**Measuring Convergence, August 2013**

**(**[**Stayton, 2005**](#_ENREF_35)**)**

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_36)**)**

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 they used *a priori* 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_37)**)**

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_28)**)**

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_23)**)** 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_26)**)** 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_25)**)**

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_19)**) 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_26)**)**

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_22)**)**

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_40)**)**

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_16)**)**

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_18)**)**

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_5)**) and (**[**Brusatte et al., 2008b**](#_ENREF_6)**)**

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

([Brusatte et al., 2008a](#_ENREF_5)) 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_6)) 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)**

**(**[**Foote, 1997**](#_ENREF_14)**)**

Background to general morphological disparity studies and good justification for why it’s important to extend disparity studies across new taxa (see read cube notes)

**(**[**Zelditch et al., 2012**](#_ENREF_41)**)**

Remember to go back to the marked disparity sections in this book – good theory but the accompanying workbook doesn’t have any practical examples for R code. It includes calculating morphological disparity by shape variance and the idea of partial disparity (partial disparity of subgroups will sum to the overall disparity for the entire sample).

Different disparity metrics for continuous and categorical/ordinal data since only continuous variables are measured on an unambiguous scale (true values of differences between taxa).

Metrics for continuous variables can either be Euclidean or non-Euclidean distances and they can be metrics of linear distances between forms (standard deviation), squared distances (variance) or volumes. Volume metrics aren’t great because they are multiplicative so if you multiply a very small distance from one dimension that deflates the space (e.g. multiply 0.4, 0.3 and 0.002 and you get an answer which is very close to 0).

Standard deviations and variances are not linearly related.

Equation (page 281 of Zelditch book) to measure morphological disparity based on the Procrustes distance between the average mean shape of an individual species and the grand mean shape. You can get this shape disparity directly by estimating the Procrustes distances, or calculate the variance of coordinates obtained by a generalised least squares Procrustes superimposition (is this the same as a GPA?) or by the variances of partial warp scores. All three approaches give the same result.

**(**[**Erwin, 2007**](#_ENREF_12)**)**

Nice introduction about the long history of interest in the diversity of morphological form - Cuvier used shape as the basis for grouping animals into clusters. Early approaches to disparity, including Gould's Wonderful Life, relied on taxonomic rank as a reliable index of disparity.

Null model that disparity, like taxonomic diversity, should increase with the age of a clade - important to try and estimate the length of time for evolution of a clade. Ciampaglio 2001 compared measures of disparity - no single best measures, different metrics capture different aspects. Average pairwise dissimilarity is a good metric because it's relatively immune to differences in sample size. Refers to Harmon 2003 paper's method of including phylogenetic information - avoids having to map nodes into the morphospace. Discrete characters may underestimate disparity compared to using continuous characters (but see Foth 2012).

I've only read as far as page 8; I need to come back to the rest of it for a conceptual overview.

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

Disparity calculations using different types of morphological data. In this case, different proxies for morphological form converge on the same disparity signal

To cite tpsDig 2 they just did Rohlf (2010).

GPA on landmark coordinates were converted into a covariance matrix and subjected to a PCA. They used those PC scores as a proxy for skull shape -> used them in the disparity analysis

sum and product of the ranges and variances on the PC axes which account for more than 90% of total variance. Bootstrapping to get 95% confidence intervals (they don't specifically say whether that's with replacement but presumably that's implied). Similar disparity results to another study using discrete character sets. Villier and Eble 2004 reference (behind a paleobiology pay wall) on echinoid morphology also found similar results from disparity studies based on different morphological proxies

**(**[**Ruta et al., 2013**](#_ENREF_32)**)**

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 – ecological opportunity doesn’t necessarily correlate with morphological disparity.

Really good description of the disparity calculations, especially in the supplementary information. There’s also a good discussion about the difference between character based (usually nut not always cladistic) and geometric (shape based) disparity analyses

**Back to convergence papers**

**(**[**Ojeda et al., 1999**](#_ENREF_29)**)**

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_9)**)**

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_8)**)**

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_39)**)**

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_31)**)**

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. Do we see 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_23)**)**

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_24)**)**

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

He gives convergence examples e.g. toxic animals and their mimics.

**More convergence papers added 10/12/13**

**(**[**Tseng, 2013**](#_ENREF_38)**)**

Not quite quantifying convergence but it is a novel approach; compare actual evolutionary trends to predicted evolution under biomechanically optimal parameters. Two questions: are morphologically convergent species actually convergent in functional capability? Do those morphologies occupy local optimal peaks in a functional landscape?

Convergent morphologies can arise from either convergent or parallel evolutionary pathways - Tseng and Wang 2011 palaeobiology paper. Combined functional simulations, Finite Element Analysis (FEA for studying biomechanics) and theoretical morphospace

Created a theoretical morphospace, put a wire mesh model on top of it and then created functional landscapes for mechanical advantage and strain energy. Actual skulls evolved over an optimal trajectory in the theoretical space

But, the most optimised theoretical shapes in the functional landscapes are not represented by real species so there must be a constraint on skull shape disparity within the hybrid morphospace of theoretical possible shapes - It makes sense since the skull is constrained by far more factors than just biomechanics.

Macroevolutionary ratchet; evolutionary process of moving up in elevation on the adaptive landscape (specialists are at higher elevations than generalists). The alternative idea is that mobile and dynamic adaptive peaks through time so organisms may follow more of an evolutionary adjustment to current peaks.

**(**[**Parker et al., 2013**](#_ENREF_30)**)**

This is the first evidence for genome-wide convergence rather than just in specific candidate genes. 6 bat species, bottlenose dolphins and 5 mammalian outgroups

Convergent changes in genes associated with the shift in primary sensory modality (vision->echolocation) either directly or through the associated complex changes in ecology and natural history.

Bats and cetaceans - shifts in spectral tuning and other adaptations in response to living in low light environments -> also found convergence in genes implicated in vision - similar to tenrecs/nocturnal mammals in general?

Stronger sequence convergence for hearing genes in echolocating bats and dolphins compared to other genes.

Many of the convergent loci have unknown functions - some which are definitely not involved in sensory perception may instead be associated with phenotypic traits that are correlated with aspects of echolocation.

Measured strength of selection as the ratio between non-synonymous substitutions and synonymous substitutions - indicates molecular adaptation.

**(**[**Moen et al., 2013**](#_ENREF_27)**)**

Many questions still remain to be resolved e.g. does similarity in ecology necessarily translate to similarity in morphology and performance? Two reasons for similar traits in species from different regions; convergent evolution and ecologically conservative dispersal (ECD) - lineages disperse and conserve the relative ecological trait during and after dispersal.

Most studies assume convergence and don't test for dispersal similarity. It's important to look for similarity in ecology, morphology and performance e.g. locomotion or feeding.

Three different frog assemblages in field sites in China (n=11 species), Colombia (n=19) and Australia (n=14). Samples don't include all of the species at each site but they're probably representative of the ecological diversity. They captured male frogs and used video analysis of behavioural trials of clinging, swimming and jumping abilities. Killed the frogs after the trials and measured morphological variables that are related to performance activity. They divided species into different microhabitat classes; arboreal, burrowing, semi-aquatic or terrestrial.

Phylogenetic PCAs based on Revell's 2009 paper. NB; there's a Polly 2013 paper from Hystrix on the application of phylogenetic PCAs to geometric morphometric data; mainly saying that the resulting scores are harder to interpret for shape change compared to ordinary PCAs. Phylogenetic MANOVA on PC scores for morphology and performance to test whether microhabitat use was associated with particular morphological or performance traits. Species in different microhabitats were similar for PC1 so they only did MANOVAs on the PC axes after PC1 to look at the axes which distinguish among microhabitat specialists - did the same thing for analyses of conservatism and convergence

Tested relationships between morphological and performance variables; otherwise you can't do a clear ecomorphological study. They identified microhabitat states as either in-situ evolution or ECD.

They did a novel test for conservatism; compared pairwise Euclidean distance between similar species from different locations to the distances among all species with the same ecology and among all the species from the same location. They also had new tests to see whether the previous evolutionary history of a clade limits the ability of descendants to evolve into diverse microhabitats. There were three groups; focal group with the ancestral ecology (Fanc), focal group with novel ecology (Fnov), unrelated species that have the same ecology as species in the focal group with novel ecology (nonF).

If history is important then expect Fnov not to have diverged far from Fanc -> compare the expected distance (Fanc to nonF) to the observed distance (Fanc to Fnov). They have a simple test of convergence; shorter distance between two groups sharing the same microhabitat than between two groups that are closely related.

Second test looks at vector of divergence of the Fnov from their ancestral Fanc type - measure what proportion of that divergence is in the direction expected by convergence. They tested significance by comparison to null distributions from simulations of phenotypic evolution.

These are all species mean approaches but they did try OU models of phenotypic evolution towards selective optima as well which gave similar results. NB: most OU methods require single values for selective regimes at internal nodes - which can be highly uncertain and therefore give poor results - not sure what SURFACE does about this?

Microhabitat use was related to morphology and performance but traits were more distinctive in aquatic, arboreal and fossorial forms - so my general terrestrial species might not be clearly separated by this kind of analysis.

Morphology and performance gave similar results but those for morphology were statistically stronger. Convergence analyses; adaptation to different ecologies can largely erase the imprint of past adaptation to ancestral ecology - so, at least in this one arboreal frog clade, history doesn't constrain convergence. NB: both dispersal (ECD) and convergence for producing trait similarity, even across continents. ECD may be more important in biogeographically connected regions while in-situ evolution is more important on islands - but frogs only partly follow these expectations

NB: lots more detail to read in the supplemental

**(**[**Segar et al., 2013**](#_ENREF_34)**)**

Wasp communities associated with figs; include both herbivore and parasitoid species. Clustering approach to put species into guilds -> calculate ecological distances between species. Diagram for data analysis on page 2; null hypotheses for different models of community convergence structure. Defined guilds of ecological similarity based on different detailed traits e.g. timing of oviposition, gall size...

I don't understand how they calculated ecological distance. The guilds approach might be too specific for me because the wasp/fig system is much clearer for defining the different roles of the species. They analysed traits by generating Euclidean distances to obtain "ecological" branch lengths. Clustered species using Ward's hierarchical method with k-means analysis to determine the guilds and assessed the support using AU p-values based on bootstrapping. Community diversity calculated using mean pairwise distance and mean nearest taxon distance across both the molecular phylogeny and e neighbour-joining tree built from ecological Euclidean distances- I don't know what they mean by that part.

Tested the explanatory power of ecological role and phylogeny as predictors of log (relative species abundance) ->control for phylogeny - if ecological role is still significant then it suggests convergence in the community structure rather than just inheritance through phylogenetic niche conservatism. Phylogenetic Eigenvector Regression (PVR) to quantify the relative contributions of ecological role and phylogeny- Diniz-Fikho 1998 reference.

Used PCoA on the ecological distance matrix and selected the eigenvectors which explained the most variation in log (relative species abundance). Decomposed the phylogenetic distance matrix and did a PVR with the ecological eigenvectors as explanatory variables.

They made a new index: the proportion of phylogenetic distance/proportion of ecological distance occupied by each pairwise comparison. They considered cases in the 95th quantile of the distribution to reflect phylogenetic>>ecological distance and therefore ecological convergence - similar idea to the pretty morphological vs. phylogenetic graphs in Muschick 2012.

**(**[**Harmon et al., 2010**](#_ENREF_17)**)**

Body size and disparity through time – more relevant for disparity background rather than convergence.

Time course of morphological evolution varies substantially among clades. Results were roughly similar for body size and shape but body shape appears to be constrained more often than body size. Most comparative methods assume models of constant-rate BM but that has a poor fit for some clades. So early burst patterns appear to be rare but this is in contrast to other work which suggests that slowdowns in lineage diversification through time are common in comparative data - contrast between patterns of lineage diversification and the accumulation of morphological disparity through time

**(**[**Elias et al., 2008**](#_ENREF_11)**)**

Müllerian mimicry as an example of mutualism - drives convergence along multiple ecological axes. They found stable coexistence of several mimicry complexes in communities. First test of adaptive ecological convergence at the community level in Müllerian mimics. Ithomiines are Müllerian mimetic butterflies in the neotropics. Mutualism drives convergence in flight height and forest habitat and these effects outweigh common ancestry and competition. Ecological distances regressed onto phylogenetic distances - tested the residuals for convergence (-ve) and divergence (+ve) patterns among co-mimics and non-co-mimics. Convergent microhabitat use in both simulation and regression analyses.

**(**[**Fleischer et al., 2008**](#_ENREF_13)**)**

DNA sequences from Hawaiian museum specimens - the Hawaiian birds became extinct in the 1980s. Hawaiian honeyeaters are only distantly related to Australasian ones. They have similar morphologies, behaviour and song so their convergent life histories led many taxonomists to place them into the same groups (similar to early taxonomy of tenrecs). Convergence is seen in at least two independent radiations. They are undoubtedly convergent because the two groups look and behaved more similarly to each other than to their closest relatives but there's no measure of convergence.

**(**[**Jones and Holderied, 2007**](#_ENREF_21)**)**

Good reference for discussing the influence of similar environments in phenotypic and functional/behavioural convergence. Phylogenetic analyses; particular types of echolocation signals have evolved independently in several lineages of bats - call design is often more influenced by perceptual challenges from the environment than by the phylogeny.

They use improved technology for recording flight paths and 3D models of the environment. Most insectivorous bats have dominant frequencies between 20 and 60 kHz. Calls with broad bandwidths are better in cluttered environments. Good review of call features and structure; useful for my echolocation call analyses but I haven't read them all yet. Echolocation calls using clicks are unlikely to be ancestral in bats - also found in whales, swiftlets, oilbirds and insectivores. Convergence; high duty cycle echolocation has evolved twice - speed-dependent compensation for Doppler shifts during their flight. There’s similar convergence in large-eared bats from two different families.

**(**[**Scheffer and van Nes, 2006**](#_ENREF_33)**)**

This is a reference to go with the Muschick paper; convergent species occupying similar niches within a particular species assemblage. Convergent species can evolve by spontaneous coevolution of competitors - prediction only applies to species-saturated communities.

There are two options to co-exist; be sufficiently different or sufficiently similar. They use a Lotka-Voltera model of competition with coefficients that mimic competition between species along a niche gradient. They run a simulation of competing species in an infinite niche axis (circle). Run a competition model - simulations converge to a transient pattern of self-organised lumps that contain multiple coexisting species of similar size. Lumps are more spread apart if the niches are broader. So co-existence of different lumps is avoidance competition and similar species can exist within lumps. Very slow competitive displacement - relatively easy for other processes to stabilise coexistence e.g. predation. Coexistence lumps seem to be even more stable on an evolutionary rather than ecological time scale. They give examples; convergence between fish in streams and preferential invasion of relatives of resident plants in New Zealand. Another example is the lumpiness of species distributions for various species.

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

Similar chemical defences in neotropical ants and endemic Malagasy ants which are not closely related. Two levels of convergence: convergent evolution in production of defensive alkaloids by the ants and subsequent convergence in poisonous frogs in the Neotropics and Madagascar. There’s variation among frogs in Madagascar; alkaloid profiles seem to be mainly influenced by the distribution of local arthropod alkaloid sources rather than ecological or evolutionary differences among frog species.

**(**[**Bernal et al., 2001**](#_ENREF_3)**)**

Suite of similar physiological and behavioural traits evolved separately in tunas and laminid sharks. Strong selective influences (e.g. hydromechanics) can lead to modification of different body plans to result in similar morphologies. Continuous swimming - convergent design features; endothermy, energetics... Argue that the convergence has been strongly influenced by hydrodynamic factors governing continuous swimming. But complete understanding is limited by a lack of data about the two groups' sister taxa.

**(**[**Donley et al., 2004**](#_ENREF_10)**)**

They use more of a quantitative approach; comparing convergent pair to other closely related species. Convergence between laminid sharks and tunas is more than skin deep - convergent morphological and functional adaptations in mechanical design. They made in vivo quantitative measurements of swimming kinematics and muscle dynamics in laminid sharks. Quantitative swimming data; sharks kinematically resemble tuna more than other sharks. Both groups use the same mechanism to swim with the same method of propulsion.

**(**[**Jones et al., 2012**](#_ENREF_20)**)**

Genetic loci consistently associated with marine-freshwater adaptation. The paper is very dense but Ed Yong's blog (in macroevolution tutorial reading) has a good summary. Main point is that pairs of marine and freshwater cichlids from similar locations have similar genetic divergence to other pairs - so repeated evolution of similar genetic changes to produce divergent phenotypes. Seems to mainly involve changes in regulatory rather than protein coding regions but that may be because of their whole-genome rather than candidate genes approach.

Nice system: both phenotypic and genetic convergence.

**(**[**Blount et al., 2008**](#_ENREF_4)**)**

NB; Science magazine article about this paper - the article is part of the reading notes for the macroevolution tutorial

There was evolution of citrate metabolism in some *E.coli* lineages but only after many generations. Historical contingency can have a profound and lasting impact even under simple conditions. It is especially important when it facilitates the evolution of key innovations that don't easily evolve by gradual, cumulative selection. Gould; replay the tape of life would lead to very different results. Conway Morris; NS constrains to adaptive peaks so the evolutionary routes are many but the destinations are limited. *E.coli* population went through billions of mutations; far more than the total possible number of points mutations so the population tried each typical one step point mutation multiple times?

Late evolution of citrate metabolism; it’s difficult to explain but also interesting that it was so late in the experiment since the rate of fitness improvement had declined in all populations. Contingent adaptations; independent origins should be rare and significant time lags should occur. Overall increase in diversity; population gave rise to an ecological community with two members: a resource specialist and a resource generalist

**Papers**

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