Organismal Diversification

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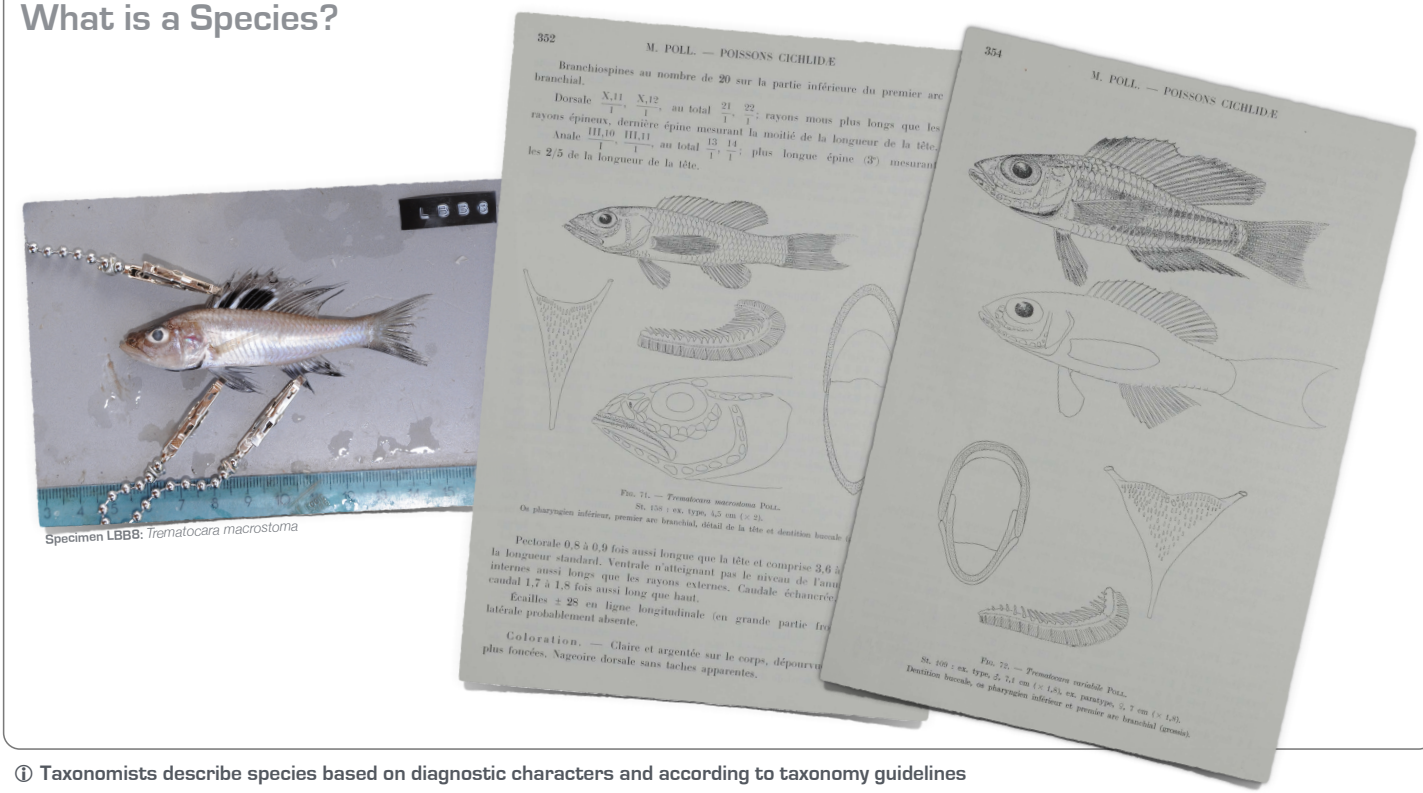
What is a Species?



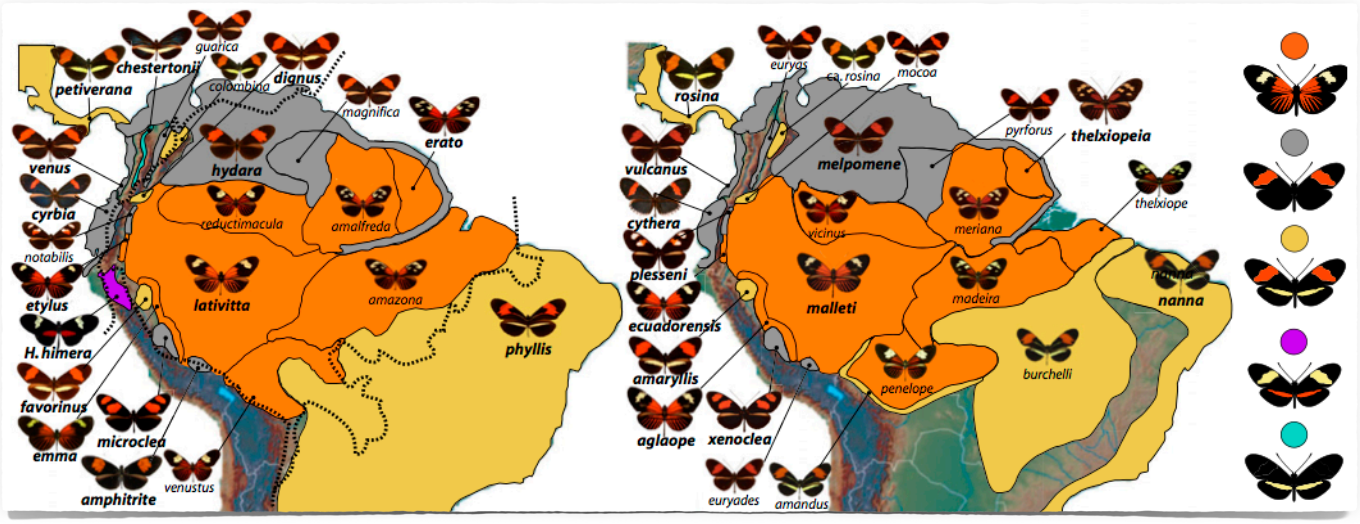
Specimen LBB8: *Trematocara macrostoma*

Poll (1956)

ⓘ Taxonomists describe species based on diagnostic characters and according to taxonomy guidelines

What is a Species?

- Individuals within a species are **variable**. There is usually no "ideal" or "typical" individual.



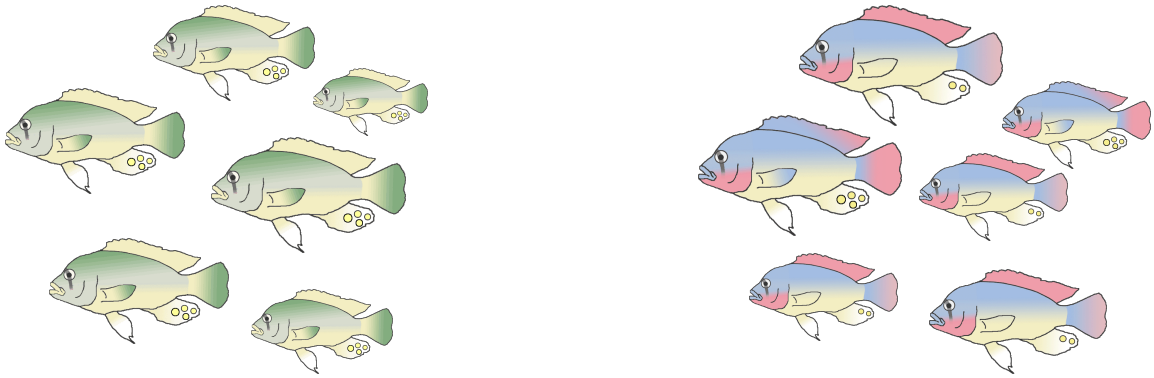
Heliconius erato | *Heliconius malpomene*

modified from www.heliconius.org

ⓘ *Heliconius erato* and H. *melpomene* are morphologically similar because of mimicry

What is a Species?

- Members of a species share a **gene pool**. Selection and drift operate within species.



Species X | Species Y

ⓘ Evolutionary biologists interpret species as independent (real) evolutionary units

What is a Species?

- The category species is defined according to a **species concept**. Not one of the available species concepts provides a universally valid definition of the category species.

biological species concept	A species is a group of interbreeding natural populations that is reproductively isolated from other such groups (Mayr 1963).
cohesion species concept	A species is the most inclusive populations of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms (Templeton 1989).
ecological species concept	A species is a lineages (or a closely related set of lineages), which occupies an adaptive zone minimally different from that of any other lineage in range, and which evolve separately from all lineages outside its range (Van Valen 1976).
evolutionary species concept	A species is a single lineage of ancestral-descendant lineages that evolve separately from other such lineages and have their own evolutionary tendencies and historical fate (Simpson 1961; Wiley 1978).
phylogenetic species concepts	A species is the smallest monophyletic group of common ancestry (de Querioz & Donoghue 1988). A phylogenetic species is a basal cluster of organisms that is diagnosably distinct from other such clusters (Cracraft 1989).

after Coyne & Orr (2004), Zachos (2016)

What is a Species?

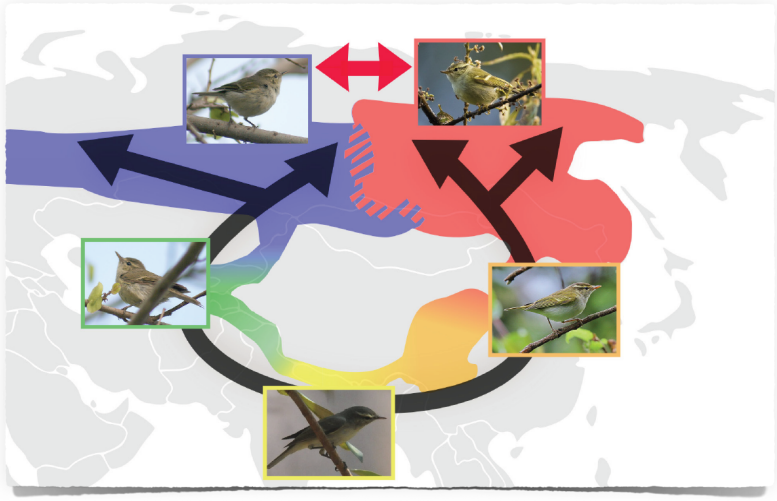
- According to the **biological species concept**, a species is a group of interbreeding natural populations that is **reproductively isolated** from other such groups (Mayr 1963).

ⓘ The biological species concept places the category species within the framework of population genetics

What is a Species?

- **Conceptual problems with species definitions: ring species.**

Ensantia eschscholtzii **in the western USA**



Greenish warbler *(Phylloscopus nitidus)* **in Eurasia**

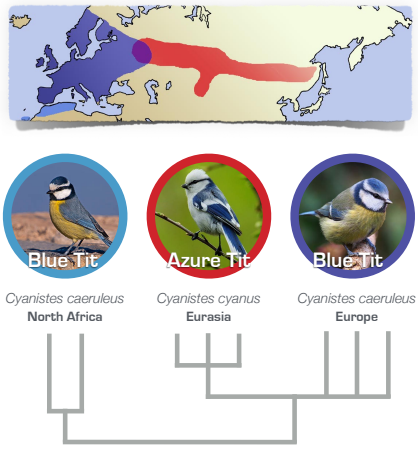
Images: Stebbins (1994), wikimedia.org

ⓘ In a "ring species" two reproductively isolated populations are connected by a geographic ring of interbreeding populations

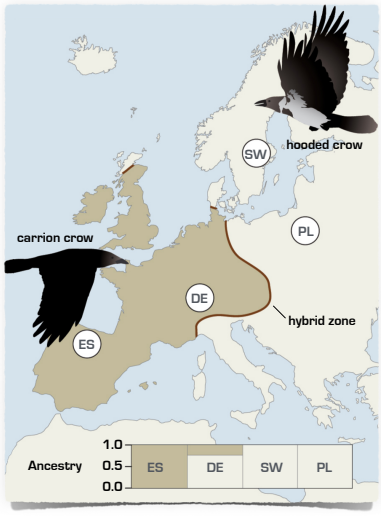
What is a Species?

- **Conceptual problems with species definitions:**

paraphyletic species



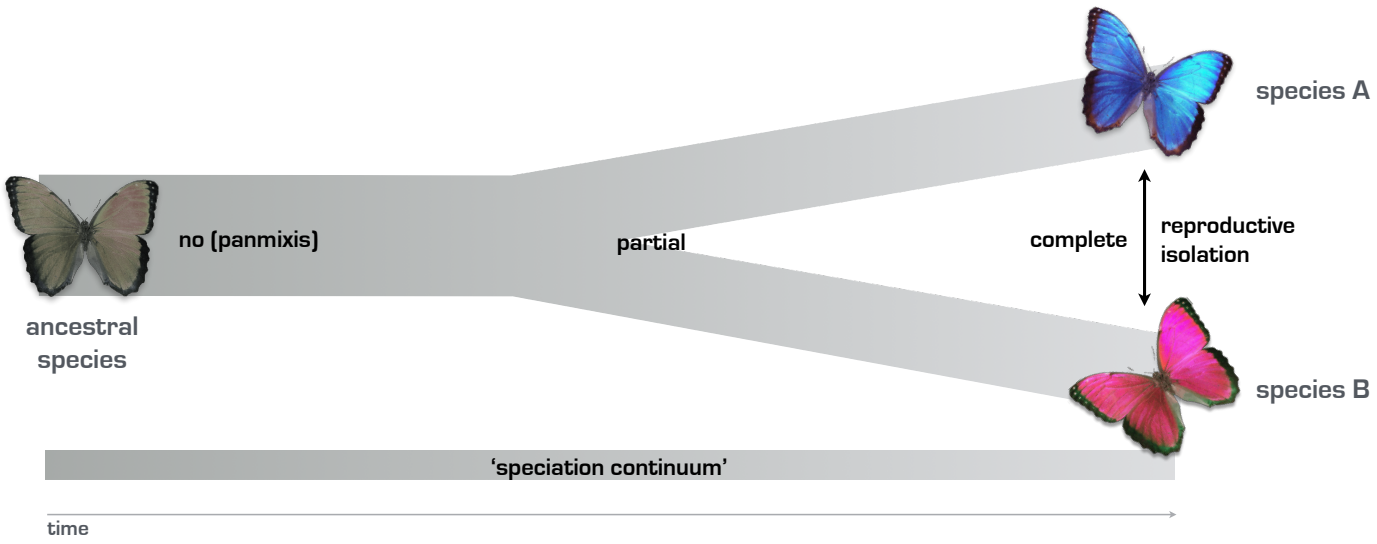
hybridization



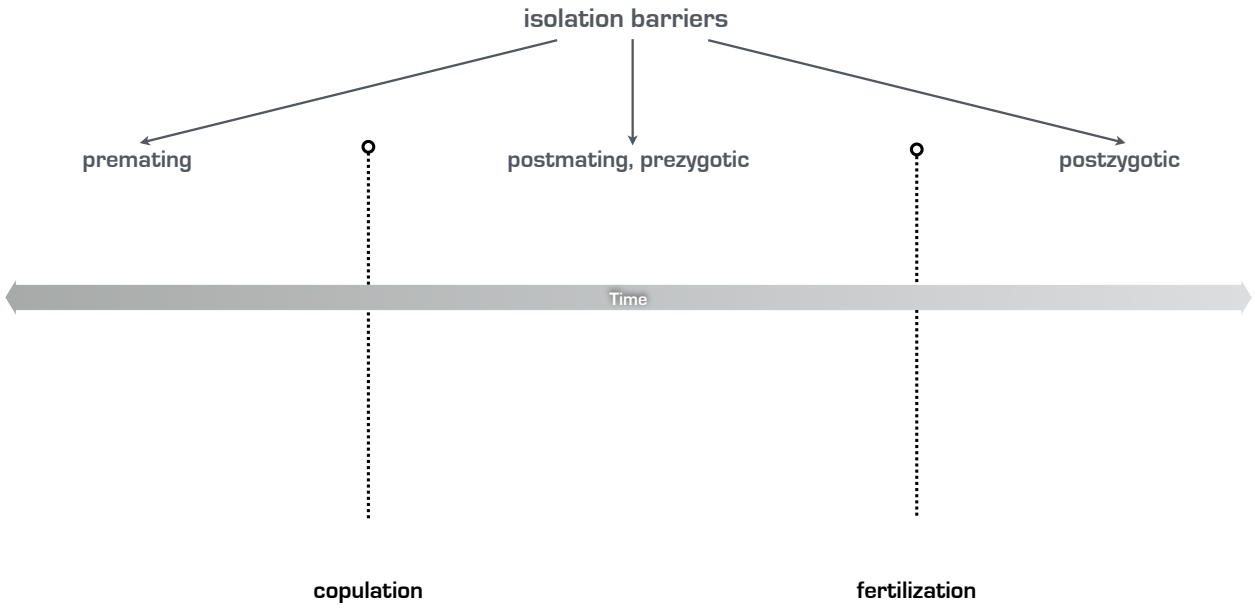
modified from Salzburger et al. (2002), de Knijff (2014)

ⓘ The African Blue Tit *(C. teneriffae)* has meanwhile been given species rank, "solving" the paraphyly situation

Reproductive Isolation

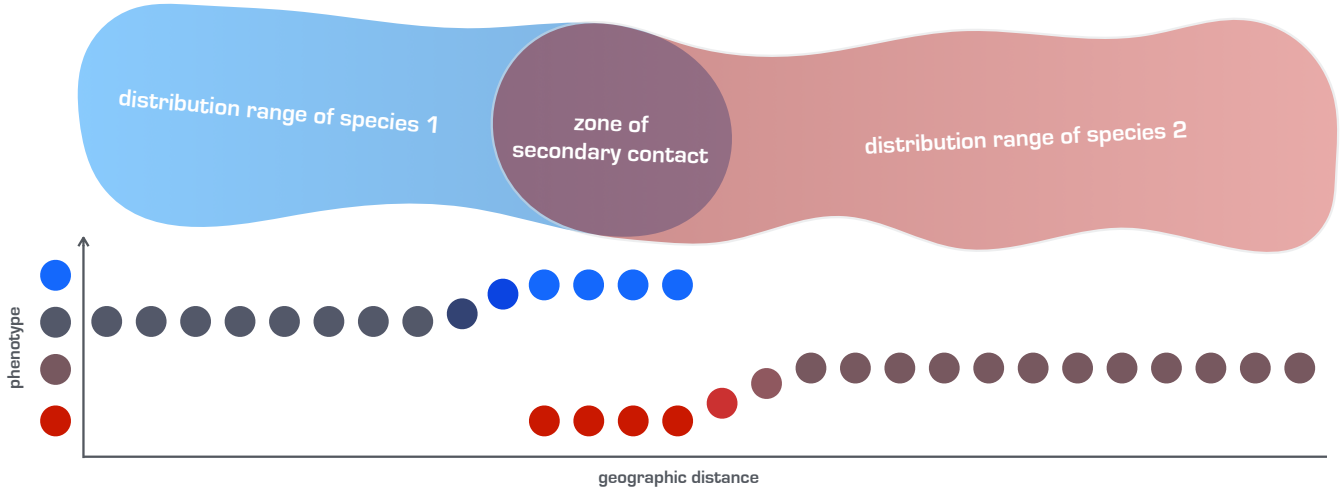


Reproductive Isolation

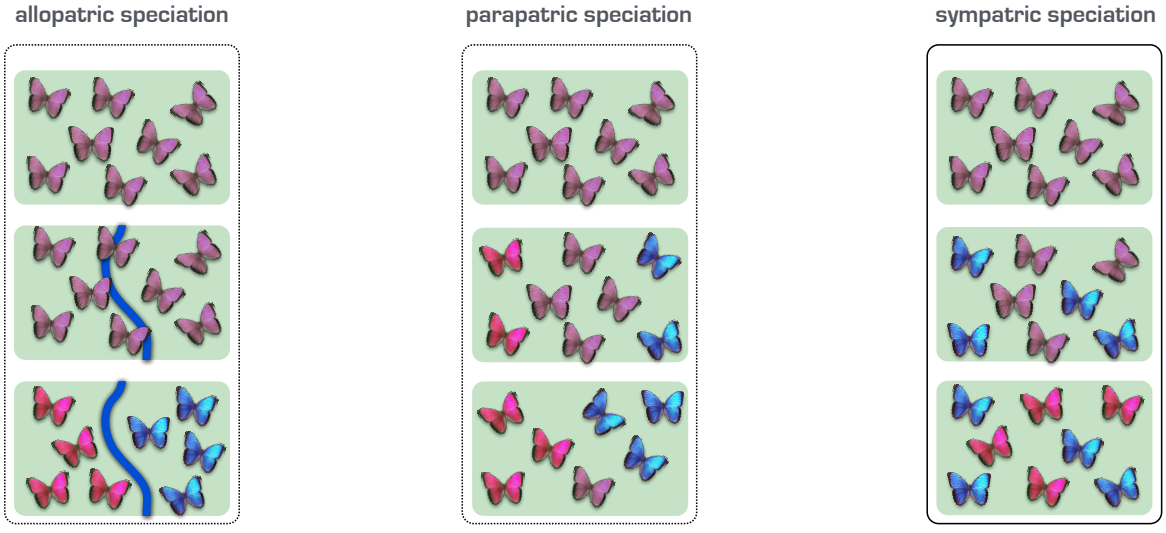


Isolation Barriers

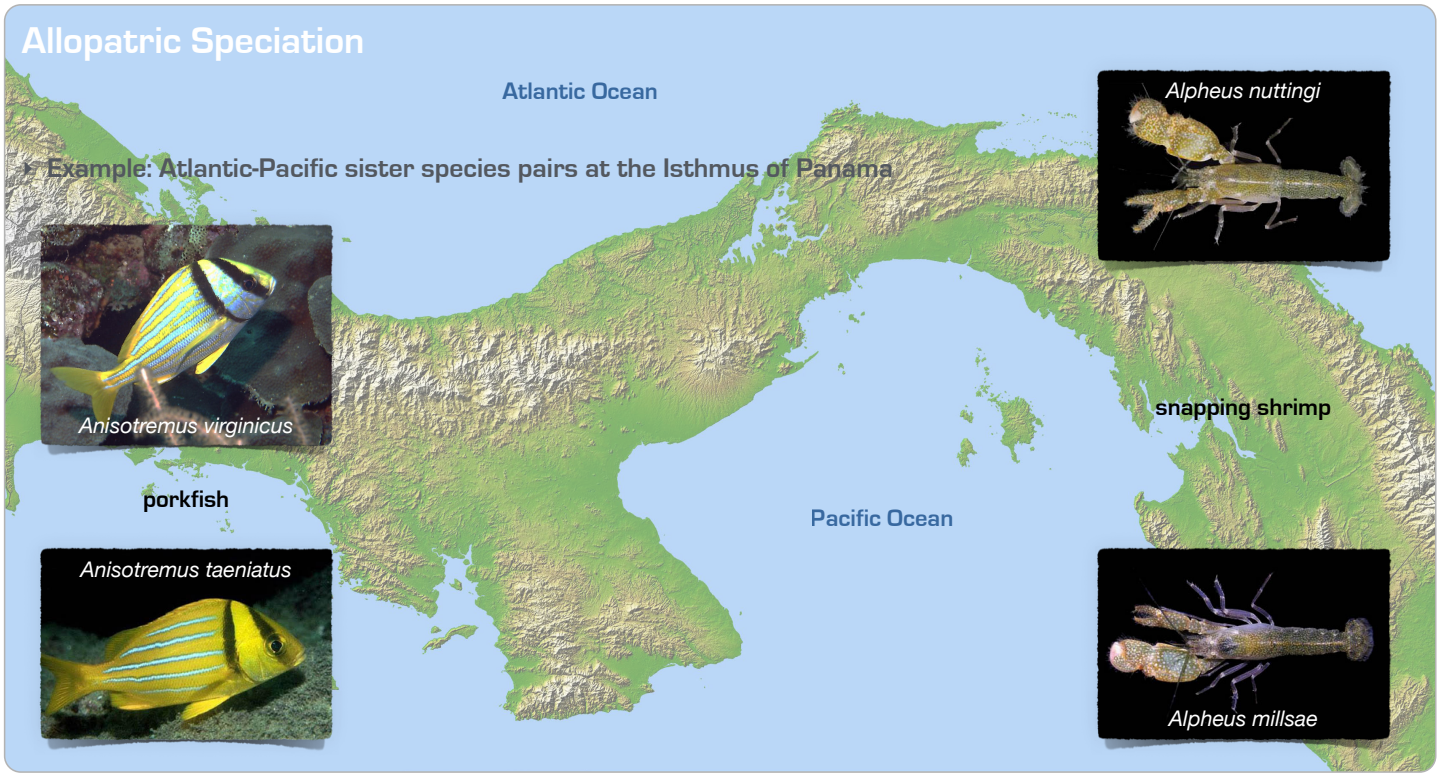
- Reinforcement: Increase of reproductive isolation as a result of selection against the production of hybrids.



Geographic Conditions of Speciation



Allopatric Speciation

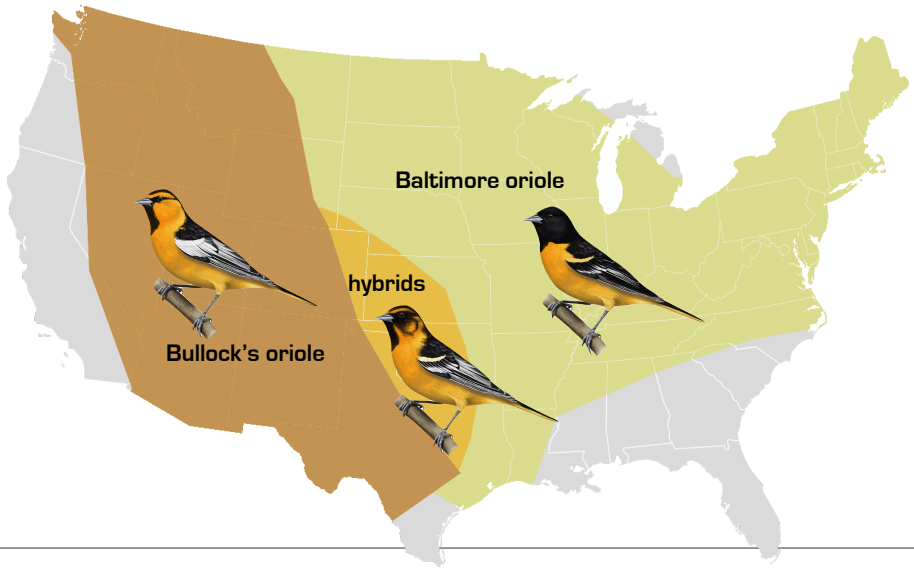


Images: NASA, wikimedia.org, fishbiosystems.ru

ⓘ The Isthmus of Panama formed between 3.5-10 million years ago, establishing a land-bridge between the Americas

Parapatric Speciation

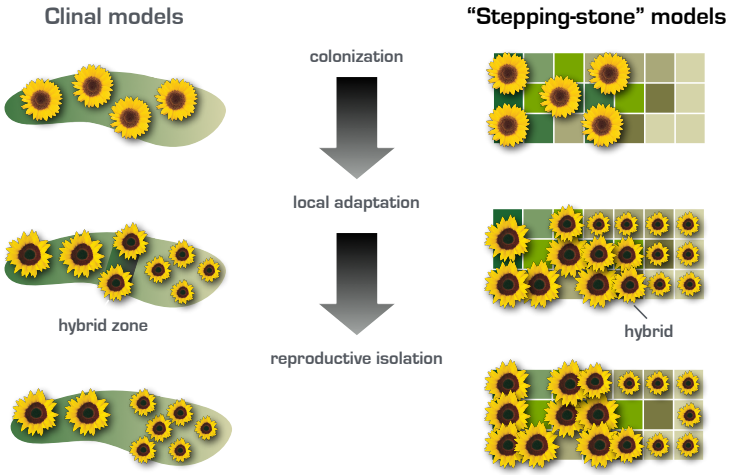
- Example: Bullock's oriole and Baltimore oriole in the United States of America



Images: Meghan Bishop

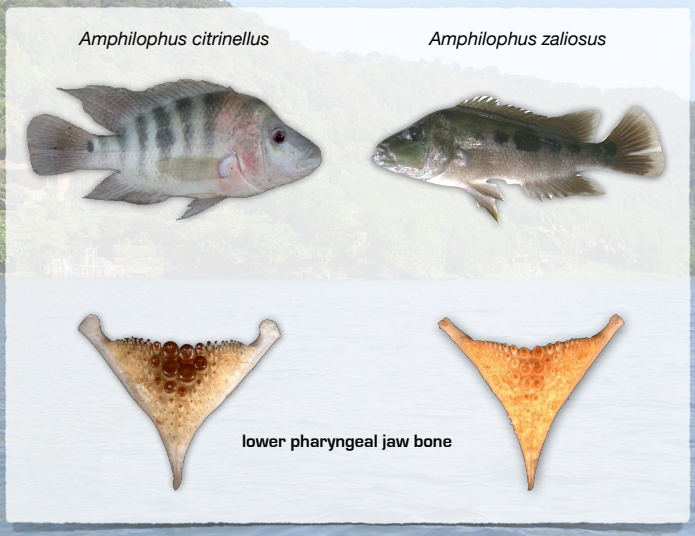
Parapatric Speciation

- Models of parapatric speciation typically involve a gradient (ecological, geographic) and occasional hybridization



Sympatric Speciation

- Example: Cichlid fishes in Crater Lake Apoyo in Nicaragua



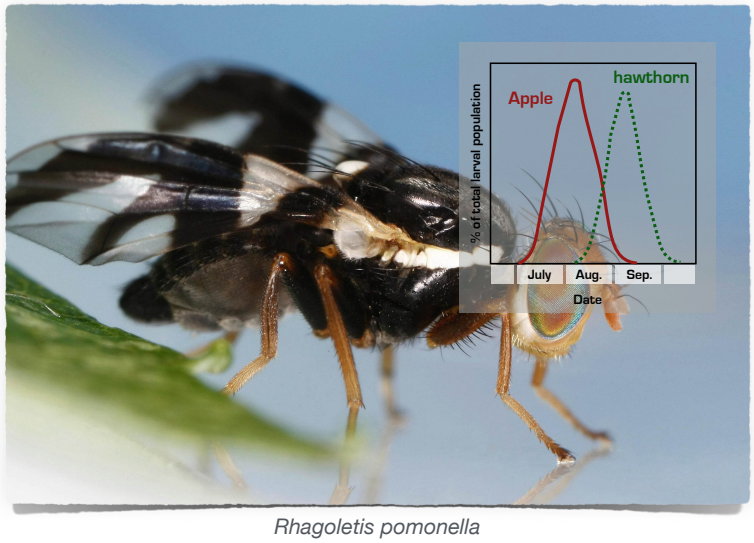
modified from Barluenga et al. (2006)

ⓘ The 'Laguna de Apoyo' is a small but deep volcanic crater lake

Sympatric Speciation

- Examples: Palm trees on Lord Howe Island and apple maggot flies in North America

Howea forsteriana *Howea belmoreana*



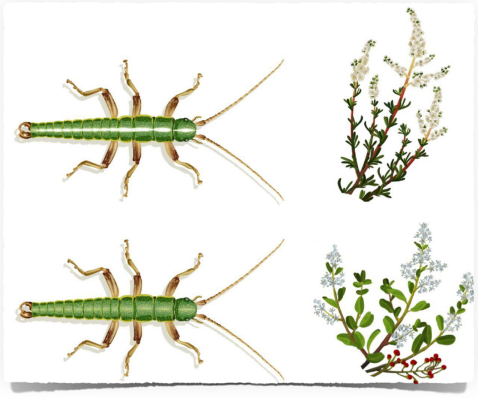
Rhagoletis pomonella

modified from Savolainen et al. (2006), Filchak et al. (2000), image: wikimedia.org

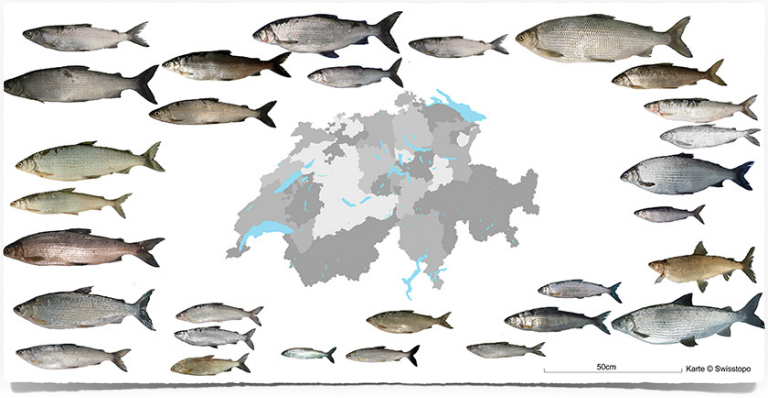
Ecological Speciation

- Ecological speciation is the evolution of reproductive isolation between populations by adaptation to different environments or ecological niches

Timema stick insects

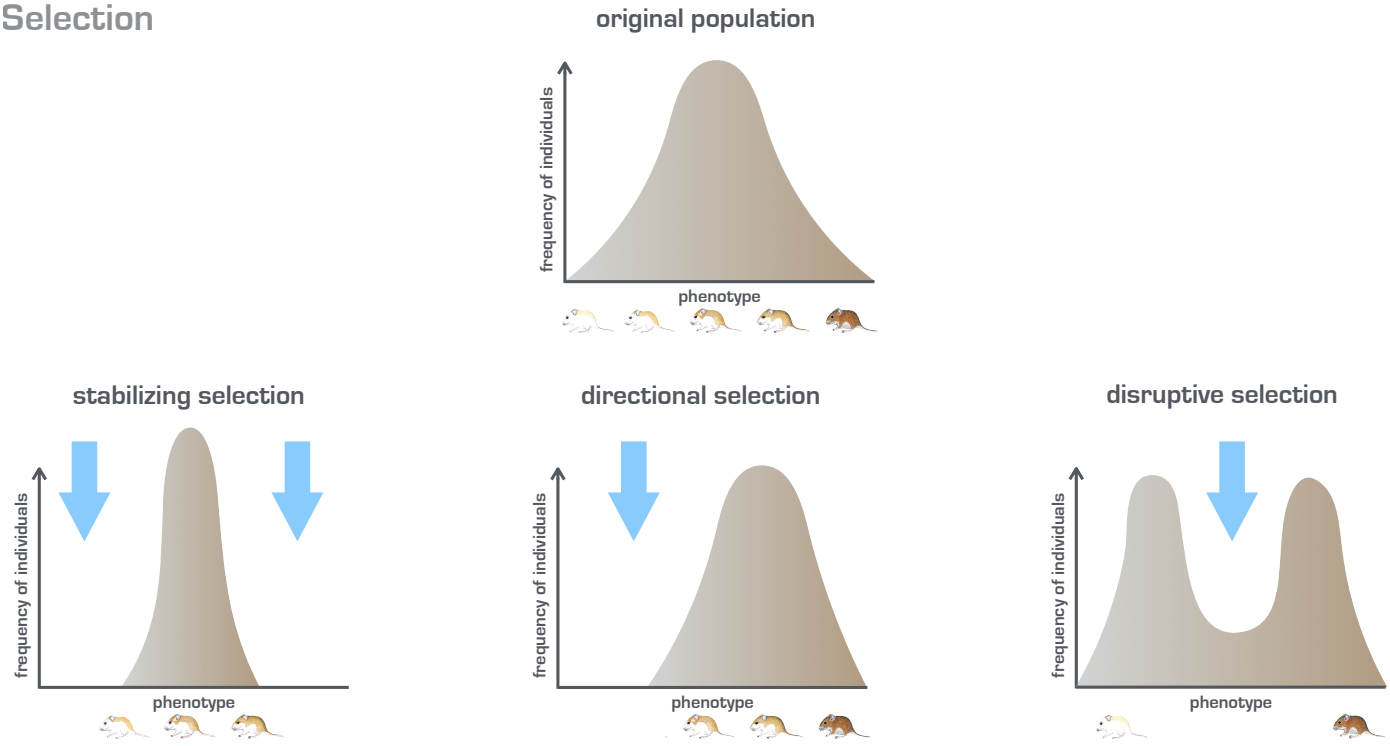


Lake whitefish



ⓘ Ecological speciation can occur in allopatry, parapatry and sympatry

Selection



Selection

- **Natural selection** is the process by which the forms of organisms in a population that are best adapted to the environment **increase in frequency** relative to less well-adapted forms over **a number of generations** (Ridley 2004)

Images: www.idscaro.net, www.wikipedia.com

Selection

- **Sexual selection** is the selection on mating behavior, either through **competition among members of one sex** (usually males) for access to members of the other sex, or **choice by members of one sex** (usually females) for certain members of the other sex (Ridley 1996)

Images: National Geographic, www.smh.com.au

Selection

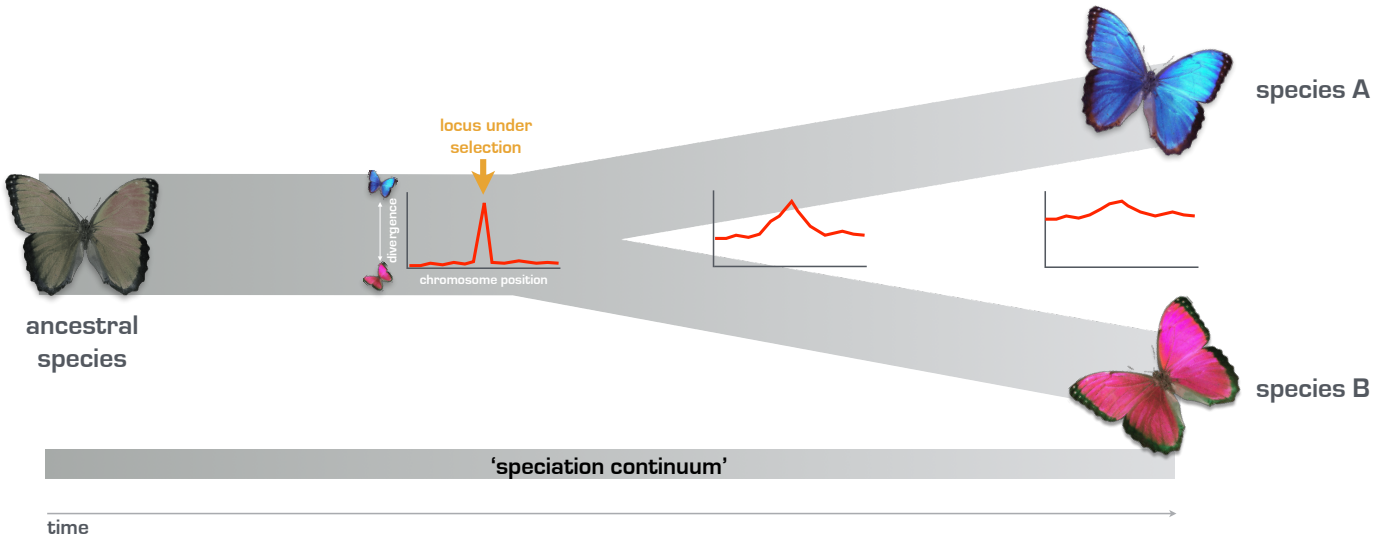
- Both **natural and sexual selection** operate if the following conditions are met:

reproduction	organisms must reproduce to form new generations
heredity	offspring resemble parents ("like must produce like")
trait variation	individuals in natural populations vary in (adaptive) traits
variation in fitness	individuals in natural populations vary in the number of their offspring that survive to reproduce ('lifetime reproductive success')

Selection

- (Natural) selection versus drift:

Speciation Continuum | Genomics



Speciation Continuum | Genomics

- **Cichlid fishes (*Astatotilapia sp.*) in crater lake Massoko (Malinsky et al. 2015, Science)**


benthic ecomorph


limnetic ecomorph

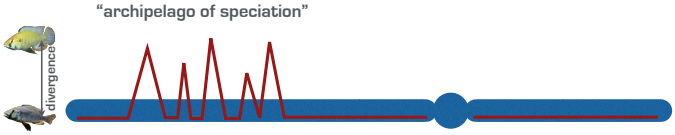
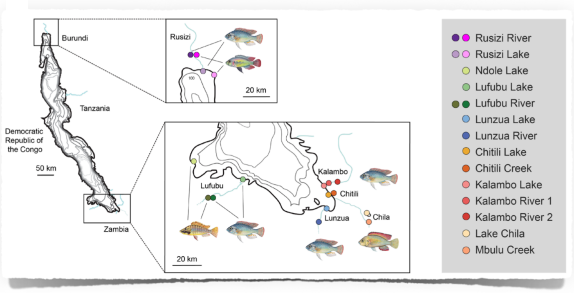
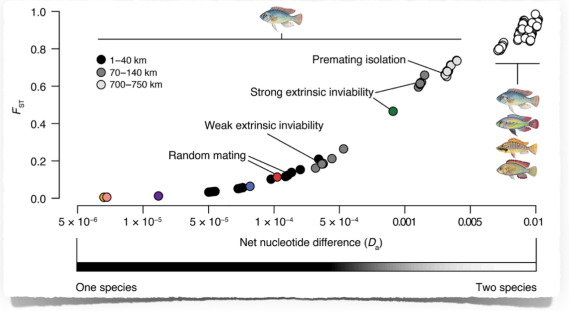
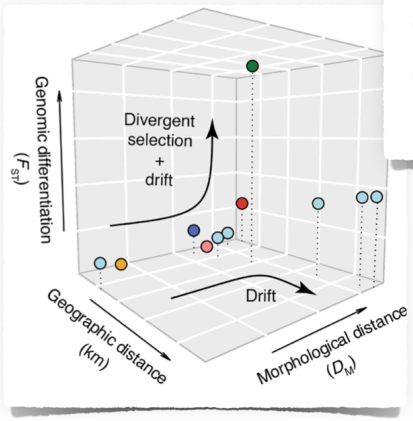


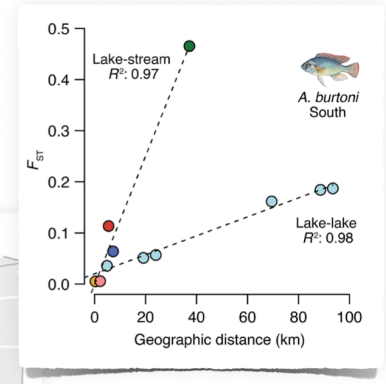
Figure: Ronco & Salzburger (2016) Current Biology

Speciation Continuum | Genomics



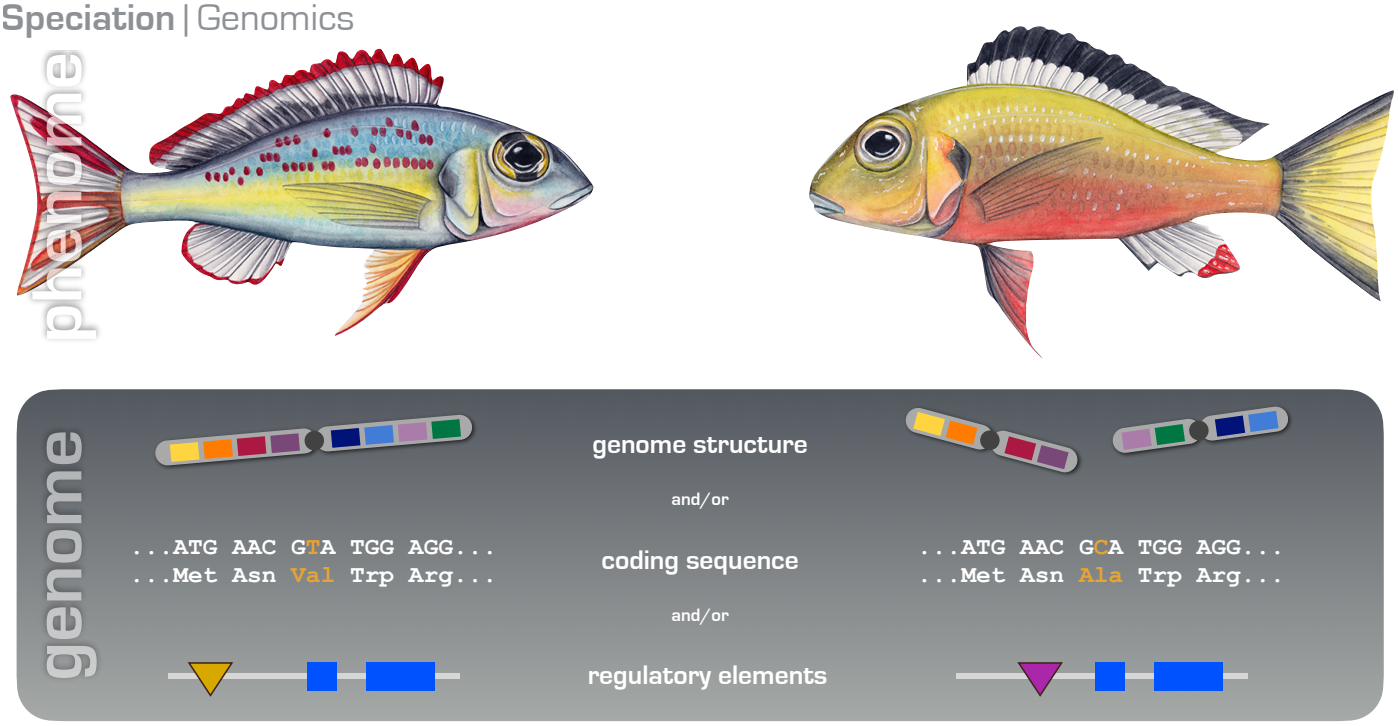






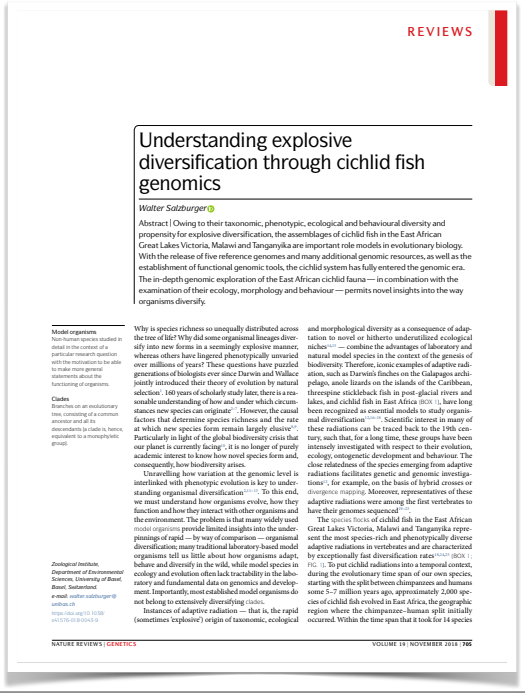
• • • AAT Weber, J Rajkov, K Smailus, B Egger & W Salzburger (2021) Science Advances

Speciation | Genomics



Paintings: Julie Johnson/Uni Basel

Literature (second part)



REVIEWS

Understanding explosive diversification through cichlid fish genomics

Walter Salzburger

Abstract | Owing to their taxonomic, phenotypic, ecological and behavioural diversity and propensity for explosive diversification, the assemblages of cichlid fish in the East African Great Lakes Victoria, Malawi and Tanganyika are important role models in evolutionary biology. With the release of five reference genomes and many additional genomic resources, as well as the establishment of functional genomic tools, the cichlid system has fully entered the genomic era. The in-depth genomic exploration of the East African cichlid fauna — in combination with the examination of their ecology, morphology and behaviour — permits novel insights into the way organisms diversify.

Model organisms
Non-human species studied in detail in the context of a particular research question with the motivation to be able to make more general statements about the functioning of organisms.

Clades
Branches on an evolutionary tree, consisting of a common ancestor and all its descendants (a clade is, hence, equivalent to a monophyletic group).

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Why is species richness so unequally distributed across the tree of life? Why did some organismal lineages diversify into new forms in a seemingly explosive manner, whereas others have lingered phenotypically unvaried over millions of years? These questions have puzzled generations of biologists ever since Darwin and Wallace jointly introduced their theory of evolution by natural selection[1]. 160 years of scholarly study later, there is a reasonable understanding of how and under which circumstances new species can originate[2–7]. However, the causal factors that determine species richness and the rate at which new species form remain largely elusive[8–11]. Particularly in light of the global biodiversity crisis that our planet is currently facing[12], it is no longer of purely academic interest to know how novel species form and, consequently, how biodiversity arises.

Unravelling how variation at the genomic level is interlinked with phenotypic evolution is key to understanding organismal diversification[13–15]. To this end, we must understand how organisms evolve, how they function and how they interact with other organisms and the environment. The problem is that many widely used model organisms provide limited insights into the underpinnings of rapid — by way of comparison — organismal diversification; many traditional laboratory-based model organisms tell us little about how organisms adapt, behave and diversify in the wild, while model species in ecology and evolution often lack tractability in the laboratory and fundamental data on genomics and development. Importantly, most established model organisms do not belong to extensively diversifying clades.

Instances of adaptive radiation — that is, the rapid (sometimes 'explosive') origin of taxonomic, ecological and morphological diversity as a consequence of adaptation to novel or hitherto underutilized ecological niches[16,17] — combine the advantages of laboratory and natural model species in the context of the genesis of biodiversity. Therefore, iconic examples of adaptive radiation, such as Darwin's finches on the Galapagos archipelago, anole lizards on the islands of the Caribbean, threespine stickleback fish in post-glacial rivers and lakes, and cichlid fish in East Africa (BOX 1), have long been recognized as essential models to study organismal diversification[9,10,18–20]. Scientific interest in many of these radiations can be traced back to the 19th century, such that, for a long time, these groups have been intensely investigated with respect to their evolution, ecology, ontogenetic development and behaviour. The close relatedness of the species emerging from adaptive radiations facilitates genetic and genomic investigations[21], for example, on the basis of hybrid crosses or divergence mapping. Moreover, representatives of these adaptive radiations were among the first vertebrates to have their genomes sequenced[22–25].

The species flocks of cichlid fish in the East African Great Lakes Victoria, Malawi and Tanganyika represent the most species-rich and phenotypically diverse adaptive radiations in vertebrates and are characterized by exceptionally fast diversification rates[19,26,27] (BOX 1; FIG. 1). To put cichlid radiations into a temporal context, during the evolutionary time span of our own species, starting with the split between chimpanzees and humans some 5–7 million years ago, approximately 2,000 species of cichlid fish evolved in East Africa, the geographic region where the chimpanzee–human split initially occurred. Within the time span that it took for 14 species

Article

Drivers and dynamics of a massive adaptive radiation in cichlid fishes

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Fabrizia Ronco[1,2], Michael Matschiner[1,2,3], Astrid Böhne[1,4], Anna Boila[1], Heinz H. Büscher[1], Athimed El Taher[5], Adrian Indermaur[1], Milan Malinsky[1], Virginia Ricci[1], Ansgar Kahmen[6], Sissel Jentoft[7] & Walter Salzburger[1,2]✉

Adaptive radiation is the likely source of much of the ecological and morphological diversity of life[1–4]. How adaptive radiations proceed and what determines their extent remains unclear in most cases[5,6]. Here we report the in-depth examination of the spectacular adaptive radiation of cichlid fishes in Lake Tanganyika. On the basis of whole-genome phylogenetic analyses, multivariate morphological measurements of three ecologically relevant trait complexes (body shape, upper oral jaw morphology and lower pharyngeal jaw shape), scoring of pigmentation patterns and approximations of the ecology of nearly all of the approximately 240 cichlid species endemic to Lake Tanganyika, we show that the radiation occurred within the confines of the lake and that morphological diversification proceeded in consecutive trait-specific pulses of rapid morphospace expansion. We provide empirical support for two theoretical predictions of how adaptive radiations proceed, the 'early-burst' scenario[3,4] (for body shape) and the stages model[5,6,7] (for all traits investigated). Through the analysis of two genomes per species and by taking advantage of the uneven distribution of species in subclades of the radiation, we further show that species richness scales positively with per-individual heterozygosity, but is not correlated with transposable element content, number of gene duplications or genome-wide levels of selection in coding sequences.

At the macroevolutionary level, the diversity of life has been shaped mainly by two antagonistic processes: evolutionary radiations increase, and extinction events decrease, organismal diversity over time[8,9]. Evolutionary radiations are referred to as adaptive radiations if new lifeforms evolve rapidly through adaptive diversification into a variety of ecological niches, which typically presupposes ecological opportunity[1–3,10]. Whether or not an adaptive radiation occurs depends on a variety of extrinsic and intrinsic factors as well as on contingency, whereas the magnitude of an adaptive radiation is determined by the interplay between its main components, speciation (minus extinction) and adaptation to distinct ecological niches[11,12,6]. Despite considerable scientific interest in the phenomenon of adaptive radiation as the cradle of organismal diversity[1,2,10,12,13], many predictions regarding its drivers and dynamics remain untested, particularly in exceptionally species-rich instances. Here, we examine what some consider as the "most outstanding example of adaptive radiation"[14], the species flock of cichlid fishes in Lake Tanganyika. This cichlid assemblage comprises about 240 species[15], which together feature an extraordinary degree of morphological, ecological and behavioural diversity[16–18]. We construct a species tree of Lake Tanganyika's cichlid fauna on the basis of genome-wide data, demonstrate the adaptive nature of the radiation, reconstruct eco-morphological diversification along the species tree, and test general and cichlid-specific predictions related to adaptive radiation.

In situ radiation in Lake Tanganyika

To establish the phylogenetic context of cichlid evolution in Lake Tanganyika, we estimated the age of the radiation through divergence time analyses based on cichlid and other teleost fossils[19], and constructed time-calibrated species trees using 547 newly sequenced cichlid genomes (Supplementary Table 1). Our new phylogenetic hypotheses (Fig. 1, Extended Data Figs. 1–4, Supplementary Figs. 1, 2) support the assignment of the Tanganyikan cichlid fauna into 16 subclades — corresponding to the taxonomic grouping of species into tribes[20] — and confirm that the Tanganyikan representatives of the tribes Coptodonini, Oreochromini and Tylochromini belong to more ancestral and widespread lineages that have colonized the lake secondarily[21,22] (Supplementary Discussion). It has been under debate whether all endemic Tanganyikan cichlid tribes evolved within the confines of Lake Tanganyika or whether some of them evolved elsewhere before the formation of the lake[20–22]. Our time calibrations establish that the most recent common ancestor of the cichlid radiation in Lake Tanganyika lived around 9.7 million years ago (Ma) (95% highest posterior density

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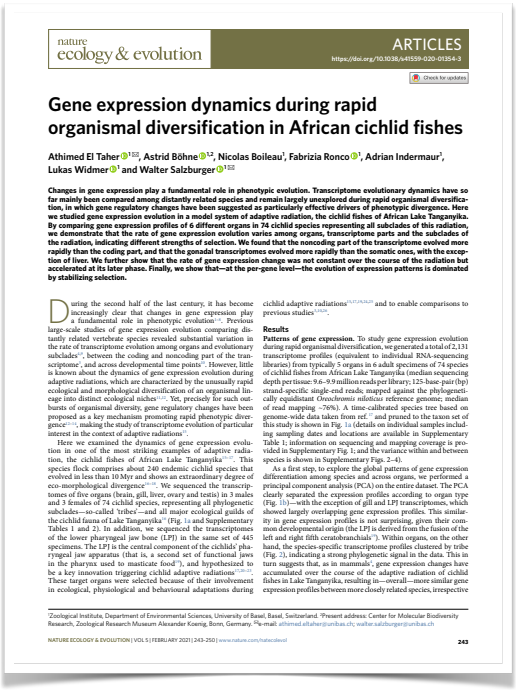
Literature (second part)



nature ecology & evolution

ARTICLES

https://doi.org/10.1038/s41559-020-01354-3

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Gene expression dynamics during rapid organismal diversification in African cichlid fishes

Athimed El Taher[1,2], Astrid Böhne[1,2], Nicolas Boileau[1], Fabrizia Ronco[1], Adrian Indermaur[1], Lukas Widmer[1] and Walter Salzburger[1,2]

Changes in gene expression play a fundamental role in phenotypic evolution. Transcriptome evolutionary dynamics have so far mainly been compared among distantly related species and remain largely unexplored during rapid organismal diversification, in which gene regulatory changes have been suggested as particularly effective drivers of phenotypic divergence. Here we studied gene expression evolution in a model system of adaptive radiation, the cichlid fishes of African Lake Tanganyika. By comparing gene expression profiles of 6 different organs in 74 cichlid species representing all subclades of this radiation, we demonstrate that the rate of gene expression evolution varies among organs, transcriptome parts and the subclades of the radiation, indicating different strengths of selection. We found that the noncoding part of the transcriptome evolved more rapidly than the coding part, and that the gonadal transcriptomes evolved more rapidly than the somatic ones, with the exception of liver. We further show that the rate of gene expression change was not constant over the course of the radiation but accelerated at its later phase. Finally, we show that—at the per-gene level—the evolution of expression patterns is dominated by stabilizing selection.

During the second half of the last century, it has become increasingly clear that changes in gene expression play a fundamental role in phenotypic evolution[1–5]. Previous large-scale studies of gene expression evolution comparing distantly related vertebrate species revealed substantial variation in the rate of transcriptome evolution among organs and evolutionary subclades[6–9], between the coding and noncoding part of the transcriptome[7], and across developmental time points[10]. However, little is known about the dynamics of gene expression evolution during adaptive radiations, which are characterized by the unusually rapid ecological and morphological diversification of an organismal lineage into distinct ecological niches[11–13]. Yet, precisely for such outbursts of organismal diversity, gene regulatory changes have been proposed as a key mechanism promoting rapid phenotypic divergence[14–16], making the study of transcriptome evolution of particular interest in the context of adaptive radiations[17].

Here we examined the dynamics of gene expression evolution in one of the most striking examples of adaptive radiation, the cichlid fishes of African Lake Tanganyika[18–21]. This species flock comprises about 240 endemic cichlid species that evolved in less than 10 Myr and shows an extraordinary degree of eco-morphological divergence[22–24]. We sequenced the transcriptomes of five organs (brain, gill, liver, ovary and testis) in 3 males and 3 females of 74 cichlid species, representing all phylogenetic subclades—so-called 'tribes'—and all major ecological guilds of the cichlid fauna of Lake Tanganyika[25] (Fig. 1a and Supplementary Tables 1 and 2). In addition, we sequenced the transcriptomes of the lower pharyngeal jaw bone (LPJ) in the same set of 445 specimens. The LPJ is the central component of the cichlids' pharyngeal jaw apparatus (that is, a second set of functional jaws in the pharynx used to masticate food[26]), and hypothesized to be a key innovation triggering cichlid adaptive radiations[27,28,17]. These target organs were selected because of their involvement in ecological, physiological and behavioural adaptations during cichlid adaptive radiations[14,17,19,20,29] and to enable comparisons to previous studies[7,10,30].

Results

Patterns of gene expression. To study gene expression evolution during rapid organismal diversification, we generated a total of 2,131 transcriptome profiles (equivalent to individual RNA-sequencing libraries) from typically 5 organs in 6 adult specimens of 74 species of cichlid fishes from African Lake Tanganyika (median sequencing depth per tissue: 9.6–9.9 million reads per library; 125-base-pair (bp) strand-specific single-end reads; mapped against the phylogenetically equidistant *Oreochromis niloticus* reference genome; median of read mapping ~76%). A time-calibrated species tree based on genome-wide data taken from ref. [25] and pruned to the taxon set of this study is shown in Fig. 1a (details on individual samples including sampling dates and locations are available in Supplementary Table 1; information on sequencing and mapping coverage is provided in Supplementary Fig. 1; and the variance within and between species is shown in Supplementary Figs. 2–4).

As a first step, to explore the global patterns of gene expression differentiation among species and across organs, we performed a principal component analysis (PCA) on the entire dataset. The PCA clearly separated the expression profiles according to organ type (Fig. 1b)—with the exception of gill and LPJ transcriptomes, which showed largely overlapping gene expression profiles. This similarity in gene expression profiles is not surprising, given their common developmental origin (the LPJ is derived from the fusion of the left and right fifth ceratobranchials[31]). Within organs, on the other hand, the species-specific transcriptome profiles clustered by tribe (Fig. 2), indicating a strong phylogenetic signal in the data. This in turn suggests that, as in mammals[7], gene expression changes have accumulated over the course of the adaptive radiation of cichlid fishes in Lake Tanganyika, resulting in—overall—more similar gene expression profiles between more closely related species, irrespective

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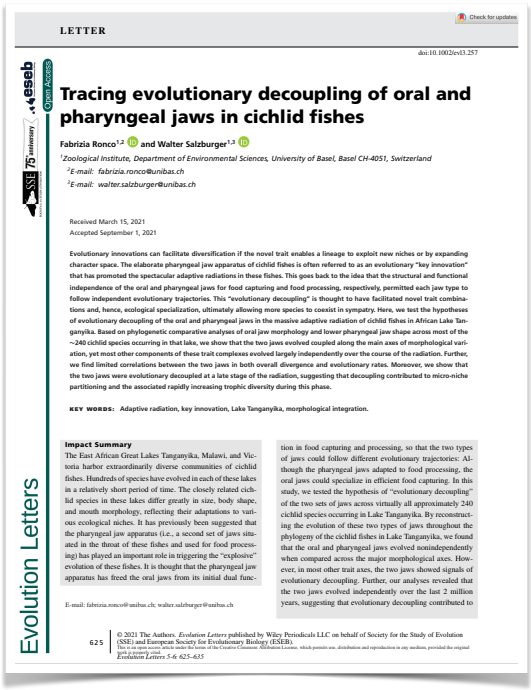

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Tracing evolutionary decoupling of oral and pharyngeal jaws in cichlid fishes

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Evolutionary innovations can facilitate diversification if the novel trait enables a lineage to exploit new niches or by expanding character space. The elaborate pharyngeal jaw apparatus of cichlid fishes is often referred to as an evolutionary "key innovation" that has promoted the spectacular adaptive radiations in these fishes. This goes back to the idea that the structural and functional independence of the oral and pharyngeal jaws for food capturing and food processing, respectively, permitted each jaw type to follow independent evolutionary trajectories. This "evolutionary decoupling" is thought to have facilitated novel trait combinations and, hence, ecological specialization, ultimately allowing more species to coexist in sympatry. Here, we test the hypotheses of evolutionary decoupling of the oral and pharyngeal jaws in the massive adaptive radiation of cichlid fishes in African Lake Tanganyika. Based on phylogenetic comparative analyses of oral jaw morphology and lower pharyngeal jaw shape across most of the ~240 cichlid species occurring in that lake, we show that the two jaws evolved coupled along the main axes of morphological variation, yet most other components of these trait complexes evolved largely independently over the course of the radiation. Further, we find limited correlations between the two jaws in both overall divergence and evolutionary rates. Moreover, we show that the two jaws were evolutionary decoupled at a late stage of the radiation, suggesting that decoupling contributed to micro-niche partitioning and the associated rapidly increasing trophic diversity during this phase.

KEY WORDS: Adaptive radiation, key innovation, Lake Tanganyika, morphological integration.

Impact Summary

The East African Great Lakes Tanganyika, Malawi, and Victoria harbor extraordinarily diverse communities of cichlid fishes. Hundreds of species have evolved in each of these lakes in a relatively short period of time. The closely related cichlid species in these lakes differ greatly in size, body shape, and mouth morphology, reflecting their adaptations to various ecological niches. It has previously been suggested that the pharyngeal jaw apparatus (i.e., a second set of jaws situated in the throat of these fishes and used for food processing) has played an important role in triggering the "explosive" evolution of these fishes. It is thought that the pharyngeal jaw apparatus has freed the oral jaws from its initial dual function in food capturing and processing, so that the two types of jaws could follow different evolutionary trajectories: Although the pharyngeal jaws adapted to food processing, the oral jaws could specialize in efficient food capturing. In this study, we tested the hypothesis of "evolutionary decoupling" of the two sets of jaws across virtually all approximately 240 cichlid species occurring in Lake Tanganyika. By reconstructing the evolution of these two types of jaws throughout the phylogeny of the cichlid fishes in Lake Tanganyika, we found that the oral and pharyngeal jaws evolved nonindependently when compared across the major morphological axes. However, in most other trait axes, the two jaws showed signals of evolutionary decoupling. Further, our analyses revealed that the two jaws evolved independently over the last 2 million years, suggesting that evolutionary decoupling contributed to

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