Oikos

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Appendix 1–4

Appendix 1 – Individual-based Simulations

It is straightforward to run individual-based simulations following the model description in the main text. For efficiency, individuals were here aggregated in 'clones' of identical individuals. Each clone produced a Poisson distributed number of offspring, with a mean equal to the sum of the individual fitness values. This procedure was much faster than, but mathematically equivalent to, a truly individual based approach. Most simulations, unless otherwise stated, were run for 2×10^6 generations and sampled every 1000 generation for analysis and plotting. The simulations were run in C++ and plotted in Matlab (Matlab R2016a, MathWorks, Inc.). Code is available in Dryad Digital Repository https://doi.org/10.5061/dryad.jn44bq4

Appendix 2 – Clustering and phylogenetic analysis

To analyse the results it was necessary to track the evolving phenotypes through time. This was done by sorting the individuals (or clones) into *clusters* of similar phenotypes (cf. Pontarp et al. 2012). A cluster was defined as a set of individuals with common ancestry and a maximal Euclidian nearest-neighbour distance of $\Delta_{\max}$ in the (α, β) trait space. Each individual in a cluster had the same *cluster id*, which was inherited from parent to offspring. Before each population sampling, all clusters were checked to see if a branching event had occurred or if a cluster had gone extinct. A branching had occurred if a cluster could be divided into smaller clusters, i.e. subsets where no individual was within a distance $\Delta_{\max}$ to an individual of another subset. If there had been a branching, new clusters were formed by labelling each individual in each new sub-cluster with a new cluster id. An extinction was noted if a cluster no longer had any member individuals. A separate table was kept in order to track the birth and death time of each cluster, its mean phenotype at birth and death, its parent cluster, and its possible descendant clusters. The parameter $\Delta_{\max}$ was set to 0.15 after a bit of trial and error. With a too large $\Delta_{\max}$, the algorithm fails to identify clusters that are easily identified by visual inspection. A too small $\Delta_{\max}$ generates many small, ephemeral, clusters that take time and computer memory to track and complicate the subsequent analysis. Sub-clusters containing less than 10 individuals were for the same reasons not considered for branching (but could, if they survived and multiplied, be identified as a new cluster at a later sampling event).

The heritability of cluster id assured that cluster merging was not possible, even if two clusters would temporarily evolve to similar phenotypes. It also made it possible to reconstruct and analyse the phylogeny of the final clusters, identified as (asexual) species. The time since divergence of two extant species was calculated by back-tracking the table of cluster information. This information, together with the mean phenotype of each species, was used to calculate Pagel's λ (Pagel 1999) of the α-trait and the β-trait, respectively. The PHYLOSIG function of the PHYTOOLS R package (v. 0.6-20, Revell 2012) was adapted to Matlab for this purpose. Pagel's λ measures to what extent a shared evolutionary history can explain trait similarities and is often used as a measure of phylogenetic signal or niche conservatism. The difference in λ between the α- and β-trait was here used to determine which trait was most evolutionarily conserved. Blomberg’s K (Blomberg et al. 2003) was also tested as a measure of niche conservatism. The results were qualitatively similar to those of Pagel’s λ but showed somewhat less correspondence to what could be expected by visual inspection of the phylogenies.

Appendix 3 – Invasion fitness

The fitness landscapes in Fig. 5 were calculated using the standard technique of dominant eigenvalues (Metz et al. 1992). The transition matrix A of a phenotype $[\alpha, \beta]$ was calculated as

$$A = MF,$$

where F is a diagonal $n_H \times n_H$ matrix with the fecundities in the different habitats (eq. 3) as the diagonal elements. The dispersal matrix M is likewise $n_H \times n_H$ with diagonal elements $1 - m$ and off-diagonal elements $\frac{m}{n_H - 1}$, corresponding to global dispersal with dispersal probability m. Invasion fitness was calculated as the dominant eigenvalue of A, given the equilibrium abundance of resources in all habitats, as determined by the current distribution of consumers (eq. 2).

Appendix 4 – Ecological Stability Analysis

Rescaling system units such that $I = k = c = 1$ (see Parameter values section), setting the system size parameter K to 1, and combining eq. (3) with eqs. (2), (4) and (5) gives the fecundity of a single resource and single habitat specialist feeding on its preferred resource (but nothing else) in its preferred habitat as

$$f = a_0 R^* - d = \frac{a_0}{1 + a_0 n} - d,$$

where n is the local number of identical specialist consumers. Since the generations are discrete, the fecundity is equal to the *per capita* growth rate and the local dynamics (ignoring dispersal) follow

$$n_{t+1} = F(n_t) = f n_t = \left(\frac{a_0}{1 + a_0 n} - d\right) n_t,$$

introducing $F(n)$ as a Solving $f = 1$ for n gives the equilibrium population size

$$n^* = \frac{a_0 - d - 1}{a_0(d + 1)}.$$

It follows directly that $a_0 > d + 1$ is necessary for a positive equilibrium size. The local dynamic stability is dependent on the derivative dF/dn evaluated at the equilibrium population size, which gives

$$\left.\frac{dF}{dn}\right|_{n=n^*} = \frac{(d + 1)^2}{a_0} - d.$$

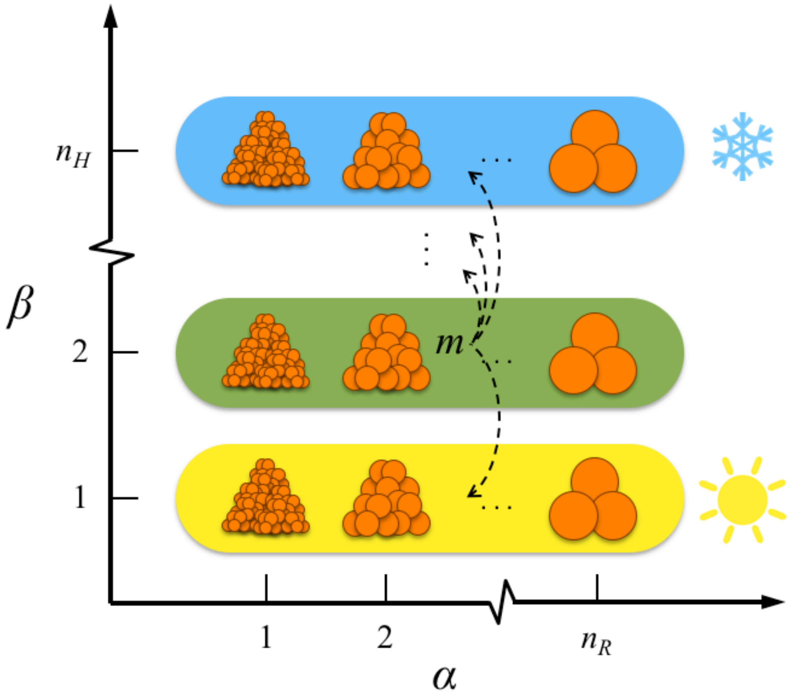
This entity should fall in the interval $(-1, +1)$ to ensure dynamic stability of the equilibrium. The condition for the upper boundary ($\frac{dF}{dn} < 1$) coincides with the condition for $n^* > 0$, so it is fulfilled as long as there is population persistence. The lower boundary condition ($\frac{dF}{dn} > -1$) is met as long as $d < 1$ or $a_0 < \frac{(d+1)^2}{d-1}$.

Strictly speaking, these conditions only apply to the case of a single specialist feeding on a single resource in a single habitat, but they should work as useful guidelines for finding suitable parameter values for the extended system, i.e. parameter values that allow long term persistence of the evolving species.

Additional References

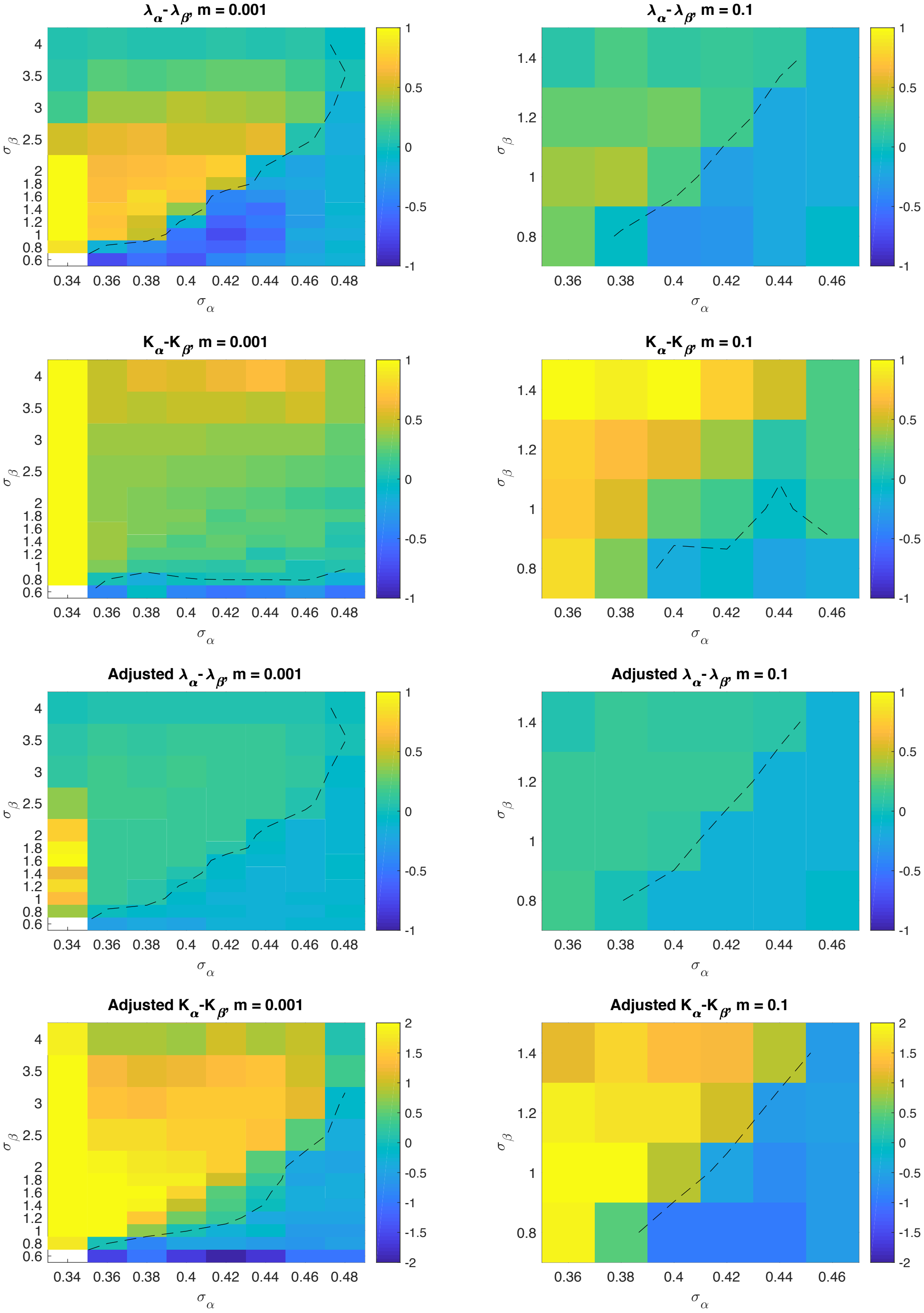
Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217-223.

Supplementary Fig. A1



A schematic illustration of the model structure. A sequence of habitats, 1, …, n_H, here drawn as differently coloured patches, each contains a suite of resources, 1, …, n_R, drawn as piles of differently sized food items. The two evolving traits, α and β, correspond to two niche axes. The α-trait maps onto the available resources such that an α-value equal to i represents a specialist of resource i. Likewise does the β-trait correspond to adaptation to the physical environment of the different habitats. Individuals disperse each generation with a probability m to a randomly chosen habitat.

Supplementary Fig. A2



A comparison of different measures of phylogenetic signal.

The top two panels are identical to Fig. 3 in the main text, showing the average difference in Pagel's λ between the α-trait and the β-trait across parameter space. The dashed black lines show the contour of $\lambda_\alpha - \lambda_\beta = 0$, separating a pattern of α-niche conservatism (bright yellow) from β-niche conservatism (dark blue). The second row shows the same results using Blomberg's K statistic instead of Pagel's λ. The overall pattern is the same, but there is a consistent bias towards α-niche conservatism. However, both these statistics change with time after the completion of an adaptive radiation, since they depend on *relative* path lengths between species. Adjusting for this by measuring the phylogenetic signal a fixed waiting time (2×10^4 generations) after the last speciation event gives different results, presented in rows three and four. The difference in Pagel's λ is smaller in magnitude but the boundary between α- and β-niche conservatism is preserved (row three). The adjusted results for Blomberg's K (row four) are now qualitatively very similar to those of Pagel's λ (rows one and three). Choosing a longer waiting time gives results more similar to the unadjusted results.