

# Evolution in fossil time series reconciles observations in micro- and macroevolution

Kjetil Lysne Voje<sup>1</sup>, Megumi Saito-Kato<sup>2</sup>, Trisha L. Spanbauer<sup>3</sup>

<sup>1</sup>Natural History Museum, P.O. 1172, Blindern, Oslo 0318, Norway

<sup>2</sup>Department of Geology and Paleontology, National Museum of Nature and Science, Tsukuba, Japan

<sup>3</sup>Department of Environmental Science and Lake Erie Center, University of Toledo, Toledo, OH, United States

Handling editor: Luke Holman, Guest editor: Théo Gaboriau

Corresponding author: Kjetil Lysne Voje, Natural History Museum, P.O. 1172, Blindern, 0318 Oslo, Norway. Email: [k.l.voje@nhm.uio.no](mailto:k.l.voje@nhm.uio.no)

## Abstract

Extrapolating microevolutionary models does not always provide satisfactory explanations for phenotypic diversification on million-year time scales. For example, short-term evolutionary change is often modelled assuming a fixed adaptive landscape, but macroevolutionary changes are likely to involve changes in the adaptive landscape itself. A better understanding of how the adaptive landscape changes across different time intervals and how these changes cause populations to evolve has the potential to narrow the gap between micro- and macroevolution. Here, we analyze two fossil diatom time series of exceptional quality and resolution covering time intervals of a few hundred thousand years using models that account for different behaviours of the adaptive landscape. We find that one of the lineages evolves on a randomly and continuously changing landscape, whereas the other lineage evolves on a landscape that shows a rapid shift in the position of the adaptive peak of a magnitude that is typically associated with species-level differentiation. This suggests phenotypic evolution beyond generational timescales may be a consequence of both gradual and sudden repositioning of adaptive peaks. Both lineages show rapid and erratic evolutionary change and are constantly readapting towards the optimal trait state, observations that align with evolutionary dynamics commonly observed in contemporary populations. The inferred trait evolution over a span of a few hundred thousand years in these two lineages is, therefore, chimeric in the sense that it combines components of trait evolution typically observed on both short and long timescales.

**Keywords:** diatom, ancient lakes, phenotypic evolution, anagenesis, cladogenesis

## Introduction

Relating phenomena across different scales is a general challenge in science. Biology is no exception (Levin, 1992), and connecting generational processes (microevolution) to the larger-scale patterns of phenotypic diversification (macroevolution) is one example (e.g., Hansen, 2012, 2024; Harmon et al., 2021; Holstad et al., 2024; Jablonski, 2000, 2008; Rolland et al., 2023). More specifically, on generational timescales, strong selection (Hereford et al., 2004) on highly evolvable traits (Hansen & Pélabon, 2021; Houle, 1992) predict rapid evolution, which indeed seems to be a common feature of evolution on short timescales (e.g., Kinnison & Hendry, 2001; Sanderson et al., 2022; Uyeda et al., 2011). The high level of trait differentiation on microevolutionary timescales does not typically lead to much net evolution on longer timescales, however, as the overall mode of phenotypic evolution covering time intervals up to a few million years is characterized by stationarity trait dynamics (Estes & Arnold, 2007; Gingerich, 1983, 2001; Holstad et al., 2024; Uyeda et al., 2011). Stationary trait dynamics is equivalent to a white noise process, a type of evolutionary dynamic that does not predict increased divergence with time (Hansen, 2024). The overall mode of phenotypic evolution on shorter time intervals is therefore apparently not able to explain the diversification of morphology among species in a clade (Estes and Arnold, 2007; Hansen, 2012, 2024), nor the common

observation of strong phylogenetic effects where sister taxa are generally more similar to each other compared to more distantly related taxa (e.g., Ashton, 2004; Freckleton et al., 2002). Evolutionary processes on generational and longer time scales have indeed been suggested to be different by nature, thus making any attempt to merge our understanding of phenotypic evolution across the timescale continuum a futile endeavour (e.g., Gould, 1980, 1985; Stanley 1975). However, recent work has detected strong predictability of estimates of population genetic variance (i.e., evolvability sensu Houle 1992), a microevolutionary parameter, on phenotypic divergence across thousands and millions of years (e.g., Bolstad et al., 2014; Houle et al., 2017; McGlothlin et al., 2018, 2022; Opdal et al., 2023; Holstad et al., 2024; reviewed in Voje et al., 2023) indicating a potential for synthesis.

The adaptive landscape has been proposed as a conceptual bridge for how we can reconcile evolution across micro- and macroevolutionary timescales (Arnold et al., 2001; Hansen, 2012; Simpson, 1944). The adaptive landscape is a representation of possible combinations of phenotypic traits where elevations in the landscape represent peaks with high population fitness. Natural selection causes populations to evolve towards peaks in the landscape (Lande, 1979), and populations will attempt to track peaks when they change positions. According to Simpson (1944), most phenotypic evolution occurs within adaptive zones, which can be understood as

Received November 8, 2023; accepted July 15, 2024

© The Author(s) 2024. Published by Oxford University Press on behalf of the European Society of Evolutionary Biology.

This is an Open Access article distributed under the terms of the Creative Commons Attribution License (<https://creativecommons.org/licenses/by/4.0/>), which permits unrestricted reuse, distribution, and reproduction in any medium, provided the original work is properly cited.

collections of niches occupied by species with similar traits and, therefore, abilities to utilize similar habitats. One way to reconcile the rapid changes often observed on shorter timescales with stationary trait dynamics across thousands and up to a few millions of years is to assume that minor and erratic changes in the adaptive landscape lead to rapid microevolutionary events within the boundaries of an adaptive zone. Lineages will remain within the boundaries of the adaptive zones as long as such changes in the adaptive landscape do not accumulate (Arnold, 2014; Hansen, 2012, 2024; Uyeda et al., 2011; Voje, 2016). Lineages may break free of their bounded evolution due to rare and substantial changes in the positions of adaptive peaks (“quantum evolution” in Simpson’s (1944) terminology). In their analysis of a large collection of phenotypic size data from vertebrate lineages, Uyeda et al. (2011) estimated an average waiting time for a substantial change in the position of a peak to be several million years. Consistent with this expectation, studies of phenotypic evolution that cover microevolutionary timescales are usually analyzed using models that assume a fixed adaptive landscape. However, even though the predominant mode of evolution over generational timescales up to a few million years is characterized by stationary trait dynamics (i.e., bounded fluctuations in the trait mean) (Estes & Arnold, 2007; Gingerich 1983, 2001; Holstad et al., 2024; Uyeda et al., 2011), it is well-established that individual lineages can deviate from this pattern and evolve according to other modes of evolution at these timescales (Hopkins & Lidgard 2012; Hunt 2007; Hunt et al., 2015; Voje, 2016). It is therefore likely that the adaptive landscape can change in many different ways across both short and longer timescales. Large shifts in the adaptive landscape on macroevolutionary timescales are usually explored using phylogenetic comparative methods (e.g., Beaulieu et al., 2012; Butler & King, 2004; Hansen et al., 2008; Landis & Schraiber, 2017; Uyeda & Harmon, 2014), but whether these large shifts are due to the accumulation of many small changes over time or whether they represent sudden shifts in the positions of peaks is unknown (Uyeda & Harmon, 2014). A better understanding of if and how the adaptive landscape changes across different time intervals is likely to enable a better understanding of some of the seemingly contrasting observations of phenotypic evolution across different time scales.

Here, we analyze size evolution in two independent diatom lineages from the fossil record to assess the dynamics of the adaptive landscape on time intervals covering a few hundred thousand years. The size of an organism is a fundamental ecological (Peters, 1986), physiological (Schmidt-Nielsen, 1984) and life-history trait (Charnov, 1993) and diatoms show remarkable adaptations in size and shape as they colonized various marine, freshwater, and terrestrial habitats (Armbrust, 2009; Falkowski et al., 1998). Both analyzed datasets have an exceptional time resolution constrained by modelled chronologies (Saito-Kato et al., 2015; Spanbauer et al., 2018). The high quality of the data thus allows robust assessment of the fit of models that differ in their assumptions regarding if and how the adaptive landscape changes. In this study, we assess (1) if evolution of size beyond generational timescales is best explained by models assuming fixed or dynamical adaptive landscapes, (2) if typical microevolutionary observations—rapid evolution, directional selection, maladaptation as a common state—fit the observed trait evolution, and (3) whether the observed trait evolution is compatible

with processes explaining larger-scale patterns of phenotypic change typically associated with species-level differentiation.

## Materials and methods

### Evolutionary time series

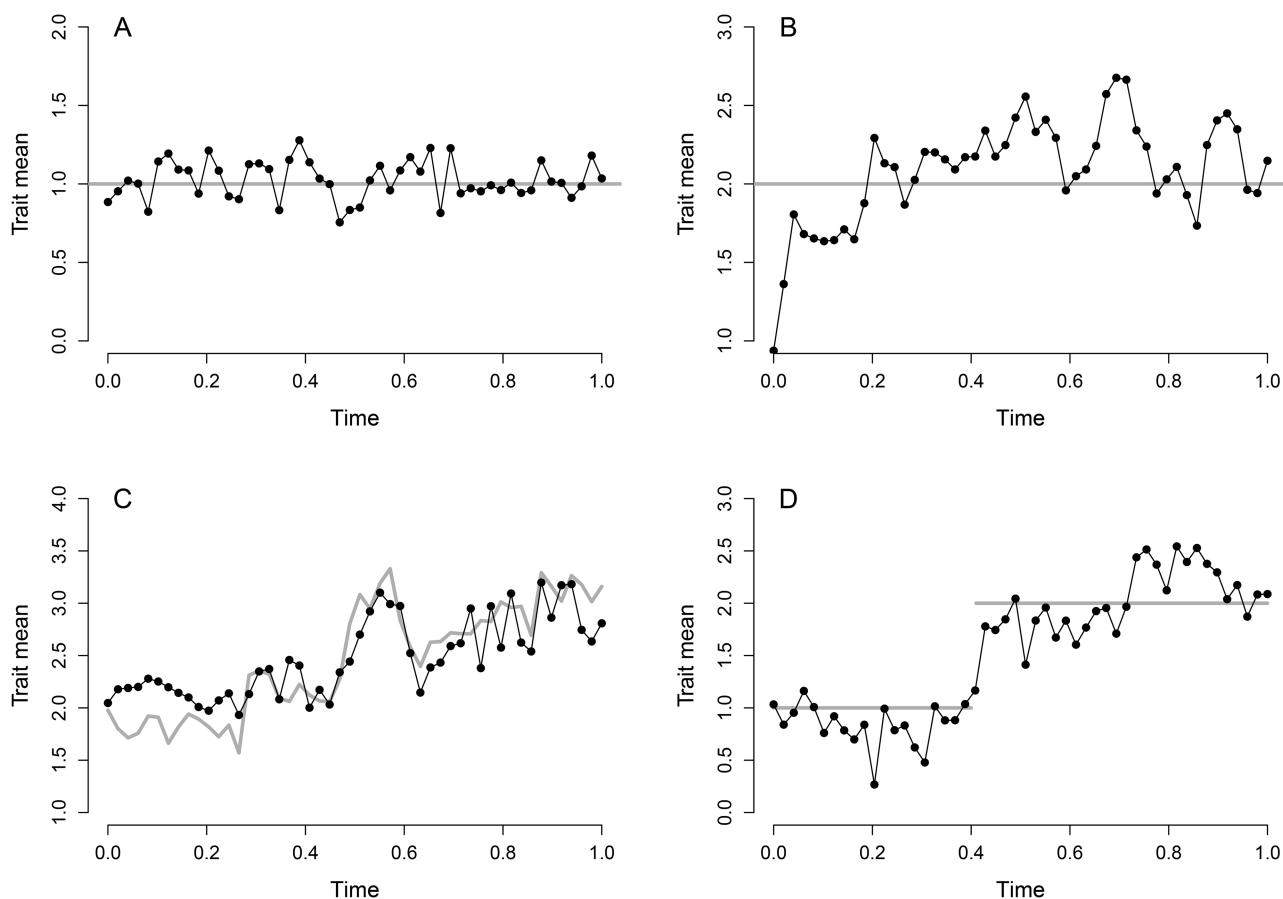
The sedimentary record of ancient lakes, such as Lake Titicaca and Lake Biwa, are good model systems for investigating phenotypic evolution within lineages due to their high rates of endemism coupled with continuous archives of paleoclimatic and paleoecological change (Cohen, 2012; Wilke et al., 2016). The sedimentary record from ancient lakes often produces high-resolution paleoecological (e.g., Fritz et al., 2012; Khursevich & Prokopenko, 2009; Sadori et al., 2016) and evolutionary records (e.g., Saito-Kato et al., 2015; Spanbauer et al., 2018) of communities and populations of organisms, making them especially useful for testing models of evolutionary dynamics (Ivory et al., 2016).

The *Cyclostephanos andinus* dataset describes size evolution in a diatom lineage from Lake Titicaca and was first published by Spanbauer et al. (2018). Lake Titicaca is a large monomictic lake located in the Andean Plateau along the border of Bolivia and Peru at 3810 m above sea level. The lake consists of two basins separated by the Straits of Tiquina. A 136-m drill core record (LT01-2B) was recovered in 2001 from 235 m water depth in the larger, deeper basin of Lake Titicaca (Fritz et al., 2007). Through a combination of radiocarbon dating, Uranium series dating, and calcium carbonate peak tuning to the Vostok CO<sub>2</sub> record, this sedimentary record was found to reconstruct ~370,000 years of paleoclimatic and paleoecological history (Fritz et al., 2007, 2012).

*C. andinus* is a large centric diatom endemic to Lake Titicaca and several other altiplano lakes (Tapia et al., 2004). For each sample, we used a Zeiss Axioskop 2 plus with an AxioCam under 1,000× magnification to measure 50 well-preserved *C. andinus* frustules. Despite the stable presence of *C. andinus* in Lake Titicaca throughout the sedimentary history of the lake, the morphology had a great deal of variation over time (Spanbauer et al., 2018). However, there is no robust support for elevating this diversity of morphology to separate species, and the data most likely represents a single evolving lineage through time (Spanbauer et al., 2018). The time series of *C. andinus* spans about 312,000 years and contains 266 samples. The average (median) time interval separating the samples is 1,177 (494) years, and the average (median) number of specimens measured per sample is 48 (50).

The second dataset describes size evolution in a diatom lineage from Lake Biwa in Japan, originally published in Saito-Kato et al. (2015). Lake Biwa is a tectonic lake ca. 1.5 Ma old in central Japan (Danbara et al., 2010). Since the 1970s, several long sediment cores have been taken from this lake, revealing over 200 m of continuous clay deposited under the lake (Takemura, 2012). Tephrochronology, palaeomagnetism, and fission track dates estimate a 430,000-year for the continuous clay sediment (Meyers et al., 1993), which suggests perennial pelagic environments over multiple glacial-interglacial cycles, which have been used to reconstruct past climates from the Middle–Late Pleistocene to the present (Miyoshi et al., 1999; Nakagawa et al., 2008). Diatom siliceous valves in these sediments are thus an excellent model system for investigating phenotypic evolution (Saito-Kato et al., 2015).

Biwa *Stephanodiscus* is an independent and distinct evolutionary lineage which is the ancestor of extant species in Lake



**Figure 1.** Trait evolution on static and dynamic adaptive landscapes. Panel (A) shows trait evolution according to the stasis model, where the trait mean (black dots) fluctuates randomly around a non-changing optimum (grey line). Panel (B) shows trait evolution according to an Ornstein–Uhlenbeck (OU) model with a fixed and non-changing optimum. Panel (C) shows an OU model where the trait tracks a randomly and continuously changing optimum. Panel (D) shows an OU model where a fixed optimum changes position abruptly, causing the trait to readapt to the new optimal state. The models in the first row (A and B) are examples of trait evolution on a constant adaptive landscape, while the models in the last row (C and D) are examples of evolution on changing adaptive landscapes.

Biwa. It originates from *S. cf. vestibulis* Håkansson, Theriot & Stoermer synonymous to *S. triporus* Genkal & G.V. Kuzmin in the sediment dated back to ca. 240,000 years B.P. Saito-Kato et al. (2015) classified 3 (chrono-)species stratigraphically, *S. umbilicatus* Saito-Kato, *S. praestephanos* Saito-Kato and *S. suzukii* (Tuji & Kocielek) Saito-Kato et al. (2015) with distinct morphological features and combinations of them. All these Biwa *Stephanodiscus* species have been placed in a newly established genus *Praestephanos* Tuji & M. Julius (Tuji et al., 2014), based on their valve morphology with the pattern of the areolae changing at the level of the marginal fultoportulae but not at the level of the rimoportulae or spines. In this article, the chrono-species are jointly referred to as the lineage Biwa *Stephanodiscus* following Saito-Kato et al. (2015) who provided original morphometric data for this study. Valve diameters were measured at 1,000 $\times$  magnification in the light microscope using an optical micrometre with 0.5  $\mu\text{m}$  precision. The time series consists of 229 samples spanning a time interval of 238,000 years. The average (median) time interval separating the sedimentary horizons is 1,045 years (median = 796 years), and size was measured on 11–50 randomly selected specimens (mean = 47, median = 50) in each horizon.

### Models of trait evolution

We fitted models of within-lineage evolution to each time series that differ in their assumptions regarding the dynamics

of the adaptive landscape. Some of the models assume a constant adaptive landscape, while other models allow continuous or sudden changes in the position of peaks (Figure 1). Models assuming a fixed adaptive landscape include stasis (white noise), unbiased random walk, biased random walk, and an Ornstein–Uhlenbeck (OU) process with a fixed optimum and were fitted using the paleoTS R package (Hunt, 2006, 2008; Hunt et al., 2008, 2015). We used the evoTS R package (Voje, 2023) to fit models that allow the adaptive landscape to change. These models include OU models, where the position of the adaptive peak continuously changes through a random walk or where fixed peaks experience sudden shifts in position. Both datasets were log-transformed prior to model fitting.

The stasis model describes stationary trait dynamics where a trait fluctuates with a variance ( $\omega$ ) around an optimal/central phenotype ( $\theta$ ), basically a white noise process with uncorrelated normally distributed trait values around the fixed mean through time (Hunt, 2006; Sheets & Mitchell, 2001). The unbiased random walk model portrays random changes in the trait mean across time. Evolutionary steps are drawn from a normal distribution (a step distribution) with a mean equal to zero ( $\mu = 0$ ), where the variance ( $\sigma^2$ ) describes the rate of evolution per discrete time step (Hunt, 2006). The expected difference between ancestor and descendant populations according to this model is therefore normally distributed with a zero mean and a variance of  $t\sigma^2$ , where  $t$  is

the number of discrete time steps separating the two populations. The unbiased random walk model is a special case of the general (biased) random walk as the latter allows the mean of the step distribution to be different from zero ( $\mu \neq 0$ ) (Hunt, 2006). The mean of the step distribution reflects the expected direction of evolution per time step, while  $\sigma^2$  represents the stochastic fluctuations around the trend. The OU model contains a deterministic and a stochastic part, where the former represents adaptation at a rate of  $\alpha$  towards an optimal trait value ( $\theta$ ) and where the latter is a white noise process where the fluctuations around the adaptive trend are given by a variance parameter  $\sigma^2$  (Hansen, 1997; Hunt et al., 2008). The optimal trait value is fixed in the OU model implemented in paleoTS but is allowed to change according to an unbiased random walk in evoTS (Hansen et al., 2008; Voje, 2023). The trait value at time zero ( $z_0$ ) can either be assumed to be approximately equal to the ancestral optimum ( $z_0 \approx \theta_0$ ), or the ancestral state of the optimum is estimated as a free parameter. A common way to reparameterize the rate of adaptation ( $\alpha$ ) in the OU model is to calculate its half-life, represented as  $\ln(2)/\alpha$ , which is defined as the time it takes for the trait to move halfway from the ancestral state to the optimum. The stationary variance,  $\sigma^2/(2\alpha)$ , represents the equilibrium variance of the OU process (Hansen et al. 2008) and describes the variance expected in the trait after it has reached the optimum. We also fitted two mode-shift models to each time series. The first model involved fitting two separate OU models, each with their own fixed optimum, to two separate segments of the time series. The second mode-shift model involved fitting two separate unbiased random walk models to each segment. In both cases, we considered all possible switch points in each time series, provided that the shortest segment consisted of at least 10 samples.

All fitted models assume that the sample means in a sequence of ancestor-descendants have a joint distribution that is multivariate normal with an expected mean vector and covariance matrix that are functions of the parameters of each model, the time intervals separating the samples in the sequence, and the sampling variances of the trait means calculated for each sample. Given the assumption of multivariate normality of sample means, their expected distribution is given by their first, second, and mixed moments (covariance). Note that multivariate here refers to multiple samples within a sequence, not multiple phenotypic traits. Also, it is the trait means that are assumed to be normally distributed, while no assumption is made about how traits themselves are distributed within each sample. The expected distribution of differences between samples in a time series allows for the computation of the likelihood for a set of parameter estimates in the evolutionary models when fitted to an empirical dataset. Time from the first to last sample in the time series was scaled to unit length before fitting the models to ease parameter estimation and interpretation of model parameters. Estimation (sampling) error of sample means contributes to the expected variance between sample means. Estimation error was taken into account by adding the population sample variance divided by the number of measured specimens for that sample to the diagonal of the variance–covariance matrix (Hunt, 2006). To account for variation in model complexity in the different candidate models, we estimated relative model fit using the small sample-corrected version of the AICc (Akaike, 1974). We also calculated Akaike weights, which are standardized AICc scores such that scores across

all candidate models sum to unity (Wagenmakers & Farrell, 2004). AICc weights correspond to the relative likelihood of each of the candidate models. The model with the lowest AICc value shows the best relative fit, with the degree of support quantified by Akaike weights. We obtain estimates of uncertainty in all model parameters from the square root of the inverse of the diagonal of the Hessian matrix. For the models showing the best relative fit to each of the two data sets, we used evoTS (Voje, 2023) to calculate support sets, defined here as the values of the parameters that are within two units of support relative to the best (maximum-likelihood) estimate (Edwards, 1992).

### Assessing model adequacy

Measures of relative model fit (e.g., AIC) cannot assess to what extent a model adequately describes the data (see, e.g., Pennell et al., 2015). One model among a set of candidates will always be best according to a relative model fit criterion, but that does not mean it is appropriate for the data in the sense that it represents a good statistical explanation of the evolution of the trait. We applied two tests to investigate whether the model showing the best relative model fit also represents an adequate statistical representation of the trait dynamics in the time series (Voje, 2018; Voje et al., 2018). The procedure for assessing model adequacy followed here evaluates how likely it is that a particular model X with parameters Y can produce trait dynamics similar to what is observed in a time series Z. This is assessed by a parametric bootstrap approach: The model passes the adequacy test if the test statistic calculated on the real data falls inside 95% of the calculated test statistic on the simulated time series. The two tests we applied investigate whether the data contain the expected levels of autocorrelation and the number of runs (one run is a sequence of consecutive numbers with the same sign on the residuals from the expected trait value) under the assumption that the observed trait dynamics are generated by a given model. A detailed description of the parametric bootstrap procedure to assess model adequacy of phyletic models can be found in Voje (2018). Data and R scripts for replicating all analyses are available in the [Supplementary Material](#).

## Results

### Trait dynamics in *Cyclostephanos andinus*

The two best models describing the trait dynamics in *C. andinus* are both OU models with an optimum that is constantly changing according to an unbiased random walk process (Table 1; Figure 2). The only difference between the two best models is the assumption of whether the ancestral trait state is close to the optimal state or not at the beginning of the time series. The former has the lowest (best) AICc score for the *C. andinus* data. The highest-ranked OU model successfully passed both adequacy tests, which examined whether the level of autocorrelation and the number of runs in the data align with data generated by an OU process. This outcome increases our confidence in considering the highest-ranked OU model as an appropriate statistical representation of the trait dynamics in the lineage (Supplementary Figure S1). The life cycle of diatoms results in a diminution of valve size, which results in a right-skewed size distribution. Applying the same evolution models to a dataset comprising only 20% of the largest individuals per sample yielded comparable results regarding relative model fit. This finding suggests that sampling error

**Table 1.** Relative model fit of candidate models.

Model	# of parameters	<i>Cyclostephanos andinus</i>		<i>Biwa Stephanodiscus</i>	
		AICc	AICc weight	AICc	AICc weight
Stasis (white noise)	2	133.363	0.000	13.075	0.000
Unbiased Random Walk	2	-65.032	0.000	-229.856	0.000
General Random Walk	3	-63.009	0.000	-227.842	0.000
Ornstein–Uhlenbeck fixed optimum	4	-97.942	0.000	-236.723	0.000
Ornstein–Uhlenbeck evolving optimum	4	<b>-153.573</b>	1.000	-265.666	0.000
Ornstein–Uhlenbeck evolving optimum*	5	-137.172	0.000	-263.576	0.000
<i>Two Unbiased Random Walks</i>	4	-77.385	0.000	-267.610	0.000
<i>Ornstein–Uhlenbeck two fixed optima</i>	8	-114.937	0.000	<b>-289.521</b>	1.000

Note. AICc = small sample-corrected Akaike information criterion. # of param = number of parameters in the model. Model names in italics are mode-shift models, meaning two separate segments of the time series are described by different parameterizations of the same model. The best models are given in bold.

among individuals at different stages of the life cycle did not contribute significantly to the main analysis results, thus further strengthening the interpretation of adaptation towards a continuously moving optimum ([Supplementary Figure S2](#)).

The average percent change in size between consecutive samples in *C. andinus* is 16.16% ([Table 2](#); [Figure 2B](#); see [Supplementary Figure S3](#) for a similar plot of rates of change). The variance of the step distribution that defines the rate of change in the optimum is  $2.53 \log (\mu\text{m})^2$  when the time interval of the time series is scaled to unit length, which means the adaptive peak shows high volatility across the studied time interval ([Table 2](#)). The point estimate for the time it takes for the ancestral trait state to evolve halfway towards the constantly changing position of the optimum is 12 years, and immediate adaptation (half-life = 0) cannot be excluded based on the confidence region of the parameter describing the rate of evolution towards the optimum ([Figure 2C](#)). The equilibrium variance of the stochastic trait changes around the optimum is  $0.015 \log (\text{micrometre})^2$ , which is comparably small relative to the observed variance in the optimum. It is, therefore, the deterministic part of the OU process—the tracking of the constantly moving optimum—that dominates the evolutionary dynamics of the trait. Given the random movement of the optimum, a pure unbiased random walk model might have been expected to explain the trait dynamics well. The reason why the OU model does much better in comparison to the unbiased random walk is because of the size of the fluctuations around the optimum, which is sufficiently large not to be accounted for by measurement error in the samples. Not controlling for error in the samples would, therefore, unduly favour the unbiased random walk instead of the OU process. The trait dynamics is therefore compatible with a process of rapid trait adaptation to a quickly and randomly moving optimum.

### Trait dynamics in *Biwa Stephanodiscus*

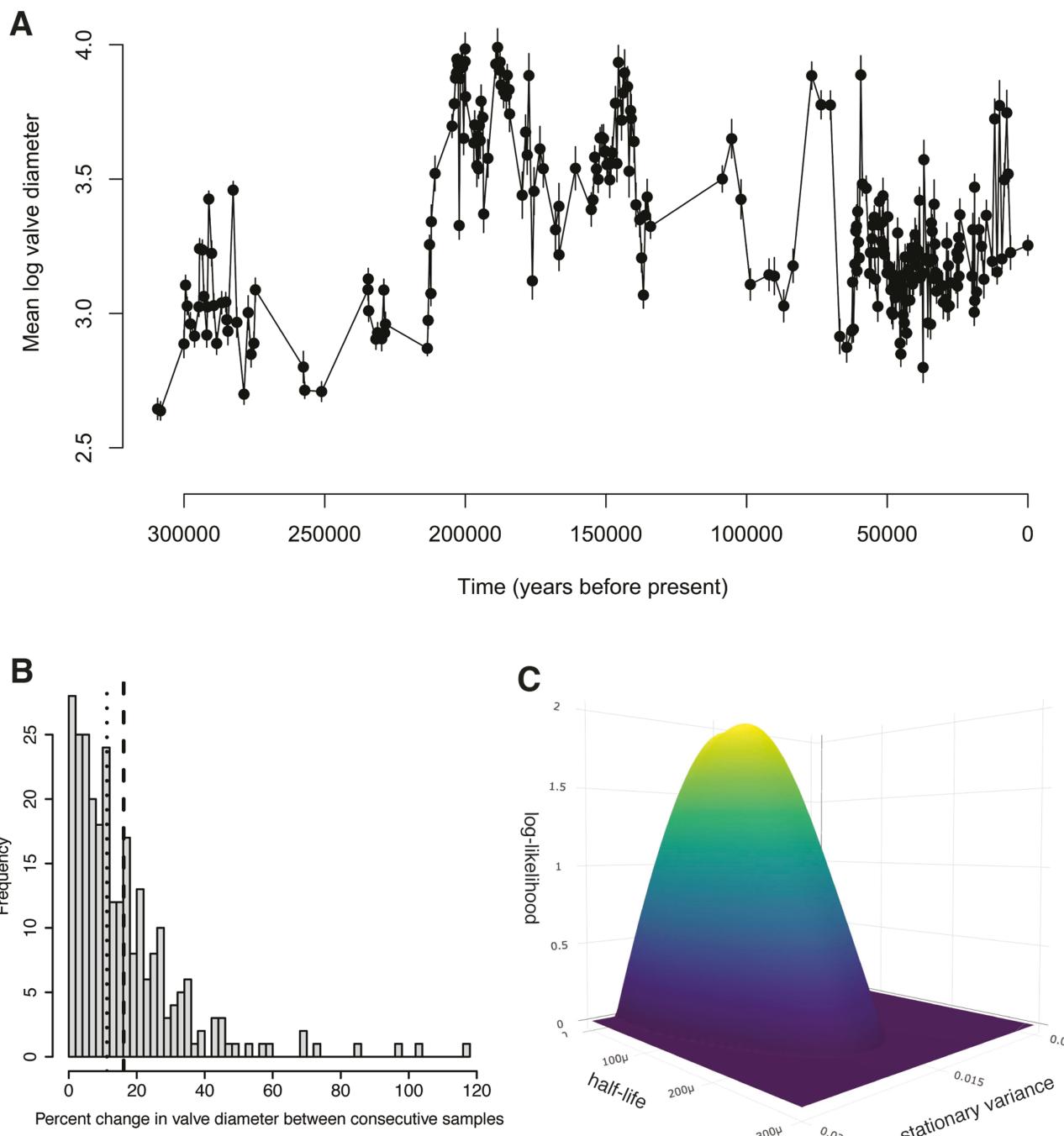
An OU model with a fixed optimum that “jumps” to a new fixed position fitted the *Biwa Stephanodiscus* data best ([Table 1](#); [Figure 3](#)). The adaptive peak is, therefore, not constantly changing its position as in the model describing the trait dynamics in *C. andinus*, but abruptly changes its position around 120,000 years after the start of the time series. The peak change equates to a change of  $0.41 \log (\mu\text{m})$  in the optimal value, which is equivalent to a 50% change (increase) in size

on the original (non-logarithmic) scale. The adequacy of the OU model was assessed using the same adequacy test applied to *C. andinus*. The data passed both tests ([Supplementary Figure S4](#)). Re-fitting all models to a dataset consisting of the 20% largest individuals in each sample shows that the same trait dynamics are detected for this “extreme” dataset, indicating sampling error of individuals at different stages in the life cycle is not driving the result ([Supplementary Figure S5](#)).

Evolution is slower in *Biwa Stephanodiscus* compared to *C. andinus*. The average percent change in size between consecutive samples is 11.96%. During the 13,000 years that span the time from when the position of the peak changed until the lineage reached the new optimum, there is no evidence to suggest that evolution occurred at a faster rate compared to the amount and pace of evolution around the fixed peaks ([Figure 4A](#), see [Supplementary Figure S6](#) for a comparison of rates of change). However, the rate of adaptation differs before and after the change in the optimum ([Table 2](#)). The half-lives are 1737 (95% CI: 715–2,694) and 675 (95% CI: 477–1,811) years before and after the shift in the position of the peak, respectively ([Figure 4B](#) and C). Immediate adaptation can be excluded as a likely scenario, suggesting some type of constraints may prevent very rapid adaptation. The stationary (equilibrium) variance is  $0.007 \log (\text{micrometre})^2$  and  $0.021 \log (\text{micrometre})^2$  for the two parts of the time series, respectively, suggesting a threefold increase in factors like drift and indirect selection on the trait dynamics in the time period after the change in the optimum. These equilibrium variances can be interpreted as the width of the adaptive zone the lineage is inhabiting before and after the change in the position of the peak. The width of the first adaptive zone is accordingly almost half as wide (standard deviation = 8.3% change in the trait mean) as the width of the adaptive zone the lineage is evolving into after the peak shift (standard deviation = 14.5% change in the trait mean).

### Discussion

Size evolution in *C. andinus* and in *Biwa Stephanodiscus* across some hundred thousand years are compatible with observations of evolution on both generational and macroevolutionary timescales. A large body of theoretical and empirical insight from evolutionary quantitative genetics suggests selection on phenotypic traits generally is “strong,



**Figure 2.** (A) Mean log valve-face diameter of the *Cyclostephanos andinus* lineage across 320,000 years. Vertical lines represent one standard deviation of the mean trait. (B) The percent change in the size of *C. andinus* between consecutive samples. The dotted and broken vertical lines represent the median (11.22%) and average (16.16%) change between consecutive sample means, respectively. (C) The log-likelihood support surface for the half-life and the stationary (equilibrium) variance parameter. The best estimate of the half-life is equivalent to 12 years, while the best estimate for the stationary (equilibrium) variance is 0.015 (Table 2).

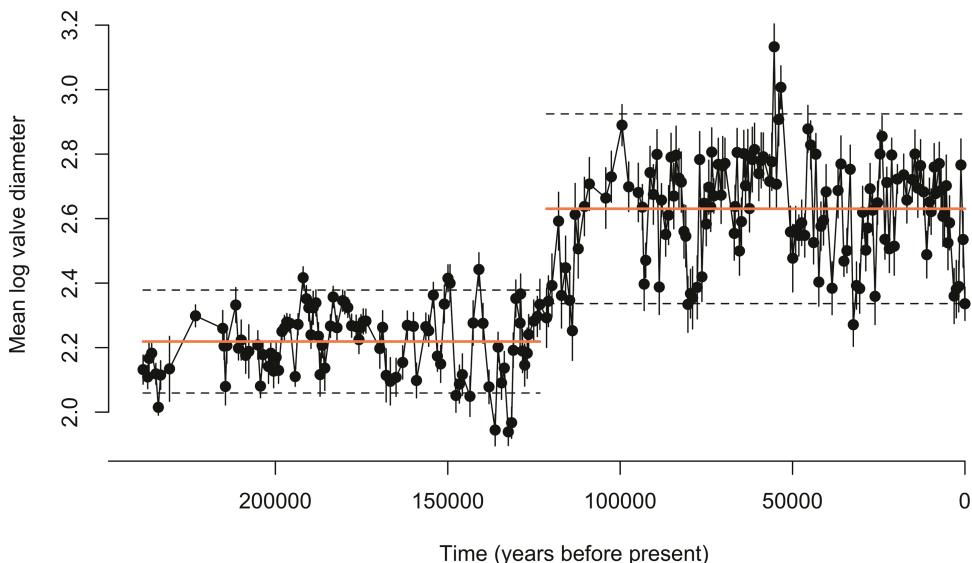
directional and fluctuating on short time scales” (Hansen, 2023, pp. 96). The rapid tracking of the volatile adaptive peak in the *C. andinus* lineage is in accordance with these observations. The size evolution in Biwa *Stephanodiscus* is less erratic in comparison, but fluctuations around the optimum cover distances in phenotype space that are much larger than what can be explained by sampling error alone and can potentially be explained by strong and temporarily fluctuating selection. Neither of the two lineages reside at their local adaptive peak but instead constantly find themselves

displaced from their optimum. Maladaptation, in the sense of being displaced from the peak in the adaptive landscape, is therefore a frequent state in both lineages, an observation overlapping well with the common detection of maladaptation in microevolutionary studies (e.g., Brady et al., 2019b, 2019a; Crespi, 2000). Based on a large-scale analysis of selection coefficients, the majority of populations deviated more than one standard deviation from the estimated optimum for 64% of the cases, and this deviation was more than two standard deviations in about one-third of the investigated

**Table 2.** Maximum-likelihood parameter estimates for the best models.

Model	Dataset	$z_0$	$\sigma^2_{\theta_i}$	$\theta_1$	$\alpha_1$
OU—two fixed optima	<i>C. andinus</i>	2.104 ( $\pm 0.092$ )	1.872 ( $\pm 0.901$ )	2.219 ( $\pm 0.016$ )	146.917 ( $\pm 66.063$ )
		$\sigma^2_{\theta_2}$	$\theta_2$	$\alpha_2$	shift
		8.044 ( $\pm 2.131$ )	2.631 ( $\pm 0.023$ )	185.965 ( $\pm 51.691$ )	97
OU—changing optimum	<i>Biwa Stephanodiscus</i>	$z_0/\theta_0$	$\sigma^2_z$	$\sigma^2_{\theta_0}$	$\alpha$
		2.645 ( $\pm 0.057$ )	2152.526 ( $\pm 298.730$ )	2.532 ( $\pm 0.627$ )	73318.010 ( $\pm 1498.604$ )

**Note.** The parameters are the ancestral trait value at the start of the fossil sequence ( $z_0$ ), the position of the adaptive peak in phenotype space in segment  $i$  of the time series ( $\theta_i$ ), the step variance of the trait in segment  $i$  of the time series ( $\sigma^2_{\theta_i}$ ), the strength of the pull towards the optimum in segment  $i$  ( $\alpha_i$ ), the sample in the time series where the shift in optimum happens (shift), the ancestral state of the optimum at time 0 ( $\theta_0$ ), the step variance of the trait ( $\sigma^2_z$ ), the step variance of the moving optimum ( $\sigma^2_{\theta_0}$ ). The numbers in parentheses are standard errors calculated from the square root of the inverse of the diagonal of the Hessian matrix. OU = Ornstein–Uhlenbeck model.

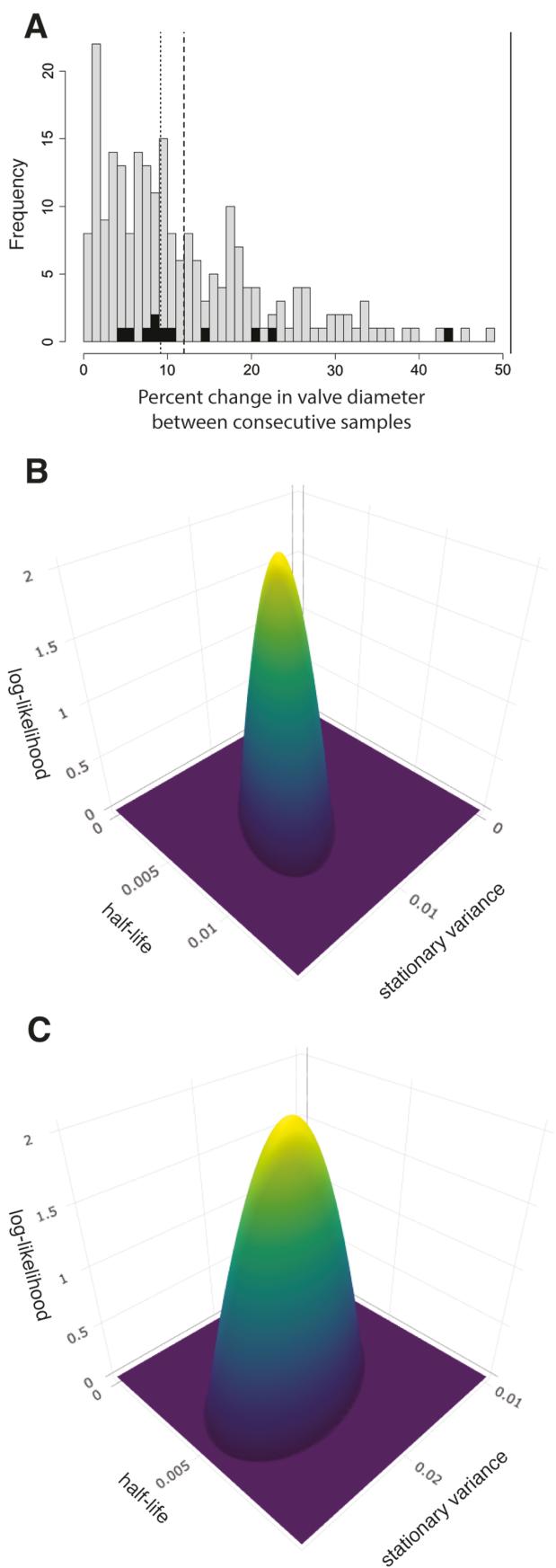


**Figure 3.** Mean log valve diameter of the *Biwa Stephanodiscus* lineage across 240,000 years. Vertical lines represent one standard deviation of the mean trait. The best model fitting the data is an Ornstein–Uhlenbeck model, where the size optimum (horizontal line) changes its position in the adaptive landscape approximately 123,000 years before present. The broken horizontal lines represent two times the standard deviation (based on the equilibrium variance of the Ornstein–Uhlenbeck process, see *Materials and methods* section) around the optimum and can be interpreted as an estimate of the width of the adaptive zone.

populations (Estes & Arnold, 2007; see also Lisle et al., 2020). Typical observations from microevolutionary studies are therefore present throughout the evolutionary time series in both the investigated lineages. Plasticity is an important explanation for phenotypic change in many contemporary species (e.g., Stamp & Hadfield, 2020), and we consider it likely that parts of the phenotypic changes across samples in both diatom lineages are due to plasticity (e.g., Kamakura et al., 2022; Toseland et al., 2013). However, size in diatoms is at least partly under genetic control (Kirkham et al., 2017), and diatoms are often characterized by a substantial within-population genetic variation (Godhe & Rynearson, 2017), which lends support to the claim that at least part of the changes in size observed across the timespan of a few hundred thousand years in *Biwa Stephanodiscus* and *C. andinus* are due to evolution.

The observed evolution in the two lineages deviates from common patterns or models of phenotypic change beyond generational timescales. Neither lineage follows the stationary pattern (fluctuations around a fixed optimum) that has been found to be the overall mode of evolution when compilations

of data on phenotypic change up to a few million years are jointly analyzed (Estes & Arnold, 2007; Gingerich, 1993, 2001). *C. andinus* evolves on a randomly changing adaptive landscape, while *Biwa Stephanodiscus* evolves on a landscape that experienced a substantial and sudden change. The observed evolution does also not support the Punctuated Equilibrium model, where within-lineage evolution is dominated by stasis (a form of stationary trait change), with bursts of change in connection with lineage-splitting (speciation) events (Eldredge & Gould, 1972; Gould & Eldredge, 1977; Stanley, 1975). The rapid tracking of a random and constantly changing optimum in *C. andinus* aligns poorly with stasis, and also, the net evolution is large across various time intervals during the sequence. *Biwa Stephanodiscus* shows substantial evolution between samples, and evolution towards the new position of the optimum is anagenesis and not a cladogenetic event. Even if the change of the optimum represents a lineage-splitting event in *Biwa Stephanodiscus*, the pace of evolution is not more rapid during the re-adaptation phase compared to the rest of the within-lineage trait dynamics.

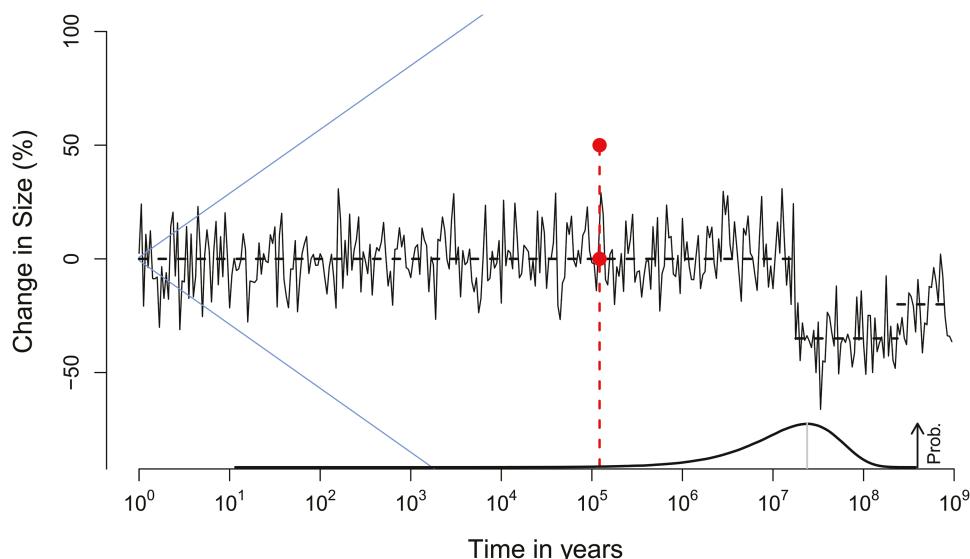


**Figure 4.** (A) The percent change in the size of Biwa *Stephanodiscus* between consecutive samples. Black represents changes in the trait mean between consecutive samples from the time the optimum

A different explanation for macroevolutionary change is the “blunderbuss” model in Uyeda et al. (2011), where trait dynamics are stationary within wide limits with substantial bursts of change happening with an average waiting time of 25 million years. Although the observed evolution in *C. andinus* and Biwa *Stephanodiscus* show some similarity to the blunderbuss model, it also deviates from it on two important accounts (Figure 5). First, the optimum tracked by *C. andinus* is found to evolve randomly (modelled as a random walk), which means the evolutionary dynamics are not stationary in the sense documented by Uyeda et al. (2011). The variance of a random walk process scales linearly with time, which means trends towards increased trait divergence are likely for lineages evolving according to this model. It is reasonable to argue that the movements of the optimum are probably more bounded on million-year timescales than what a model of random change predicts (Holstad et al. 2024). However, and independent of the exact dynamics of the adaptive peak, the amount of evolution in the *C. andinus* lineage is much larger than what is predicted by the blunderbuss model. For example, in less than 50,000 years, the size increased by a factor of four, which is far outside the predicted limits of the bounded evolution in Uyeda et al.’s (2011) blunderbuss model. Also, Biwa *Stephanodiscus* experienced changes that exceeded expectations from the blunderbuss model. The shift in the size optimum for Biwa *Stephanodiscus* happens after about 120,000 years since the start of the time series, in contrast to the average waiting time of 25 million years in the blunderbuss model. Simulating a Poisson process 100,000 times using the parameter estimates from the waiting time in the blunderbuss model (Uyeda et al. 2011) indicates that a burst this rapid has a probability of 0.41%. Furthermore, the average change in the position of the peak in the blunderbuss model represents a 27% change in the trait mean, while the peak shift in the case of Biwa *Stephanodiscus* represents a 50% change in the trait on the original scale (Figure 5). It is worth noting that only size data in vertebrates were analyzed by Uyeda et al. (2011), so it is possible that the dynamics predicted by the blunderbuss model only apply to vertebrates. However, it is also possible that large-scale changes in the adaptive landscape might be more common than the blunderbuss model suggests.

Utilizing fossil time series data for the analysis of changes, or the absence of changes, in the adaptive landscape presents a promising avenue for gaining knowledge about evolutionary dynamics across different timescales. However, a shortcoming of the current work is that the causal factors responsible for changing the adaptive landscape in the two datasets are unknown. It has been suggested that regional environmental change, including tectonically driven basin evolution and glacial-interglacial cycles, drove lake level changes and alterations in thermal stratification in Lake Titicaca (Fritz et al.,

changes its position until the trait has reached the new optimum, i.e., the data points between about 123,000 to 110,000 years on the x-axis in Figure 3. The rightmost vertical line represents the change in optimal size before and after the change in the optimum in Figure 3. The dotted and broken vertical lines represent the median (9.17%) and average (11.96%) change between consecutive sample means. (B and C) The log-likelihood support surface for the half-life and the stationary (equilibrium) variance parameters before (B) and after (C) the position of the optimum changes its position. Immediate adaptation can be excluded as a likely scenario for both segments, as the support surfaces do not contain a half-life of zero. See Table 2 for parameter estimates.



**Figure 5.** The figure shows an expected pattern of phenotypic trait evolution according to the blunderbuss model (black, wiggly line) Uyeda et al. (2011). Stationary trait dynamics modelled as a white noise process is the dominant mode of evolution. The standard deviation of the white noise process is 9.6% trait change, which can be interpreted as the average width of an adaptive zone (*sensu* Simpson, 1944). The broken horizontal lines represent the average trait value for the white noise process, i.e., the average position of the adaptive peak during the stationary trait dynamics. Large and more permanent changes in the adaptive peak happen according to a Poisson process with a probability distribution shown along the x-axis, where the average waiting time for a large and permanent change is about 25 million years (grey vertical line). The x-axis is time in millions of years on a  $\log_{10}$  scale. The trait evolution shown has two large and permanent changes in the peak. The two solid (blue) lines show the 95% confidence interval of the movement of the adaptive peak in the model fitted to the *C. andinus* time series, which suggests the peak can rapidly move outside the range of bounded stationary peak movements suggested by the blunderbuss model. The lower and upper dots indicate the magnitude of the sudden change in the position of the adaptive peak in the best model for the *S. biwa* dataset. The change in the peak happens at a time when the blunderbuss model gives a 0.41% probability of observing a major change in the adaptive landscape (broken vertical line).

2012), which may have affected the size optimum in *C. andinus* (Spanbauer et al., 2018). Whether these factors alone are sufficient to explain the random fluctuations in the position of the optimum remains unknown, however, as an optimum changing in a random fashion is also compatible with being influenced by a large number of stochastic factors, which together combine to generate random changes in the optimum across time (Hansen et al., 2008). In the case of Biwa *Stephanodiscus*, it has been suggested that changes in temperature, particularly the transitions from a cold to a warm climate at the onset of the last interglacial period, influenced the size evolution within this lineage (Saito-Kato et al., 2015). However, similar size change did not happen during the latest climate transition from the last glacial period to the Holocene interglacial period during the studied interval, indicating these types of climate change cannot be the only explanation for the rapid and large shift in the adaptive landscape of the Biwa *Stephanodiscus* lineage. Multivariate models allowing changes in the adaptive landscape to be parameterized based on empirical data are available (Reitan & Liow, 2019; Voje, 2023), but such data are not currently available for the two datasets analyzed here.

Independently of the causal factors causing the adaptive landscapes to change, trait evolution in both *C. andinus* and Biwa *Stephanodiscus* exemplifies how large changes in phenotypes can happen, either due to the accumulation of continuous changes in the position of adaptive peaks or through sudden and large shifts in the position of adaptive peaks. Interestingly, if gradual and more pulsed changes in the position of peaks are random, they will generate the often observed phylogenetic signal among species in comparative data (Hansen, 2012, 2024). Since both lineages also show

clear signs of common microevolutionary observations (rapid and erratic evolution, maladaptation), the trait dynamics estimated in the two lineages can be interpreted as “chimeric,” containing elements of both micro- and macroevolution. Evolution in fossil time series thus has the potential to reconcile observations of phenotypic change across disparate timescales and may contribute to a more comprehensive quantitative theory of phenotypic change across different parts of the timescale continuum.

## Supplementary material

Supplementary material is available at *Journal of Evolutionary Biology* online.

## Data availability

All necessary data and R code to replicate our results have been uploaded to DRYAD: <https://doi.org/10.5061/dryad.bk3j9kdmj>.

## Author contributions

Kjetil Lysne Voje (Conceptualization [lead], Formal analysis [lead], Funding acquisition [lead], Investigation [lead], Methodology [lead], Project administration [lead], Visualization [lead], Writing—original draft [lead], Writing—review & editing [lead]), Megumi Saito-Kato (Data curation [lead], Investigation [equal], Methodology [supporting], Validation [supporting], Visualization [supporting], Writing—original draft [equal], Writing—review & editing [equal]), and Trisha Spanbauer (Data curation [lead], Investigation

[equal], Methodology [supporting], Validation [supporting], Visualization [supporting], Writing—original draft [equal], Writing—review & editing [equal])

## Funding

This study was partly supported by Grant-in-Aid for Scientific Research (C) 17K05695 to M.S.-K. This material is based upon work supported by the National Science Foundation under Grant No. 1625040 and Grant No. 1251678 to T.L.S. The work was also supported by an ERC–2020-STG to K.L.V. (grant agreement ID: 948465).

## Conflicts of interest

None declared.

## References

- Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, 19(6), 716–723. <https://doi.org/10.1109/TAC.1974.1100705>
- Armbrust, E. V. (2009). The life of diatoms in the world's oceans. *Nature*, 459(7244), 185–192. <https://doi.org/10.1038/nature08057>
- Arnold, S. J. (2014). Phenotypic evolution: The ongoing synthesis: (American Society of Naturalists Address). *The American Naturalist*, 183(6), 729–746. <https://doi.org/10.1086/675304>
- Arnold, S. J., Pfrender, M. E., & Jones, A. G. (2001). The adaptive landscape as a conceptual bridge between micro- and macroevolution. *Genetica*, 112–113, 9–32.
- Ashton, K. G. (2004). Comparing phylogenetic signal in intra-specific and interspecific body size datasets. *Journal of Evolutionary Biology*, 17(5), 1157–1161. <https://doi.org/10.1111/j.1420-9101.2004.00764.x>
- Beaulieu, J. M., Jhwueng, D., Boettiger, C., & O'Meara, B. C. (2012). Modeling stabilizing selection: Expanding the Ornstein-Uhlenbeck model of adaptive evolution. *Evolution*, 66(8), 2369–2383. <https://doi.org/10.1111/j.1558-5646.2012.01619.x>
- Bolstad, G. H., Hansen, T. F., Pélabon, C., ... Armbruster, W. S. (2014). Genetic constraints predict evolutionary divergence in *Dalechampia blossoms*. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 369(1649), 20130255. <https://doi.org/10.1098/rstb.2013.0255>
- Brady, S. P., Bolnick, D. I., Angert, A. L., ... Hendry, A. P. (2019a). Causes of maladaptation. *Evolutionary Applications*, 12(7), 1229–1242. <https://doi.org/10.1111/eva.12844>
- Brady, S. P., Bolnick, D. I., Barrett, R. D. H., ... Hendry, H. (2019b). Understanding maladaptation by uniting ecological and evolutionary perspectives. *The American Naturalist*, 194, 495–515.
- Butler, M. A., & King, A. A. (2004). Phylogenetic comparative analysis: A modeling approach for adaptive evolution. *The American Naturalist*, 164(6), 683–695. <https://doi.org/10.1086/426002>
- Charnov, E. L. (1993). *Life history invariants*. Oxford University Press.
- Cohen, A. S. (2012). Scientific drilling and biological evolution in ancient lakes: Lessons learned and recommendations for the future. *Hydrobiologia*, 682(1), 3–25. <https://doi.org/10.1007/s10750-010-0546-7>
- Crespi, B. J. (2000). The evolution of maladaptation. *Heredity*, 84(Pt 6), 623–629. <https://doi.org/10.1046/j.1365-2540.2000.00746.x>
- Danhara, T., Yamashita, T., Iwano, H., ... Hayashida, A. (2010). Chronology of the 1400-m core obtained from Lake Biwa in 1982–1983: Re-investigation of fission-track ages and tephra identification. *The Quaternary Research (Daiyonki-Kenkyu)*, 49(3), 101–119. <https://doi.org/10.4116/jaqua.49.101>
- Edwards, A. W. F. (1992). *Likelihood: Expanded edition*. Johns Hopkins.
- Eldredge, N., & Gould, S. J. (1972). Punctuated equilibria: An alternative to phyletic gradualism. In Schopf T. J. M. (Ed.), *Models in paleobiology* (pp. 82–115). Freeman Cooper.
- Estes, S., & Arnold, S. J. (2007). Resolving the paradox of stasis: Models with stabilizing selection explain evolutionary divergence on all timescales. *The American Naturalist*, 169(2), 227–244. <https://doi.org/10.1086/510633>
- Falkowski, P. G., Barber, R. T., & Smetacek, V. (1998). Biogeochemical controls and feedbacks on ocean primary production. *Science*, 281(5374), 200–207. <https://doi.org/10.1126/science.281.5374.200>
- Freckleton, R. P., Harvey, P. H., & Pagel, M. (2002). Phylogenetic analysis and comparative data: A test and review of evidence. *The American Naturalist*, 160(6), 712–726. <https://doi.org/10.1086/343873>
- Fritz, S. C., Baker, P. A., Seltzer, G. O., ... Edwards, R. L. (2007). Quaternary glaciation and hydrologic variation in the South American tropics as reconstructed from the Lake Titicaca drilling project. *Quaternary Research*, 68(3), 410–420. <https://doi.org/10.1016/j.yqres.2007.07.008>
- Fritz, S. C., Baker, P. A., Tapia, P., ... Westover, K. (2012). Evolution of the Lake Titicaca basin and its diatom flora over the last ~370,000 years. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 317–318, 93–103. <https://doi.org/10.1016/j.palaeo.2011.12.013>
- Gingerich, P. D. (1983). Rates of evolution: Effects of time and temporal scaling. *Science*, 222(4620), 159–161. <https://doi.org/10.1126/science.222.4620.159>
- Gingerich, P. D. (2001). Rates of evolution on the time scale of the evolutionary process. *Genetica*, 112–113, 127–144.
- Godhe, A., & Rynearson, T. (2017). The role of intraspecific variation in the ecological and evolutionary success of diatoms in changing environments. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 372(1728), 20160399. <https://doi.org/10.1098/rstb.2016.0399>
- Gould, S. J. (1980). The promise of paleobiology as a nomothetic, evolutionary discipline. *Paleobiology*, 6(1), 96–118. <https://doi.org/10.1017/s0094837300012537>
- Gould, S. J. (1985). The paradox of the first tier: An agenda for paleobiology. *Paleobiology*, 11(1), 2–12. <https://doi.org/10.1017/s0094837300011350>
- Gould, S. J., & Eldredge, N. (1977). Punctuated equilibria: The tempo and mode of evolution reconsidered. *Paleobiology*, 3(2), 115–151. <https://doi.org/10.1017/s0094837300005224>
- Hansen, T. F. (1997). Stabilizing selection and the comparative analysis of adaptation. *Evolution*, 51(5), 1341–1351. <https://doi.org/10.1111/j.1558-5646.1997.tb01457.x>
- Hansen, T. F. (2012). Adaptive landscapes and macroevolutionary dynamics. In I. E. Svensson, & R. Calsbeek (Eds.), *The adaptive landscape in evolutionary biology* (pp. 205–226). Oxford: Oxford University Press.
- Hansen, T. F. (2023). Variation, inheritance, and evolution: A primer on evolutionary quantitative genetics. In T. F. Hansen, D. Houle, M. Pavlicev, & C. Pélabon (Eds.), *Evolvability: A unifying concept in evolutionary biology?* (pp. 73–100). MIT Press.
- Hansen, T. F. (2024). Three modes of evolution? Remarks on rates of evolution and time scaling. *Journal of Evolutionary Biology*, 37(12), 1523–1537. <https://doi.org/10.1093/jeb/voae071>
- Hansen, T. F., & Pélabon, C. (2021). Evolvability: A quantitative-genetics perspective. *Annual Review of Ecology, Evolution, and Systematics*, 52(1), 153–175. <https://doi.org/10.1146/annurev-ecolsys-011121-021241>
- Hansen, T. F., Pienaar, J., & Orzack, S. H. (2008). A comparative method for studying adaptation to a randomly evolving environment. *Evolution*, 62(8), 1965–1977. <https://doi.org/10.1111/j.1558-5646.2008.00412.x>
- Harmon, L. J., Pennell, M. W., Henao-Díaz, L. F., ... Uyeda, J. C. (2021). Causes and consequences of apparent timescaling across all estimated evolutionary rates. *Annual Review of Ecology, Evolution, and Systematics*, 52(1), 587–609. <https://doi.org/10.1146/annurev-ecolsys-011921-023644>
- Hereford, J., Hansen, T. F., & Houle, D. (2004). Comparing strengths of directional selection: How strong is strong? *Evolution*, 58(10), 2133–2143. <https://doi.org/10.1111/j.0014-3820.2004.tb01592.x>

- Holstad, A., Voje, K. L., Opedal, O. H., ... Pélabon, C. (2024). Evolvability predicts evolutionary divergence in extant and extinct species. *Science*, 384(6696), 688–693. <https://doi.org/10.1126/science.adis8722>
- Hopkins, M. J. & Lidgard, S. (2012). Evolutionary mode routinely varies among morphological traits within fossil species lineages. *Proceedings of the National Academy of Sciences of the United States of America*, 109(50) 20520–20525.
- Houle, D. (1992). Comparing evolvability and variability of quantitative traits. *Genetics*, 130(1), 195–204. <https://doi.org/10.1093/genetics/130.1.195>
- Houle, D., Bolstad, G. H., van der Linde, K., & Hansen, T. F. (2017). Mutation predicts 40 million years of fly wing evolution. *Nature*, 548, 447–450.
- Hunt, G. (2006). Fitting and comparing models of phyletic evolution: Random walks and beyond. *Paleobiology*, 32(4), 578–601. <https://doi.org/10.1666/05070.1>
- Hunt, G. (2007). The relative importance of directional change, random walks, and stasis in the evolution of fossil lineages. *Proceedings of the National Academy of Sciences of the United States of America*, 104(47), 18404–18408.
- Hunt, G. (2008). Gradual or pulsed evolution: When should punctational explanations be preferred? *Paleobiology*, 34(3), 360–377. <https://doi.org/10.1666/07073.1>
- Hunt, G., Bell, M. A., & Travis, M. P. (2008). Evolution toward a new adaptive optimum: Phenotypic evolution in a fossil stickleback lineage. *Evolution*, 62(3), 700–710. <https://doi.org/10.1111/j.1558-5646.2007.00310.x>
- Hunt, G., Hopkins, M. J., & Lidgard, S. (2015). Simple versus complex models of trait evolution and stasis as a response to environmental change. *Proceedings of the National Academy of Sciences of the United States of America*, 112(16), 4885–4890. <https://doi.org/10.1073/pnas.1403662111>
- Ivory, S. J., Blome, M. W., King, J. W., ... Cohen, A. S. (2016). Environmental change explains cichlid adaptive radiation at Lake Malawi over the past 1.2 million years. *Proceedings of the National Academy of Sciences of the United States of America*, 113(42), 11895–11900. <https://doi.org/10.1073/pnas.1611028113>
- Jablonski, D. (2000). Micro- and macroevolution: Scale and hierarchy in evolutionary biology and paleobiology. *Paleobiology*, 26(S4), 15–52. <https://doi.org/10.1017/s0094837300026877>
- Jablonski, D. (2008). Biotic interactions and macroevolution: Extinctions and mismatches across scales and levels. *Evolution*, 62(4), 715–739. <https://doi.org/10.1111/j.1558-5646.2008.00317.x>
- Kamakura, S., Ashworth, M. P., Yamada, K., ... Sato, S. (2022). Morphological plasticity in response to salinity change in the euryhaline diatom *Pleurosira laevis* (Bacillariophyta). *Journal of Phycology*, 58(5), 631–642. <https://doi.org/10.1111/jpy.13277>
- Khursevich, G. K., & Prokopenko, A. A. (2009). Diatom record from Lake Hovsgol, Mongolia, during the last 1 Ma: The results from the HDP-04 drill core. *Quaternary International*, 205(1–2), 84–97. <https://doi.org/10.1016/j.quaint.2009.02.003>
- Kinnison, M. T., & Hendry, A. P. (2001). The pace of modern life II: From rates of contemporary microevolution to pattern and process. *Genetica*, 112–113, 145–164.
- Kirkham, A. R., Richthammer, P., Schmidt, K., ... Mock, T. (2017). A role for the cell-wall protein silacidin in cell size of the diatom *Thalassiosira pseudonana*. *The ISME Journal*, 11(11), 2452–2464. <https://doi.org/10.1038/ismej.2017.100>
- Lande, R. (1979). Quantitative genetic analysis of multivariate evolution, applied to brain: Body size allometry. *Evolution*, 33(1Part2), 402–416. <https://doi.org/10.1111/j.1558-5646.1979.tb04694.x>
- Landis, M. J., & Schraiber, J. G. (2017). Pulsed evolution shaped modern vertebrate body sizes. *Proceedings of the National Academy of Sciences of the United States of America*, 114(50), 13224–13229. <https://doi.org/10.1073/pnas.1710920114>
- Levin, S. A. (1992). The problem of pattern and scale in ecology: The Robert H. MacArthur award lecture. *Ecology*, 73(6), 1943–1967. <https://doi.org/10.2307/1941447>
- Lisle, S. P. D., Punzalan, D., Rollinson, N., & Rowe, L. (2020). Extinction and the temporal distribution of macroevolutionary bursts. *Journal of Evolutionary Biology*, 34, 380–390. <https://doi.org/10.1111/jeb.13741>
- McGlothlin, J. W., Kobiela, M. E., Wright, H. V., ... Brodie, E. D. III (2018). Adaptive radiation along a deeply conserved genetic line of least resistance in *Anolis* lizards. *Evolution Letters*, 2(4), 310–322. <https://doi.org/10.1002/evl3.72>
- McGlothlin, J. W., Kobiela, M. E., Wright, H. V., ... Brodie, E. D. (2022). Conservation and convergence of genetic architecture in the adaptive radiation of *Anolis* lizards. *The American Naturalist*, 200(5), E207–E220. <https://doi.org/10.1086/721091>
- Meyers, P. A., Takemura, K., & Horie, S. (1993). Reinterpretation of late Quaternary sediment chronology of Lake Biwa, Japan, from correlation with marine glacial-interglacial cycles. *Quaternary Research*, 39(2), 154–162. <https://doi.org/10.1006/qres.1993.1019>
- Miyoshi, N., Fujiki, T., & Morita, Y. (1999). Palynology of a 250-m core from Lake Biwa: A 430,000-year record of glacial-interglacial vegetation change in Japan. *Review of Palaeobotany and Palynology*, 104(3–4), 267–283. [https://doi.org/10.1016/s0034-6667\(98\)00058-x](https://doi.org/10.1016/s0034-6667(98)00058-x)
- Nakagawa, T., Okuda, M., Yonenobu, H., ... Horie, S. (2008). Regulation of the monsoon climate by two different orbital rhythms and forcing mechanisms. *Geology*, 36(6), 491–494. <https://doi.org/10.1130/g24586a.1>
- Opedal, O. H., Armbruster, W. S., Hansen, T. F., ... Bolstad, G. H. (2023). Evolvability and trait function predict phenotypic divergence of plant populations. *Proceedings of the National Academy of Sciences of the United States of America*, 120(1), e2203228120. <https://doi.org/10.1073/pnas.2203228120>
- Pennell, M. W., FitzJohn, R. G., Cornwell, W. K., & Harmon, L. J. (2015). Model adequacy and the macroevolution of angiosperm functional traits. *The American Naturalist*, 186(2), E33–E50. <https://doi.org/10.1086/682022>
- Peters, R. H. (1986). *The ecological implications of body size*. Cambridge University Press.
- Reitan, T., & Liow, L. H. (2019). layeranalyzer: Inferring correlative and causal connections from time series data in R. *Methods in Ecology and Evolution*, 10(12), 2183–2188. <https://doi.org/10.1111/2041-210x.13299>
- Rolland, J., Henao-Diaz, L. F., Doebeli, M., ... Schlüter, D. (2023). Conceptual and empirical bridges between micro- and macroevolution. *Nature ecology & Evolution*, 7(8), 1181–1193. <https://doi.org/10.1038/s41559-023-02116-7>
- Sadori, L., Koutsodendris, A., Panagiotopoulos, K., ... Donders, T. H. (2016). Pollen-based paleoenvironmental and paleoclimatic change at Lake Ohrid (south-eastern Europe) during the past 500 ka. *Biogeosciences*, 13, 1423–1437.
- Saito-Kato, M., Tanimura, Y., Mori, S., & Julius, M. L. (2015). Morphological evolution of *Stephanodiscus* (Bacillariophyta) in Lake Biwa from a 300 ka fossil record. *Journal of Micropalaeontology*, 34(2), 165–179. <https://doi.org/10.1144/jmpaleo2014-015>
- Sanderson, S., Beausoleil, M., O'Dea, R. E., ... Hendry, A. P. (2022). The pace of modern life, revisited. *Molecular Ecology*, 31(4), 1028–1043. <https://doi.org/10.1111/mec.16299>
- Schmidt-Nielsen, K. (1984). *Scaling: Why is animal size so important?* Cambridge University Press.
- Sheets, H. D., & Mitchell, C. E. (2001). Why the null matters: Statistical tests, random walks and evolution. *Genetica*, 112–113, 105–125.
- Simpson, G. G. (1944). *Tempo and mode in evolution*. Columbia University Press.
- Spanbauer, T. L., Fritz, S. C., & Baker, P. A. (2018). Punctuated changes in the morphology of an endemic diatom from Lake Titicaca. *Paleobiology*, 44(1), 89–100. <https://doi.org/10.1017/pab.2017.27>
- Stamp, M. A., & Hadfield, J. D. (2020). The relative importance of plasticity versus genetic differentiation in explaining between population differences; a meta-analysis. *Ecology Letters*, 23(10), 1432–1441. <https://doi.org/10.1111/ele.13565>

- Stanley, S. M. (1975). A theory of evolution above the species level. *Proceedings of the National Academy of Sciences of the United States of America*, 72(2), 646–650. <https://doi.org/10.1073/pnas.72.2.646>
- Takemura, K. (2012). The history of Lake Biwa drilling. *PAGES News*, 20(2), 68–69. <https://doi.org/10.22498/pages.20.2.68>
- Tapia, P. M., Theriot, E. C., Fritz, S. C., ... Rivera, P. (2004). Distribution and morphometric analysis of *Cyclostephanos andinus* comb. nov., a planktonic diatom from the Central Andes. *Diatom Research*, 19(2), 311–327. <https://doi.org/10.1080/0269249x.2004.9705877>
- Toseland, A., Daines, S. J., Clark, J. R., ... Mock, T. (2013). The impact of temperature on marine phytoplankton resource allocation and metabolism. *Nature Climate Change*, 3(11), 979–984. <https://doi.org/10.1038/nclimate1989>
- Tuji, A., Mohri, Y., Ki, J. -S., ... Julius, M. L. (2014). Phylogeny of *Praestephanos* gen. nov. (Thalassiosirales, Bacillariophyceae) based on *Stephanodiscus suzukii*, and related freshwater thalassiosiroid diatoms. *Plankton and Benthos Research*, 9(2), 132–140. <https://doi.org/10.3800/pbr.9.132>
- Uyeda, J. C., Hansen, T. F., Arnold, S. J., & Pienaar, J. (2011). The million-year wait for macroevolutionary bursts. *Proceedings of the National Academy of Sciences of the United States of America*, 108(38), 15908–15913. <https://doi.org/10.1073/pnas.1014503108>
- Uyeda, J. C., & Harmon, L. J. (2014). A novel Bayesian method for inferring and interpreting the dynamics of adaptive landscapes from phylogenetic comparative data. *Systematic Biology*, 63(6), 902–918. <https://doi.org/10.1093/sysbio/syu057>
- Voje, K. L. (2016). Tempo does not correlate with mode in the fossil record. *Evolution*, 70(12), 2678–2689. <https://doi.org/10.1111/evo.13090>
- Voje, K. L. (2018). Assessing adequacy of models of phyletic evolution in the fossil record. *Methods in Ecology and Evolution*, 9(12), 2402–2413. <https://doi.org/10.1111/2041-210x.13083>
- Voje, K. L. (2023). Fitting and evaluating univariate and multivariate models of within-lineage evolution. *Paleobiology*, 49(4), 747–764. <https://doi.org/10.1017/pab.2023.10>
- Voje, K. L., Grabowski, M., Holstad, A., ... Bolstad, G. (2023). Does lack of evolvability constrain adaptation? If so, on what time scales? In T. F. Hansen, D. Houle, M. Pavlicev, & C. Pélabon (Eds.), *Evolvability. A unifying concept in evolutionary biology?* The MIT Press.
- Voje, K. L., Starrfelt, J., & Liow, L. H. (2018). Model adequacy and microevolutionary explanations for stasis in the fossil record. *The American Naturalist*, 191(4), 509–523. <https://doi.org/10.1086/696265>
- Wagenmakers, E. -J., & Farrell, S. (2004). AIC model selection using Akaike weights. *Psychonomic Bulletin & Review*, 11(1), 192–196. <https://doi.org/10.3758/bf03206482>
- Wilke, T., Wagner, B., Bocxlaer, B. V., ... Wonik, T. (2016). Scientific drilling projects in ancient lakes: Integrating geological and biological histories. *Global and Planetary Change*, 143, 118–151.