

1 Climatic niches in phylogenetic comparative studies: a review of  
2 challenges and approaches

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4 Running title: Climatic niche in phylogenetic comparative studies

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10 Key words: Climatic niche, phylogenetic comparative studies, ancestral niche reconstruction,  
11 evolutionary models

12 **Abstract** Studying the evolution of climatic niches through time in a phylogenetic  
13 comparative framework combines species distribution modeling with phylogenies.  
14 Phylogenetic comparative studies aid the understanding of the evolution of species'  
15 environmental preferences by revealing the underlying evolutionary processes and causes,  
16 detecting the differences among groups of species or relative to evolutionary pattern of other  
17 phenotypic traits, but also act as a yardstick to gauge the adaptational potential under  
18 climate change. Because several alternatives exist on how to compute and represent the  
19 climatic niche, we here review and discuss the current state of the art and propose a best  
20 practice to use in comparative studies. Moreover we outline the common evolutionary models  
21 and available model-fitting methods and describe the procedure for ancestral niche  
22 reconstruction with the intention to give a broad overview and highlight the most advanced  
23 approaches for optimal niche-related comparative studies.

## 24 Introduction

25

26 Phylogenetic comparative studies use a wide range of methods to explore patterns and  
27 processes linked to phylogenetic trees and species traits (Pennell and Harmon, 2013). These  
28 studies uncover how a certain trait evolves among different taxa, how evolution of one trait  
29 influences another, whether a trait represents adaptation to the environment etc. In this  
30 review we focus exclusively on studies testing hypotheses about species' climatic niches  
31 evolution through phylogeny.

32 The aim of such studies is typically not only to suggest the trajectories of niche evolution,  
33 but rather to test specific hypothesis about the timing of appearance, causation or  
34 evolutionary processes responsible for observed patterns. Such studies aim to discover, for  
35 instance, whether shifts in the climate niche occur at the same time as shifts in a particular  
36 trait (such as C3/C4 photosynthesis: Edwards and Smith, 2010), whether it was a key driver  
37 for developing specific life-histories (e.g. cactus life-form: Edwards and Donoghue, 2006), or  
38 whether temporal and/or spatial fluctuation of climate caused species to evolve and diversify  
39 (Evans et al., 2009). Furthermore, linking climate niche evolution to population demography  
40 through time could reveal whether major niche shifts occur in small or large populations  
41 (Jakob et al., 2010). The analyses are based on current trait values, the phylogenetic  
42 relationship between species and an evolutionary model. Climate niche is treated as if it was a  
43 phenotypic trait and the analysis of, say, temperature values follows the same logic as  
44 evolutionary analysis of body mass. The actual reconstruction of ancestral trait values is  
45 unnecessary for testing correlations between characters. Being an integral part of the  
46 procedure, ancestral states along the phylogeny are implicitly inferred but not actually  
47 presented. However, other hypotheses might require reconstruction of ancestral values, such as  
48 tests of niche overlap between specific ancestral nodes, pinpointing the exact time of  
49 appearance of certain values, identifying reversals in evolutionary progression or visualization  
50 of trait changes through time.

51 Given that understanding the evolution of species' niches through time attracts extensive  
52 interest and is highlighted as a priority research question in paleoecology (Seddon et al.,  
53 2014), we discuss and propose guidelines for optimal use of species distribution and climatic  
54 data in comparative studies.

55 The aim of this review is to (1) introduce the concepts relating niche space to its evolution  
56 through time, (2) discuss and propose the optimal niche representation to be used in  
57 phylogenetic comparative studies, (3) introduce most common evolutionary models (4)  
58 describe the methods for ancestral reconstruction and discuss future directions of the field.

### 59 **Climate niche in space and time**

60 Hutchinson (1957, 1978) defined a species' fundamental niche as all combinations of  
61 environmental conditions where a species can persist and maintain a viable population in the  
62 absence of predators or competitors (Kearney and Porter, 2004). Although the ecological  
63 niche is not strictly a heritable phenotypic trait for which these methods were developed,  
64 niche characteristics are defined and constrained by species physiology, which *is* heritable, and  
65 as such can be analyzed in a phylogenetic framework (Kozak and Wiens, 2010a).

66 Biologists are generally interested in the "fundamental niche", which represents species  
67 physiological limits and is the actual evolvable trait, although what we actually observe in  
68 nature is the "realized niche". Unfortunately we are currently unable to determine the  
69 fundamental niche without manipulative experimental studies, so we are bound to analyse the  
70 realized niche, a restricted section where a species lives, limited by biotic interaction or  
71 dispersal limitation (Jackson and Overpeck, 2000; Soberón and Nakamura, 2009).

72 It is currently impossible to tell how closely the realized niche approximates the  
73 fundamental niche, and for this reason it is difficult to guess whether the observed change  
74 really demonstrates niche evolution, or if this change is merely a shift of the realized niche  
75 within the species' fundamental niche (e.g. due to changed biotic interactions: Graham et al.,  
76 2004; Dormann et al., 2010). High within-species plasticity (e.g. in mammals, Réale et al.,  
77 2003) may lead to changes in realised habitats as biotic and/or abiotic conditions change.

78 A further complication is introduced by the existence of no-analog climate conditions at  
79 different time slices, e.g. in the past (Williams et al., 2001) or future (Williams et al., 2007,  
80 see Fig.1), which indicates that only a portion of a species' fundamental climatic niche  
81 (termed "potential niche") actually exists in the world at a given time. Therefore, whole  
82 sections of fundamental niche might be unobserved because they are nonexistent in space at  
83 that time (Fig. 1). Moreover, in the presence of facilitative biotic interactions or mutualism,  
84 species' niche could even extend beyond the fundamental niche (e.g. in lichens or corals; see  
85 Fig. 1, Bruno et al., 2003; Afkhami et al., 2014). Given the tremendous complexity of

86 confounding factors it seems incredibly difficult to be certain how to interpret the observed  
87 change in the climate niche. Distinguishing evolutionary change from shifts within unknown  
88 niche limits certainly merits attention, and comparative studies could potentially disentangle  
89 one from another: if a trait tightly linked to physiology changes along with the niche  
90 (assuming this change is at the genetic level, i.e. it goes beyond phenotypic plasticity), this  
91 could indicate the species is adapting to new environmental conditions, and hence its niche is  
92 evolving. For example, Edwards and Smith (2010) found that the origin of C4 photosynthesis  
93 in grasses coincided with shifts to drier environments. Without considering the exact  
94 mechanism, or excluding other hypotheses, it should be reasonable to interpret this finding as  
95 species adaptation to novel climate conditions (i.e. evolutionary change of the fundamental  
96 niche). In this review we consider the “realized” niche, since this is the most common  
97 situation for which we have data although we acknowledge it is far from a consistent  
98 approximation of the fundamental niche, and encourage using direct physiological estimates of  
99 climatic tolerance whenever available.

## 100 Representing the climatic niche

101 To test hypotheses about the climatic niche in phylogenetic comparative methods, it is  
102 necessary to infer the present climate niche of extant species. There is no standard protocol  
103 and the way the niche is represented varies widely among studies. For example, some authors  
104 represent the niche with climate niche models (Graham et al., 2004; Yesson and Culham,  
105 2006a,b; Eaton et al., 2008; Dormann et al., 2010), others use raw climate data (Evans et al.,  
106 2005; Ackerly et al., 2006), some combine the two approaches (Fig. 3, Evans et al., 2009;  
107 Smith and Donoghue, 2010), and others represent the niche with ordination techniques  
108 (principal component analysis, outlying mean index: Eaton et al., 2008; Boucher et al., 2012;  
109 Bystriakova et al., 2011). Here we define the optimal climate niche representation for the most  
110 common circumstance, where data derive from occurrence data and the hypothesis to be  
111 tested is specific to that region. In this case, niches based on **raw** data consist only of climate  
112 values extracted at species locations: generally the mean of those values is representing the  
113 niche (e.g. mean annual temperature, total annual precipitation). Climate niche models, a  
114 subset of species distribution models, are the most frequently used approach to represent the  
115 niche (Franklin and Miller, 2009; Peterson et al., 2011). Algorithms relate a species’

116 geographical locations to climate characteristics in order to describe its environmental niche  
117 (Guisan and Zimmermann, 2000; Kozak et al., 2008, a review of prediction ability of numerous  
118 modeling algorithms is provided by Elith et al. 2006). Modeling the niche to get insights of  
119 the functional relationship between a species and its environment is statistically preferable to  
120 the use of raw data (Peterson et al., 2011), because it accounts for the fact that species  
121 occurrences in an area might be determined by habitat availability and is not only a function  
122 of species preferences. For instance, a higher abundance in valleys compared to mountain tops  
123 could be due to a higher availability of valleys in that area, despite species' higher preference  
124 for mountains (see Fig. 3 c,d and examples below).

## 125 **Niche statistics**

126 The niche is a multidimensional entity and as such difficult to analyze phylogenetically as a  
127 whole. In general, it is decomposed into its marginal components (e.g. annual precipitation),  
128 each of which is examined separately along the phylogenetic tree. Most if not all variables  
129 describing the climate niche are continuous and the statistic most commonly chosen to  
130 represent them is the mean (e.g. mean annual precipitation). As some authors acknowledged,  
131 the mean may or may not be the most informative descriptor of the niche (see Fig. 3d,  
132 Graham et al., 2004). Different solutions have been proposed, particularly among studies  
133 where ancestral climate niche was reconstructed along the phylogeny. Graham et al. (2004)  
134 and Hardy and Linder (2005) proposed to consider the upper and lower niche limits  
135 separately, in order to infer the whole range of conditions of the ancestral niche, the so called  
136 “MaxMin” coding, which was used in a number of later studies (Yesson and Culham, 2006a,b;  
137 Lo Presti and Oberprieler, 2009; Lawing and Polly, 2011; Töpel et al., 2012). Instead of using  
138 maximum and minimum, which could be outliers, Vieites et al. (2009) proposed to consider  
139 95% confidence values. In any case, mean, minimum or maximum temperature still do not  
140 fully describe the distribution of species climatic tolerances. To tackle this issue Evans et al.  
141 (2009) proposed the “predicted niche occupancy” (PNO) profiles: histograms obtained by  
142 combining response curves from niche models with climate layers of actual species distribution  
143 in geographic space. With this approach, each climate variable is represented by a histogram,  
144 which is especially appropriate for species whose niche variables are multimodal or, more  
145 generally, do not approximate a normal distribution. Working with histograms (or rather,  
146 empirical densities) requires sampling from the distribution of values and thus repeating the

147 same analysis for each sampled value.

148 Analyzing the whole distribution of preferences is certainly more desirable than using single  
149 values. It would, however, be more appropriate to consider response curves obtained from  
150 niche models in parameter space, rather than combining them with geographic space. This  
151 avoids spurious results arising when large areas with low suitability are present in geographic  
152 space: the total sum of suitabilities (as used in Evans et al., 2009) could still be higher for  
153 those suboptimal conditions, only because of their high frequency in geographic space. This is  
154 illustrated in Fig. 3c, where a great portion of sites with the temperature of 9-10°C are not  
155 occupied by the species, therefore the probability of species occurrence at that temperature is  
156 relatively low (see Fig. 3d), but the sum of those probabilities in space will be high because  
157 there are many sites with that temperature. On the other hand, a temperature of 12-13°C is  
158 highly suitable (probability of 0.8), but there are so few sites with these conditions that the  
159 sum of suitabilities is low, despite the species' high preference for those sites. The statistical  
160 model would pick it up and discriminate between use and availability (the maximum in  
161 Fig. 3d), while the histogram of suitability in geographic space (PNO) will be biased towards  
162 common environmental conditions. Therefore, model output allows an unbiased representation  
163 of preferences, irrespective of geographic availability (Hurlbert, 1978; Manly et al., 1993;  
164 Matthiopoulos et al., 2011). This is relevant also when considering large-scale climate change  
165 and the existence of no-analog climates in different time periods - climate conditions that  
166 cover large areas today might have been very restricted at a different time, and vice versa.

167 In principle, the same resampling scheme can be used for multivariate distributions (as in  
168 Boucher et al., 2012), obviating the need to study each climate variable separately. However,  
169 given the no-analog conditions, the problem of assuming the same correlation structure  
170 between variables for different time periods arises again, an issue still waiting to be solved.

### 171 **Ecological variability**

172 Species are often polymorphic; populations of the same species may live, for example, on  
173 different types of soil, or along a wide gradient of temperature (Pearman et al., 2010). The  
174 approach described above, where species' climatic preferences are expressed with empirical  
175 densities, automatically takes into account the ecological variability within species by  
176 resampling from climatic values based on species' preferences. Theoretically the same  
177 approach could be employed for categorical variables, with preferences determining the  
178 probability of drawing from each character state (e.g. in case of higher species' preference for

179 soil-type A compared to B). This way ecological variability can be taken into account in any  
180 comparative analysis. Another method to accommodate polymorphism in discrete characters  
181 is through the quantitative genetic threshold model (Felsenstein, 2005), which models a  
182 discrete character as a continuous trait and is described in more detail in Box 1. See also  
183 Hardy and Linder (2005) and Hardy (2006) for additional methods and discussion on this  
184 topic.

## 185 Evolutionary analyses

186 How did the niche evolve among different species? Under which processes? What were the  
187 drivers? Are niches conserved or labile? What was the ancestral niche like? These are some of  
188 the most intriguing questions in comparative studies about climatic niches. We next describe  
189 the available methods to tackle some of them: we discuss the utility of phylogenetic  
190 conservatism tests, describe the most common evolutionary models, explain the procedure to  
191 infer the ancestral climatic niche and end with a summary and recommendations of best  
192 approaches.

193 As the name suggests, phylogenetic tree is the backbone of phylogenetic comparative  
194 studies. A detailed description on building a phylogeny is beyond the scope of this review, and  
195 we refer the interested readers to Holder et al. (2003); Bininda-Emonds (2004) and Roquet  
196 et al. (2012). At the coarsest level, a distinction can be drawn between phylograms (trees with  
197 branch lengths proportional to molecular distance), and chronograms (or ultrametric trees,  
198 with branch lengths proportional to time). Unless the aim of the study specifically requires  
199 the use of a phylogram, the general consensus is to use ultrametric trees because niche  
200 evolution is assumed to be proportional to time. Although sophisticated methods are  
201 continually reducing uncertainty, phylogenies still remain only hypotheses of how species  
202 evolved (Webb et al., 2002). Alternative trees often have almost the same support, which is  
203 problematic because for instance, niche reconstruction on different trees may produce different  
204 results. Therefore the best way to incorporate phylogenetic uncertainty is to carry out the  
205 analyses on a sample of plausible phylogenetic trees instead of using the single best phylogeny.

### 206 **Phylogenetic niche conservatism**

207 Phylogenetic niche conservatism (PNC) is the tendency of species to retain their ancestral  
208 niches through time (Boucher et al., 2014). The most common way to assess the PNC is by



209 measuring the phylogenetic signal: a measure indicating whether a trait evolves according to  
210 the null expectation of neutral drift model. There is still disagreement and it remains a  
211 debated topic at which similarity level phylogenetic signal can be interpreted as phylogenetic  
212 niche conservatism (Losos, 2008a; Wiens et al., 2010).

213 Here we want to highlight how testing for PNC by measuring phylogenetic signal can be  
214 potentially misleading and special caution is needed when interpreting the results. For  
215 instance, no phylogenetic signal is a pattern where species niches appear to be independent  
216 from phylogenetic relationship among them (Losos, 2011). This is usually interpreted as no  
217 niche conservatism, as it can arise when the niche evolved more than expected from random  
218 evolution. Niche diverged to such an extent that the similarity among closely related species is  
219 lost (Fig. 1c). Another cause leading to the same pattern is convergence, when species  
220 belonging to separate clades adapt to the same types of environment, and therefore the  
221 pattern of niche values distribution among clades is similar (Fig. 1c, Kraft et al., 2007).  
222 Again, this is seen as no niche conservatism. But a highly problematic and less obvious cause  
223 of observing no phylogenetic signal is *perfect* conservatism: if the evolution is extremely  
224 conserved, all species will have the same or very similar niches, and no phylogenetic signal can  
225 be detected (Fig. 1d, Revell et al., 2008; Kozak and Wiens, 2010b). This occurs under  
226 strongly stabilizing selection, where all species evolve towards the same optimum value (Revell  
227 et al., 2008; Kozak and Wiens, 2010b), or when strong biological constraints bound the niche  
228 values to a narrow interval (Revell et al., 2008; Losos, 2011). Hence no signal could indicate  
229 either divergent evolution, strong stabilizing selection with one optimum (i.e. stasis), or  
230 bounded evolution. Therefore, the same pattern can be caused by completely different  
231 processes, which cannot be distinguished among each other by measuring the level of  
232 phylogenetic signal alone. To identify whether the niche evolved under, e.g., directional  
233 selection or genetic drift, the recommended approach is to fit different evolutionary models to  
234 data, rather than measuring the phylogenetic signal (Revell et al., 2008; Cooper et al., 2010).

235 Furthermore, the detection of a phylogenetic signal depends on the size of the phylogenetic  
236 tree and the section analyzed (Fig. 1e). It is extremely important to interpret the patterns  
237 only according to the climatic/temporal boundaries within which they were identified; niche  
238 lability in a strictly tropical species does not preclude PNC at larger scales (Losos, 2008b;  
239 Wiens, 2008).

240 To summarize: (a) phylogenetic signal and niche conservatism are patterns which do not

241 necessarily reveal the underlying processes (Losos, 2011; Crisp and Cook, 2012); (b)  
242 completely different processes can lead to the same pattern (see Revell et al., 2008); (c) the  
243 detection of patterns is context-dependent (Fig. 1e).

244 Therefore, a better approach to assess niche conservatism among different clades is to test  
245 for mechanisms and evolutionary processes.

### 246 **Models of evolution**

247 Evolutionary models describe and approximate the natural processes responsible for trait  
248 evolution (Fig. 4). Fitting various models to the data permits to test hypotheses about the  
249 processes driving evolution of particular trait (e.g. the climatic niche). Before actually fitting  
250 models to the data, it is advisable to first identify plausible evolutionary processes based on  
251 prior biological knowledge, and afterwards proceed to fit only the corresponding models  
252 (Fig. 5). By fitting all the models without distinction one runs the risk of selecting a model  
253 with good statistical fit, but biologically improbable premises (as demonstrated in Wiens  
254 et al., 2007). The model with best fit is chosen in most cases through likelihood ratio tests  
255 (LRT, Johnson and Omland, 2004). Model selection criteria such as Akaike information  
256 criterion (AIC, Akaike, 1973) or Schwarz criterion (BIC, Schwarz, 1978) provide several  
257 advantages; they can compare multiple models simultaneously, rank them, give relative  
258 supports and are not influenced by the hierarchical order in which the models are compared  
259 (Burnham and Anderson, 2002; Johnson and Omland, 2004; Posada and Buckley, 2004).

260 Nonetheless, recent criticism about information theoretic approaches cast a doubt on their  
261 ability to discern the correct model. As Boettiger et al. (2012) and Slater and Pennell (2013)  
262 argue, in comparative studies *predictive approaches* are more robust and powerful means for  
263 model selection. While information theoretic approaches select the model which maximizes  
264 the posterior probability of the observed values, predictive approaches prefer the model which  
265 best predicts the observed values through simulation (Slater and Pennell, 2013). In this  
266 approach the models are first fitted and parameters for each model of evolution are estimated,  
267 and subsequently used to simulate new data. The models are then evaluated based on how  
268 closely they predicted the observed data. This procedure is available in the R-package  
269 “geiger” (Harmon et al., 2008), so far to test for early burst, Brownian motion and rate shift  
270 models. Package “pmc” (Boettiger et al., 2012) allows a simulation based method to choose  
271 between models fitted in “geiger”, “ape” (Paradis et al., 2004) and “ouch” (King and Butler,  
272 2009). Given that complex models have a higher number of parameters, the phylogenies have

## 273 **Evolutionary models for continuous characters**

274 The simplest evolutionary model is the **Brownian motion model** (BM, Cavalli-Sforza and  
275 Edwards, 1967; Felsenstein, 1985, 1988). Under this model the traits are evolving randomly in  
276 any direction from the mean at each instant of time, with a net change of zero. The  
277 probability of character change is thus proportional to branch length, and the correlation  
278 among trait values at the tips of the tree decreases linearly with increasing phylogenetic  
279 distance between species (i.e. the more closely related the species, the more similar their traits  
280 are, Hansen and Martins, 1996). Exactly the same correlation structure is also expected when  
281 traits evolve under some other processes, such as directional or stabilizing selection with  
282 fluctuating optimum or punctuated change (periods of stasis alternated by abrupt changes,  
283 Hansen and Martins, 1996; O'Meara et al., 2006; Thomas and Freckleton, 2011). The  
284 assumptions of BM are violated if the values of a trait are near their biological limits and  
285 therefore cannot decrease or increase independently of the current value, or if the trait is  
286 under stabilizing selection (O'Meara et al., 2006). In those cases trait evolution is better  
287 described by the **Ornstein-Uhlenbeck model** (OU, Hansen, 1997; Butler and King, 2004;  
303 288 Estes and Arnold, 2007), an extension of BM which has an additional term describing the  
289 “pull” towards an optimum value (known as mean-reversion rate in financial mathematics).  
290 When the value of this constraint equals zero, the model is equal to BM. On the other hand,  
291 the higher the pull towards an optimal value is, the lower the correlation among closely related  
292 species will be, as all species evolve towards the same optimum.

293 Another process of great evolutionary importance is “adaptive radiation”, which traces back  
294 to Simpson (1944). According to this process, species traits initially evolve rapidly and then  
295 slow down as the niche space becomes filled, which is basically opposing the idea of gradual  
296 evolution as described by simple BM (Harmon et al., 2003, 2010; Slater et al., 2010). It is  
297 modeled as BM with decelerating rates of evolution through time, a model commonly known  
298 as **early-burst (EB)** or **ACDC** (accelerating versus decelerating rates of character evolution,  
299 Blomberg et al., 2003), which can also be tested with **Pagel's  $\delta$**  (Pagel, 1997; Pagel et al.,  
300 1999). Another way of detecting the pattern of decelerating evolutionary rates is to infer rate  
301 shifts through phylogeny, as described in Eastman et al. (2011), or by calculating the  
302 morphological disparity index (MDI, Harmon et al., 2003).

304 **Box 1: continued**

305 A further option is to perform the node height test: EB occurs when the standardized  
306 independent contrasts of trait values are higher deeper in the tree than among more recent  
307 nodes in the phylogeny (Freckleton and Harvey, 2006). Although the model of adaptive  
308 radiation is generally well supported in paleontology, it has not been often observed in  
309 comparative studies (Harmon et al., 2010). Slater and Pennell (2013) argue the inability of  
310 detecting EB may be because of lack of power of currently employed methods, rather than the  
311 absence of such pattern in nature. Several other models describing adaptive radiation exist  
312 which assume a decrease of evolutionary rates as a function of the number of competing  
313 lineages (Mahler et al., 2010), or are refinements of Price's **niche-filling** models (Price, 1997;  
314 Harvey and Rambaut, 2000; Freckleton and Harvey, 2006). Adaptive radiation can also be  
315 fitted with a stabilizing selection model where different clades in the tree evolve towards  
316 different optima (multiple-optimum OU model Butler and King, 2004).

317 Similarly, to investigate the tempo of evolution – whether traits evolved rapidly immediately  
318 after speciation events followed by a long period of stasis – it is necessary to fit

319 **punctuational** or **speciational** models of evolution, where the evolutionary change is a  
320 function of speciation events and is independent of branch lengths (Gould and Eldredge, 1972;  
321 Huey and Bennett, 1987; Pagel, 1997; Pagel et al., 1999; Pagel, 2002). This type of evolution  
322 can also be detected by testing for a cladogenetic component of trait evolution with Bayesian  
323 MCMC test (Bokma, 2008). Models can also assign different rates of trait evolution to  
324 different parts of a tree (O'Meara et al., 2006; Thomas et al., 2006; Eastman et al., 2011;  
325 Venditti et al., 2011; Beaulieu et al., 2012; Revell, 2012). It is possible to identify the location  
326 of a rate shift in the phylogeny with R-packages “phytools” (evol.rate.mcmc Revell, 2012), or  
327 “geiger” (rjmcmbm).

328 Different evolutionary models for continuously varying trait can be fitted with R-package  
329 “geiger” (Harmon et al., 2008), “ouch” (Butler and King, 2004), ‘ouwie” (Beaulieu et al.,  
330 2012), whereas Mahler et al. (2010) model can be fitted by fitDiversityModel in phytools.

331 **Discrete characters**

332 Statistical models describing the evolution of discrete characters are based on continuous-time  
333 Markov process, equivalent to the Brownian motion model for continuous characters (Schluter  
334 et al., 1997; Cunningham et al., 1998; Pagel et al., 1999; Ronquist, 2004). The earliest and  
335 simplest such model is the Jukes-Cantor model proposed for nucleotide substitution with  
336 equal transition rates (Jukes and Cantor, 1969; Galtier et al., 2005).

338 **Box 1: continued**

339 Kimura (1980) extended it to a two-rate model to allow the transition rates between  
340 nucleotides to differ. Today this family of models are known as Mk models, Markov models  
341 which can assume  $k$  states. (Lewis, 2001). The central feature of the model is the rate matrix,  
342 which contains the instantaneous transition rates between different character states (Pagel,  
343 1997; Pagel et al., 1999). With a 3-states trait, this transition matrix is a  $3 \times 3$  matrix with  
344 forward and backward transition rates represented on the off-diagonals (Revell, 2014). The  
345 model can assume different rates among characters (the rate  $A \rightarrow B$  may differ from  $B \rightarrow C$ ),  
346 and the direction of change (the forward transition  $A \rightarrow B$  may differ from the backward  
347 direction  $B \rightarrow A$ ). Until recently, the transition rates were fixed and applied to the entire  
348 phylogeny, without the possibility, for instance, to assume a different rate of  $A \rightarrow B$  transition  
349 on different parts of the tree. This is now possible with the R package “corHHM”, which  
350 handles the different rate classes as hidden character states (e.g. fast and slow; Beaulieu et al.,  
351 2013). Another innovative way to model the evolution of discrete characters is through the  
352 “threshold” model, first described by (Wright, 1934), in which the discrete trait is practically  
353 transformed to a continuous character, an unobserved trait called “liability” with fixed  
370 354 thresholds (Felsenstein, 2012; Revell, 2014). For example, a trait with two states (A, B) can  
355 be represented by a continuous scale liability axis with an arbitrary threshold (e.g. at 0), so  
356 that when the liability assumes negative values, the trait is in state A, otherwise in state B.  
357 The threshold model is biologically reasonable because it models a discrete character as a  
358 continuous trait where the probability of the character to change states decreases with time:  
359 the longer the time after the character crossed the threshold and moved to another state, the  
360 less probable it is the return to previous state, in contrast to Mk model, in which the amount  
361 of time at a certain state does not influence the probability of change (Felsenstein, 2002). The  
362 threshold model is implemented in R package “phytools” (Revell, 2012) and permits ancestral  
363 reconstruction of discrete characters under BM and OU models of evolution. Several other R  
364 packages are available for reconstruction of discrete traits under both joint and marginal  
365 methods, allowing multistate characters and different transition rates: diversitree (FitzJohn,  
366 2012), geiger (Harmon et al., 2008), ape (Paradis et al., 2004), as well as other software such  
367 as MESQUITE, BayesTraits and SIMMAP (Bollback, 2006). J. Felsenstein’s webpage  
368 (<http://evolution.genetics.washington.edu/phylip/software.html>) provides an overview of  
369 other available phylogeny software.

371 to be large enough to allow a reasonable inference of the evolutionary model (Boettiger et al.,  
372 2012). Thanks to the increasing availability of molecular data, phylogenetic trees are growing  
373 to include many thousand species (Bininda-Emonds et al., 2007; Smith and Donoghue, 2008;  
374 Thuiller et al., 2011; Jetz et al., 2012). With such a variety of life forms it becomes reasonable,  
375 even necessary, to assume and test much more complex models of evolution than a simple  
376 Brownian motion.

377 **Integrating fossil records** Incorporating known ancestral values dramatically improves the  
378 inference of the evolutionary model, in particular by allowing the detection of directional  
379 evolutionary trends, which are virtually unobservable with extant taxa only (Oakley and  
380 Cunningham, 2000; Finarelli and Flynn, 2006; Albert et al., 2009; Slater et al., 2012).  
381 Substantial improvements were shown for model detection for all tested models (BM, AC/DC  
382 and OU: Slater et al., 2012). Integrating prior information by directly assigning values to  
383 specific ancestral nodes in the phylogeny is now possible and technically straightforward (e.g.  
384 in R-packages “phytools” and “geiger”; Slater et al., 2012). Constraining values from  
385 wandering too far from the optimum value can be achieved by simulating “bounded evolution”  
386 by varying the “pull” parameter of the OU model, which in turn determines the width around  
387 the optimum, or by setting absolute limits (as proposed by Revell, 2007; Revell et al., 2008).  
388 Given that the interpretation of results in comparative methods largely depend on the model  
389 of evolution, it will be important to integrate all available prior knowledge from paleosciences,  
390 continue developing realistic evolutionary models, as well as establishing reliable techniques to  
391 choose among them.

## 392 **Ancestral niche reconstruction**

393 Rapidly developing statistical reconstruction methods permit the estimation of ancestral  
394 trait values based on its present-day value, the phylogenetic relationship among species and an  
395 evolutionary model. Therefore the inference of the best evolutionary model should be an  
396 integral part of the reconstruction procedure. If a model is not specified, most reconstruction  
397 methods will follow a BM model by default, and their output will be identical or very similar  
398 (see Table 2).

399 As in model-fitting, the methods for continuous and discrete traits are slightly different.  
400 Climate variables are most commonly expressed on a **continuous** scale and ancestral climate  
401 niches can be reconstructed following the methods for continuous characters. Squared-change

402 parsimony (or weighted squared-change parsimony) was initially the most widely used  
403 method. The optimal values for ancestral characters are found when the sum of their squared  
404 changes over the whole phylogenetic tree reaches the minimum value (Maddison, 1991;  
405 Garland et al., 1997). Weighted squared-change parsimony takes into account branch lengths  
406 (i.e. evolutionary time), so that the resulting reconstruction corresponds to BM evolution  
407 (Maddison, 1991; Webster and Purvis, 2002). Another widely used method was Felsenstein's  
408 (1985) independent contrasts (IC). Although weighted squared-change parsimony and IC both  
409 implicitly assume a BM model of evolution, those two methods will yield slightly different  
410 reconstructed values for all nodes except the basal, because independent contrasts use "local"  
411 optimization (only daughter nodes are considered to infer the value of the ancestor), as  
412 opposed to "global" optimization used in squared-change parsimony (Maddison, 1991;  
413 Garland et al., 1997; Webster and Purvis, 2002). Nowadays more commonly used methods are  
414 maximum likelihood (ML) (Schluter et al., 1997; Cunningham et al., 1998), generalized least  
415 squares (GLS) (Grafen, 1989; Martins and Hansen, 1997; Pagel et al., 1999; Martins, 1999)  
416 and Bayesian approaches (Pagel et al., 2004). Ancestral traits, and hence also climate niches  
417 can be estimated using R-packages "ape", "phytools" and "phyloclim" (Heibl et al., 2013) and  
418 other software as MESQUITE (Maddison and Maddison, 2001), BayesTraits (Pagel and  
419 Meade, 2007) or COMPARE (Martins, 2004). Table 3. summarizes the approaches used in  
420 climatic niche reconstruction studies, indicating methodological improvements over time.

421 One could represent climate preferences as **discrete** characters (e.g. by categorising  
422 temperature values into "arid" and "mesic" conditions). Performing this categorization *after*  
423 the reconstruction of continuous climate variables allows more precision and avoids spurious  
424 results due to arbitrarily chosen thresholds. Maximum parsimony reconstructs the ancestral  
425 values by minimizing the number of changes needed to reach the observed present-day values  
426 (Pagel et al., 1999; Pedersen et al., 2007). Maximum likelihood and Bayesian methods are  
427 broadly grouped into "joint" or "global" and "marginal" or "local" reconstructions. Joint  
428 reconstruction finds the states which jointly maximize the likelihood over the whole phylogeny.  
429 In contrast, marginal reconstruction singles out the state with the highest likelihood at each  
430 node separately, which can be useful to test a specific hypothesis at a certain node in the tree  
431 (Pagel, 1999). Models which describe the evolution of discrete characters are based on the  
432 Markov-transition process of the probability of the character (see Box 1, Pagel et al., 1999).

433 Reconstruction procedures take into account evolutionary models by transforming the

434 branch lengths, the path separating species pairs from their common ancestor in the  
435 phylogenetic tree. For instance, according to early burst model, evolution is faster closer to  
436 the root of the tree, therefore after transformation those branches will be longer compared to  
437 the branches closer to the tips where the rate of evolution is slowing down. Reconstructing the  
438 values according to a specific model of evolution in R can be done in two steps: first, it is  
439 necessary to transform the phylogenetic tree according to the previously tested best fitting  
440 model (e.g. `rescale` function in “`geiger`”), and afterwards this rescaled tree can be used for  
441 ML-based ancestral niche reconstruction under the default BM model of evolution (e.g. `ace`  
442 function in “`ape`”). The obtained ancestral values correspond to values evolved according to  
443 the evolutionary model used to transform the tree. Accordingly, weighted squared change  
444 parsimony or independent contrasts can fit different models of evolution in a computationally  
445 efficient way, by employing appropriate transformations of the phylogeny (see Table 1).

446       Regardless of the character type or method of choice, estimating trait history on a sample  
447 of possible phylogenetic trees instead of using only the single best tree allows to incorporate  
448 phylogenetic uncertainty in the analysis. Reconstructed estimates of all trees are then  
449 averaged and their distribution provides uncertainty estimates. This procedure is not limited  
450 to Bayesian analysis, but can be applied to any ancestral reconstruction method (Donoghue  
451 and Ackerly, 1996; Martins and Hansen, 1997; de Villemerueil et al., 2012).

452 **Visualizing and validating the ancestral range and climatic niche** If the aim of niche  
453 reconstruction was exploring the unfolding of evolutionary changes through time, we may  
454 want to visualize the ancestral climatic niche in an abstract multidimensional climate space  
455 (e.g. Veloz et al., 2012). On the other hand, to visualize the historical distribution and  
456 appreciate the extent of range shift through time, ancestral niche is often projected to a  
457 geographic map along with the current climatic niche (e.g. Yesson and Culham, 2006a; Lawing  
458 and Polly, 2011; Töpel et al., 2012). This may be problematic because environmental variables  
459 today are most likely correlated differently among each other than they were in the past  
460 (Boucher et al., 2012), given that non-analog climate conditions were already present at  
461 different time steps even on a short time scale, such as in the Quaternary (Jackson and  
462 Overpeck, 2000; Williams and Jackson, 2007). Therefore, projecting the ancestral niche to  
463 today’s world and vice-versa will not accurately represent the ancestral range, as parts of the  
464 range may be missing while some other areas might be wrongly assigned. It practically shows



465 where the ancestor would live today, but not necessarily where it actually lived in the past.  
466 The ideal solution would be to project to paleoclimate maps, but because they become less  
467 reliable the further one goes back in time, it is difficult to infer the correct ancestral range  
468 solely with SDMs, without fossil records. Fossil records are scarce for most species and are  
469 often biased with respect to climate, topography, species size and abundance, yielding fewer  
470 traces of rare and small-sized animal species especially in wet tropical climates (Kidwell and  
471 Flessa, 1995). Still, whenever available they are a valuable indicator of a species' past  
472 distribution as they are generally buried within the species' range so spatial displacements  
473 between past and present are likely due to a range shift of species (Kidwell and Flessa, 1995).  
474 Fossil records of species occurrences can prove that species were present in the study area at  
475 the specific time (Vieites et al., 2009), and/or in the predicted ancestral range.

476 Known ancestral climatic values from paleodata add valuable information and should either  
477 be used to aid a better approximation of evolutionary models by constraining specific nodes to  
478 known values, as previously seen, or be employed for validating the reconstructed niche values.  
479 Validation may be more important when current data already yield a well-constrained model.  
480 In contrast, poorly defined models may profit from integrating paleoclimate data into the  
481 estimation process.

## 482 Summary and recommendations

483 Here we summarize and propose tentative guidelines for optimal use of species occurrence and  
484 climatic data in phylogenetic comparative studies.

### 485 **Niche representation**

- 486 • When present-day climate niches are inferred from spatial occurrences, niche models are  
487 a better choice than raw data.
- 488 • Each climatic variable should ideally be expressed by species preference for the full range  
489 of values (i.e. empirical densities), instead of being summarized by the mean or other  
490 point estimates (e.g. mean temperature).

### 491 **Ancestral niche reconstruction**

- 492 • Before reconstructing the niche, a best-fitting evolutionary model should be estimated  
493 for each climatic variable.

- 494 • Known paleoclimate data can either be used to improve the evolutionary model
- 495 inference or to validate the reconstructed values.
- 496 • Evolutionary changes are best visualised in an abstract climatic space.
- 497 • Ancestral species range should be projected to a paleoclimate map.

## 498 Concluding remarks

499 Analysing the evolution of climatic niches integrates species distribution modeling,  
500 phylogenies, evolutionary models as well as elements of paleosciences. Such a complex research  
501 question requires careful consideration of each component to minimize potential bias and  
502 information loss. We primarily focused and discussed the most appropriate methods to  
503 represent the climatic niche through species distribution modeling and outlined the procedure  
504 for ancestral niche reconstruction. This research field has a lot to gain from improvements in  
505 other areas, particularly from developing new evolutionary models, which would better  
506 approximate processes on macroevolutionary scale. Available paleodata has the potential to  
507 greatly improve the detection of evolutionary models (Slater et al., 2012), and we expect the  
508 future efforts in this interdisciplinary field to focus especially on a better integration of  
509 phylogenetic, paleontological and climatic data.

510 **Acknowledgments** We would like to thank Jan Schnitzler and Marten Winter for providing  
511 valuable comments that greatly improved the manuscript. This research was supported by the  
512 German Research Foundation, DFG (DO 786/5-1). The authors declare no conflict of interest.

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## Tables

895 Table 1: Reconstruction outcome from different methods for continuous characters. Under default conditions -  
 896 untransformed ultrametric tree and/or no model specification - all methods will produce roughly the same  
 897 ancestral states, as all assume Brownian motion model of evolution. Note: independent contrast (IC) method  
 898 will yield the same ancestral state estimates as the other methods only when each node of the tree is separately  
 899 re-rooted during the reconstruction process (Maddison, 1991; Garland et al., 1997). Weighted squared-change  
 900 parsimony (WSqCP) and independent contrasts can also assume different models of evolution by reconstructing  
 901 the trait values on a transformed phylogeny. Bayesian estimate can lead to a different result under the same  
 902 model due to different prior distributions for model parameters.

IC [untransformed tree]	≈	WSqCP [untransformed tree]	=	ML [BM]	=	GLS [BM]	≈	Bayesian [BM]
IC [OU tree]	≈	WSqCP [OU tree]	=	ML [OU]	=	GLS [OU]	≈	Bayesian [OU]

903 Table 2: A proposal of best practice and data format for phylogenetic comparative studies

	<b>Best choice</b>	<b>Alternative</b>
<b>Phylogeny</b>	Sample of trees Chronogram	Single tree Phylogram/topology
<b>Climate niche from occurrence data</b>	Modelled data	Raw data
<b>Climate niche from experimental data</b>	Direct measures	-
<b>Niche statistics</b>	Empirical distribution	Point values
<b>Evolutionary model</b>	Selected according to prior knowledge, followed by model selection based on fit	No selection
<b>Ancestral niche projection</b>	To paleoclimate maps, if reliable	To present-day maps
<b>Validation</b>	Fossil records	-

904 Table 3: List of studies reconstructing the ancestral climate niche in chronological order. The fields with missing values indicate either that the tests were not performed or  
 905 no information is available in the text. An overview of R packages implementing comparative phylogenetic methods is available in O'Meara (2012).

Study	Phylogeny	N° of species	Niche representation	Reconstruction method	Model selection/ additional indices	Software
Rice et al. (2003)	Phylogram	19	Modelled mean and st. error	GLS (BM)	Randomization	Compare
Graham et al. (2004)	Phylogram	2,3,5	Raw min/max values	ML/GLS (BM)	LR	
Hoffmann (2005)	Phylogram	15	Raw distribution	SqCP		MacClade
Edwards and Donoghue (2006)	Phylogram	9, 8	Mean climatic and physiological parameters	GLS (BM,OU <sub>1</sub> )		Compare
Yesson and Culham (2006b)	Topology	21	Mean/st.dev/min/max of raw data	SqCP	Randomization	Mesquite
Yesson and Culham (2006a)	Chronogram	45	Mean/st.dev/min/max of raw data	SqCP	Randomization	Mesquite
Eaton et al. (2008)	Phylogram	19,23,39	PC axes centroids	SqCP (BM)		Mesquite
Crisp et al. (2009)	Chronogram/ phylogram	11064 in 4 trees	7 biomes	SqCP, ML (Mk1)	Randomization	Mesquite

Table 3: continued

Author (Year)	Chronogram	n	Modelled distribution	ML (BM)	MDI <sup>1</sup>	R <sup>2</sup>
Evans et al. (2009)	Chronogram	20	Raw mean, min, max values	SqCP	QVI, K	Mesquite
Lo Presti and Oberprieler (2009)	Chronogram	147	PC axes	GLS (BM)	Disparity ratios, rates of evolution (AIC <sub>c</sub> )	R, Brownie
Smith and Beaulieu (2009)	Chronogram phylogram	301,351, 889,3174	Raw mean/min/max	ML	$\lambda, K, LR$	R <sup>3</sup>
Verbruggen et al. (2009)	Chronogram	52	Raw mean, 95% CI	ML (BM)	$\lambda, K, \delta, LR$	Mesquite
Vieites et al. (2009)	Chronogram	80	C3/C4 physiology, mean climate values	IC/ML (BM), ML (OU2)	AIC <sub>c</sub>	Phylocom, LASRdisc, Brownie
Edwards and Smith (2010)	Chronogram sample	1230, 299	Modelled distribution	GLS (BM)		R <sup>4</sup>
Jakob et al. (2010)	Chronogram sample	12				

<sup>1</sup>Morphological Disparity Index calculated in R package Geiger

<sup>2</sup>geiger

<sup>3</sup>ape, geiger

<sup>4</sup>phyloclim

Table 3: continued

Smith and Donoghue (2010)	Chronogram sample	19	Modelled distribution	ML (BM)	Niche overlap/ similarity/equivalency
Boucher et al. (2012)	Chronogram sample	51	OMI	JL (OU3)	AICc R <sup>5</sup>
Bystriakova et al. (2011)	Phylogram	53	Mean values/OMI centroids	ML (BM)	Permutation R <sup>6</sup>
Holstein and Renner (2011)	Chronogram	24	Biomes	ML (Mk1)	Randomization Mesquite
Rivera et al. (2011)	Phylogram	5	Raw mean	GLS (BM)	Compare
Heibl and Renner (2012)	Chronogram sample	43	Biomes	ML, Bayesian RJMCMC (Mk1)	AICc Bayestrats
Kellermann et al. (2012)	Chronogram	92, 95	Cold/dessication resistance	ML (BM)	$K, \lambda$ , Moran's I R <sup>7</sup>
Schnitzler et al. (2012)	Chronogram sample	89	Raw mean values	PIC (BM,OU)	$\lambda, AIC_c$ R <sup>8</sup>

<sup>5</sup> ade4, ape, geiger, picante, diversitree

<sup>6</sup> ape

<sup>7</sup> picante, geiger

<sup>8</sup> ape

Table 3: continued

Töpel et al. (2012)	Chronogram	38	Min, max values	ML (BM)	R <sup>9</sup>
Ahmadzadeh et al. (2013)	Chronogram sample	8	Modelled	ML (BM)	R <sup>10</sup>
Koecke et al. (2013)	Chronogram	19	Modelled distribution	ML (BM)	R <sup>11</sup>
Nyári and Reddy (2013)	Chronogram	29	Modelled distribution	ML (BM)	R <sup>12</sup>
Wiens et al. (2013)	Chronogram	117	Raw mean values	GLS (OU <sub>1</sub> )	Compare, R <sup>13</sup>
Guerrero et al. (2013)	Chronogram	73, 96, 25, 24	Raw mean, min, max values	GLS (BM,OU <sub>1</sub> )	Compare, R <sup>14</sup>
Jara-Arancio et al. (2014)	Chronogram	17,25	Biomes,raw median values	MP,ML,GLS (OU)	Mesquite,R <sup>15</sup> , Compare

<sup>9</sup>ape

<sup>10</sup>phyloclim

<sup>11</sup>Phyloclim

<sup>12</sup>Phyloclim, Phyloch

<sup>13</sup>ape,geiger

<sup>14</sup>geiger

<sup>15</sup>OUCH

## Figure legends

Figure 1: Climatic space represents all the combinations of two climatic variables existing at a certain time, which may differ at different times in history ( $t_1$ ,  $t_2$ ). The fundamental niche of a species includes all the possible conditions where a species could persist, some of which may lie outside conditions currently existing in the world. The intersection of the two represents the potential niche, which the species would fill in the absence of biotic interactions and dispersal limitations. The realized niche is the segment actually occupied by the species; it may occasionally extend towards climatic conditions outside its fundamental niche if facilitative biotic interactions are present. Adapted from Jackson and Overpeck (2000).

Figure 2: A hypothetical illustration of different degrees of phylogenetic signal. (a) Situation where trait values follow the expectations of a BM model of evolution (i.e. traits similarity is proportional to shared evolutionary history among species). (b) Strong phylogenetic signal is found when the trait values among closely related species are more similar than would be expected from BM. (c) A situation with no or low phylogenetic signal as a consequence of over-dispersion or convergence to habitat-specific trait values. Closely related species are not more similar than species drawn at random. (d) No phylogenetic signal as a consequence of trait stasis or convergence of all the species to the same trait value. (e) A signal (or its absence) may be restricted to a specific clade of a phylogenetic tree.

Figure 3: Climate niche representation. Niches are inferred by combining a) species distribution maps with b) climatic layers (temperature, precipitation, etc). c) The simplest niche representation that combines those data can be plotted as a histogram, with grey bars being the number of species occurrences at a certain temperature and white bars representing the entire area. Alternatively, niches can be statistically modeled, as shown in diagram d). The parameters finally obtained from those two approaches, in this example the mean values, may differ. Fig d) illustrates why the mean value is not necessarily the optimal statistic; instead reconstructing the whole distribution is preferable.

Figure 4: Evolutionary processes shaping the evolution of species traits are approximated by evolutionary models. Some processes, such as adaptive radiation or speciation processes can be approximated or tested by a number of slightly different models. See Box 1 for abbreviations and details.

Figure 5: Fitting the evolutionary models to data. Based on prior biological knowledge plausible evolutionary processes responsible for shaping the evolution of species traits are identified, and the corresponding evolutionary models are fitted to the data (see Fig. 4 for a readable version of this step). The model that fits best to the data (trait values and phylogeny) is commonly selected with likelihood ratio test (LRT), or with model selection criteria such as Akaike information criterion (AIC) or Schwarz criterion (SC=BIC).

## Figures

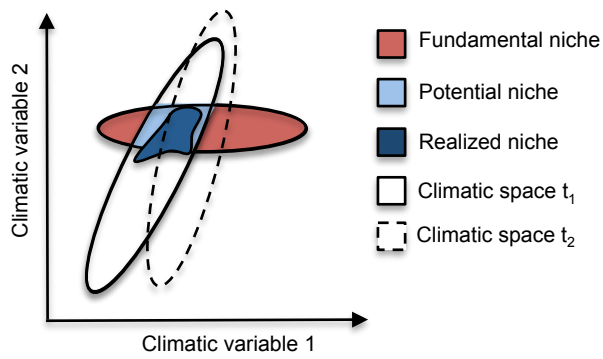


Figure 1:

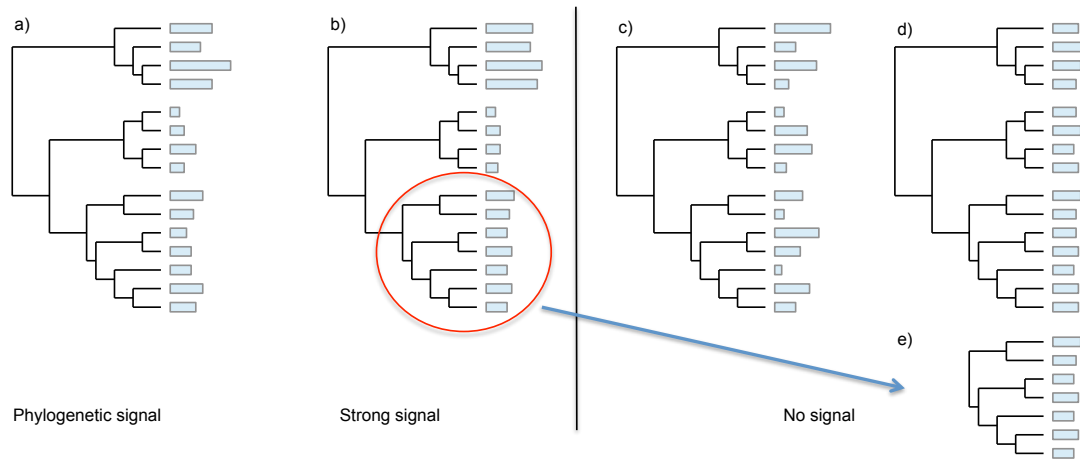


Figure 2:



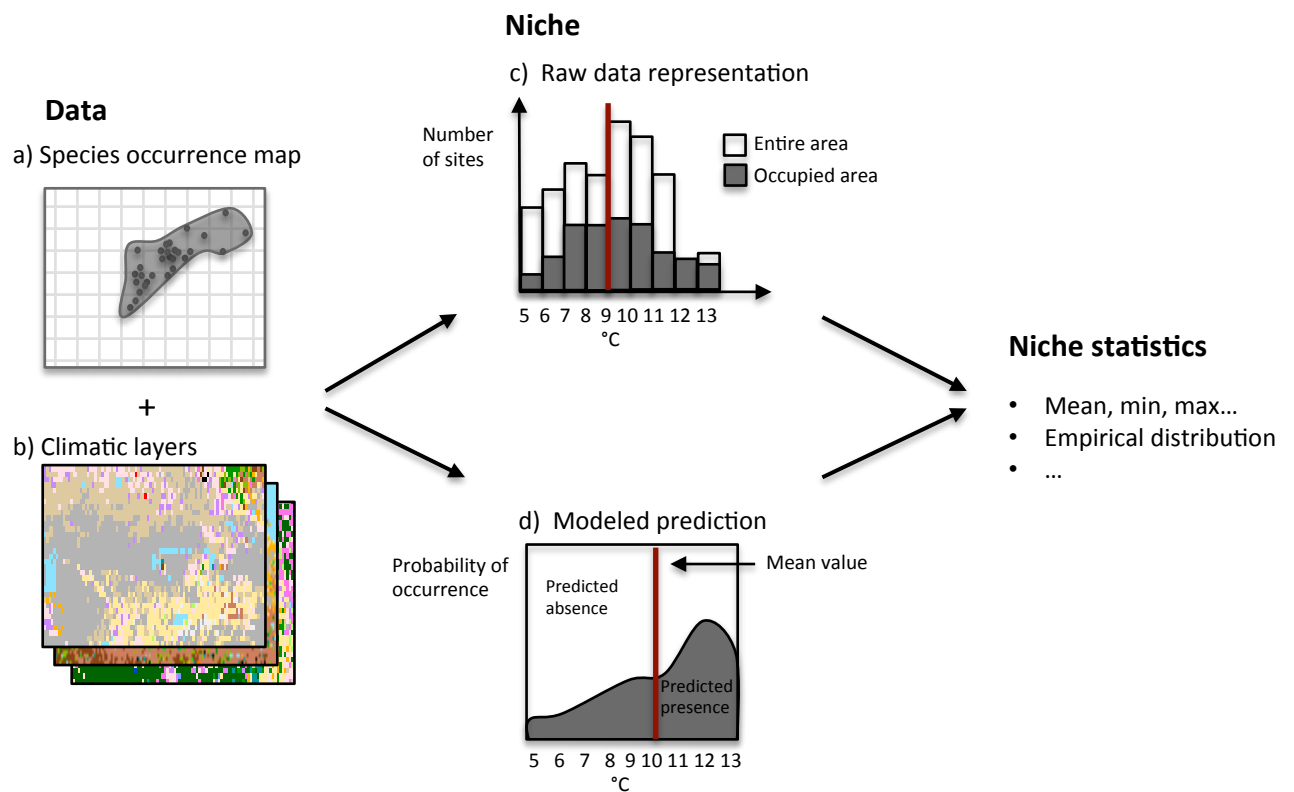


Figure 3:

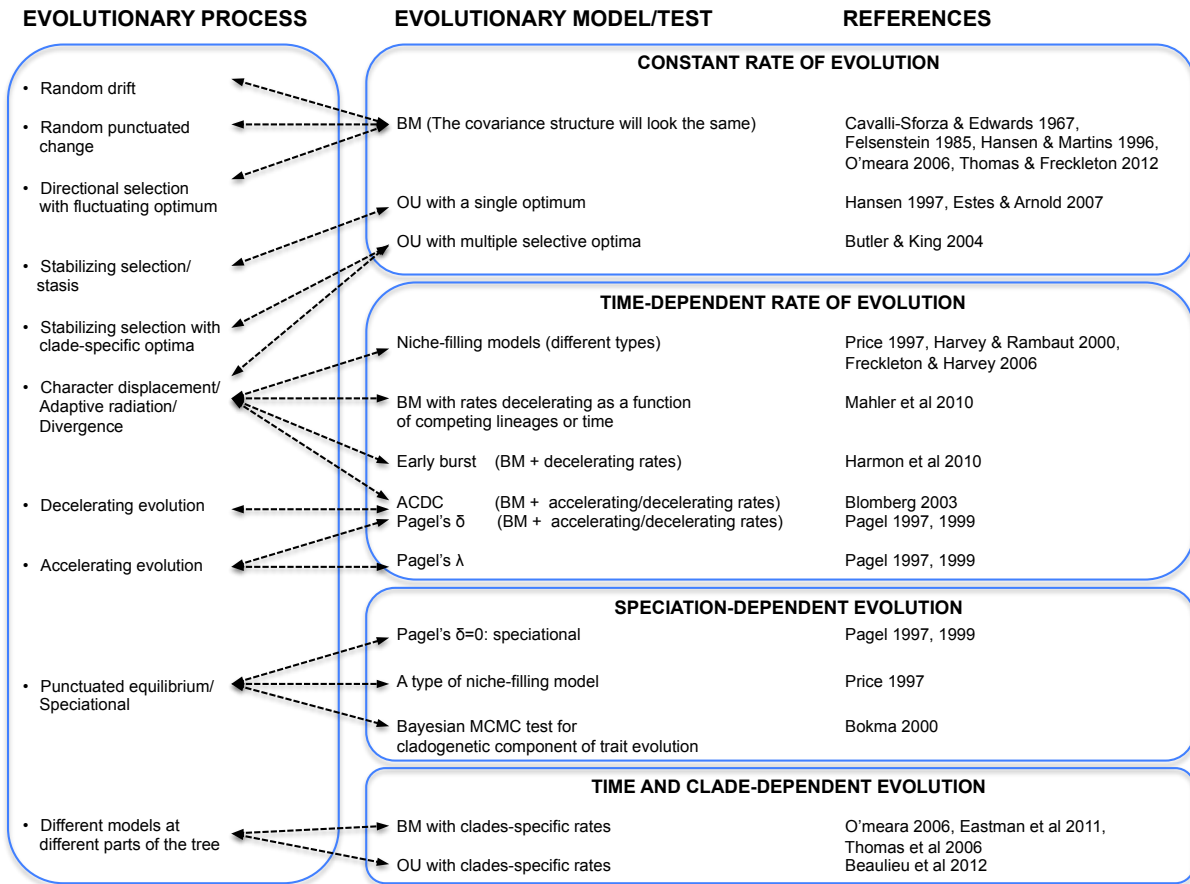


Figure 4:

Identifying plausible evolutionary processes

Model fitting

Model evaluation

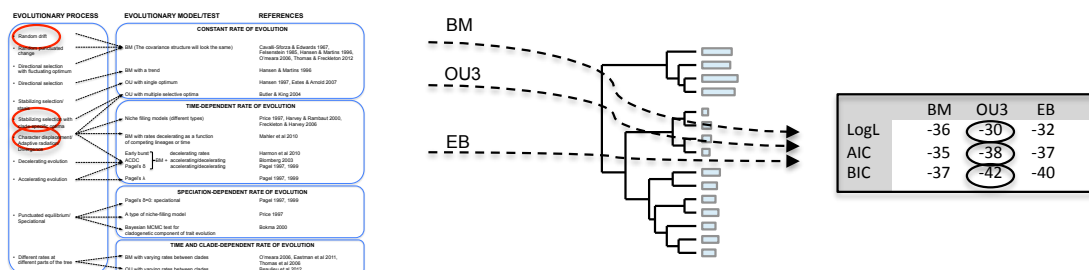


Figure 5: