OIKOS

Research

Ecology and macroevolution – evolutionary niche monopolisation as a mechanisms of niche conservatism

Jörgen Ripa

J. Ripa (http://orcid.org/0000-0002-9211-1941) (jorgen.ripa@biol.lu.se), Dept. of Biology, Lund Univ., Sölvegatan 37, SE-223 62 Lund, Sweden.

Explaining macroevolution from microevolution is a key issue in contemporary evolutionary theory. A recurrent macroevolutionary pattern is that some niche-related traits consistently evolve slower than others, so called niche conservatism. Despite a growing amount of data, the underlying evolutionary processes are not fully understood. I here analyse adaptive radiations in an individual-based eco-evolutionary model. I find a coevolutionary mechanism – evolutionary niche monopolisation – as a possibly important generator of niche conservatism. A single lineage of a radiating clade can monopolise, and later diversify within, a substantial part of the available niche space – much larger than what can be explained by limiting similarity. This leads to niche conservatism, since no species evolves into or out of the monopolised region. The region can in this sense also be described as an adaptive zone. The model indicates that evolutionary niche monopolisation is operative in a large part of parameter space, underlining its possible importance. The mechanism is driven by competitive interactions and differences in niche widths in alternative niche dimensions. I discuss plausible examples of evolutionary niche monopolisation in well-studied natural systems.

Keywords: adaptive radiation, coevolution, adaptive zone

Introduction

Which traits evolve and how they diversify is a central question in evolutionary biology. One prediction is that ecological opportunity, i.e. unexploited regions of niche space, will be filled by whatever organism has the appropriate 'Bauplan' and lacks serious genetic constraints. Given a multitude of opportunities – such as after a key innovation, a mass extinction of competitors, or the colonisation of a new geographic region – a single lineage can rapidly diversify into a suite of closely related species, each adapted to a unique ecological niche. Such adaptive radiations have been studied both empirically and theoretically, and the process itself is considered a main generator of biodiversity on Earth (Schluter 2000). In the wake of recent technological developments, the detailed phylogenies of an increasing number of taxa have been mapped and we are now in a better position than ever to understand the finer details of the adaptive radiation process.

NSO
NORDIC SOCIETY OIKOS

www.oikosjournal.org

One common observation is that some traits consistently evolve slower than others, i.e. some traits are evolutionarily conserved and some are more labile (Peterson et al. 1999, Blomberg et al. 2003, Wiens and Graham 2005, Wiens et al. 2010, Pienaar et al. 2013). Some data indicate that specific 'types' of traits tend to be more conserved than others. Streelman and Danley (2003) proposed that, at least among vertebrates, there is a specific sequence of trait divergence in an adaptive radiation. Habitat-specific traits tend to diverge first, followed by traits corresponding to resource utilisation and finally traits coupled to sexual selection. The emergent pattern of character evolution is that habitat niche traits have deep phylogenetic roots or show a strong phylogenetic signal, which can also be classified as a pattern of habitat niche conservatism.

Pickett and Bazzaz (1978) introduced the conceptual framework of α- and β-niches, useful in this context. An organism's α-niche is associated with local, competitive, interactions. A typical α-niche trait is the mouth morphology or feeding behaviour of a fish, which affects the strength of local competition with closely related species. Local coexistence of two species requires α-niche separation. The β-niche is simply the habitat niche – it dictates in which physical environments an organism can survive and reproduce. A typical β-niche trait would be a plant's adaptation to drought or a fish's adaptation to different salinity or depth. The β-niche is closely related to, if not identical to, the 'Grinnelian' niche concept (niche concepts reviewed by Leibold 1995). In the conceptual framework of Chesson (2000), the β-niche determines a species local 'average fitness', whereas α-niche differences correspond to general 'niche differences' enhancing local coexistence.

Using the concepts of the α- and β-niche framework, the Streelman and Danley (2003) proposition is that β-niches and their associated traits are typically conserved relative to α-niches. Such a pattern of β-niche conservatism has been found in a suite of organisms, ranging from fish (Danley and Kocher 2001, Koblmuller et al. 2004) to plants (Silvertown et al. 2006) and marine invertebrates (Hopkins et al. 2014). However, other authors have found the opposite pattern, i.e. α-niche conservatism (Richman and Price 1992, Ackerly et al. 2006, Sallan and Friedman 2012, Muschick et al. 2014, Anderson and Wiens 2017), and sometimes there is no clear signal (Ingram and Shurin 2009, Bernard-Verdier et al. 2013).

Niche conservatism is here used as a 'relative' concept, i.e. it is only by comparing the evolutionary rates of different traits that some can be classified as conserved and others not. In fact, all definitions of niche conservatism I have found in the literature rely in one way or the other on such relative measures, and it is in hard to come up with one that does not.

Understanding the origin of niche conservatism patterns is not only interesting in its own right, but may teach us something important about the evolution of natural communities, what mechanisms drive the diversification of fitness-related traits or how natural communities are assembled and structured. Several possible explanations for niche conservatism have been put forward, mainly to explain β-niche conservatism (Wiens et al. 2010): 1) genetic constraints – the necessary genetic variation is not possible within the 'Bauplan' of the focal organism or is simply missing. 2) Sharp environmental contrasts, e.g. between marine and terrestrial environments, makes transitions difficult and rare. Adaptations to specific environments are therefore conserved. 3) Adaptation to alternative habitats is hampered through demographic effects of extensive dispersal (Holt and Gaines 1992, Kawecki and Holt 2002) or strong gene-flow (Kirkpatrick and Barton 1997). 4) Competition – a species may be prevented from adapting to a certain habitat if strong competitors have already occupied that niche. The ecological opportunity is simply not there (Case and Taper 2000, De Meester et al. 2002).

Although the mechanisms above have been used repeatedly to explain patterns of niche conservatism, there are several gaps in our understanding. For instance, it is uncertain when to expect a pattern of α-niche conservatism instead of β-niche conservatism. Can ecological interactions, the coevolution within a radiating clade, generate one pattern or the other or is it all about genetic constraints? I here investigate adaptive radiations in an eco-evolutionary, individual-based model, flexible and general enough to produce different patterns of niche conservatism. I find all the proposed mechanisms operating, usually in concert, but also a new mechanism – 'evolutionary niche monopolisation', which turns out to be important in large parts of parameter space. These results offer new key insights into the inner machinery of niche coevolution.

Methods

Model

The model is designed within an α/β-niche framework, as introduced above, but many of the conclusions are applicable to arbitrary niche dimensions. The model meets the minimal requirements to be able to generate both α- and β-niche conservatism. The model organism has two evolving traits, one associated with an α-niche and one β-niche trait. More precisely, the organism has one trait, α, that controls its utilisation of n_R different resources and another trait, β, that determines its adaptation to n_H different habitats. All resources occur in all habitats, and the habitats are connected by passive (i.e. random) dispersal (a schematic illustration of the model is given in the Supplementary material Appendix 4 Fig. A1). Disruptive, frequency-dependent selection can drive the diversification of both traits (Geritz et al. 1998). In this way, a single ancestral (asexual) species can diversify into a saturated meta-community of maximally $n_R \times n_H$ co-existing consumer species, occupying distinct positions in trait space (Fig. 1). The corresponding phylogeny can show patterns of α- or β-niche conservatism.
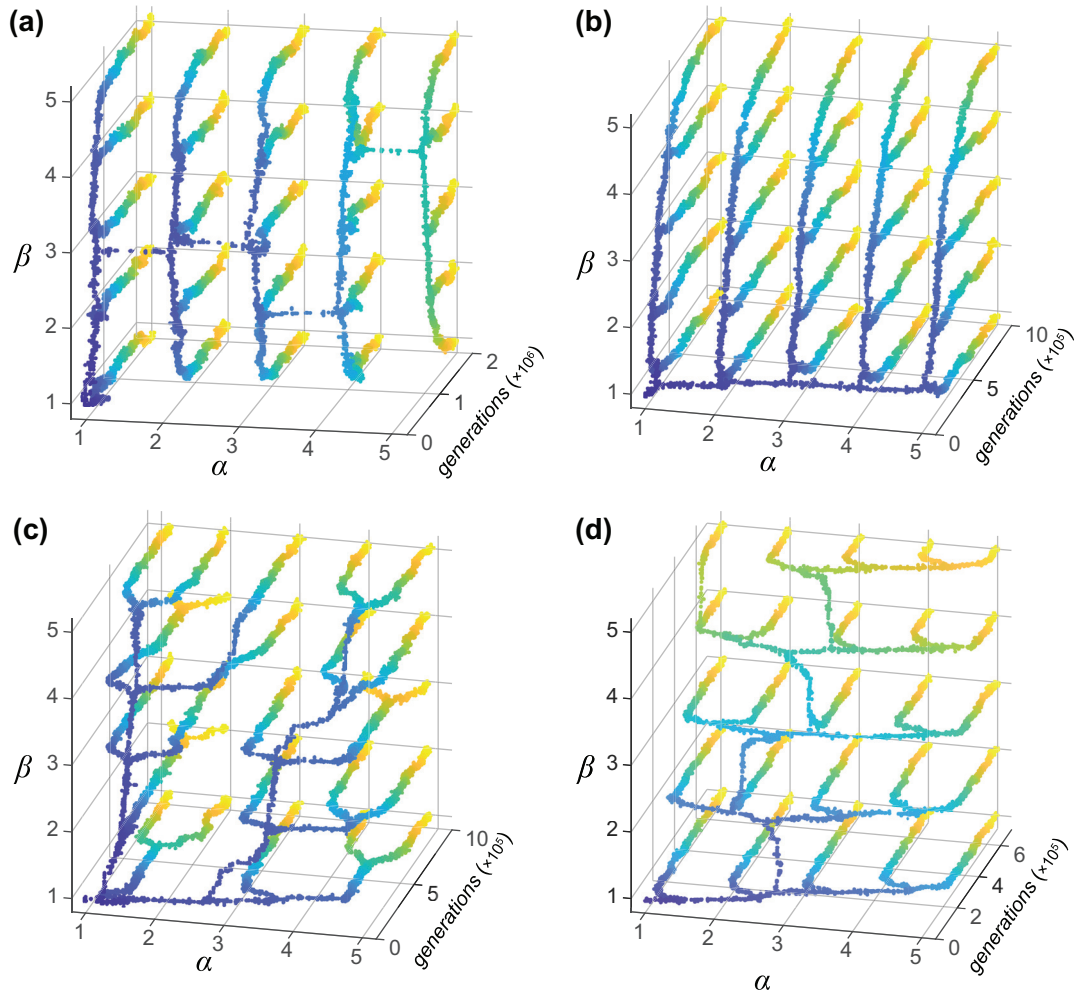
Figure 1. Each panel shows a sample simulated adaptive radiation, as it unfolds in trait-space (α, β) over time. The coloured dots represent the phenotypes (α, β) present in the population at any given time. For clarity, time is also colour-coded, ranging from dark blue (early) to bright yellow (late). In all cases the initial population at [α = 1, β = 1] diversifies into a community of 5 × 5 = 25 well-separated clusters (species), but the radiations show very diverse phylogenetic patterns depending on the values of the two niche width parameters, σ_α and σ_β. (a) $\sigma_\alpha = 0.34$, $\sigma_\beta = 2$; a narrow α-niche creates fitness valleys that only rarely can be crossed and a pattern of α-niche conservatism, i.e. rare evolution of the α-trait. (b) $\sigma_\alpha = 0.36$, $\sigma_\beta = 2$; an only slightly higher value of σ_α removes the fitness valleys. Instead, the rate of divergence in α is much faster than that in β, but α-evolution after the initial rapid divergence is constrained by niche monopolisation (see main text). Again, the emergent pattern is α-niche conservatism. (c) $\sigma_\alpha = 0.46$, $\sigma_\beta = 0.8$; a broad α-niche and relatively narrow β-niche promotes patterns of β-niche conservatism, but only on local phylogenetic scales (there are many small subclades where β is conserved). The pattern is driven by local niche monopolization. (d) $\sigma_\alpha = 0.38$, $\sigma_\beta = 0.6$; an even narrower β-niche gives hard-to-cross fitness valleys for the β-trait and a corresponding pattern of β-niche conservatism. Other parameters: $m = 0.001$, $n_R = 5$, $n_H = 5$, $K = 1000$, $I = 1$, $k = 1$, $c = 1$, $d = 0$, $a_0 = 4$, $\mu = 10^{-4}$ and $\nu_\alpha = \nu_\beta = 0.02^2$.

Resource dynamics

The n_R resources in each habitat are regulated by chemostat-type dynamics and a type I functional response of the consumers. These assumptions assure ecological stability while keeping the number of parameters to a minimum. It is also assumed that local resource dynamics (in continuous time, within season) is much faster than consumer dynamics (in discrete time), such that the resources are always at an equilibrium set by the current local consumer population (see Rueffler et al. 2006 and Nilsson and Ripa 2010 for similar resource model assumptions). The dynamics of resource i in habitat h are given by

$$\frac{dR_{ih}}{d\tau} = KI - kR_{ih} - \sum_{j \in S_h} \frac{a_{ij}}{K} R_{ih}, \; i = 1, \ldots, n_R; \, h = 1, \ldots, n_H \quad (1)$$

where R_{ih} is the biomass of resource i in habitat h, τ is time on the fast time-scale, I is a constant inflow of resources per time unit (in units of τ), k is the resource outflow per mass unit per time unit, a_{ij} is the consumption per time unit of resource

i by individual *j*, and the sum is taken across the set S_h of individuals occurring in habitat *h*. *K* is a unit-free scaling constant, used to adjust the total size of the system and thereby the total number of consumers. Given that the resource dynamics are much faster than the consumer dynamics, the equilibrium biomass of resource R_{ih} becomes

$$R_{ih}^* = \frac{KI}{k + \sum_{j \in S_h} \dfrac{a_{ij}}{K}} \qquad (2)$$

Consumer dynamics

The consumer dynamics occur on a longer, discrete, time-scale denoted *t*. Within a single time-step, from *t* to *t* + 1, all consumers reproduce and then die. Each offspring disperses with probability *m* to a randomly chosen habitat, which completes the time-step. The average number of offspring by consumer *j* in habitat *h* is a linear function of its total resource consumption, which depends on the available amount of local resources according to

$$f_{hj} = b_{hj} \left(c \frac{\sum_{i=1}^{n_R} a_{ij} R_{ih}^*}{K} - d \right) \qquad (3)$$

where b_{hj} ($0 < b_{hj} < 1$) represents the adaptation of individual *j* to the abiotic environment in habitat *h*, *c* is a conversion factor and *d* sets a minimal level of consumption below which the consumer dies immediately without reproducing (f_{hj} is truncated below at zero). Since the resource abundances (R_{ij}^*) are contingent on the local consumer community (Eq. 2), the fecundity expressed in Eq. 3 is limited by local resource competition. The actual number of offspring of each individual is drawn from a Poisson distribution with a mean given by Eq. 3. All offspring are born into the same habitat as their respective parents (but may disperse, as described above).

Trait evolution

All consumers have two heritable, continuous traits – α and β, representing their α- and β-niche, respectively. The α-trait dictates a consumer's ability to utilise the different resources according to a Gaussian function (following Nilsson and Ripa 2010)

$$a_{ij} = a_0 \exp \left(-\frac{(\alpha_j - i)^2}{2\sigma_\alpha^2} \right) \qquad (4)$$

where a_0 is the maximal consumption rate, σ_α represents the width of the consumer resource niche and α_j is the trait-value of individual *j*. It follows from Eq. 4 that a consumer with an α-value close to *i* is specialised on resource *i*. A small σ_α implies that deviations from a specialist strategy renders a high cost in terms of a lower consumption rate, i.e. there is a strong tradeoff between different resource types. A large σ_α, i.e. a broad niche, implies a weak tradeoff and that a single consumer can feed efficiently from more than one resource.

The model habitats differ in a sense that requires specific adaptations, and the β-trait represents an individual's local adaptation. The local growth rate of consumer *j* is modified by a factor b_{hj} (Eq. 3), which depends on the consumer's trait β_j according to

$$b_{hj} = \exp \left(-\frac{(\beta_j - h)^2}{2\sigma_\beta^2} \right) \qquad (5)$$

such that a β-value equal to *h* implies perfect adaptation to habitat *h* (see also Meszéna et al. 1997). The habitat niche width, σ_β, controls the strength of the tradeoff between habitats, analogous to the resource niche width, σ_α.

Both traits (α and β) are faithfully inherited from parent to offspring except for mutation events. Each trait mutates independently with probability μ to a new value. Mutated α- and β-values are drawn from a normal distributions with means equal to the parent values and variances equal to ν_α and ν_β, respectively.

Evolutionary branching and ecological diversification

In order to study adaptive radiations some mechanism of diversification is necessary. Large mutations, from one adaptive peak to another, are conceivable but unlikely. As an alternative, it is possible to find a region of parameter space where 'evolutionary branching' is possible. The process is described and analysed in detail within the adaptive dynamics framework (Geritz et al. 1998), but first conceived by Rosenzweig (1978). Evolutionary branching allows a lineage to diverge in trait space despite small mutational steps, entirely driven by (frequency-dependent) natural selection. Loosely described, the process begins with directional selection towards, say, an unexploited niche. Assuming the focal organism starts off in a pre-existing, ancestral, niche, frequency dependent selection will make it gradually adapt to the empty niche. The ancestral niche will thus become increasingly under-utilised. At some intermediate phenotype, called a branching point, the organism is subject to disruptive selection, leading to splitting and divergent selection towards both niches, the new and the ancestral. A huge benefit of this approach is that speciation is an emergent process, driven by ecological feedback and natural selection, and does not require extra parameters or assumptions (see Kisdi and Geritz 1999, Dieckmann and Doebeli 1999, Van Doorn and Weissing 2001 or Ripa 2009 for model examples with a sexually reproducing species).

Previous analyses of similar models indicate that this model should exhibit evolutionary branching in both the α-trait (Rueffler et al. 2006) and the β-trait (Brown and Pavlovic 1992, Meszéna et al. 1997). The α-trait, dictating consumption rates of the different resources, can typically branch if the corresponding niche width, σ_α, is of intermediate value. A too broad niche makes an intermediate type an evolutionarily stable strategy (ESS) and the expected evolutionary outcome is a single generalist. If the niche is too narrow, a consumer will get 'stuck' at a single specialist ESS, separated from the unexploited alternative resources by a fitness valley.

Branching in the β-trait is similarly dictated by the corresponding niche width, σ_β, but is also contingent on the dispersal rate, m. Frequent dispersal promotes an intermediate ESS, whereas a low m makes evolutionary branching more likely (Brown and Pavlovic 1992, Meszéna et al. 1997, Nilsson and Ripa 2010). A narrow β-niche (a small σ_β) will prevent colonisation of alternative habitats whereas a broad niche will select for an intermediate type, a habitat generalist. At intermediate niche-widths, evolutionary branching is possible (Brown and Pavlovic 1992, Meszéna et al. 1997, Nilsson and Ripa 2010).

Taken together, the previous experiences of related one-dimensional models indicate that there should be a region, a 'window of opportunity', in parameter space where evolutionary branching in both evolving traits is possible. This region should appear at intermediate values of both niche width parameters, at least at low to moderate levels of dispersal.

Parameter values

Two of the parameters, I, and k, can be set to 1 by rescaling the units of τ and R, respectively (Eq. 1). The conversion factor c can be set to 1 by rescaling the size (in biomass) of a consumer individual. This affects the strength of demographic stochasticity and genetic drift but is otherwise neutral. The parameters a_0 and d both affect ecological stability and persistence. A simple analysis (Supplementary material Appendix 4) gives that $a_0 > 1 + d$ is required for a specialist consumer to persist on a single resource. The same calculation implies that either $d < 1$ or $a_0 < \dfrac{(d-1)^2}{d-1}$ is necessary for ecological stability. Intermediate phenotypes require larger values of a_0 for persistence. I chose $a_0 = 4$ and $d = 0$, which keeps the population dynamics stable and maintains sizeable consumer populations throughout phenotype space. The scaling parameter K was set to 1000 such that a single consumer species would contain about 750 individuals – large enough to avoid substantial genetic drift but small enough to keep simulation length at a manageable level. The mutation probability μ was set to 10^{-4} and the variances of the mutation effect sizes were set to $\nu_\alpha = \nu_\beta = 0.02^2$. With these settings, it took more than just a handful of mutations to evolve from one species position to another. Yet, the evolutionary rate was high enough that ecological saturation could be reached within reasonable simulation time.

Individual-based simulations

Individual-based simulations followed the model description above. Each simulation was initiated with 100 identical individuals in habitat 1 with phenotype [$\alpha = 1$, $\beta = 1$] and ran for 2×10^6 generations. Details are given in Supplementary material Appendix 1.

Clustering and phylogenetic analysis

To analyse the results, it was necessary to track the evolving phenotypes and their ancestry through time. This was done by sorting the individuals into 'clusters' of similar phenotypes of common ancestry, here referred to as species. Cluster identity was heritable and could only change during branching events, when a single cluster was found to actually consist of two (or more) distinct phenotypic clusters. In such a case, the new clusters were given new, unique, cluster IDs. The identity of the parent cluster and its descendants was saved, together with the time of the event. Note here that the clustering was merely a matter of book-keeping and had no effect on the evolutionary process, which was all individual-based. The saved cluster information was later used to calculate the phylogenetic distance between the evolved species, which in turn was used to calculate Pagel's λ (Pagel 1999) of the α-trait and the β-trait, respectively. 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. More specifically, the length of the shared phylogenetic history raised to the power λ is used to explain the covariance of trait values between species. The λ that maximises the likelihood of the data is used as a measure of phylogenetic signal. A λ of 1 corresponds to random walk evolution (giving a strong signal), whereas a λ of 0 implies no signal, i.e. no relationship between shared phylogeny and trait value. Results using Blomberg's K (Blomberg et al. 2003) were qualitatively similar (Supplementary material Appendix 4 Fig. A2). Further details on the clustering and phylogenetic analysis are given in Supplementary material Appendix 2.

Fitness landscapes

Fitness landscapes of evolved communities were in some cases calculated for illustrational purposes (Fig. 5). The fitness measure, 'invasion fitness' (Metz et al. 1992), is based on individual fecundity (Eq. 3), but also takes dispersal between habitats into account (cf. Brown and Pavlovic 1992, Meszéna et al. 1997). The fitness of a phenotype is evaluated depending on its emergent, stationary, distribution across habitats, given the current equilibrium abundance of resources. Details are given in Supplementary material Appendix 3.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.jn44bq4> (Ripa 2018).

Results

Simulations show that a complete adaptive radiation from a single ancestral species to a saturated (meta-)community is possible in this model (Fig. 1). As predicted, both evolving traits diversify and the community reaches high levels of diversity within a bounded region of parameter space (Fig. 2).

It can also be seen from the simulations that the phylogenetic structure of the evolved communities varies considerably. In some cases, transitions in α are rare whereas β diversifies repeatedly (Fig. 1a–b). Such a pattern can be classified as α-conservatism. Other simulations show the
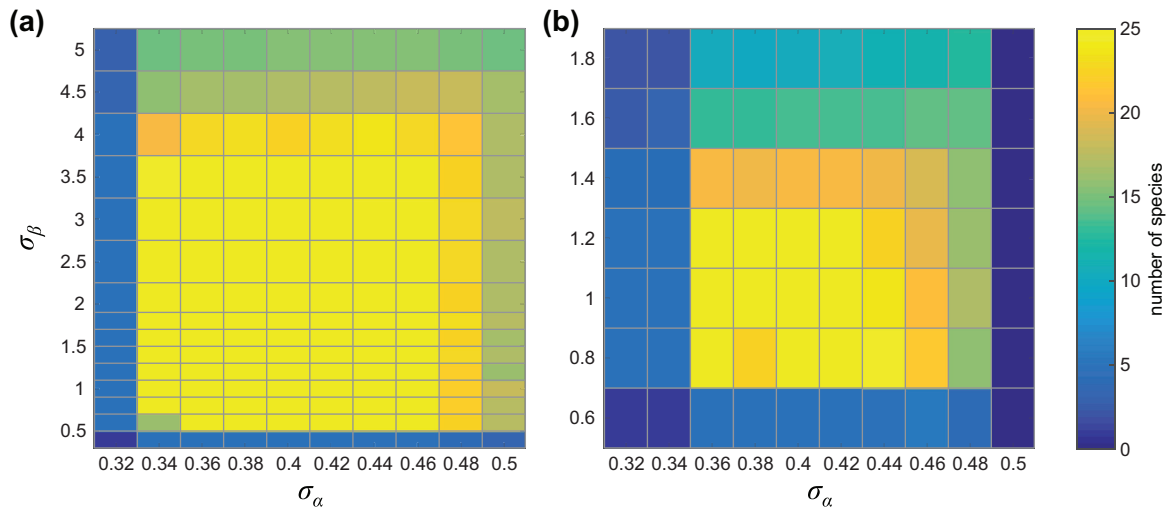
Figure 2. The number of species (phenotypic clusters) at the end of a simulation for different parameter combinations. Each rectangle is centred at the coordinates of the corresponding niche width parameters σ_α (x-axis) and σ_β (y-axis), and its colour indicates the average of 10 replicate runs (see colour scale to the right). Note the change of scale on the y-axis. (a) Dispersal rate $m = 0.001$; (b) $m = 0.1$. All other parameter values as in Fig. 1.

opposite, i.e. a pattern of β-conservatism (Fig. 1d). Yet others show a combination of the two (Fig. 1c). Fig. 3 shows the difference in phylogenetic signal of the two traits illustrated as the difference in Pagel's λ between the α- and β-trait. The dashed line is the contour level where $\lambda_\alpha = \lambda_\beta$, which can be interpreted as the boundary between a region of α-niche conservatism (bright yellow) and β-niche conservatism (dark blue). A narrow α-niche and broad β-niche (upper left corner) generates a pattern of α-niche conservatism, and the opposite condition generates β-niche conservatism (Fig. 3). The major mechanisms driving this pattern are discussed below.

Mechanism 1. Sharp niche contrasts

It is hard to adapt to an alternative niche if it is too different from an organism's current niche. For this model, that situation occurs at small values of the niche width parameters, corresponding to strong trade-offs. In the case of a narrow α-niche, i.e. a small σ_α, it is difficult to adapt to alternative resources. A single resource specialist is separated from alternative resource strategies by a fitness valley. Large, rare, mutations may be necessary to cross that valley. The emergent phylogeny shows rare transitions in α and repeated small radiations in β (Fig. 1a). Figure 4a shows the rate of divergence of the α-character
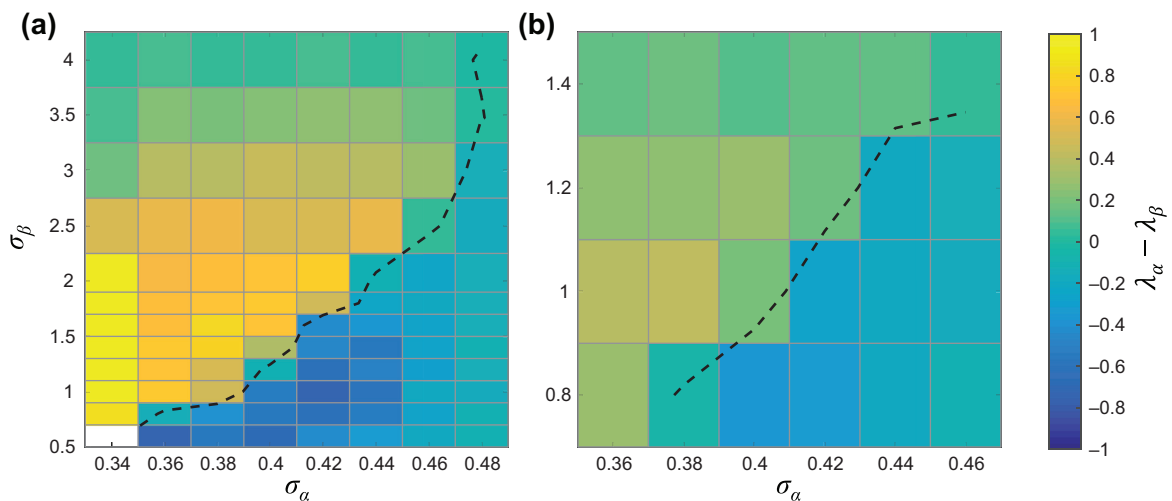

Figure 3. The mean difference in Pagel's λ, a measure of phylogenetic signal, between the two evolving traits (α and β), based on the simulations in Fig. 2. The dashed line is where $\lambda_\alpha = \lambda_\beta$, i.e. none of the traits has a stronger phylogenetic signal or is more conserved than the other. Bright yellow/orange colours represent a large positive difference, i.e. the α-trait is relatively conserved. Dark blue colours correspond to a strong negative difference and β-niche conservatism. (a) $m = 0.001$; (b) $m = 0.1$. All other parameter values as in Fig. 1.
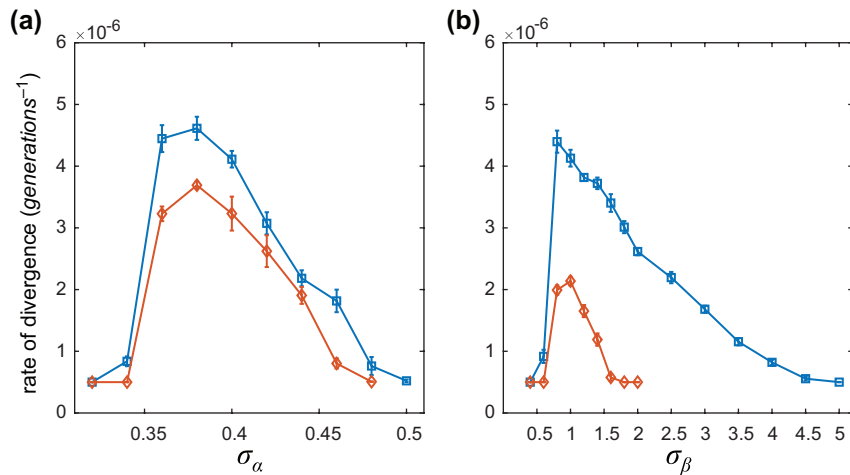
Figure 4. The average rate of ecological divergence (±1 SE) in the α-trait (a) and the β-trait (b). The rate is calculated as the mean of $1/T$, where T is the time (in generations) to reach a phenotypic range of 3.5 of the respective trait, corresponding to an almost complete filling of the available niche space. The mean is calculated from 10 replicated simulations from a part of parameter space where only one of the two ecological traits diversifies. In (a), σ_β is set to 0.4, preventing diversification of β. In (b), σ_α is set to 0.32, preventing diversification of α. In this way, the two rates of divergence are measured independently. In the case of no divergence, T was set to the maximal simulation time, 2×10^6, corresponding to a lowest divergence rate of 0.5×10^{-6}. The rate of dispersal, m, is 0.001 (blue squares) and 0.1 (red diamonds). All other parameter values as in Fig. 1.

evolving without the simultaneous divergence of β. It can be seen that low values of σ_α do not allow α-divergence at all, and that there is a small range of values (approximately at $0.34 < \sigma_\alpha < 0.36$) where divergence is hampered, before it actually reaches maximal speed around $\sigma_\alpha = 0.38$. A narrow niche width stops or slows down divergence as described above. A slightly broader niche will remove the fitness valley, since intermediate phenotypes are better off, and allow for evolutionary branching. That process is, in turn, speeded up by a relatively narrow niche, since a narrow niche implies stronger selection, directional as well as disruptive, which explains the peak divergence rate at the low end of the range (Fig. 4a). The same patterns and the same mechanisms apply to divergence of the β-trait (Fig. 4b). Figure 1d shows an example radiation where β-divergence is contingent on rare mutations crossing a fitness valley between habitat niches.

The part of parameter space that generates niche conservatism due to rare crossings of fitness valleys consists of narrow strips of small niche width values (around $\sigma_\alpha = 0.34$ or $\sigma_\beta = 0.6$, Fig. 4). A more narrow niche prevents diversification altogether, whereas a wider niche makes diversification very likely and swift. As an example, Fig. 1b differs from Fig. 1a by only a small increase in σ_α, from 0.34 to 0.36. Yet, the α-trait now diversifies rapidly – there is no apparent difference between the rates at which the two evolving traits reach full divergence. If anything, the last resource niche is filled slightly before the last habitat niche. Despite this, there is a clear pattern of α-niche conservatism, which begs for other explanations (Mechanism 3 below).

Mechanism 2. Weak selection

Niche conservatism as a pattern of relative evolutionary rates may be driven by overall differences in selection strengths,

causing some traits to evolve faster or slower than other traits. In this model, the two niche width parameters have a large impact on the overall rate of divergence. If a single trait evolves on its own, the maximal rate of divergence is reached at low values of the corresponding niche width, as explained above (Fig. 4).

A possible explanation for patterns of niche conservatism in this model may thus be that the corresponding trait has an intrinsic slow rate of divergence, caused by weak disruptive or directional selection, or both. This occurs at high values of the corresponding niche width parameter (Fig. 4). However, the patterns of niche conservatism found in this model (Fig. 3) go in the opposite direction. A wide niche width typically induces conservation of the other trait. Further, large changes of the rate of divergence of one trait can have little or no effect on the emergent pattern of conservatism (compare Fig. 1a and 1b). My conclusion is that the overall, 'intrinsic', rate of divergence of a particular trait plays a subordinate role for the emergent phylogenetic pattern. It is overshadowed by another mechanism, described in the next section.

Mechanism 3. Evolutionary niche monopolisation

Niche conservatism will emerge if a large part of niche space, an adaptive zone rather than a single niche, can be 'monopolised' once a single lineage is established within it. Figure 1b shows a possible example of this – a suite of resource specialists evolve early on. Subsequently, each of them diversifies in the β-dimension while remaining within the same α-niche. The resulting phylogeny has five subclades, one per resource niche. The adaptation to a particular resource niche occurs only once, although the subclades do not diversify completely in parallel and there should be opportunities for more shifts between resource niches.

To test to what extent a single species can prevent other lineages from evolving into the same region of niche space, the same resource niche or the same habitat niche, I made a new set of simulations, replicated across parameter space. They also serve as good illustrations of the monopolisation effect. Figure 5 shows a few samples of the tests of resource monopolisation (Fig. 5a, c) and habitat monopolisation (Fig. 5d). In Fig. 5a, a single, non-evolving, resource 2 specialist (marked with a solid black circle at generation 0) prevents a suite of six evolving resource 1 specialists from adapting to resource 2. Resource 2 is in this way monopolised, despite the presence

of empty niches at higher or lower β-values. These empty niches could easily be invaded if the right invading type should appear, as apparent from the large area of phenotypes with positive fitness centred around the unexploited niches (black area, Fig. 5a). However, the resource 1 specialists do not evolve into those niches. They sit on local fitness peaks and are separated from the invadable niche space by fitness valleys. The fitness valleys are due to the presence of the single resource 2 specialist, which at least partly exploits resource 2 in all habitats and makes the corresponding niche position less evolutionarily attractive. Removing the monopoliser
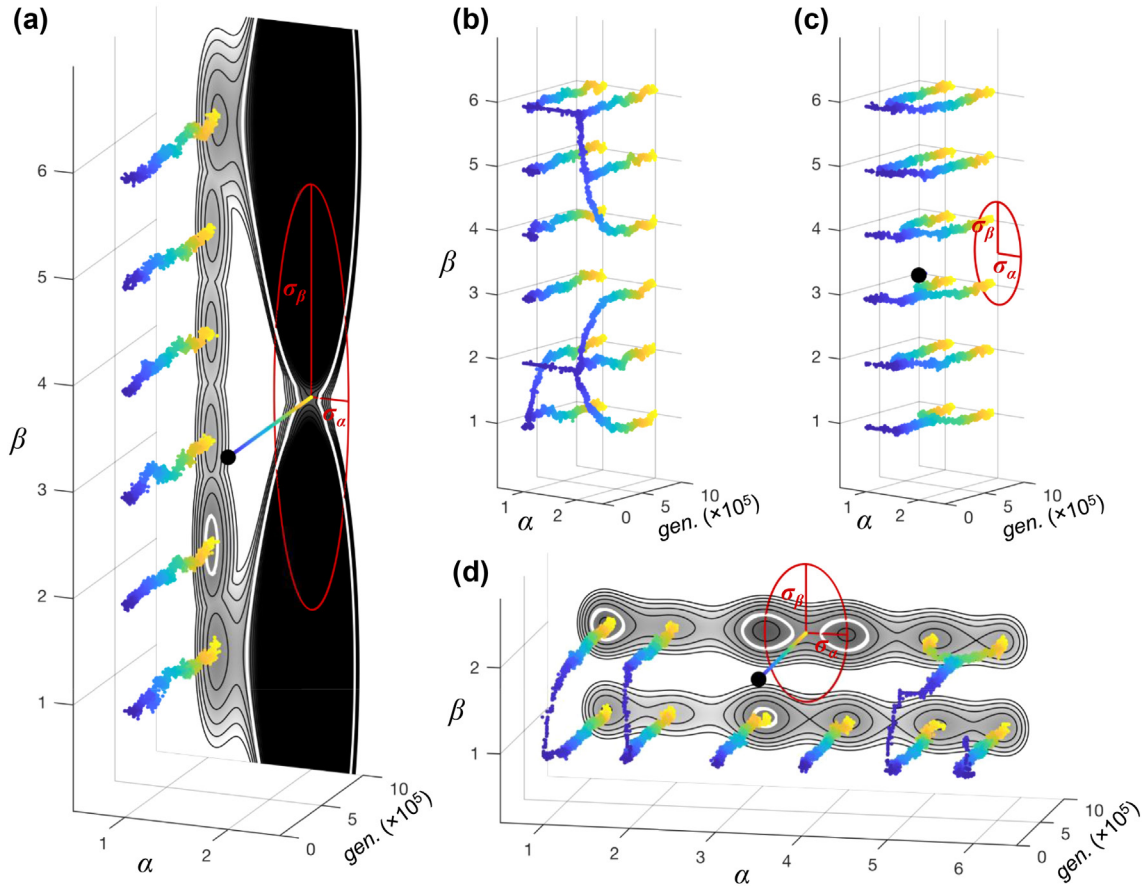

Figure 5. Simulations to illustrate evolutionary niche monopolisation, depicted as individual phenotypes through time as in Fig. 1. The ecological setup is in panels (a)–(c) that of two resources, corresponding to phenotypic values $\alpha = 1$ and $\alpha = 2$, and six habitats ($\beta = 1, \ldots,$ 6). (d) shows the reciprocal case with six resources ($\alpha = 1, \ldots, 6$) and two habitats ($\beta = 1, 2$). In (a) and (c) a single, non-evolving, resource 2 specialist is fixed at [$\alpha = 2$, $\beta = 3.5$] (marked with a solid black circle in generation 0) while a suite of six species initiated as resource 1 specialists [$\alpha = 1$, $\beta = 1, \ldots, 6$] evolve freely. (b) has the same setup as (a), but without the fixed species. In (c) the monopolisation is not effective and the fixed species rapidly goes extinct due to competition from the evolving species. In (d) there is a fixed habitat 2 specialist and six freely evolving species initiated as habitat 1 specialists. The red ellipses (a, c, d) have their main axes scaled as the corresponding niche width parameters (σ_α, σ_β) and thus indicate the size of the ecological niche in each case. In (a) and (d) the fitness landscape (see Methods) of the final generation is depicted as shades of grey ranging from 0.9 (white) to 1.1 (black), enhanced with black contour lines 0.02 fitness units apart and a single white contour line at fitness 1. The dark regions inside the white contours thus correspond to phenotypes that could increase in abundance if they appeared. The evolving species finalise on one fitness peak each, whereas the non-evolving species is stuck in a fitness valley (a, d) (note: none of the species is exactly at ecological equilibrium, i.e. exactly at fitness = 1, due to demographic stochasticity). The monopolisation effect is the strongest in panel (a), where a single (fixed) species can fence off other species from a large part of trait space, even though there is plenty of invadable niche space. (b) shows that the evolving species can readily evolve into the unoccupied niche space if the fixed species is removed. (a, b) $\sigma_\alpha = 0.35$, $\sigma_\beta = 2$; (c) $\sigma_\alpha = 0.44$, $\sigma_\beta = 0.8$; (d) $\sigma_\alpha = 0.48$, $\sigma_\beta = 0.8$; The dispersal rate $m = 0.001$ in all panels. All other parameters take values as in Fig. 1.

removes the fitness valleys and the resource 1 specialists can quickly adapt to the alternative resource and diversify within that region of niche space (Fig. 5b). A contrasting example is seen in Fig. 5c, where the six evolving species quickly become intermediate phenotypes and outcompete the non-evolving resource 2 specialist. Subsequently, resource 2 niche space is filled through six parallel evolutionary branching events.

There are two reasons for the successful monopolisation in Fig. 5a: 1) the β niche width (σ_β) is wide (see the red ellipse in Fig. 5a), which means the non-evolving species can colonise and exploit alternative habitats to some extent, despite not being fully adapted to them. 2) The α niche width is narrow, which makes resource 2 less exploitable to the evolving resource 1 specialists and further decreases selection in that direction. Taken together, the single resource 2 specialist creates a fitness valley that the evolving resource 1 specialists cannot cross, as they would otherwise (Fig. 5b). Figure 5c shows that resource monopolisation is not efficient if the appropriate conditions – a broad β-niche and a narrow α-niche – are not met.

Habitat niches can be monopolised in a similar way, given the analogous conditions, although not as efficiently. Figure 5d shows an example where the habitat 2 niche is only partly monopolised – three of the original habitat 1 specialist lineages manage to evolve into the alternative habitat niche, and even diversify within it. The non-evolving species can only monopolise the most nearby parts of niche space due to its still quite narrow resource niche, σ_α (Fig. 5d). A broader resource niche would enhance the monopolisation effect but at the same time impede diversification.

Figure 5a also illustrates the important difference between limiting similarity and niche monopolisation. The six evolving resource 1 specialists quickly settle on local fitness peaks leaving the nearby parts of niche space uninvadable. Another resource 1 specialist cannot invade this community, regardless

of its β-phenotype. The competition from the established species is too strong. This is a case of limiting similarity. On the other hand, almost any resource 2 specialist, i.e. with an $\alpha = 2$, has invasion fitness above 1. That part of niche space is totally open to invasion, should the right invader appear, but niche monopolisation prevents the already established species from evolving into that region, as described above, unless they are bestowed with large enough mutations in the right direction. In a sense, limiting similarity is about claiming niche space on an ecological time scale, operating directly through ecological interactions, whereas niche monopolisation is more indirect and on evolutionary time scales – ecological interactions control the fitness landscape which directs evolution away from the monopolised region.

Figure 6 summarises the results of the monopolisation test runs across parameter space. It shows how many lineages from the ancestral niche region, out of six, were prevented to evolve into the alternative, partly unoccupied, region of niche space. A high score (yellow colours) thus means strong monopolisation. Figure 6 confirms that both niche width parameters have an effect on both types of monopolisation. A larger β-niche will both strengthen resource monopolisation (Fig. 6a) and weaken habitat monopolisation (Fig. 6b). The opposite effects are produced by increasing the α-niche width.

Figure 6b also shows that habitat monopolisation is mostly efficient in the regions of parameter space where habitat niche evolution is already hampered by fitness valleys ($\sigma_\beta \lesssim 0.6$, cf. Fig. 4b). Above that region, habitat monopolisation is very limited in its extent. The same effect can be seen in the adaptive radiation simulations. I found no cases where a whole habitat niche was monopolised by a single lineage, except when transition between habitat niches was dependent on a jump across a fitness valley (Fig. 1d). Instead, habitat monopolisation was more local, extending to two or possibly three
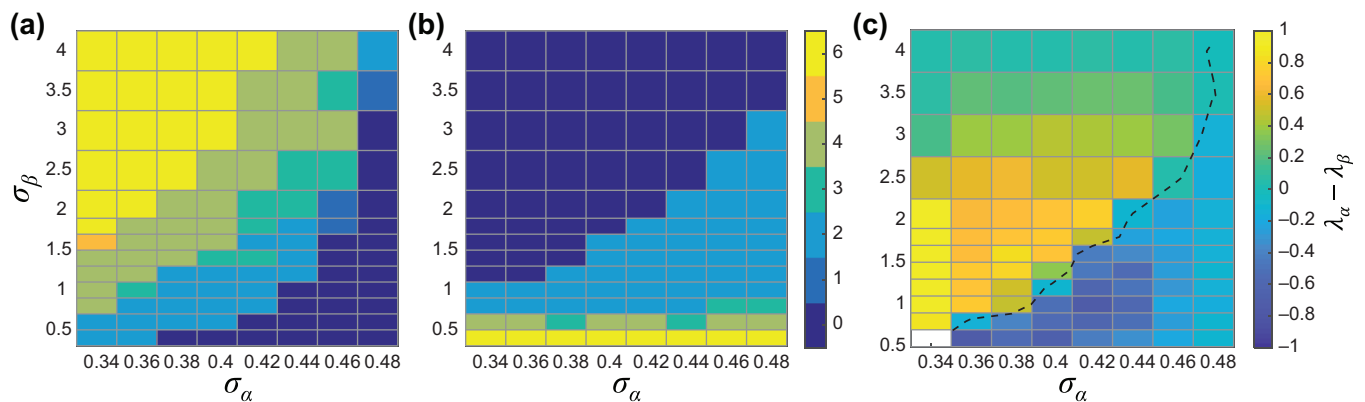

Figure 6. A summary of the monopolisation runs, showing the degree of monopolisation as a function of the two niche width parameters σ_α and σ_β. Each grid cell represents a single simulation as exemplified in Fig. 5. (a) Resource monopolisation. Grid cell colour indicates the number of evolving lineages, out of six, that were prevented to evolve into the monopolised region (evolve to an α-value > 1.3) (see colour scale to the right of (b)). For example, the simulation in Fig. 5a scores 6 and that in Fig. 5c scores 0. (b) The analogous measure of habitat monopolisation. The simulation in Fig. 5d scores 3 with this measure. (c) is a copy of Fig. 3a, to show that the contour lines of niche monopolisation (a, b) are well aligned with the dividing line between α- and β-niche conservatism (c, dashed line). All panels: $m = 0.001$ and other parameter values as in Fig. 1.

resource niches (Fig. 1c). This can be explained by the limited range of the resource niche width, σ_α. A too high value of σ_α prevents diversification altogether and an intermediate, generalist type is selected for instead. A broad resource niche thus reduces each habitat to a single species niche and niche monopolisation is reduced to a case of limiting similarity.

Resource monopolisation is not restricted in the same way as habitat monopolisation. A diversification of β is possible also for high values of σ_β, at least as long as the dispersal rate is low to moderate (compare Fig. 4a and 4b). Habitat adaptation evolves more easily than resource specialisation because the spatial distribution in itself contributes to disruptive selection on habitat-related traits. Incipient habitat specialists tend to occur in the environment to which they are already partly adapted, due to local competitive exclusion, which strengthens the selection for further habitat specialisation. There is thus a larger range of σ_β-values that allows diversification of β, and where resource monopolisation can be effective.

As a final point, the contour lines in Fig. 6 match the shape and position of the boundary between α- and β-niche conservatism in Fig. 3a, further corroborating evolutionary niche monopolisation as an important mechanism of niche conservatism patterns. For comparison, Fig. 3a is replicated as Fig. 6c.

Note: The qualifier 'evolutionary' is necessary to distinguish the concept discussed here from the niche monopolisation concept used in the niche construction literature, where, briefly put, a constructed niche can be monopolised by the 'constructor' in order to reap its benefits without competition (Krakauer et al. 2009).

Discussion

I have used a simple, conceptual model to investigate patterns of phylogenetic niche conservatism and the underlying eco-evolutionary mechanisms. Two traits evolve simultaneously in the model, representing an α-niche-trait and a β-niche-trait. The emergent phylogenetic pattern, α- or β-niche conservatism, depends on the organism's niche width in the two niche dimensions, and to some extent on the rate of dispersal. I studied the possible mechanisms underlying these patterns, in particular evolutionary niche monopolisation.

The simplicity of the model necessarily means that many factors of potential importance have been left out. However, the purpose of the model is to evaluate possible eco-evolutionary mechanisms driving the diversification of a clade and the relative evolutionary inertia of α- and β-niche-related traits. For that purpose, the model has the necessary ingredients – at least two evolving traits, one of each kind, a spatial structure and the possibility for ecological diversification in both niche dimensions.

The results highlight two non-exclusive mechanisms driving niche conservatism: 1) hard-to-cross fitness valleys generated by a narrow niche or a strong tradeoff and 2) evolutionary niche monopolisation. To disentangle which mechanism is the most important in what part of parameter space may be difficult, since they sometimes operate in parallel, but I found mechanism 1) limited to narrow strips of parameter space. Evolutionary niche monopolisation thus stands out as a potentially important driver of phylogenetic patterns of niche conservatism. Tentative results confirm that the other mechanisms suggested in the literature may also be operational. Genetic constraints, implemented as letting one trait have much smaller mutations than the other, makes the corresponding pattern of conservatism more likely. However, the qualitative results above pertaining to niche monopolisation remain (not shown). Demographic effects of high dispersal rates can prevent diversification altogether, also resulting in niche conservatism (Holt and Gaines 1992, Kawecki and Holt 2002). That effect is here reflected by the up-shifted lower bound of σ_β-values that allow full diversification in Fig. 2b as compared to Fig. 2a.

Some previous theoretical work has also pointed to the importance of niche monopolisation. Loeuille and Leibold (2008), Urban and De Meester (2009) and Vanoverbeke et al. (2016) showed how a locally adapted type can efficiently prevent a close relative from invading the same habitat niche. Niche monopolisation as described here extends beyond the niche of the single species into other niche dimensions where the organism has a relatively broad niche. A region of niche space can thus be monopolised against other species that are not necessarily the closest relatives but subject to the same underlying tradeoffs, i.e. typically members of the same genus or family. Evolutionary niche monopolisation should thus also apply to traits other than those explicitly analysed here – the underlying concepts and principles of niche widths, niche separation and niche exploitation are generally applicable.

There are a couple of examples from the empirical literature that hint at niche monopolisation as an explanatory mechanism. Richman and Price (1992) studied eight species of *Phylloscopus* warblers with a conspicuous pattern of niche conservatism – traits associated with resource utilisation were evolutionarily conserved relative to traits associated with habitat choice. In other words, diet niche traits evolved early in the phylogeny and were later conserved when other traits diversified. Richman and Price (1992) concluded that "Once a new ecological zone [diet niche] was occupied, subsequent morphological change along these niche axes was limited, accounting for the similarity of closely related species". It is important to note here that the diet niches of these warblers eventually harbour several species, adapted to separate habitat niches. Nonetheless, the full diet niche seems to be monopolised already by its first occupant.

Another example is the well-studied *Anolis* lizards of the Greater Antilles (Losos 2009). On each large island (Cuba, Hispaniola, Jamaica, Puerto Rico) a multitude of *Anolis* species have evolved, but most of them can be classified into one of six *ecomorphs*, specialised on different microhabitats and resource use. With few exceptions, each ecomorph has evolved only once on each island. Losos et al. (1998)

conclude: "Interspecific competition, which is intense among anoles and may drive their adaptive radiation, is probably responsible; once an ecomorph niche is filled on an island, other species are excluded from utilising that niche". This is evolutionary niche monopolisation in a nutshell. The different species within an ecomorph clade have in many cases adapted to different (macro-) habitats (Losos et al. 2006). In the light of my results, it can be hypothesised that the 'ecomorph niche width' is narrower than the 'habitat niche width' in anoles. In other words, utilising an alternative ecomorph niche has a higher fitness cost to an *Anolis* than utilising an alternative habitat (e.g. a different climate region or type of forest).

The monopolisation of entire habitat niches seems difficult judging from this study, at least if the habitat is complex enough to contain a multitude of alternative resource niches. Either, the monopolising species is enough of a generalist to fully exploit all resources, which makes monopolisation efficient but inhibits local diversification. Alternatively, a narrower niche makes local diversification possible, but does not prevent other species from evolving into the same niche region in the meantime (Fig. 5d). There seems to be little opportunity for large scale patterns of β-niche conservatism (often simply called niche conservatism), where species-rich habitat niches are filled by closely related species (Fig. 1d). Yet, such patterns are regularly observed (Danley and Kocher 2001, Koblmuller et al. 2004, Silvertown et al. 2006, Hopkins et al. 2014). However, the evolutionary processes studied here are on a relatively small temporal and taxonomic scale, representing evolution within a single genus rather than family or above. Niche space is filled rapidly, driven by directional and disruptive selection, and the standing genetic variation may be more important than mutations. Rare, unlikely events, such as the crossing of wide fitness valleys or the rare colonisation of unexploited habitats, may be more important at larger taxonomic scales. One conclusion is that evolutionary niche monopolisation is relatively more important on small phylogenetic scales. At larger scales it may compete with genetic constraints or biogeographic contingencies. As an example, Peixoto et al. (2017) find climatic (β-) niche conservatism among bats at the level of order or family, but not at lower levels. The same pattern was found in the geophylogenetic patterns of Floridian plant communities (Cavender-Bares et al. 2006). Patterns of niche conservatism can thus be different at different scales and so can the responsible mechanisms (Cavender-Bares et al. 2006, Emerson and Gillespie 2008).

I have here highlighted the possible importance of niche widths, or tradeoffs, and niche monopolisation mechanisms for patterns of niche conservatism, i.e. the order in which different types of traits diverge during an adaptive radiation. Niche monopolisation operates between two or more coevolving species, and in more than one niche dimension. It is only by comparing different traits and the corresponding tradeoffs or niche widths that patterns of niche conservatism can be fully understood. This calls for more complex models

and theories than usual, but the reward can be substantial. Processes at the macroevolutionary level are often analysed using phenomenological models, where rates of speciation and trait evolution are dictated by model parameters. In contrast, the ideas of niche co-evolution discussed here have already been used as heuristic explanations of empirical patterns (Richman and Price 1992, Losos et al. 1998). This theory, developed from an eco-evolutionary model with trait evolution and ecological divergence as emergent properties, nicely corroborates the earlier ideas but also offers a generalisation and deeper understanding of the evolutionary niche monopolisation concept. It will hopefully be a useful conceptual tool for the interpretation of the evolution of a wide range of natural systems.

References

Ackerly, D. D. et al. 2006. Niche evolution and adaptive radiation: testing the order of trait divergence. – Ecology 87: S50–S61.

Anderson, S. R. and Wiens, J. J. 2017. Out of the dark: 350 million years of conservatism and evolution in diel activity patterns in vertebrates. – Evolution 71: 1944–1959.

Bernard-Verdier, M et al. 2013. Partitioning phylogenetic and functional diversity into alpha and beta components along an environmental gradient in a Mediterranean rangeland. – J. Veg. Sci. 24: 877–889.

Blomberg, S. P. et al. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. – Evolution 57: 717–745.

Brown, J. S. and Pavlovic, N. B. 1992. Evolution in heterogeneous environments – effects of migration on habitat specialization. – Evol. Ecol. 6: 360–382.

Case, T. J. and Taper, M. L. 2000. Interspecific competition, environmental gradients, gene flow, and the coevolution of species' borders. – Am. Nat. 155: 583–605.

Cavender-Bares, J. et al. 2006. Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. – Ecology 87: S109–S122.

Chesson, P. 2000. General theory of competitive coexistence in spatially-varying environments. – Theor. Popul. Biol. 58: 211–237.

Danley, P. D. and Kocher, T. D. 2001. Speciation in rapidly diverging systems: lessons from Lake Malawi. – Mol. Ecol. 10: 1075–1086.

De Meester, L. et al. 2002. The monopolization hypothesis and the dispersal–gene flow paradox in aquatic organisms. – Acta Oecol. 23: 121–135.

Dieckmann, U. and Doebeli, M. 1999. On the origin of species by sympatric speciation. – Nature 400: 354–357.

Emerson, B. C. and Gillespie, R. G. 2008. Phylogenetic analysis of community assembly and structure over space and time. – Trends Ecol. Evol. 23: 619–630.

Geritz, S. A. H. et al. 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. – Evol. Ecol. 12: 35–57.

Holt, R. D. and Gaines, M. S. 1992. Analysis of adaptation in heterogeneous landscapes – implications for the evolution of fundamental niches. – Evol. Ecol. 6: 433–447.

Hopkins, M. J. et al. 2014. Differential niche dynamics among major marine invertebrate clades. – Ecol. Lett. 17: 314–323.

Ingram, T. and Shurin, J. B. 2009. Trait-based assembly and phylogenetic structure in northeast Pacific rockfish assemblages. – Ecology 90: 2444–2453.

Kawecki, T. J. and Holt, R. D. 2002. Evolutionary consequences of asymmetric dispersal rates. – Am. Nat. 160: 333–347.

Kirkpatrick, M. and Barton, N. H. 1997. Evolution of a species' range. – Am. Nat. 150: 1–23.

Kisdi, É. and Geritz, S. A. H. 1999. Adaptive dynamics in allele space: evolution of genetic polymorphism by small mutations in a heterogeneous environment. – Evolution 53: 993–1008.

Koblmuller, S. et al. 2004. Evolutionary relationships in the sand-dwelling cichlid lineage of Lake Tanganyika suggest multiple colonization of rocky habitats and convergent origin of biparental mouthbrooding. – J. Mol. Evol. 58: 79–96.

Krakauer, D. C. et al. 2009. Diversity, dilemmas and monopolies of niche construction. – Am. Nat. 173: 26–40.

Leibold, M. 1995. The niche concept revisited: mechanistic models and community context. – Ecology 76: 1371–1382.

Loeuille, N. and Leibold, M. A. 2008. Evolution in metacommunities: on the relative importance of species sorting and monopolization in structuring communities. – Am. Nat. 171: 788–799.

Losos, J. B. 2009. Lizards in an evolutionary tree – ecology and adaptive radiation of anoles. – UC Press, Berkeley, CA.

Losos, J. B. et al. 1998. Contingency and determinism in replicated adaptive radiations of island lizards. – Science 279: 2115–2118.

Losos, J. B. et al. 2006. Adaptation, speciation, and convergence: a hierarchical analysis of adaptive radiation in Caribbean *Anolis* lizards. – Ann. MO Bot. Gard. 93: 24–33.

Meszéna, G. et al. 1997. Adaptive dynamics in a 2-patch environment: a toy model for allopatric and parapatric speciation. – J. Biol. Sys. 5: 265–284.

Metz, J. A. J. et al. 1992. How should we define 'fitness' for general ecological scenarios? – Trends Ecol. Evol. 7: 198–202.

Muschick, M. et al. 2014. Testing the stages model in the adaptive radiation of cichlid fishes in East African Lake Tanganyika. – Proc. R. Soc. B 281: 20140605.

Nilsson, J. and Ripa, J. 2010. Adaptive branching in source–sink habitats. – Evol. Ecol. 24: 479–489.

Pagel, M. 1999. Inferring the historical patterns of biological evolution. – Nature 401: 877–884.

Peterson, A. T. et al. 1999. Conservatism of ecological niches in evolutionary time. – Science 285: 1265–1267.

Peixoto, F. P. et al. 2017. Phylogenetic conservatism of climatic niche in bats. – Global Ecol. Biogeogr. 26: 1055–1065.

Pickett, S. T. A. and Bazzaz, F. A. 1978. Organization of an assemblage of early successional species on a soil-moisture gradient. – Ecology 59: 1248–1255.

Pienaar, J. et al. 2013. Macroevolution of life-history traits in passerine birds: adaptation and phylogenetic inertia. – Ecol. Lett. 16: 571–576.

Richman, A. D. and Price, T. 1992. Evolution of ecological differences in the old-world leaf warblers. – Nature 355: 817–821.

Ripa, J. 2009. When is sympatric speciation truly adaptive? An analysis of the joint evolution of resource utilization and assortative mating. – Evol. Ecol. 23: 31–52.

Ripa, J. 2018. Data from: Ecology and macroevolution – evolutionary niche monopolisation as a mechanisms of niche conservatism. – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.jn44bq4>.

Rosenzweig, M. L. 1978. Competitive speciation. – Biol. J. Linn. Soc. 10: 275–289.

Rueffler, C. et al. 2006. The evolution of resource specialization through frequency-dependent and frequency-independent mechanisms. – Am. Nat. 167: 81–93.

Sallan, L. C. and Friedman, M. 2012. Heads or tails: staged diversification in vertebrate evolutionary radiations. – Proc. R. Soc. B 279: 2025–2032.

Schluter, D. 2000. The ecology of adaptive radiation. – Oxford Univ. Press.

Silvertown, J. et al. 2006. Phylogeny and the hierarchical organization of plant diversity. – Ecology 87: S39–S49.

Streelman, J. T. and Danley, P. D. 2003. The stages of vertebrate evolutionary radiation. – Trends Ecol. Evol. 18: 126–131.

Urban, M. C. and De Meester, L. 2009. Community monopolization: local adaptation enhances priority effects in an evolving metacommunity. – Proc. R. Soc. B 276: 4129–4138.

Van Doorn, G. S. and Weissing, F. J. 2001. Ecological versus sexual selection models of sympatric speciation: a synthesis. – Selection 2: 17–40.

Vanoverbeke, J. et al. 2016. Community assembly is a race between immigration and adaptation: eco-evolutionary interactions across spatial scales. – Ecography 39: 858–870.

Wiens, J. J. and Graham, C. H. 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. – Annu. Rev. Ecol. Evol. Syst. 36: 519–539.

Wiens, J. J. et al. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. – Ecol. Lett. 13: 1310–1324.