Chapter 18
Phylogenetic Comparative Methods for Studying Clade-Wide Convergence

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Abstract A recurring question in ecology and evolutionary biology is whether deterministic evolutionary convergence ever occurs among large sets of species, such as ecological communities or entire evolutionary radiations. Questions about large-scale convergence have featured prominently in discussions of the nature of community assembly and in debates about the relative roles of contingency versus determinism in macroevolution. Until recently, however, there have been relatively few attempts to use a phylogenetic comparative approach to answer questions about clade-level convergence. This is beginning to change with the development of new and more flexible comparative techniques for studying macroevolutionary convergence. In this chapter, we discuss ecological and evolutionary questions that have motivated interest in convergence at large spatial and phylogenetic scales. We review the statistical approaches that have been used to investigate clade-wide convergence, then describe SURFACE, a recently developed method for objectively studying convergence using macroevolutionary adaptive landscape models. We introduce new features within this framework for testing hypotheses about the biogeography of large-scale convergence and for visualizing the relative contributions of different traits to multidimensional convergence, and demonstrate these features using convergent Caribbean *Anolis* lizard faunas. We conclude by discussing the limitations of current approaches for studying clade-wide convergence and highlighting some directions for future research.

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18.1 Why Study Convergent Evolution at the Clade Scale?

The fact that organisms experiencing similar selective pressures often converge by evolving similar adaptations is not controversial, and many studies have elucidated the ecological conditions and genetic and developmental mechanisms responsible for convergence among particular populations or species (Arendt and Reznick 2008; Conway Morris 2003; Losos 2011; Manceau et al. 2010). By contrast, the notion that entire communities or clades could evolve to be deterministically similar remains a source of disagreement among both ecologists and evolutionary biologists (Blondel 1991; Cody and Mooney 1978; Gould 1989; Ricklefs and Miles 1994; Samuels and Drake 1997; Schluter 2000; Schluter and McPhail 1993; Segar et al. 2013).

In ecology, discussions of community convergence have played a role in debates about the mechanisms governing community assembly and structure. Inspired by the perception that similar but historically isolated environments were often host to what appeared to be suites of 'ecologically equivalent' species (e.g., Karr and James 1975; Pianka 1974), a number of workers in the 1970s and 1980s became interested in whether similar ecological settings could lead to the evolution of deterministically similar communities (Cody 1974; Cody and Mooney 1978; Gatz 1979; Karr and James 1975; Keast 1972; Lawton 1984; Melville et al. 2006; Orians and Paine 1983; Orians and Solbrig 1977a; Ricklefs and Miles 1994; Ricklefs and Schluter 1993). Most early community similarity research focused on the non-evolutionary assembly of communities from existing species pools (Cody and Diamond 1975; Fox 1987; Strong et al. 1984), but evidence for similar communities on different continents raised the question of whether matched communities in similar environments could arise through evolutionary processes (Cody and Mooney 1978; Karr and James 1975; Kelt et al. 1996; Ricklefs and Miles 1994; Ricklefs and Travis 1980; Schluter 1986, 1990; Emerson and Gillespie 2008; Segar et al. 2013). Community similarity is most often measured using the phenotypic or functional attributes of species, but related approaches have asked whether communities are similar in other features such as richness and abundance in ecological guilds (Orians and Solbrig 1977b; Segar et al. 2013), the degree of species packing (Gatz 1979; Orians and Solbrig 1977b; Ricklefs and Travis 1980), the axes of variation among species (Wiens 1991; Young et al. 2009), or the relationship between morphology and ecology (Cody and Mooney 1978; Karr and James 1975; Melville et al. 2006; Miles et al. 1987; Montaña and Winemiller 2013; Ricklefs and Miles 1994).

In evolutionary research, the notion of clade-wide convergence has featured most prominently in the debate over the importance of contingency and determinism in macroevolution. Trajectories of evolutionary change are conventionally viewed as being at least somewhat predictable at microevolutionary scales, but idiosyncratic and unpredictable over the longer timescales over which clades diversify. According to this view, commonly referred to as the contingency hypothesis, both the inevitable differences in the initial conditions for evolution in different lineages and the influence of chance events during the course of evolution are sufficient to preclude highly similar macroevolutionary outcomes (Gould 1989, 2002, 2003; Price et al. 2000; Simpson 1950); (discussed in Beatty 2006, 2008; Erwin 2006; Inkpen and Turner 2012; Pearce 2012; Powell 2009, 2012). Many have challenged this view, citing the apparent emergence of so-called 'replicated adaptive radiations'—independent clades containing similar sets of species that have resulted from diversification in similar environments. With the rise of molecular systematics, phylogenetic investigations of many groups of organisms have revealed patterns of frequent ecological and morphological convergence, often among species that were previously thought to be close relatives based on superficial similarities (Givnish 1997; Losos and Mahler 2010). Such large-scale convergence would provide support for evolutionary determinism and would suggest a more limited role for initial conditions and chance events in determining macroevolutionary outcomes. Phylogenetic patterns suggestive of replicated adaptive radiation have now been reported for cichlid fishes (Clabaut et al. 2007; Kocher et al. 1993; Rüber et al. 1999; Stiassny and Meyer 1999; Young et al. 2009), *Anolis* lizards (Losos et al. 1998; Mahler et al. 2013), Hawaiian spiders (Blackledge and Gillespie 2004; Gillespie 2004, 2005) and plants (Givnish 1999; Givnish et al. 2009), continental radiations of mammals (Madsen et al. 2001; Springer et al. 1997), frogs (Bossuyt and Milinkovitch 2000; Moen and Wiens 2009), damselfishes (Cooper and Westneat 2009; Frédérich et al. 2013), land snails (Chiba 2004), and many other groups (e.g., Alejandrino et al. 2011; De Busschere et al. 2012; Kozak et al. 2009; Patterson and Givnish 2003; Ruedi and Mayer 2001; Ellingson 2013).

Many questions about macroevolutionary convergence remain unanswered. First, because some degree of convergence is expected among any large clades that have diversified from similar ancestors, it is possible that much of the celebrated convergence in replicated radiations is actually unremarkable and not indicative of deterministic evolution (Stayton 2008). Even assuming that replicated radiations are deterministically similar, there has been little investigation into the evolutionary process responsible for such convergence. In particular, while conceptual models of replicated radiation typically involve lineages in different regions being attracted to similar adaptive peaks, methods for inferring the number and position of such peaks on a macroevolutionary landscape have been lacking. In addition, there has been much recent discussion about whether convergence only occurs among members of geographically distinct clades, as might be expected if ecological opportunity and competition regulate the evolution of novel niche specialists (Losos 1996; Wiens et al. 2006), or whether convergence may occur repeatedly within the same region (Kozak et al. 2009; Muschick et al. 2012; Scheffer and van Nes 2006; Ingram and Kai 2014).

Testing hypotheses about processes underlying large-scale convergence has been a challenge, as the long timescales over which clades typically diversify preclude direct observation in nature. As a result, many of our insights into evolutionary contingency and determinism have come from experimental studies of microorganisms evolving in laboratory settings (Hekstra and Leibler 2012; Kassen 2009; Lenski and Travisano 1994; MacLean 2005; Rainey and Travisano 1998; Saxer et al. 2010; Tyerman et al. 2005) or from computer simulations (Gavrilets and Vose 2005; Pie and Weitz 2005; Scheffer and van Nes 2006; Stayton 2008; Wagenaar and Adami 2004; Yedid and Bell 2002; Yedid et al. 2008). However, in recent years, phylogenetic comparative methods have increasingly been employed to investigate questions about clade-wide convergence in natural systems. To date, most such studies have used phylogenies to identify instances of convergence or to test whether the frequency or fidelity of convergence within or among clades exceeds expectations under simple null models. However, comparative tools that incorporate evolutionary processes into models of convergence on macroevolutionary adaptive landscapes are now available, allowing tests of a wider range of hypotheses about evolutionary convergence using phylogenetic comparative data.

18.2 Historical Development of Methods for Studying Clade-Wide Convergence

Interest in clade-wide convergence predated the advent of modern phylogenetic comparative methods, meaning that the first quantitative techniques for studying convergence among evolutionarily distinct communities were necessarily nonphylogenetic. Starting in the 1970s, community ecologists tested for community convergence by directly comparing the ecological or morphological attributes of species in independent communities (reviewed in Cody and Mooney 1978; Orians and Paine 1983; Blondel 1991; Ricklefs and Miles 1994; Samuels and Drake 1997; Schluter 2000). A common technique for making such comparisons was to construct a multidimensional Euclidean 'morphospace' (Ricklefs and Travis 1980; Wiens 1991; Gatz 1979) and to ask whether the communities showed phenotypic matching (e.g., exceptionally small mean Euclidian distances between species and their nearest neighbors from the other community in morphospace). If the sets of species were well-matched despite their different evolutionary histories, then a case could be made that the communities were convergent (Cody and Mooney 1978; Ricklefs and Travis 1980; Gatz 1979; Ricklefs and Miles 1994). Using this framework, one could test whether communities were more similar than expected using a given null distribution, usually obtained by randomization.

A drawback of this approach is that it is ahistorical and thus does not explicitly test whether organisms have evolved to be more similar to one another than were their ancestors (i.e., whether they are truly convergent or just similar). This point was certainly appreciated by many early workers, and led some to focus on comparisons of communities on different continents (Karr and James 1975; Orians and Solbrig 1977a; Ricklefs and Travis 1980). Schluter (1986) indirectly addressed this problem by comparing the similarity observed among communities in matching habitats from different regions (and different evolutionary origins, presumably) to the similarity observed among communities in contrasting habitats from the same region. Such a pattern of differences among relatives and similarities with species in similar communities would be consistent with community convergence. However, an alternative explanation for the same pattern is that community matching might be due to ecological sorting from a larger species pool in each region rather than convergent evolution.

A critical step in testing for convergence of communities or radiations was thus the incorporation of evolutionary history into statistical null models. According to this approach, the investigator quantifies the similarity of communities or clades using a standard statistical measure as described above, such as the mean nearest-neighbor distance in morphospace, and then evaluates this statistic against an evolutionary null distribution (Fig. 18.1). We refer to this as the 'statistical' approach in what follows. The null distribution may be generated by simulating trait data on a phylogenetic tree using an evolutionary model that lacks deterministic evolutionary convergence, such as random-walk Brownian motion (BM) (Fig. 18.2) or a single-optimum Ornstein–Uhlenbeck (OU) model. The OU model (Uhlenbeck and Ornstein 1930) includes stochastic evolution as well as attraction toward an 'optimum' trait value, which has the effect of eroding the signal of evolutionary history and reducing the volume of trait space that can be explored (Felsenstein 1988). These features make it useful as a null model that can result in phenotypically similar species without deterministic convergence. The observed measure of convergence can then be compared to this null distribution to test whether putatively convergent groups of species are more similar than expected by chance. A related approach uses phylogenetic simulations to generate a null distribution of a test statistic for ANOVA-like designs (Garland et al. 1993), where the goal is to quantify the phenotypic similarity of unrelated species belonging to categories representing putatively convergent niches (e.g., Brandley et al. 2014; Glor et al. 2003; Harmon et al. 2005; Johnson et al. 2009; Winchester et al. 2014).

Thus far, we have focused on testing for convergence among clades from different regions or among multiple clades that have radiated within a shared region, but another form of 'clade-wide convergence' occurs when multiple sets of lineages in a single large clade converge on one another within a broad geographic region. An alternative method for identifying exceptional convergence in such cases considers how the phenotypic similarity of species is related to the phylogenetic distance between them (Muschick et al. 2012). Stochastic models such as BM predict a general increase in phenotypic distance at increasing evolutionary scales, and despite a high variance in phenotypic distance among distantly related pairs of species, relatively few such pairs are expected to have highly similar phenotypes. In contrast, if convergence is widespread, one can predict an overrepresentation of pairs of phenotypically similar distant relatives. Muschick et al. (2012) devised a test for this pattern that summarizes a plot of phenotypic versus phylogenetic distances using hexagonal binning and tests for a surplus of pairs in bins representing high phylogenetic distance and low phenotypic distance compared to

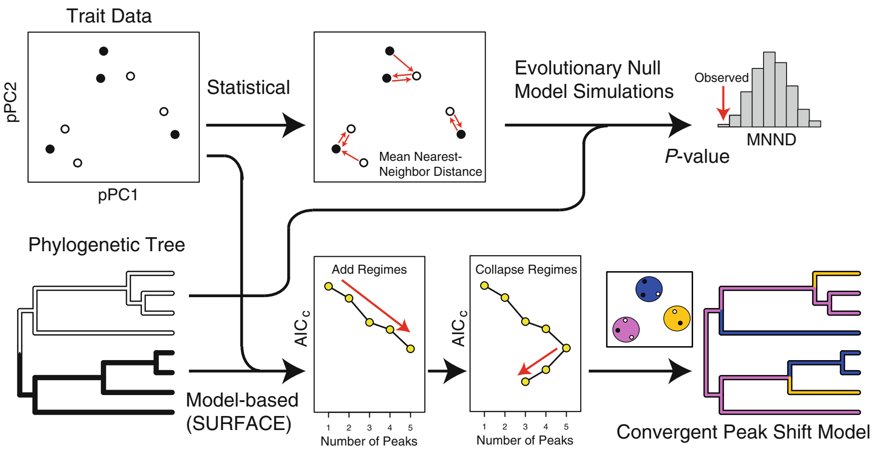

Fig. 18.1 Workflow for two approaches to studying clade-wide convergence using a phylogenetic tree and trait data (multiple phenotypic axes, such as from a phylogenetic principal components analysis). The example data set shown here contains clades in two regions (*white* and *black*), which form three clusters in trait space. The *upper* path illustrates the 'statistical' approach to accounting for phylogeny, in which trait data are used to calculate a statistic summarizing the extent of among-region similarity which is then compared to the same value calculated for data simulated on the tree using an evolutionary null model such as Brownian motion. In this example, the mean of the nearest-neighbor distances between each species and its most similar counterpart in the second region or clade is employed as the summary statistic. The summary statistic can be compared to the null distribution to test for significant clade-wide convergence, but does not incorporate a process model required for model comparison or predictive simulations. The *lower* path shows the approach used by SURFACE to fit macroevolutionary models that incorporate convergence to the tree and trait data. The two stages use stepwise $\mathrm{AIC_c}$ first to place peak shifts on the tree and then to identify shifts that are to the same, convergent peak. The method outputs a mapping of the peaks to each branch of the tree and estimates of the peak positions in trait space and the rates of adaptation and stochastic evolution. This 'Hansen' model can then be used in comparison with null or alternative models or to characterize features such as the geographic context (see Fig. 18.3) or dimensionality (see Fig. 18.4) of convergence

evolutionary null models. As long as stasis over long timescales can be ruled out as a cause of similarity between distant relatives, this method provides a means to detect widespread convergence within a clade. While the first application focused on convergence within a region (Lake Tanganyika cichlids), one could also focus on pairs of species from the same or from different regions to test the prevalence of convergence in both geographic contexts.

A drawback of all of these statistical approaches is that they do not explicitly model a process underlying convergent evolution. Instead, they at best compare a measured empirical pattern to a model such as BM that lacks convergent processes, to determine whether the empirical pattern differs from the null expectation in a manner consistent with clade-wide deterministic convergence. While this

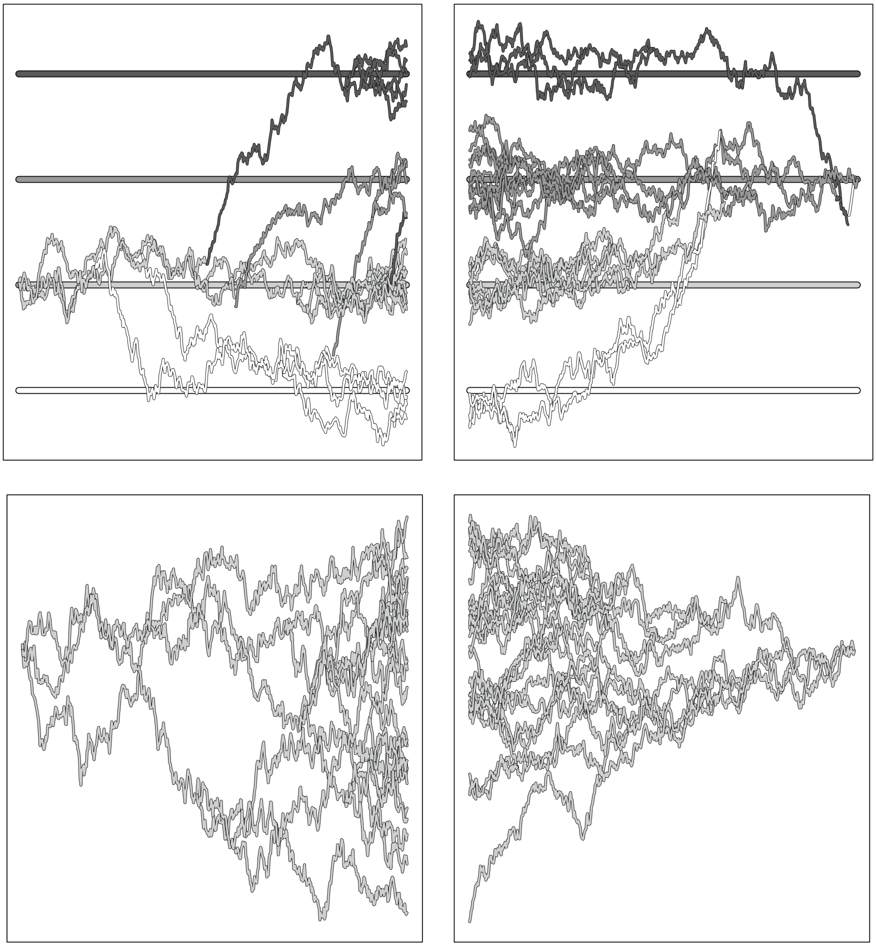

Fig. 18.2 Visualization of deterministic convergence versus chance similarity in two clades. The *top panels* show trait values over time of two clades diversifying to occupy the same set of four adaptive peaks (Ornstein–Uhlenbeck optima, denoted by *horizontal lines*). While the clades differ in ancestral state and the sequence of peak shifts, the resulting faunas are deterministically similar as a result of diversification on the same macroevolutionary landscape. This can be contrasted with the *lower panels*, which show traits evolving under Brownian motion during diversification. In one or a few trait dimensions, some lineages are expected to evolve similar trait values purely by chance; an important goal of any tests for clade-wide convergence is ruling out chance as an explanation for faunal similarity

remains a useful technique for hypothesis testing, it does not provide the means to estimate evolutionary parameters that can result in convergence or allow for comparison with alternative models.

18.3 Development of the Phylogenetic Ornstein–Uhlenbeck Model of the Macroevolutionary Adaptive Landscape and its Utility for the Study of Clade-Wide Convergence

The incorporation of processes that underlie convergence into model-based phylogenetic comparative methods presents new opportunities to gain a mechanistic understanding of replicated radiations. BM does not include the deterministic component necessary to represent adaptive evolution on a macroevolutionary landscape, which makes it useful as a null model but unsuitable if we wish to model convergence explicitly. An important advance was achieved with the realization that versions of the OU model (Uhlenbeck and Ornstein 1930) could be applied to models of adaptive evolution (Chaps. 14 and 15). The deterministic component of the OU process causes a species' mean trait value to be pulled toward an optimum, with a force proportional to its distance from the optimum (Chap. 15). Lande (1976) showed that this model can describe the evolution of a continuous trait in a population under a balance of stochastic mutation and genetic drift and deterministic selection that is directional when the population is approaching the optimum and stabilizing when it is at the optimum. While the parameters of the OU model estimated from comparative data often do not correspond well to population genetic parameters (Harmon et al. 2010), the model has proven to be a useful representation of adaptive evolution, in which the optimum can be interpreted as the location of an adaptive peak (Felsenstein 1988; Martins 1994).

An important advance came when Hansen (1997) demonstrated how the OU model could be used to model peak shifts on a macroevolutionary adaptive landscape (e.g., Simpson 1944). If certain lineages within a clade begin evolving toward a new peak, such as equids shifting from browsing to grazing, this can be modeled as these lineages becoming attracted to a new optimum trait value. Hansen (1997) showed how this peak-shift model could be fit to a phylogenetic tree and trait data, and Butler and King (2004) subsequently introduced the 'OUCH' methodology as a generalized framework for fitting such 'Hansen' models by 'painting' the branches of a tree with multiple selective regimes, each corresponding to a hypothesized peak. The multipeak OU model can thus be interpreted as a representation of the macroevolutionary landscape (Simpson 1944) and can be used to test hypotheses such as whether clades in multiple regions have reached the same set of peaks (Fig. 18.2). The parameters of the model are the positions of one or more optima $\boldsymbol{\theta}$; the rate α at which species adapt toward their present optimum; and the Brownian rate parameter σ^2 that governs the magnitude of stochastic fluctuations in trait values (an additional parameter represents the root state and is typically assumed to come from the stationary distribution of the OU process rather than being estimated—see Chap. 15 for additional discussion). The macroevolutionary landscape is characterized by one or more adaptive peaks, with the relative rates of adaptation and stochastic evolution roughly indicative of the steepness of the peaks. We deal here with 'Simpsonian' macroevolutionary landscapes that measure individual fitness as a function of phenotypic values, in contrast to 'Wrightian' landscapes that measure population mean genotype fitnesses (Hansen 2012; Svensson and Calsbeek 2012).

The Hansen model has been widely used to test adaptive hypotheses, such as whether species in different regimes (typically defined based on ecological contexts such as discrete habitats) repeatedly evolve toward different phenotypic optima. Other elaborations of the OU model allow variation among regimes in α and σ^2 in addition to the positions of optima (Beaulieu et al. 2012; Chap. 15), increasing the variety of hypotheses that can be tested. The Hansen model is a valuable tool for comparative hypothesis testing, but there is an important caveat that limits its applicability to testing for replicated radiation. The method requires an a priori adaptive hypothesis, such that one must paint the hypothesized regimes onto specific branches to reflect taxa already thought to be convergent in advance of testing for clade-wide convergence. This approach is suitable for testing certain hypotheses about convergent evolution, such as whether particular ecological or behavioral shifts consistently lead to adaptation of similar morphological traits (e.g., Collar et al. 2011; Frédérich et al. 2013; Lapiedra et al. 2013). However, if we wish to assess the extent of convergence using phenotypic data alone, it would be circular to first use phenotypic similarity to assign species to regimes. To deal with this limitation, we devised an algorithm for fitting Hansen models to a data set in the absence of a priori hypotheses and thus objectively identifying convergent peak shifts (Ingram and Mahler 2013).

18.4 Using SURFACE to Infer a Macroevolutionary Adaptive Landscape from Comparative Data

As we have described, tests for clade-wide convergent evolution have been dominated by two approaches. One statistically quantifies the similarity of communities or faunas and uses null model comparisons to assess whether the observed similarity exceeds what would be expected by chance. This method has the benefit of objectivity, but does not incorporate a mechanism underlying convergence. The second approach uses model-based comparative methods to test whether independent shifts to shared selective regimes result in convergent phenotypic evolution. This method incorporates adaptive processes, but its reliance on potentially subjective regime specification is problematic if we wish to test for clade-wide phenotypic convergence without using independent data to define regimes.

To bridge this gap, we introduced the SURFACE method, which constructs a representation of the macroevolutionary adaptive landscape, taking as inputs only continuous trait data and a tree (Ingram and Mahler 2013). SURFACE (a recursive acronym for 'SURFACE Uses Regime Fitting and AIC to model Convergent Evolution') uses stepwise AIC (Alfaro et al. 2009; Thomas and Freckleton 2012) to first identify peak shifts well supported by the data and then to identify whether any of these shifts involve convergence toward the same peaks (Fig. 18.1). The method is implemented as the R package ‘surface’, which contains functions for running the analysis, simulating data sets, and visualizing the results.

Here, we briefly outline the steps involved in a SURFACE analysis, and refer the reader to Ingram and Mahler (2013) for a detailed description. First, a single-peak OU model is fit to the phylogeny and continuous trait data using maximum likelihood. This approach can handle multidimensional trait data by making the simplifying assumption that there are no covariances between traits in the rates of adaptation (α) or stochastic evolution (σ^2), which is most likely to be valid if the traits are orthogonal axes such as those obtained from a principal components analysis. This assumption allows the log likelihoods calculated separately for each trait to be added together to give the overall model log likelihood L. A set of all candidate models in which a peak shift is added to one branch in the tree is then generated (in the present implementation, each branch may experience only a single peak shift, which occurs at its origin). Each model is fit, and log likelihoods are added across traits as before. For each candidate model, the small sample size-corrected Akaike Information Criterion ($\mathrm{AIC_c}$) is calculated as a measure of model performance that accounts for the model complexity (number of parameters, p) and sample size n (number of species k multiplied by number of traits m).

$$\mathrm{AIC_c} = -2\log L + 2k + \frac{2p(p+1)}{n-p-1} \tag{18.1}$$

The addition of one peak shift adds one parameter per trait to account for the new estimated optima and one parameter to represent the phylogenetic placement of the peak shift. The candidate model that most improves (i.e., reduces) the $\mathrm{AIC_c}$ is selected, a peak shift is placed at the origin of the corresponding branch, and the process is iterated to place additional peak shifts until the $\mathrm{AIC_c}$ ceases to improve.

This ‘forward’ phase of the method yields a Hansen model containing some number of peak shifts, each of which is toward a different peak. The second, ‘backward’ phase evaluates the fit of models in which sets of shifts are toward to the same convergent peak. Reducing the number of peaks (and optima) in the model may improve the $\mathrm{AIC_c}$ if the model likelihood remains high despite the reduction in model complexity. This second stepwise process is iterated until model improvement stops and a final model is identified. The extent of convergence in this model can be quantified in a number of ways, including the reduction in the number of peaks in the backward phase and the number of peak shifts that are toward convergent peaks (see 18.5). Once quantified, measures of convergence from the fitted model can be compared to a null distribution obtained by running SURFACE on data simulated under BM or other models that lack deterministic convergence. Additionally, parametric bootstrapping can be carried out to construct approximate confidence intervals on the convergence parameters or other parameters of interest, by running SURFACE on many data sets simulated under the fitted Hansen model. These approaches allow the researcher to evaluate whether the extent of convergence in a model is greater than expected by chance.

18.5 Extending SURFACE to Ask Questions About the Nature of Convergence in Replicated Radiations

SURFACE provides a Hansen model representing the macroevolutionary adaptive landscape, as well as several measures of the extent and frequency of convergence, but additional steps are needed to interpret the details of any detected convergence. Here, we describe new methods for characterizing the biogeographic pattern of convergence and for comparing the extent of convergence among traits.

a. The geographic context of convergence

Biogeography is central to many hypotheses about clade-scale convergence and must be incorporated if we wish to use SURFACE to infer whether convergence tends to occur because radiations in different regions are replicated (e.g., Chiba 2004; Mahler et al. 2013; Ellingson 2013) or because radiations generate locally replicated adaptive diversity within regions (e.g., Kozak et al. 2009; Muschick et al. 2012). Some degree of replicated radiation can be inferred if the same peaks are occupied by lineages in each region, and such an inference may be straightforward in cases where each region is occupied by a distinct subclade. However, if the ancestral geographic locations of lineages are uncertain, we need appropriate statistical methods to account for this uncertainty in evaluating whether adaptive peak shifts occurred in the same or in different regions.

We describe a simple approach to inferring the biogeography of convergence using a Hansen model fitted by SURFACE, which contains some number of peak shifts, each assigned to a branch in the tree. We combine this information with hypothesized biogeographic histories that include the timing of dispersal events between regions and can be used to estimate the region in which each peak shift occurred. The calculations described below require that each node in the tree can be assigned to a single geographic region; if some ancestors are though to span multiple regions, a reasonable approach may be to treat this as uncertainty and sample histories that include the different regions. Biogeographic history estimates may come from a variety of techniques including ancestral character reconstruction using likelihood or parsimony and stochastic character mapping (Huelsenbeck et al. 2003). While these histories can include one or more dispersal events along a branch, we consider only the geography at the beginning and at the end of each branch. We do this so that geography is defined at the same resolution as peak shifts, as SURFACE is limited to inferring one peak shift per branch. We make the assumption that the region occupied at the end of a branch (rather than the region occupied by the parent species when the branch originated) is the region in which any peak shift occurred. Unless specified otherwise, the peak shift placed at the root of the tree in the Hansen model is assumed not to correspond to a geographic shift.

To illustrate our approach, we incorporate estimates of geographic history into an analysis of ecomorphological convergence in Greater Antillean anoles (Fig. 18.3). Mahler et al. (2013) used SURFACE to show that there are many more instances of convergence in this group than expected by chance, and inferred that

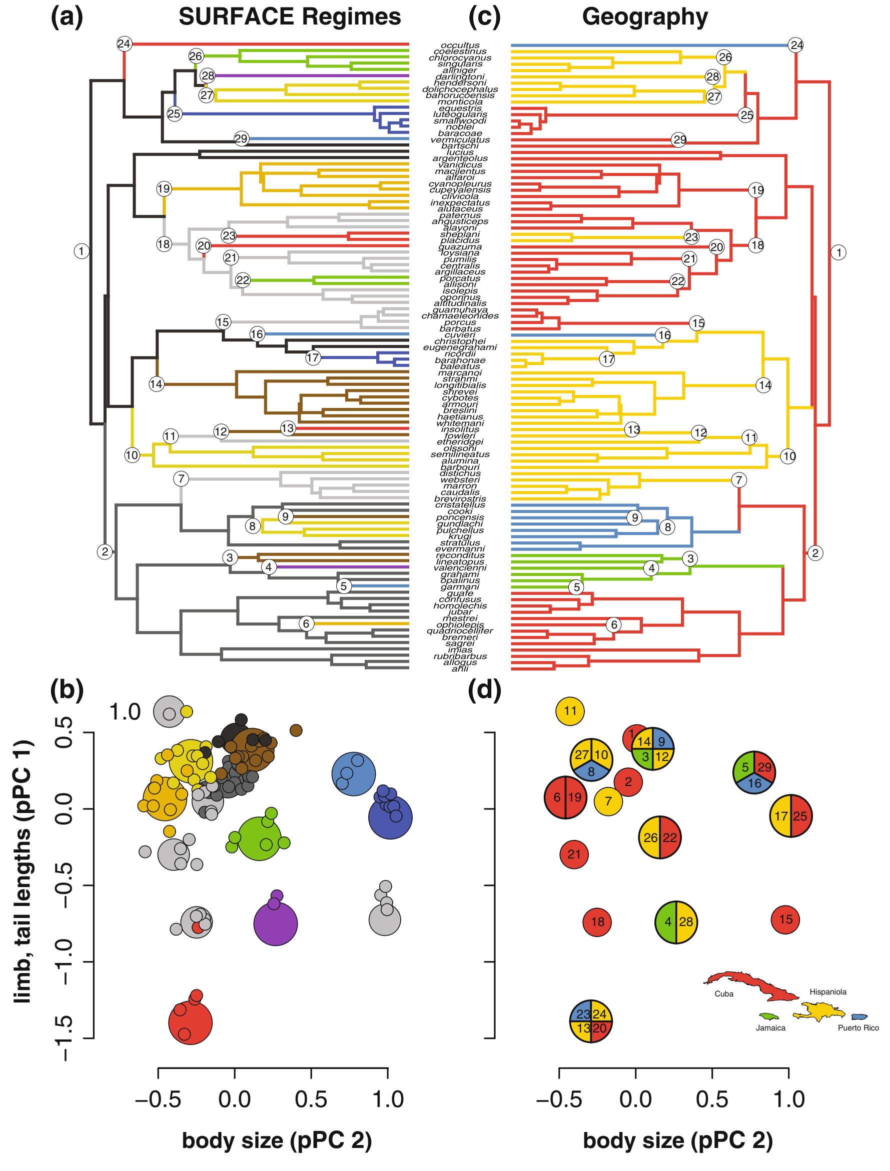

Fig. 18.3 Illustration of a Hansen model obtained using SURFACE that illustrates the biogeography of exceptional clade-wide morphological convergence in Greater Antillean *Anolis*. The *left panels*, adapted from (Mahler et al. 2013), illustrate the placement of adaptive peaks on the branches of the phylogenetic tree (**a**) and in morphospace (**b**). Branches in color indicate convergent peaks (that attract more than one lineage), while non-convergent peaks are in gray scale. **b** shows the first two dimensions of a four-dimensional morphospace for Greater Antillean anoles derived from a phylogenetic principal components analysis (pPCA). *Large circles* denote estimated positions for peaks on the macroevolutionary landscape (*circles* are slightly *larger* for convergent peaks than non-convergent ones), and small circles denote trait values for the 100

◀extant anole species in the data set. Colors of species' trait values and the optima to which they are attracted correspond to **a**. The *right panels* show the biogeography of anoles on the tree (**c**) and of the peaks in morphospace (**d**). The phylogeny in **c** is identical to **a**, but branches are colored according to the Greater Antillean island occupied at the end of the branch (see text) in one stochastic character map estimate of *Anolis* geographic history. *Panel* **d** depicts the estimated positions of adaptive peaks in morphospace as in **b**, but colored by island to indicate the geography of convergent and non-convergent peak shifts. Numbers indicate which lineages from **c** have shifted to each adaptive peak, allowing assessment of whether shifts to convergent peaks occurred within the same geographic region (e.g., shifts 6 and 19), in different regions (e.g., shifts 17 and 25) or both (e.g., shifts 8, 10 and 27). Note that for the morphospace panels, peaks that appear to overlap are distinct in other trait dimensions (not illustrated) that were part of the SURFACE analysis

most instances of convergence involved lineages from multiple islands. To formalize the latter result and to uncover additional details about the geography of Greater Antillean anole convergence, we use stochastic character mapping with the 'make.simmap' function in the 'phytools' R package (Revell 2012; Chap. 4) to generate 1,000 biogeographic histories of transitions between the four islands (Cuba, Hispaniola, Jamaica, and Puerto Rico; Fig. 18.3c). We then reconsider the macroevolutionary landscape inferred by SURFACE (Mahler et al. 2013) in an explicitly geographic context.

Having inferred the phylogenetic positions of both peak shifts and geographic shifts, we can ask a variety of questions about the geography of convergence. The biogeographic question most relevant to tests for replicated radiation is whether convergence to a shared peak typically occurs in distinct regions or within a single region. To assess this, we examine two alternative measures that categorize convergence by geography: one uses the geography of individual convergent peak shifts, while the other uses the geography of pairs of convergent lineages. While these measures provide similar information, they allow us to ask somewhat different questions about the geography of convergence.

The first approach classifies each peak shift based on the geographic context of the lineages that have reached that peak. We first count the number of peak shifts in the model fitted by SURFACE that are toward convergent peaks, denoted as c (Ingram and Mahler 2013). For each of the c convergent peak shifts, we ask whether the shift occurred toward a peak occupied only by lineages that occur in different regions from that of the focal lineage, and we count the total number of such shifts as c_{between} (e.g., shifts 3, 8 and 29, among others, in Fig. 18.3d). Next, we count the number of convergent shifts that occur toward a peak that is only occupied by lineages from the same region, c_{within} (e.g., shifts 6 and 19 in Fig. 18.3d). Finally, we count the number of shifts to peaks occupied both by other lineages from the same region, as well as lineages from different regions, c_{both} (e.g., shifts 10, 12, and 27, among others, in Fig. 18.3d). These three geographic convergent shift statistics sum to c. Note that the total number of convergent shifts to peaks occupied in more than one region is the sum of c_{between} and c_{both} and that the total number of geographically replicated convergent shifts (i.e., shifts to peaks occupied by at least one other lineage from the same region) is the sum of c_{within}

and c_{both}. For *Anolis*, we averaged these calculations across the 1,000 stochastically mapped geographic histories. As expected, most of the convergent peak shifts (91 %) were to peaks occupied on multiple islands (i.e., $c_{\text{between}} + c_{\text{both}}$), while very few (9 %) were to single-island peaks (i.e., c_{within}; Fig. 18.3d). However, it was not uncommon for independent lineages from the same island to adapt to the same adaptive peak, and 36 % of shifts were to peaks occupied by at least one other lineage from the same island (i.e., $c_{\text{within}} + c_{\text{both}}$; Fig. 18.3d).

The second approach quantifies the geography of pairwise cases of convergence, examining all pairs of peak shifts that were toward the same peak. We define the number of such cases as *cc*: a peak reached by two shifts represents a single case of convergence; a peak reached by three shifts represents three pairwise cases, and so on. For each of the *cc* pairwise cases of convergence, we identify whether the two shifts occurred in the same region (e.g., for convergent peaks in Fig. 18.3d, whether pairs of shifts have the same color) or in different regions (pairs of shifts have different colors in Fig. 18.3d). We add these values to estimate the number of within-region cases of pairwise convergence (cc_{within}) and the number of between-region cases (cc_{between}), which sum to *cc* (Ingram and Kai 2014). The alternative measures *c* and *cc* provide similar information and will differ more in cases when many lineages converge on a small number of peaks. In anoles, we found that 82 % of pairwise cases of convergence occurred between islands (Fig. 18.3d), confirming the replicated nature of Greater Antillean anole radiations.

Specific hypotheses about replicated radiation can be carried out by comparing any of these geographic measures of convergence to null distributions, generated either by randomizing the positions of geographic and/or peak shifts or by analyzing simulated data sets with SURFACE. Related approaches could be used to ask additional biogeographic questions, such as whether convergence is more common in some regions than in others, whether shifts toward certain peaks only occur in certain types of regions (e.g., large versus small; temperate versus tropical), and whether peak shifts coincide with the colonization of novel areas. In anoles, we found that on average, 20 % of peak shifts occurred on branches containing geographic shifts, while 56 % of geographic shifts occurred on branches containing peak shifts. This indicates that most peak shifts occur within islands, but that about half of the anole colonizations to new islands nonetheless coincided with an adaptive peak shift. In addition to testing new hypotheses, there is scope for extending the methods described here to accommodate common biogeographic scenarios with added complexity, such as species that span multiple regions or regions that do not have discrete boundaries.

b. Partitioning the signal of convergence among traits

Another important feature of clade-wide convergence is the degree to which convergent evolution varies among traits in a multidimensional data set. The SURFACE algorithm combines evidence across multiple traits when identifying the best-fitting model at each step, making the simplifying assumption that the evolution of each trait is governed by independent parameters (α and σ^2).

However, a signal of convergence may arise in different ways: each trait may contribute approximately equally to the model improvement, or one or more traits may show very strong convergence, while others show little or none. In such a case, the additional non-convergent traits may reduce our ability to detect the strong signal of convergence in other phenotypic dimensions, and we may draw false conclusions about the dimensionality of convergence.

Here, we describe how one can visualize the contribution of each trait to the improvement in the overall model support (i.e., $\mathrm{AIC_c}$) during the course of model selection by SURFACE. We have previously visualized the change in $\mathrm{AIC_c}$ throughout the forward and backward phases using a line graph of model $\mathrm{AIC_c}$ against the number of peaks at each step (Ingram and Mahler 2013; Mahler et al. 2013). In a data set with evidence for many convergent peak shifts, this graph will appear roughly triangular, with an $\mathrm{AIC_c}$ decrease from left to right as peaks are added during the forward phase, and a second decrease from right to left as convergent peaks are collapsed during the backward phase.

To divide the $\mathrm{AIC_c}$ among traits, we must consider both components of the $\mathrm{AIC_c}$ (Eq. 18.1). The fit of the model to each trait, captured as the deviance ($-2\log L$), can easily be partitioned among traits as it is based on the sum of trait-specific log likelihoods. The second component of the formula is the ‘penalty’ term, which captures the complexity of the model (number of parameters p) and the correction for finite sample size (n). This component is not trait-specific (because the parameters representing the phylogenetic positions of shifts are shared across traits), but for the purpose of visualization, we divide this term by the number of traits (m) and then add this value to the deviance for each trait i to obtain a ‘partial $\mathrm{AIC_c}$’:

$$\text{partial } \mathrm{AIC_c}(i) = -2logL_i + \frac{1}{m}\left(2p + \frac{2p(p+1)}{n-p-1}\right). \qquad (18.2)$$

We standardize the overall $\mathrm{AIC_c}$ and the partial $\mathrm{AIC_c}$ of each trait to initial values of zero and then plot the partial $\mathrm{AIC_c}$ values along with the overall $\mathrm{AIC_c}$ as a function of the number of peaks through both phases of the analysis. For each point on the line graph, the sum of the partial $\mathrm{AIC_c}$ values is equal to the overall $\mathrm{AIC_c}$.

The extent to which the partial $\mathrm{AIC_c}$ for each trait declines gives an indication of how much it contributes to the addition of peak shifts during the forward phase and to the identification of convergent peak shifts during the backward phase. If all traits contribute roughly equally, their lines will each show a similar decline, while if the signal is dominated by a single trait, the latter’s partial $\mathrm{AIC_c}$ will decline substantially, while those of the other traits may decline little or even increase. This visualization can be done using the function ‘surfaceAICPlot’ in the ‘surface’ package, which has an option *traitplot* that can be set to *dev* for deviance or *aic* to use the partial $\mathrm{AIC_c}$ values. If the deviance is used, the values will sum to give the total model deviance rather than the $\mathrm{AIC_c}$; as the deviance cannot improve as the number of parameters decreases during the backward phase, we find the visualization using partial $\mathrm{AIC_c}$ more intuitive.

To illustrate this approach, we show a partial $\mathrm{AIC_c}$ plot from the SURFACE analysis of ecomorphological convergence in the anole data set, which consists of four traits derived from a phylogenetic principal components analysis (Revell 2009; Fig. 18.4). This visualization shows that the first two trait axes, which correspond to relative limb length and body size and combine to explain 73 % of the total variation, each contribute strongly to the overall improvement in model fit. The third axis, which loads with relative tail and limb lengths, showed moderate improvement, while the $\mathrm{AIC_c}$ for the fourth axis, representing toepad lamella number, worsened throughout the forward phase. This trait-by-trait examination of the anole analysis reinforces the longstanding view that convergence in anoles is multidimensional (e.g., Harmon et al. 2005), but indicates that not all trait axes show the same signal. While repeating a SURFACE analysis following the post hoc removal of traits that failed to contribute to model improvement constitutes data dredging and would thus be problematic for hypothesis testing, care should be taken at the outset not to include traits that lack biological relevance (such as very minor axes of a principal components analysis) or that are unrelated to the ecological and evolutionary questions of interest.

18.6 Caveats, Future Directions, and Conclusions

18.6.1 Caveats

Direct inference of convergence requires that the similarity of putatively convergent species can be compared to that of their ancestors. Because empirical information about ancestral phenotypes is typically lacking, detecting convergence using comparative data is a challenge. By explicitly modeling processes that can cause convergence and examining the fit of such models to empirical data, we can use phylogenetic approaches to gain new insights into convergence. Nonetheless, such approaches have only recently been developed, and current methods exhibit several limitations. Here, we discuss caveats associated with the use of existing landscape models and propose several suggestions for the improvement and further development of comparative tools for studying convergence.

The SURFACE method generates an approximation of the macroevolutionary adaptive landscape in the form of a multiple-peak phylogenetic Hansen model. While this model incorporates important evolutionary processes, it is a rather simple representation of the landscape (Hansen 2012; Ingram and Mahler 2013). The Hansen model estimated by SURFACE contains estimates of the phylogenetic positions of adaptive peak shifts, the positions of the peaks in morphospace ($\boldsymbol{\theta}$), the trait-specific rate of adaptation of lineages toward those peaks (α), and the trait-specific rate of stochastic evolution (σ^2). A more general model of evolution on the macroevolutionary adaptive landscape would permit variation in the evolutionary parameters, so that peaks might vary in height or steepness or some lineages might

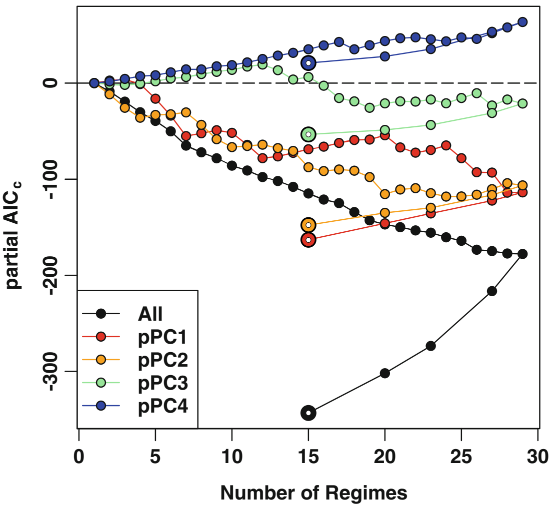

Fig. 18.4 Visualizing the relative contributions of individual traits to multidimensional convergence. This figure shows the relative 'partial AIC_c' scores for each trait axis (*colored sequences*) as well as the relative multidimensional AIC_c scores (*black sequence*) for all of the models fit during a single SURFACE analysis of Greater Antillean anoles. For each trait, partial AIC_c values are standardized relative to the partial AIC_c score of the initial single-peak Hansen model. Starting at the left with a partial AIC_c value of zero (corresponding to the single-peak OU model), each sequence records that trait's relative model support for each Hansen model (y-axis) as the number of independent adaptive peaks (x-axis) is increased during the forward SURFACE phase and then reduced during the backward phase as convergence among independent lineages is permitted. Although cumulative model support increases at each SURFACE step (decreasing AIC_c values at each step in the full model sequence), model support for individual traits does not improve uniformly as peaks are added, and peak shifts are sometimes added even if they decrease model support for some traits, provided that these losses are offset by gains in model support for other traits. An estimate of the relative contribution of each trait to the fit of the final Hansen model may be obtained by comparing the partial AIC_c values of all traits for this model (*larger circles* with *white dots* in the *center*). In the case of Greater Antillean *Anolis*, the overall fit of the final Hansen model is driven in large part by relative limb length (pPC1) and body size (pPC2), with a smaller contribution from relative tail and forelimb lengths (which have contrasting loadings on pPC3). The final model actually provides an inferior fit to toepad lamella data (pPC4) than the initial single-peak model. Note that while individual traits varied in whether they supported the addition of new peaks during the forward phase, all traits supported the simplification of the macroevolutionary landscape as similar peaks were modeled as convergent

have higher intrinsic rates of adaptation or stochastic evolution. The flexible Ornstein–Uhlenbeck 'OUwie' model described by Beaulieu et al. (2012; Chap. 15) permits α and/or σ^2 to vary across the tree, but is not presently implemented to operate in the absence of an a priori hypothesis about the phylogenetic positions of shifts in $\boldsymbol{\theta}$, α, and σ^2. While it is in theory straightforward to use stepwise model selection to compare flexible Ornstein–Uhlenbeck models, it may prove challenging in practice due to the need to fit large numbers of candidate models at each step, and the possibility that many data sets will not contain enough information to distinguish among alternative plausible parameter combinations for such complex models (Beaulieu et al. 2012).

SURFACE also assumes that the positions of peaks on the adaptive landscape are static, but both Simpson's description (Simpson 1944) and recent elaborations (Arnold et al. 2001; Hansen 2012) allow dynamic macroevolutionary landscapes on which species adapt toward peaks whose positions shift over time. If the landscape is dynamic, our ability to identify and interpret clade-wide convergence will likely depend on whether peaks move in synchrony in different regions (e.g., if they are tracking shared climatic changes) or more idiosyncratically. Recent methodology allows the incorporation of moving optima into the inference of OU model parameters (Bartoszek et al. 2012; Hansen et al. 2008), and extensions of these methods may allow the inference of convergence even in cases where the adaptive landscape is dynamic. Another possibility is to relax the assumption of SURFACE that each trait is evolutionarily independent in terms of its α and σ^2 and to evaluate the influence of correlated evolution as lineages converge to shared adaptive peaks (Bartoszek et al. 2012).

As with any statistical tool, users of SURFACE should ensure both that they have a data set that is sufficiently large and complete to support the fitting of complex models (see discussion in Ingram and Mahler 2013) and that the assumptions of the standard Hansen model yield realistic parameter estimates for their data. The examination of the estimated positions of trait optima in morphospace may aid in evaluating the appropriateness of the model, with two possible interpretations in the event that any estimated optima are extreme, falling far outside the range of trait values in morphospace. First, the assumption that all evolutionary regimes have the same rates of adaptation and stochastic Brownian evolution may be invalid, and the optimum might be estimated to be distant because the rate of adaptation to the peak is constrained to equal the lower rate supported elsewhere in the clade. Alternatively, the poorly matched species may in fact be experiencing directional selection toward a distant optimum (though the position of the optimum itself is unlikely to be estimated well). In addition to visual inspection, posterior predictive simulation may be useful for checking whether empirical measures of convergence indeed arise from the fitted model (e.g., see Mahler et al. 2013). Also, pairing a SURFACE analysis with a 'statistical' approach for testing for convergence as described above may help to confirm the robustness of the pattern of similarity implied by the model fit.

Because a Hansen model estimated by SURFACE contains a mix of parameters representing the evolutionary model ($\boldsymbol{\theta}$, α, and σ^2) and parameters describing the extent of convergence in this model (e.g., *c*, *cc*, and the geographic variables discussed in 18.5), uncertainty in the model must be considered at multiple levels. A single SURFACE analysis does not provide an estimate of this uncertainty, but it is straightforward to calculate confidence intervals for the rates and optima using parametric bootstrapping, simulating many data sets under the fitted model and re-estimating the parameters. A similar bootstrapping approach can be used to infer confidence intervals for measures of convergence, although this requires the more time-consuming process of simulating under the fitted model and running SURFACE on each resulting data set. This approach can in theory be extended to incorporate uncertainty in the topology and branch lengths of the phylogeny itself, by running analyses on a sample of trees (e.g., from the posterior distribution from a Bayesian phylogenetic analysis). While variation in topology among trees precludes direct comparisons of the Hansen models returned by SURFACE, one can combine bootstrapped estimates of convergence parameters across trees to obtain confidence intervals that more completely account for uncertainty.

There are many possible Hansen models that could be fit to a given data set, and while the stepwise algorithm used in SURFACE provides a means of navigating among candidate models, it also results in many models never being evaluated. In some cases, the early fixation of well-supported shifts may preclude the later discovery of globally superior Hansen models that do not include those shifts. Unlike with the model parameters, it is not straightforward to measure the uncertainty in the fitted model that is due to these stepwise constraints. A partial solution to this problem is provided in the *sample_shifts* option of the 'surfaceForward' and 'runSurface' functions in the 'surface' package, which permits the fixation of suboptimal shifts (chosen randomly from a sample of models above a specified support threshold) during an individual SURFACE run. By repeatedly running SURFACE using relaxed model selection criteria, it is possible to obtain a set of models for which an important element of path dependency has been relaxed (see Mahler et al. 2013 for an example). Although such a set of models is not statistically analogous to a sample of models from a Bayesian posterior distribution, it can nonetheless be used to heuristically assess the influence of path dependency on parameter estimates, as well as to potentially identify models that may be superior to the model returned by the standard SURFACE analysis.

In the future, it may be possible to simultaneously address several of these issues by exploring model and parameter space in a Bayesian framework. Bayesian Markov Chain Monte Carlo methods have recently been employed for a similar comparative purpose—identifying the locations of phylogenetic shifts in the evolutionary rate without a priori information (Eastman et al. 2011; Revell et al. 2012; Venditti et al. 2011), and a similar approach could be employed to model adaptive peak shifts. To identify shifts, it would be necessary not only to estimate Hansen model parameters, but also to estimate the numbers of total and convergent peak shifts, meaning that the algorithm would need to evaluate models that differ in the number of estimated parameters. Eastman et al. (2011) used reversible-jump MCMC to sample from models of varying complexity to determine the number and placement of evolutionary rate shifts that have occurred in a clade, and this approach may be suitable for examining shifts among evolutionary regimes. Alternatively, the clustering of convergent lineages into discrete regimes in morphospace might be modeled using a Dirichlet process prior (e.g., Heath et al. 2012) in which both the number and phylogenetic branch composition of regimes, as well as the evolutionary parameters that characterize these regimes are estimated.

18.6.2 Future Directions

The development of methods for explicitly modeling macroevolutionary convergence provides a powerful framework for studying convergence among entire communities or clades. This is leading to renewed investigation of key questions in ecology and evolution, such as whether radiations in different biogeographic regions are more similar than expected by chance and whether significant convergence occurs within single regions. In combination with suitable 'statistical' approaches to measuring the pattern of similarity, macroevolutionary models of convergence provide the means to ask many additional questions about phenotypic convergence.

One potentially useful application of SURFACE might be to directly model convergence in species' ecological attributes (e.g., continuous measures of habitat use, climatic niche preferences, or diet), rather than morphological traits that are thought to reflect ecological adaptations. The Hansen model fit to the ecological attributes of extant species might reveal whether distinct ecological niches are stable and convergent over long timescales. Further, the evolutionary correspondence between ecology and morphology could be investigated explicitly through comparison of macroevolutionary adaptive landscapes separately estimated for clades using ecological versus morphological attributes. By examining the positions of peak shifts in each Hansen model, one could use such information to ask whether species adopt novel ecological preferences prior to evolving morphological specializations, or alternatively whether morphological innovations precede novel resource use. Likewise, a comparison of ecological and morphological macroevolutionary landscapes might complement functional studies to reveal 'many-to-one mapping,' an alternative to morphological convergence in which lineages adapting to similar ecological pressures evolve different morphological solutions (Alfaro et al. 2005; Bock 1980; Bock and Miller 1959; Losos 2011).

Models of the macroevolutionary landscape may also be useful for answering longstanding questions about the sequence of adaptations during the evolutionary assembly of communities and clades. Hansen models provide an estimate of the temporal sequence of peak shifts, though we note that accurate placement of peak shifts on the branches of the phylogeny becomes more difficult for deep branches or when peak shifts are frequent (Ingram and Mahler 2013). Information about the timing of peak shifts could be used to test whether adaptive peaks in replicated radiations are colonized in the same sequence or whether the evolutionary assembly of similar radiations is more idiosyncratic (Ackerly et al. 2006; Losos et al. 1998; Sallan and Friedman 2012; Streelman and Danley 2003); reviewed in (Glor 2010). Other questions about the filling of morphospace that could be addressed are whether peak shifts tend to occur between nearby peaks (versus large jumps through morphospace) and whether peaks at the periphery of morphospace tend to be discovered later in the course of adaptive radiation (Gavrilets and Vose 2005; Price 1997; Ricklefs and Travis 1980). The continued application and elaboration of macroevolutionary adaptive landscape models has the potential to address many exciting questions about convergent evolution in adaptively radiating clades.

References

Ackerly DD, Schwilk DW, Webb CO (2006) Niche evolution and adaptive radiation: testing the order of trait divergence. Ecology 87:S50–S61

Alejandrino A, Puslednik L, Serb JM (2011) Convergent and parallel evolution in life habit of the scallops (Bivalvia: Pectinidae). BMC Evol Biol 11:164. doi:10.1186/1471-2148-11-164

Alfaro ME, Bolnick DI, Wainwright PC (2005) Evolutionary consequences of many-to-one mapping of jaw morphology to mechanics in labrid fishes. Am Nat 165:140–154. doi:10.1086/429564

Alfaro ME, Santini F, Brock C, Alamillo H, Dornburg A, Rabosky DL, Carnevale G, Harmon LJ (2009) Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. Proc Natl Acad Sci 106:13410–13414. doi:10.1073/pnas.0811087106

Arendt J, Reznick D (2008) Convergence and parallelism reconsidered: what have we learned about the genetics of adaptation? Trends Ecol Evol 23:26–32. doi:10.1016/j.tree.2007.09.011

Arnold SJ, Pfrender ME, Jones AG (2001) The adaptive landscape as a conceptual bridge between micro- and macroevolution. Genetica 112–113:9–32

Bartoszek K, Pienaar J, Mostad P, Andersson S, Hansen TF (2012) A phylogenetic comparative method for studying multivariate adaptation. J Theor Biol 314:204–215. doi:10.1016/j.jtbi.2012.08.005

Beatty J (2006) Replaying life's tape. J Philos 103:336–362

Beatty J (2008) Chance variation and evolutionary contingency: Darwin, Simpson (The Simpsons) and Gould. The Oxford Handbook of Philosophy of Biology. Oxford University Press, Oxford

Beaulieu JM, Jhwueng D-C, Boettiger C, O'Meara BC (2012) Modeling stabilizing selection: expanding the Ornstein–Uhlenbeck model of adaptive evolution. Evolution 66:2369–2383. doi:10.1111/j.1558-5646.2012.01619.x

Blackledge TA, Gillespie RG (2004) Convergent evolution of behavior in an adaptive radiation of Hawaiian web-building spiders. Proc Natl Acad Sci 101:16228–16233

Blondel J (1991) Assessing convergence at the community-wide level. Trends Ecol Evol 6:271–272

Bock WJ (1980) The definition and recognition of biological adaptation. Am Zool 20:217–227

Bock WJ, Miller WD (1959) The scansorial foot of the woodpeckers, with comments on the evolution of perching and climbing feet in birds. Am Mus Novit 1931:1–45

Bossuyt F, Milinkovitch MC (2000) Convergent adaptive radiations in Madagascan and Asian ranid frogs reveal covariation between larval and adult traits. Proc Natl Acad Sci 97:6585–6590

Brandley MC, Kuriyama T, Hasegawa M (2014) Snake and bird predation drive the repeated convergent evolution of correlated life history traits and phenotype in the Izu Island scincid lizard (*Plestiodon latiscutatus*). PLoS ONE 9:e92233. doi:10.1371/journal.pone.0092233

Butler MA, King AA (2004) Phylogenetic comparative analysis: a modeling approach for adaptive evolution. Am Nat 164:683–695

Chiba S (2004) Ecological and morphological patterns in communities of land snails of the genus *Mandarina* from the Bonin Islands. J Evol Biol 17:131–143. doi:10.1046/j.1420-9101.2004.00639.x

Clabaut C, Bunje PME, Salzburger W, Meyer A (2007) Geometric morphometric analyses provide evidence for the adaptive character of the Tanganyikan cichlid fish radiations. Evolution 61:560–578. doi:10.1111/j.1558-5646.2007.00045.x

Cody ML (1974) Competition and the structure of bird communities, pp 1–318

Cody ML, Diamond JM (1975) Ecology and evolution of communities, pp 1–545

Cody ML, Mooney HA (1978) Convergence versus nonconvergence in Mediterranean-climate ecosystems. Annu Rev Ecol Syst 9:265–321. doi:10.1146/annurev.es.09.110178.001405

Collar DC, Schulte JA II, Losos JB (2011) Evolution of extreme body size disparity in monitor lizards (*Varanus*). Evolution 65:2664–2680. doi:10.1111/j.1558-5646.2011.01335.x

Conway Morris S (2003) Life's solution: inevitable humans in a lonely universe. pp 1–464

Cooper WJ, Westneat MW (2009) Form and function of damselfish skulls: rapid and repeated evolution into a limited number of trophic niches. BMC Evol Biol 9:24. doi:10.1186/1471-2148-9-24

De Busschere C, Baert L, Van Belleghem SM, Dekoninck W, Hendrickx F (2012) Parallel phenotypic evolution in a wolf spider radiation on Galápagos. Biol J Linn Soc 106:123–136. doi:10.1111/j.1095-8312.2011.01848.x

Eastman JM, Alfaro ME, Joyce P, Hipp AL, Harmon LJ (2011) A novel comparative method for identifying shifts in the rate of character evolution on trees. Evolution 65(12):3578–3589

Ellingson RA (2013) Convergent evolution of ecomorphological adaptations in geographically isolated Bay gobies (Teleostei: Gobionellidae) of the temperate North Pacific. Mol Phylogenet Evol. doi:10.1016/j.ympev.2013.10.009

Emerson BC, Gillespie RG (2008) Phylogenetic analysis of community assembly and structure over space and time. Trends Ecol Evol 23:619–630. doi:10.1016/j.tree.2008.07.005

Erwin DH (2006) Evolutionary contingency. Curr Biol 16:825–826

Felsenstein J (1988) Phylogenies and quantitative characters. Annu Rev Ecol Syst 19:445–471. doi:10.1146/annurev.es.19.110188.002305

Fox BJ (1987) Species assembly and the evolution of community structure. Evol Ecol 1:201–213. doi:10.1007/BF02067551

Frédérich B, Sorenson L, Santini F, Slater GJ, Alfaro ME (2013) Iterative ecological radiation and convergence during the evolutionary history of damselfishes (Pomacentridae). Am Nat 181:94–113. doi:10.1086/668599

Garland T, Dickerman AW, Janis CM, Jones JA (1993) Phylogenetic analysis of covariance by computer simulation. Syst Biol 42:265–292. doi:10.1093/sysbio/42.3.265

Gatz AJJ (1979) Community organization in fishes as indicated by morphological features. Ecology 60:711–718

Gavrilets S, Vose A (2005) Dynamic patterns of adaptive radiation. Proc Natl Acad Sci 102:18040–18045. doi:10.1073/pnas.0506330102

Gillespie R (2004) Community assembly through adaptive radiation in Hawaiian spiders. Science 303:356–359. doi:10.1126/science.1091875

Gillespie RG (2005) The ecology and evolution of Hawaiian spider communities. Am Sci 93:122–131

Givnish TJ (1997) Adaptive radiation and molecular systematics: aims and conceptual issues. In: Molecular evolution and adaptive radiation, Cambridge University Press, New York

Givnish TJ (1999) Adaptive radiation, dispersal, and diversification of the Hawaiian lobeliads. The Biology of Biodiversity. Springer, Tokyo

Givnish TJ, Millam KC, Mast AR, Paterson TB, Theim TJ, Hipp AL, Henss JM, Smith JF, Wood KR, Sytsma KJ (2009) Origin, adaptive radiation and diversification of the Hawaiian lobeliads (Asterales: Campanulaceae). Proc Roy Soc B 276:407–416. doi:10.1098/rspb.2008.1204

Glor RE (2010) Phylogenetic insights on adaptive radiation. Annu Rev Ecol Evol Syst 41:251–270. doi:10.1146/annurev.ecolsys.39.110707.173447

Glor RE, Kolbe JJ, Powell R, Larson A, Losos JB (2003) Phylogenetic analysis of ecological and morphological diversification in Hispaniolan trunk-ground anoles (*Anolis cybotes* group). Evolution 57:2383–2397

Gould SJ (1989) Wonderful life: the Burgess Shale and the nature of history, pp 1–347

Gould SJ (2002) The structure of evolutionary theory, pp 1–1464

Gould SJ (2003) Contingency. In: Palaeobiology II. Blackwell Publishing Ltd, New Jersey

Hansen TF (1997) Stabilizing selection and the comparative analysis of adaptation. Evolution 51:1341–1351

Hansen TF (2012) Adaptive landscapes and macroevolutionary dynamics. In: The adaptive landscape in evolutionary biology, Oxford University Press, Oxford

Hansen TF, Pienaar J, Orzack SH (2008) A comparative method for studying adaptation to a randomly evolving environment. Evolution 62:1965–1977. doi:10.1111/j.1558-5646.2008.00412.x

Harmon LJ, Kolbe JJ, Cheverud JM, Losos JB (2005) Convergence and the multidimensional niche. Evolution 59:409–421

Harmon LJ, Losos JB, Davies TJ, Gillespie RG, Gittleman JL, Jennings WB, Kozak KH, McPeek MA, Moreno-Roark F, Near TJ, Purvis A, Ricklefs RE, Schluter D, Schulte JA II, Seehausen O, Sidlauskas BL, Torres-Carvajal O, Weir JT, Mooers AØ (2010) Early bursts of body size and shape evolution are rare in comparative data. Evolution 64:2385–2396. doi:10.1111/j.1558-5646.2010.01025.x

Heath TA, Holder MT, Huelsenbeck JP (2012) A Dirichlet process prior for estimating lineage-specific substitution rates. Mol Biol Evol 29(3):939–955

Hekstra DR, Leibler S (2012) Contingency and statistical laws in replicate microbial closed ecosystems. Cell 149:1164–1173. doi:10.1016/j.cell.2012.03.040

Huelsenbeck JP, Nielsen R, Bollback JP (2003) Stochastic mapping of morphological characters. Syst Biol 52:131–158. doi:10.1080/10635150390192780

Ingram T, Kai Y (2014) The geography of morphological convergence in the radiations of Pacific *Sebastes* rockfishes

Ingram T, Mahler DL (2013) SURFACE: detecting convergent evolution from comparative data by fitting Ornstein-Uhlenbeck models with stepwise Akaike Information Criterion. Methods Ecol Evol 4:416–425. doi:10.1111/2041-210X.12034

Inkpen R, Turner D (2012) The topography of historical contingency. J Philos Hist 6:1–19. doi:10.1163/187226312X625573

Johnson MA, Revell LJ, Losos JB (2009) Behavioral convergence and adaptive radiation: effects of habitat use on territorial behavior in *Anolis* lizards. Evolution 64:1151–1159. doi:10.1111/j.1558-5646.2009.00881.x

Karr JR, James FC (1975) Eco-morphological configurations and convergent evolution in species and communities. In: Ecology and evolution of communities. The Belknap Press of Harvard University Press, Cambridge, MA

Kassen R (2009) Toward a general theory of adaptive radiation: insights from microbial experimental evolution. Ann N Y Acad Sci 1168:3–22. doi:10.1111/j.1749-6632.2009.04574.x

Keast A (1972) Ecological opportunities and dominant families, as illustrated by the Neotropical Tyrannidae (Aves). Evol Biol 5:229–277

Kelt DA, Brown JH, Heske EJ, Marquet PA, Morton SR, Reid JRW, Rogovin KA, Shenbrot G (1996) Community structure of desert small mammals: comparisons across four continents. Ecology 77:746–761

Kocher TD, Conroy JA, McKaye KR, Stauffer JR (1993) Similar morphologies of cichlid fish in Lakes Tanganyika and Malawi are due to convergence. Mol Phylogenet Evol 2:158–165

Kozak KH, Mendyk RW, Wiens JJ (2009) Can parallel diversification occur in sympatry? Repeated patterns of body-size evolution in coexisting clades of North American salamanders. Evolution 63:1769–1784. doi:10.1111/j.1558-5646.2009.00680.x

Lande R (1976) Natural selection and random genetic drift in phenotypic evolution. Evolution 30:314–334

Lapiedra O, Sol D, Carranza S, Beaulieu JM (2013) Behavioural changes and the adaptive diversification of pigeons and doves. Proc Roy Soc B 280:20122893

Lawton JH (1984) Non-competitive populations, non-convergent communities, and vacant niches: The herbivores of bracken. In: Strong DRJ, Simberloff D, Abele LG, Thistle AB (eds) Ecological Communities: Conceptual Issues and the Evidence. Princeton University Press, Princeton, pp 67–100

Lenski RE, Travisano M (1994) Dynamics of adaptation and diversification: A 10,000-generation experiment with bacterial populations. Proc Natl Acad Sci USA 91:6808–6814

Losos JB (1996) Ecological and evolutionary determinants of the species-area relation in Caribbean anoline lizards. Philos Trans Roy Soc Lond B 351:847–854

Losos JB (2011) Convergence, adaptation and constraint. Evolution 65:1827–1840. doi:10.1111/j.1558-5646.2011.01289.x

Losos JB, Jackman TR, Larson A, de Queiroz K, Rodríguez-Schettino L (1998) Contingency and determinism in replicated adaptive radiations of island lizards. Science 279:2115–2118

Losos JB, Mahler DL (2010) Adaptive radiation: the interaction of ecological opportunity, adaptation, and speciation. In: Evolution since Darwin: The first 150 Years, vol 150. Sinauer Associates, Sunderland, MA

MacLean RC (2005) Adaptive radiation in microbial microcosms. J Evol Biol 18:1376–1386. doi:10.1111/j.1420-9101.2005.00931.x

Madsen O, Scally M, Douady CJ, Kao DJ, DeBry RW, Adkins R, Amrine HM, Stanhope MJ, de Jong WW, Springer MS (2001) Parallel adaptive radiations in two major clades of placental mammals. Nature 409:610–614. doi:10.1038/35054544

Mahler DL, Ingram T, Revell LJ, Losos JB (2013) Exceptional convergence on the macroevolutionary landscape in island lizard radiations. Science 341:292–295. doi:10.1126/science.1232392

Manceau M, Domingues VS, Linnen CR, Rosenblum EB, Hoekstra HE (2010) Convergence in pigmentation at multiple levels: mutations, genes and function. Philos Trans Roy Soc B: Biol Sci 365:2439–2450. doi:10.1098/rstb.2010.0104

Martins EP (1994) Estimating the rate of phenotypic evolution from comparative data. Am Nat 144:193–209

Melville J, Harmon LJ, Losos JB (2006) Intercontinental community convergence of ecology and morphology in desert lizards. Proc Roy Soc B 273:557–563. doi:10.1098/rspb.2005.3328

Miles DB, Ricklefs RE, Travis J (1987) Concordance of ecomorphological relationships in three assemblages of passerine birds. Am Nat 129:347–364

Moen DS, Wiens JJ (2009) Phylogenetic evidence for competitively driven divergence: body-size evolution in Caribbean treefrogs (Hylidae: *Osteopilus*). Evolution 63:195–214. doi:10.1111/j.1558-5646.2008.00538.x

Montaña CG, Winemiller KO (2013) Evolutionary convergence in Neotropical cichlids and Nearctic centrarchids: evidence from morphology, diet, and stable isotope analysis. Biol J Linn Soc 109:146–164

Muschick M, Indermaur A, Salzburger W (2012) Convergent evolution within an adaptive radiation of cichlid fishes. Curr Biol 22:2362–2368. doi:10.1016/j.cub.2012.10.048

Orians GH, Paine RT (1983) Convergent evolution at the community level. In: Coevolution, Sinauer Associates, Inc., Sunderland, MA

Orians GH, Solbrig OT (1977a) Convergent evolution in warm deserts. Dowden, Hutchinson & Ross, Inc., Stroudsburg, PA

Orians GH, Solbrig OT (1977b) Degree of convergence of ecosystem characteristics. In: Convergent evolution in warm deserts. Dowden, Hutchinson & Ross, Inc., Stroudsburg, PA

Patterson TB, Givnish TJ (2003) Geographic cohesion, chromosomal evolution, parallel adaptive radiations, and consequent floral adaptations in *Calochortus* (Calochortaceae): evidence from a cpDNA phylogeny. New Phytol 161:253–264. doi:10.1046/j.1469-8137.2003.00951.x

Pearce T (2012) Convergence and parallelism in evolution: a neo-Gouldian account. Br J Philos Sci 63:429–448. doi:10.1093/bjps/axr046

Pianka ER (1974) Evolutionary ecology, pp 1–397

Pie MR, Weitz JS (2005) A null model of morphospace occupation. Am Nat 166:E1–E13. doi:10.1086/430727

Powell R (2009) Contingency and convergence in macroevolution: a reply to John Beatty. J Philos 106:390–403

Powell R (2012) Convergent evolution and the limits of natural selection. Eur J Philos Sci 2:355–373. doi:10.1007/s13194-012-0047-9

Price T (1997) Correlated evolution and independent contrasts. Philos Trans Roy Soc Lond B 352:519–529

Price T, Lovette IJ, Bermingham E, Gibbs HL, Richman AD (2000) The imprint of history on communities of North American and Asian warblers. Am Nat 156:354–367. doi:10.1086/303397

Rainey PB, Travisano M (1998) Adaptive radiation in a heterogeneous environment. Nature 394:69–72

Revell LJ (2009) Size-correction and principal components for interspecific comparative studies. Evolution 63:3258–3268. doi:10.1111/j.1558-5646.2009.00804.x

Revell LJ (2012) phytools: an R package for phylogenetic comparative biology (and other things). Methods Ecol Evol 3(2):217–223

Revell LJ, Mahler DL, Peres-Neto PR, Redelings BD (2012) A new phylogenetic method for identifying exceptional phenotypic diversification. Evolution 66:135–146. doi:10.5061/dryad.vj310

Ricklefs RE, Miles DB (1994) Ecological and evolutionary inferences from morphology: an ecological perspective. University of Chicago Press, Chicago

Ricklefs RE, Schluter D (1993) Species diversity in ecological communities: historical and geographical perspectives, pp 1–414

Ricklefs RE, Travis J (1980) A morphological approach to the study of avian community organization. Auk 97:321–338

Rüber L, Verheyen E, Meyer A (1999) Replicated evolution of trophic specializations in an endemic cichlid fish lineage from Lake Tanganyika. Proc Natl Acad Sci 96:10230–10235

Ruedi M, Mayer F (2001) Molecular systematics of bats of the genus *Myotis* (Vespertilionidae) suggests deterministic ecomorphological convergences. Mol Phylogenet Evol 21:436–448. doi:10.1006/mpev.2001.1017

Sallan LC, Friedman M (2012) Heads or tails: staged diversification in vertebrate evolutionary radiations. Proc Roy Soc B: Biol Sci 279:2025–2032. doi:10.1098/rspb.2011.2454

Samuels CL, Drake JA (1997) Divergent perspectives on community convergence. Trends Ecol Evol 12:427–432

Saxer G, Doebeli M, Travisano M (2010) The repeatability of adaptive radiation during long-term experimental evolution of *Escherichia coli* in a multiple nutrient environment. PLoS ONE 5:e14184. doi:10.1371/journal.pone.0014184

Scheffer M, van Nes EH (2006) Self-organized similarity, the evolutionary emergence of groups of similar species. Proc Natl Acad Sci 103:6230–6235. doi:10.1073/pnas.0508024103

Schluter D (1986) Tests for similarity and convergence of finch communities. Ecology 67:1073–1085

Schluter D (1990) Species-for-species matching. Am Nat 136:560–568. doi:10.1086/285135

Schluter D (2000) The ecology of adaptive radiation, pp 1–288

Schluter D, McPhail JD (1993) Character displacement and replicate adaptive radiation. Trends Ecol Evol 8:197–200

Segar ST, Pereira RAS, Compton SG, Cook JM (2013) Convergent structure of multitrophic communities over three continents. Ecol Lett. doi:10.1111/ele.12183

Simpson GG (1944) Tempo and mode in evolution, pp 1–237

Simpson GG (1950) Evolutionary determinism and the fossil record. Sci Mon 71:262–267

Springer MS, Kirsch JAW, Chase JA (1997) The chronicle of marsupial evolution. In: Molecular evolution and adaptive radiation. Cambridge University Press, Cambridge

Stayton CT (2008) Is convergence surprising? An examination of the frequency of convergence in simulated datasets. J Theor Biol 252:1–14. doi:10.1016/j.jtbi.2008.01.008

Stiassny MLJ, Meyer A (1999) Cichlids of the rift lakes. Sci Am 280:64–69. doi:10.1038/scientificamerican0299-64

Streelman JT, Danley PD (2003) The stages of vertebrate evolutionary radiation. Trends Ecol Evol 18:126–131

Strong DRJ, Simberloff D, Abele LG, Thistle AB (1984) Ecological communities: conceptual issues and the evidence, pp 1–613

Svensson EI, Calsbeek R (2012) The past, the present, and the future of the adaptive landscape. In: Svensson EI, Calsbeek R (eds) The adaptive landscape in evolutionary biology. Oxford University Press, Oxford, pp 299–308

Thomas GH, Freckleton RP (2012) MOTMOT: models of trait macroevolution on trees. Methods Ecol Evol 3:145–151. doi:10.1111/j.2041-210X.2011.00132.x

Tyerman J, Havard N, Saxer G, Travisano M, Doebeli M (2005) Unparallel diversification in bacterial microcosms. Proc Roy Soc B 272:1393–1398. doi:10.1098/rspb.2005.3068

Uhlenbeck GE, Ornstein LS (1930) On the theory of the Brownian motion. Phys Rev 36:823–841

Venditti C, Meade A, Pagel M (2011) Multiple routes to mammalian diversity. Nature 479:393–396. doi:10.1038/nature10516

Wagenaar DA, Adami C (2004) Influence of chance, history, and adaptation on digital evolution. Artif Life 10:181–190. doi:10.1162/106454604773563603

Wiens JA (1991) Ecomorphological comparisons of the shrub-desert avifaunas of Australia and North America. Oikos 60:55–63

Wiens JJ, Brandley MC, Reeder TW (2006) Why does a trait evolve multiple times within a clade? Repeated evolution of snakelike body form in squamate reptiles. Evolution 60:123–141

Winchester JM, Boyer DM, St Clair EM, Gosselin-Ildari AD, Cooke SB, Ledogar JA (2014) Dental topography of platyrrhines and prosimians: convergence and contrasts. Am J Phys Anthropol 153:29–44. doi:10.1002/ajpa.22398

Yedid G, Bell G (2002) Macroevolution simulated with autonomously replicating computer programs. Nature 420:810–812. doi:10.1038/nature01151

Yedid G, Ofria CA, Lenski RE (2008) Historical and contingent factors affect re-evolution of a complex feature lost during mass extinction in communities of digital organisms. J Evol Biol 21:1335–1357. doi:10.1111/j.1420-9101.2008.01564.x

Young KA, Snoeks J, Seehausen O (2009) Morphological diversity and the roles of contingency, chance and determinism in African cichlid radiations. PLoS ONE 4:e4740. doi:10.1371/journal.pone.0004740