted to Central Africa and colonized Socotra about 18 Mya (Supporting information).

Several range expansions and retractions took place in *Bradypodion* but the order and timing of events is uncertain (Supporting information). The MRCA of *Bradypodion* either occupied Central Africa and Southeast Africa (body size, life history and trait-independent models) or Central Africa, Southeast and Southwest Africa (coastal distribution and dispersal syndrome models). All trait-dependent models then agreed on the MRCA of *B. pumilum* and *B. damaranum* occupying Southeast and Southwest Africa. The MRCA of *Bradypodion* excluding *B. pumilum* and *B. damaranum* (Supporting information) was estimated to have occupied the same model-specific range as the MRCA of the whole genus; only the coastal distribution model inferred a range retraction. Furthermore, in the body size and life history models the ancestor of *B. thamnobates* occupied Southeast Africa and dispersal into Central Africa only took place with *B. thamnobates*, which occurs today on the edge of both regions. In the other models, the ancestor of *B. thamnobates* was already present in both regions. Similarly, it is unclear whether *B. gutturale* expanded its range from Southeast to Southwest Africa or if the expansion happened before.

In *Trioceros*, range expansions to North Africa took place repeatedly, but the number of range expansion events differed between trait-dependent models (coastal distribution, body size: 6; life history: 4; dispersal syndrome: 5; Fig. 5, Supporting information).

Discussion

We tested on an evolutionary timescale whether three traits (coastal distribution, body size and life history) and their combination in chameleons were related to biogeographic dispersal success. Lineages of coastal chameleons and large chameleons were more likely to disperse than non-coastal and small lineages in the past. Instead of a fast life history strategy, an extreme life history strategy, i.e. either particularly early sexual maturity and short gestation time (fast) or late maturity and a long gestation time (slow) relative to body size, was linked to dispersal success. Our analyses revealed uncertainties in ancestral range estimations: there were differences in timing of dispersal events between trait-independent and trait-dependent models, as well as within trait-dependent models depending on which trait was included. However, trait-dependent models were better supported by AICc comparison than trait-independent models in all cases, demonstrating that including traits in analyses of historical biogeography is essential for more accurate estimations of species' pasts.

Trait-dependent biogeographic models

Coastal distribution and body size

Coastal distributions are positively related to biogeographic movement in chameleons, as has been shown for *Cryptoblepharus* lizards and crocodiles (Blom et al. 2019, Nicolaï and Matzke 2019). While it seems logical that coastal distributions should promote trans-oceanic dispersal, most dispersal events that we identified were continental. Possibly chameleons dispersed along the coast, either by their own movement on land, or on vegetation adrift on the sea. Alternatively, coastal lineages may have dispersed through the interior of the continent. Coastal lineages tend to have larger ranges and there may be other factors that facilitate their overland and overwater dispersal, e.g. an underlying trait correlated with coastal distribution, possibly related to microhabitat (e.g. arboreal species having a higher chance of being transported on vegetation compared to terrestrial species) or other morphological traits (da Silva and Tolley 2013, 2017).

Furthermore, body size (and associated life history trait covariation) also strongly influenced natural biogeographic dispersal processes, as in crocodilians (Nicolaï and Matzke 2019). Large size possibly favours dispersal success because the lower metabolic rate relative to body size of large species is related to lower relative energy requirements (Andrews and Pough 1985) which may improve resistance to stress, such as long periods of food and water shortage, and increase survival probability during the dispersal process. Moreover, body size in reptiles is highly correlated to clutch size (Meiri et al. 2020) and species with big clutches may have an advantage at the establishment stage. To distinguish between the correlated effects of body size and clutch size, further research should explore the role of body size in biogeographic dispersal in taxonomic groups where body size does not correlate positively with clutch size (e.g. reptile clades with relatively invariant clutch sizes, such as geckos, or in mammals).
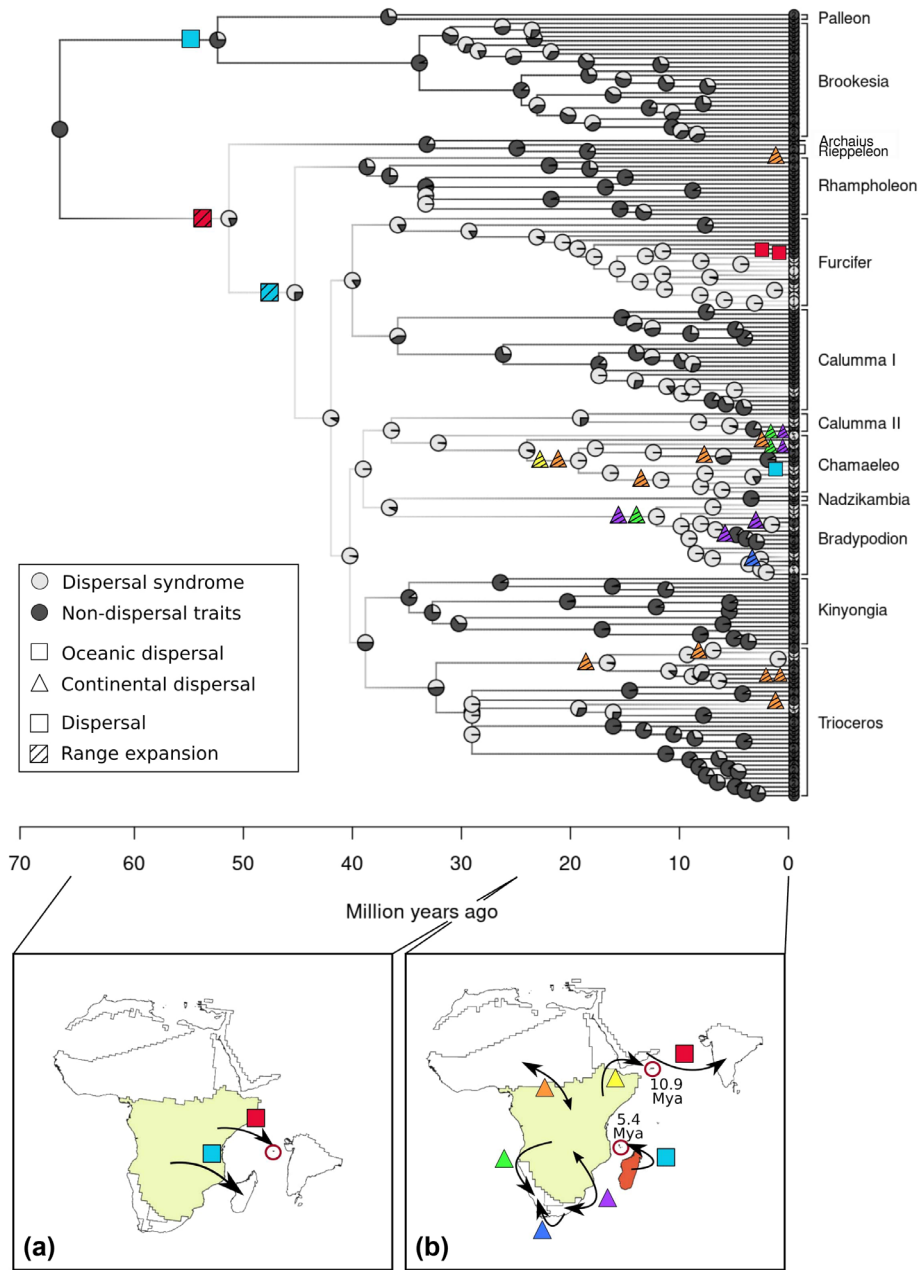
Figure 5. Biogeographical movements and evolution of the dispersal syndrome of chameleons mapped onto their phylogeny (using trait-dependent biogeographical model). The pie charts represent the probabilities of nodes being in a certain trait state: white indicates species holding all three hypothesized biogeographic dispersal traits (coastal distribution, large body and extreme life history strategy), and black indicates a form with two, one or no dispersal traits. Estimated dispersal (i.e. lineage completely left the previously occupied region; plain symbols) and range expansion events (i.e. the new regions were added to the lineage's range; striped symbols) are indicated on the tree by coloured symbols next to the pie charts. Different symbols correspond to oceanic (square) and continental (triangle) dispersal events and the colours indicate the direction of the dispersal events. The maps below the tree show where these dispersal and range expansion events took place, and where chameleons presumably occurred at the beginning of the period (coloured regions). Note: although we included five time slices in our analysis, only two maps are presented here for simplification. (a) shows the geography between 65 and 23 Mya and (b) between 23 Mya and the present. The times of emergence of the Comoros Islands and of Socotra's split-off from Africa are indicated in (b).

Life history strategy

Model selection did not confirm that chameleons with a fast life history were better dispersers than slow chameleons in the past. Instead, lineages with an extreme life history strategy had a higher dispersal probability than lineages with an intermediate life history strategy.

Our results for historical dispersal may indeed reconcile two seemingly conflicting theories on how life history strategy influences range expansion and dispersal. On one hand, species with a fast life history strategy may be successful establishers because they have the capacity for fast population growth and can quickly overcome the period in which stochastic extinction is particularly probable (Caswell et al. 2003, Reynolds 2003, Blackburn et al. 2015). Also, fast population growth facilitates local adaptation in niche requirements if newly colonized areas are ecologically different from areas of origin (Lavergne et al. 2010). In present-day invasions, for instance, a fast life history strategy was found to be more successful than a slow one in non-avian reptiles (Fujisaki et al. 2010, van Wilgen and Richardson 2012, Allen et al. 2017). On the other hand, species with a slow life history strategy can wait for favourable conditions to reproduce (Cáceres 1997) and they are less vulnerable to environmental stochasticity since they exhibit less demographic variability (Sæther and Bakke 2000, Jeppsson and Forslund 2012). This is apparent in bird invasions today where characteristics of a slow life history strategy, such as long lifespan and big brain size, are linked to success (Sol et al. 2012). Our results confirm that one strategy is not necessarily better than the other and that there might be more than one road to dispersal success.

Another reason for an extreme life history strategy being related to dispersal success in our study, rather than a fast one, may be that we did not exclusively study oceanic dispersal. Sol et al. (2012) proposed that a founder population needs to be very small for a strategy of fast population growth to be advantageous for colonization success. A small founder population is most likely the origin of island populations, but it may not always be the case for continental dispersal (e.g. climatic barriers can be temporarily alleviated over evolutionary time scales). Indeed, all recent purely oceanic dispersals in chameleons (*Furcifer polleni* and *F. cephalolepis* to the Comoros Islands and *Chamaeleo zeylanicus* to India) were associated with an extremely fast life history strategy (Fig. 3b). However, since there were few clear oceanic dispersal events in the history of chameleons, it is impossible to draw strong conclusions from this fact. More research is necessary to distinguish between the effect of life history strategy in continental versus oceanic dispersal; maybe a different strategy is advantageous for different modes of dispersal.

Dispersal syndrome

While we suggest the three traits tested are linked to specific stages of the dispersal process, it is possible that they are also linked to other stages of the dispersal process, either directly or indirectly through correlations with other traits (Uyeda et al. 2018). In addition, traits may have multiplicative effects on dispersal probability. This underlines the importance of also testing dispersal syndromes in relation to biogeographic dispersal success (Van Bocxlaer et al. 2010, Nicolaï and Matzke 2019). We found the combination of coastal distribution, large body size and an extreme history strategy had ca 98% higher dispersal rate than lineages with a non-dispersal syndrome. Moreover, more than one-third of all identified dispersal and range expansion events took place in the genus *Chamaeleo*, a relatively small genus (14/181 species) in which most extant species and their ancestors were identified to hold or to have held all three hypothesized dispersal traits. Since coastal distributions were strongly related to dispersal success (the dispersal multiplier for non-coastal species was 0 which is the maximum detectable effect), we were not able to formally detect an additive or multiplicative effect of all hypothesized dispersal traits.

The number of species that held the dispersal syndrome was significantly higher than expected by chance, which may indicate that lineages with a dispersal syndrome have higher speciation rates. In other clades (birds: *Zosterops*, Moyle et al. 2009; amphibians: Bufonidae, Van Bocxlaer et al. 2010), patterns of high dispersal ability combined with high speciation rates were found as well. Rare dispersal to distant locations may open opportunities for divergence by creating isolated populations (Gillespie et al. 2012). However, the fact that more species than expected held the dispersal syndrome may be a result of coevolving traits that produce convergent trait syndromes. Several traits can, for example, be jointly selected for by a given environment (Ronce and Clobert 2012, Stevens et al. 2014). More detailed studies are necessary to elucidate the link between dispersal and speciation in chameleons, and to determine whether the dispersal syndrome may be a product of coevolution.

New insights into the biogeographic history of chameleons

Trait-dependent models accrued 100% of the AICc weight for all four traits that we tested. This underlines the importance of including species' ecology in models of historical biogeography and emphasizes that different biogeographic processes may be relevant to different lineages, which means that they should not be treated interchangeably (Sukumaran and Knowles 2018).

The inclusion of traits allows us to pinpoint which parts of a clade's biogeographic history are subject to uncertainty. While in some nodes there were uncertainties throughout all models, two nodes were estimated identically in all trait-dependent models but differently in the trait-independent model (MRCA of *Bradypodion pumilum* and *B. damaranum*, and the ancestor of part of *Trioceros*; Supporting information). In both cases, the trait-independent model inferred a more restricted ancestral range, which led to more estimated range expansion events later on. In *Bradypodion*, there is an indication that the MRCA of *B. pumilum* and *B. damaranum* may have occupied a more widespread range including Southwest and Southeast Africa (Tolley et al. 2006), supporting results

from trait-dependent models in our study. In *Trioceros*, all trait-dependent models inferred an ancestor already occupying parts of Central Africa and the region comprising North Africa and Arabia ca 15 Mya, whereas the trait-independent model inferred two separate dispersal events later on. For clades with an uncertain biogeographic history, an analysis at a smaller spatial scale is preferable to allow a tailored definition of biogeographic regions and more detailed estimations (see Tolley et al. 2006 for *Bradypodion* and Ceccarelli et al. 2014 for *Trioceros*).

Conclusions

Our study emphasizes the importance of including species' ecological and biological characteristics in historical biogeography. Coastal distribution, body size and life history strategy are likely to have indeed played a decisive role in shaping the biogeographic history of chameleons. We found evidence that lineages with extreme life histories were more successful dispersers than lineages with an intermediate life history. Our results complement findings from invasion ecology but indicate that dispersal on an evolutionary timescale and in the Anthropocene may not be directly comparable. We show how life history strategy has influenced the biogeographic history of chameleons, which invites new key questions: Which effect has life history strategy had in the biogeographic history of other clades? How has it influenced and will it influence range shifts, invasions and global biodiversity patterns?

Author contributions

Sarah-Sophie Weil: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Writing – original draft (lead); Writing – review and editing (equal). **Laure Gallien**: Conceptualization (equal); Funding acquisition (equal); Supervision (equal); Writing – review and editing (equal). **Sébastien Lavergne**: Supervision (equal); Writing – review and editing (equal). **Luca Börger**: Supervision (equal); Writing – review and editing (equal). **Gabriel W. Hassler**: Formal analysis (supporting); Methodology (equal); Writing – original draft (supporting); Writing – review and editing (equal). **Michaël P. J. Nicolaï**: Data curation (equal); Writing – review and editing (equal). **William L. Allen**: Conceptualization (equal); Data curation (equal); Funding acquisition (equal); Supervision (equal); Writing – review and editing (equal).

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Data availability statement

Data and R code are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.hqbzkh1jx> (Weil et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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