**Measuring Convergence, August 2013**

**(**[**Stayton, 2005**](#_ENREF_19)**)**

PCA on Procrustes coordinates - interested in changes at both large and small scales so the alpha parameter (determines how the principal warps at different scales are weighted) was set to 0 - don't know if this is the default or do I need to worry about it

Three of the four disparity metrics (products of variance often produce small numbers that are difficult to interpret).

Plotted the phylogeny on the morphospace using group centroids - points on the centroid of each family (terminal nodes of family-level phylogenies), then calculated the centroids for sister groups -> points corresponding to internal nodes. He says that internal nodes are not intended to represent ancestors but rather “the centroids of successively more inclusive groups so they reveal the pattern of morphospace occupation”. But how is this not ancestral state reconstruction if the internal nodes are some average shape of the existing terminal nodes?

NB: Summary stats for morphological Euclidean distance within and between groups; min, max, mean, range, standard deviation.

I don’t understand the references to using rarefaction to correct for disparity measurements on groups of unequal size (otherwise morphological diversity and sample size are highly correlated). He has a rarefaction curve of mean range within a family vs. log (No. of species) – shows a greater morphological range for families with more species. I don’t see how he then uses this to “correct” for families with different numbers of species.

**(**[**Stayton, 2006**](#_ENREF_20)**)**

Three different morphospace patterns of convergence (examples of two of those patterns in his 2005 paper)

Multidimensional convergence index with permutation to test significance – ratio of the disparity of sister taxa to the disparity of convergent taxa in all groups. So apriori definition of convergent groups?

Used Relative Warps scores as inputs for disparity metrics (Zelditch morphometrics book: “When variation is not weighted by bending energy then RW is equivalent to PCA”. I did my Procrustes superimposition by a distance rather than bending energy method so does that mean my PCA is equivalent to RWA?)

**(**[**Stayton, 2008**](#_ENREF_21)**)**

Defines convergence only on the basis of phenetic similarity - don't need knowledge of any selective regime or any adaptive processes

True Convergence Metric - need to know the ancestral state. If data from ancestors are not available then it's never possible to conclusively establish that convergence has taken place

Weighted Count Metric: count number of taxa whose nearest neighbours in multivariate space aren’t sister taxa, multiply by patristic distance and sum scores over the entire tree, standardise by dividing all distances by maximum patristic distance between taxa. Since this gives an overall measure of convergence for the tree I’m not sure how to break it down to convergence within particular groups.

Ratio metric: patristic/phenetic distance, standardised by tree length – only use in a relevant sense to compare convergence between trees.

**(**[**Muschick et al., 2012**](#_ENREF_15)**)**

Plotted morphological vs. phylogenetic distance for each species pair and compared to simulations of trait evolution (Brownian and OU gave similar results). (Compared to **(**[**Leal et al., 2002**](#_ENREF_11)**)** who just used lack of clustering within aquatic ecomorph as evidence for non-convergence.)

I don’t understand their method for getting morphological distance: their aligned Procrustes coordinates were used for a “pooled-within-species regression of shape against centroid size” and then they used the residuals from this regression to calculate morphological (Euclidean) distance. If regressing shape against centroid size is to account for the influence of allometry then does that assume that variation in shape due to size is important? Would it be sensible to test for convergence twice; with and without controlling for size? For example, **(**[**Melville et al., 2006**](#_ENREF_14)**)** did this for their partial Mantel tests of intercontinental community convergence in lizards and found no qualitative difference when they used the residuals from regressing morphological and ecological traits by body size.

I also don’t understand what they’re regressing for the shape. Aligned Procrustes coordinates are still a set of landmarks rather than a single value so I don’t know how they translated that to a y axis value for a regression. The supplemental information doesn’t seem to explain it either.

**(**[**Mahler et al., 2013**](#_ENREF_13)**)**

New Anole convergence paper using SURFACE

Interested in convergence of the fauna as a whole rather than between individual species

"Phylogenetic comparative analysis of species similarity in a 4D Principal components morphospace generated from 11 traits important for niche partitioning" - compared to my current 301D PC morphospace (?) and traits which are purely morphological.

Measured the among-island Euclidean distance between each species and its nearest morphospace neighbour from another island - tested whether the average among-island distance for anoles was lower than expected by chance via comparison to a phylogenetic null distribution

Compared the true average distances among species from different islands to a null distribution of the same scores from simulated data

More convergent adaptive peaks than expected by chance -the number and position of peak shifts varied across phylogenies but the overall number of convergent shifts was similar for all trees. Similar adaptive peaks for anole lizards from different islands -> indicating stable adaptive landscapes

There were also some non-convergent shifts to specific island peaks but these were only found on larger islands – in-keeping with the area effect from adaptive radiation theory. So evidence for evolutionary radiation being at least partly deterministic - similar to the 2012 cichlid paper showing that whether a species radiates can be predicted from intrinsic traits of the colonist and ecological opportunities from the new habitat

Supplementary material

Simulated null models for each trait separately -Brownian, Early Burst, Time and Lineage Diversity: used the favoured model for each axis

Simulated data one axis at a time and combined axes to build morphospaces - also did other null morphospaces where all traits were simulated using the same models. Data sets with evolutionary correlated individual traits should take the correlation into account when simulating null data.

Among island faunal similarity: island-weighted average of all among-island nearest neighbour distances.

**(**[**Ingram et al., 2013**](#_ENREF_9)**) SURFACE paper**

**NB: The surface package has been removed from Cran (checked on 15/10/2013)**

Don't distinguish between convergence and parallelism; either provides evidence for non-random evolutionary change

Testing for convergence; important to rule out phenotypic similarity due to chance and avoid a priori identification of candidate convergent species

SURFACE uses two recent developments -paint selective regimes onto the branches of a phylogenetic tree -data-driven, stepwise algorithms that locate evolutionary shifts on a tree (MOTMOT models of trait macroevolution on trees package by G. Thomas and R. Freckleton)

input for runSurface-phylogenetic tree (which can include polytomies that can be left unresolved)-data for one or more continuous traits for each species in the tree

Butler and King 2004 paper (in unread list) methods for specifying adaptive hypotheses

Hansen model: expected trait values for the tip species depend on the regimes experienced during their evolutionary history

Forward phase of SURFACE

-uses OU Hansen models

-assume that the Brownian rate parameter and the rate of adaptive evolution towards a trait optimum are both constant across the tree

Input of one or more continuous traits but at least 2 trait axes are usually better

-assumes that traits evolve independently

-> problems if I was to try and use e.g. skull shape and diet?

but the Bartoszek 2012 paper in the unread list has an OU method for modelling multivariate trait adaptive evolution (correlation between traits)

Traits evolve independently-> separate likelihood estimation for each trait and then get a sum of the overall log-likelihoods estimated for individual traits

Then SURFACE adds one regime shift at a time to the origin of each branch - uses AIC to measure model performance; balances improvements in log-likelihood against increases in model complexity

Species’ means are usually used in comparative methods but this can lead to problems. Ignoring intraspecific variability can lead to increased type I error rates when intraspecific variance is large and sample sizes are small

-need to check for intraspecific variance in my skulls

NB: Phylogenetic signal; statistical non-independence where phenotypic similarity is associated with phylogenetic relatedness

Phylogenetic inertia: tendency of a trait to resist a current adaptive force

Correlational studies: PGLS models to fit regressions between matrices of shape variables and functional + ecological variables

Can also use matrix correlation methods but this is less informative and less powerful than the PGLS option

NB: be careful about interpreting results of shape principal components compared to ecological variables

Because the dimensionality of the morphometric data has been reduced into principal axes, non-significant results don't necessarily mean that there's no interaction. Non-significance just shows that the ecological variables don't have an effect on the main axes of interspecific shape variation

NB: How many principal components axes do you retain?

-use the broken stick model - compare the variance explained by each PC to that expected by a null distribution

-most studies use subjective criteria e.g. the number of PCs that explain 70-80% of the total variation

-stats method: Horn's parallel analysis

-better to use well-defined criterion to determine the number of over-dispersed PCs (account for more variance than expected in random samples)

Revell 2009; method to estimate principal components while taking phylogenetic non-independence into account - associated with the phytools R package

Phylomorphospace graph of bat skulls grouped by diet.

Nice pictures of the average skull shapes associated with PC1 and PC2 with the positive deviations from these shapes superimposed above

Phylomorphospace (with the phylogeny on top of morphospace) is controversial and probably inaccurate - more for illustration purposes and probably not relevant to me although it may be nice to show convergence??

Morphological divergence among closely related species is given greater weight in the phylogenetic PCs

NB: look at all the important (over-dispersed) PCs together when fitting a model or interpreting results rather than treating each individual PC as a separate variable

**(**[**Melville et al., 2006**](#_ENREF_14)**)**

Inter-continental community convergence in lizards. Partial Mantel test: morphological ~ microhabitat distances while controlling for phylogenetic distance. They modified the Mantel test to partition the Z statistic into between and within-continental correlations among species. Could I use a similar approach? Comparing tenrecs vs. everything else is equivalent to island vs. mainland (~intercontinental) but they may not be within the same community frameworks. Structural microhabitat characteristics – very fine scale ecological data.

Ran two sets of analyses: including and excluding body size and the results were qualitatively equivalent. Convergence may not occur in all dimensions of a community e.g. convergent locomotion and habitat but maybe not diet or thermal biology

Most examples of convergent island communities are relatively young

**(**[**Alvarado-Cárdenas et al., 2013**](#_ENREF_1)**)**

Convergence between new world vs. old world succulents; importance of modelling and quantifying environmental similarities.

WorlClim climate data, environmental models using MaxEnt, distinction between tests for niche equivalence and niche similarity.

More climatic differences than similarities between the two zones. The apparent lack of overlap in environmental space may be because of missing factors (e.g. biotic interactions) and/or due to not easily identifiable but nevertheless biologically significant differences between the supposedly convergent species.

No objective measure of similarity – any defining criteria will always be study-specific and constrained by the practicalities of your data.

Conclusions paragraph is perfect for me ☺ “The qualitative examination of "similar shape" so frequently invoked in examples of convergence bears re-examination” e.g. via techniques such as geometric morphometrics - such an approach would allow testing of whether species that are closer in shape space should also be closer in niche space

**(**[**Kawahara and Rubinoff, 2013**](#_ENREF_10)**)**

Examples of island species with similar morphologies occupying similar ecological niches: Anoles, land snails, orb-weaving spiders in Hawaii.

Convergent evolution of morphology and habitat use but morphology is based on categorical classification of larval case shape and habitat use came from detailed microhabitat characterisation.

Independent evolution of similar morphologies – predisposition to particular morphologies from similar habitat selective pressures (repeatability of evolution).

Moore 1997 reference: convergent evolution in invertebrates is more common than previously thought.

**(**[**Wroe and Milne, 2007**](#_ENREF_23)**)**

Use this paper as an example of a half way stage; not just subjective because they do measure correlations between shape and other variables but it's not measuring convergence because there's no measure of how similar the two groups are

No measures of convergence! They did a PCA on skull shapes and then calculated correlations between PC1 and other ecological variables. Then they say similar correlations indicate evidence of convergence but they don't quantify that in any way.

89 crania of 43 species - so only around 2 specimens per species.

Rotated PCs 1 and 2 by the slope of the lines representing the two mammalian groups -> calculated new axes perpendicular and parallel to the mammalian and placental lines - created new axes (W-X and Z-Y) which means that shapes at the end of these axes represent the differences between the two groups. Might be something useful?

**(**[**Harmon et al., 2005**](#_ENREF_7)**)**

Five separate morphological distance matrices for different characters (body size, head shape, lamellae number etc.)

Analyses with IMP software, PDAP (phylogenetic distance matrix), Mantel tests comparing morphological and phylogenetic matrices using Passage.

Created a binary ecomorph distance matrix for each species pair, then used three-way Mantel tests (controlling for phylogeny) to test whether each of the 5 morphological data sets differed among ecomorphs. (Whereas I want to make a single ecological distance matrix using multivariate data?)

They also used phylogenetic ANOVAs and MANOVAs on each dataset to test whether ecomorph categories differed in morphology. Significant p values based on the (number of simulated F or Wilks’ lambda values that were more extreme than the real values+1)/ (total no. of simulations +1) - calculated in a c-program, I don't understand why they put +1 into each term.

Post hoc tests for significant differences between each possible pair of ecomorph categories -compared actual distance between centroids of each ecomorph pair to the corresponding null distribution.

Multi matrix regression: residuals from each of the morphological vs. phylogenetic matrices regressed against the ecomorph residual matrix - determine which morphological data sets added significant information about ecomorph distances

Independent inter-ecomorph variation in 4 of the 5 morphological character sets -> adaptation to different aspects of the environment-> multidimensional convergence

**Disparity**

**(**[**Harmon et al., 2003**](#_ENREF_8)**)**

Morphological disparity index: difference between relative disparity of a clade (subclade disparity/entire clade disparity) compared with the expected difference under the null hypothesis.

Test statistic δ near 0: most variation is among subclades vs. near 1: lots of total variation contained within subclades -> subclades are likely to overlap -> subclades independently evolved to occupy similar regions of morphospace

**(**[**Brusatte et al., 2008a**](#_ENREF_3)**) and (**[**Brusatte et al., 2008b**](#_ENREF_4)**)**

Euclidean distance matrix (based on discrete cladistic characters) used for a principal coordinates (not PCA) analysis

([Brusatte et al., 2008a](#_ENREF_3)) Disparity metrics using the first 65 (out of 76 PO) axes encompassing 90% of the cumulative variance. They calculated the sum and product of the ranges and variances on the 65 axes using the software program Rare (product measures normalised by taking the 65th root). All metrics gave the same pattern – they use sum of ranges as their favoured one. ([Brusatte et al., 2008b](#_ENREF_4)) used NPMANOVAs to test for significant differences from the null hypothesis of equal group variance in disparity.

Supplementary of both papers: rarefaction curves of disparity (sum of ranges) vs. sample size: results are robust to sample size biases – even small sample sizes give the same overall pattern of change in disparity through time.

**More Papers (added from September 2013, after I gave Natalie the initial list of papers in mid-August)**

**(**[**Ruta et al., 2013**](#_ENREF_18)**)**

Decoupling of diversity and disparity in early herbivores; go to read cube notes for details. It includes rarefaction curves to correct for sample sizes and also a nice justification for tenrec work.

**(**[**Ojeda et al., 1999**](#_ENREF_16)**)**

Lots of convergence studies in desert rodents. Qualitative morphological and physiological similarities in desert rodents from different continents.

**(**[**Ben-Moshe et al., 2001**](#_ENREF_2)**)**

No direct measure of convergence; just that there were similar non-random patterns of over-dispersed means for size-structured rodent communities in Israel and North America.

**(**[**Conway-Morris, 2006**](#_ENREF_6)**)**

Convergence isn’t that surprising, molecular convergence is probably more common than we realise. We might be on the threshold of a general theory of evolution. “Please raise a glass to convergence.”

**(**[**Collar et al., 2011**](#_ENREF_5)**)**

Lizards; divergence among species in their use of structural habitats exerts strong influence on morphological diversification. Habitat can contribute to disparity in different ways: imposing selection towards different optima or by allowing for more or less variability. Report the estimated strength of selection in an OU model as the phylogenetic half-life - time required to evolve half the distance from the ancestral value to the optimum

**(**[**Wainwright, 2007**](#_ENREF_22)**)**

Comparative analyses of morphological and ecological diversity have lagged behind similar studies of lineage diversification rate and species richness. Don’t rely on the assumption that morphology can be used as a proxy for functional diversity.

Measuring diversity; range and variance; Range includes the furthest members in a group, which regions in morphospace have been occupied- N-dimensional minimal polygon that encloses all individuals in a group. Variance is more common - not affected by a few outliers, captures the dispersion of members of the group and doesn't scale with sample size.

([**Revell et al., 2007**](#_ENREF_17)**)**

This paper is concerned with separating adaptation and exaptation -> not very relevant to me if I stick to Stayton's (?) approach of being interested in the evolutionary pattern as it is now rather than the mechanisms by which they evolved. They also use ancestral state reconstruction so overall it's asking very different questions to me. Similarity may reflect inheritance from a common ancestor rather than convergence e.g. salamanders and lizards retaining ancestral body plans. Convergence of tenrecs and other mammals because they retain the general insectivore body plan??

So I can't separate evidence for convergence from the possibility that all other closely related species are just more derived from the generic ancestral state?? Linear measurements; took the average of 2 measurements or the average of the two closest out of 3 measurements -> reference in contrast to Natalie's error checking methods. Squared-change parsimony to reconstruct ancestral states of each of the characters

Used ancestral states to calculate multivariate changes along all internodes in the phylogeny, then used these changes for PC scores

**(**[**Leal et al., 2002**](#_ENREF_11)**)**

Evidence for non-convergence is that aquatic anoles don't cluster together in morphological space - smaller distances between each of the aquatic anoles and members of different ecomorph categories -so just based on morphological distance

Similar habitats but they're not convergent- they may actually occupy different habitats which just happen to be near water or, there may be more than one way to adapt to living in a single habitat.

**(**[**Losos, 2011**](#_ENREF_12)**)**

Nice Darwin quote about convergent traits being almost valueless to systematists. Broad definition of environment - sum of extrinsic potential selective factors encountered by a population or species. Conceptual summaries of parallel vs. nonparallel convergence, adaptation vs. exaptation, evolutionary contingencies, many to one mapping – notes in readcube for the details.

Convergence examples e.g. toxic animals and their mimics.

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