Species and Species Concepts
Diversity

- The number of living species may be as great as 100 million (but depends on who you talk to).
- First living forms (species) observed 3.8 billion years ago.
- 99% of all species are now extinct.
- All cultures recognize different forms (species) and name them.
Species

- Smallest independently evolving unit.
- Species follow independent evolutionary trajectories.
- Defining species is extraordinarily contentious.
- About 22 different species concepts exist.
Species

• Why are species definitions and recognizing species so contentious?

• Species are dynamic, evolving individuals, but we attempt to force them into rigid classes.

• Species are real evolutionary groups and not categories which are created as a direct function of perceived distinction.
Why are species important

• Much of our systematic, taxonomic, ecological, physiological, etc. studies are conducted at species level.

• The species is considered by most to be the unit of evolution. Thus, the primary unit of biogeography, selection, adaptation, speciation, etc.
Why are species important

- Evolutionary studies work with what are determined to be species. Thus, what we determine to be species will logically determine the types of processes that we will allow ourselves to discover.

- Our conceptualization of species must be one that will allow us to recognize all types of things in nature that participate in evolution (descent with modifications) or “speciation”.
Why are species important

• We must realize that hopefully the things we are placing in the taxonomic category “species” are in fact something that participants in all of the processes in nature that “real” species participate in.

• Thus understanding and recognizing what are species is fundamental for the study of evolutionary processes.
Monism versus Pluralism

• David Hull (1996) discusses the connection of monism and pluralism as they relate to generality.
• **Monism** – Refers to a singular explanation for kinds or phenomena.
• **Pluralism** – Refers to multiple possible explanations for kinds or phenomena.
Monism versus Pluralism

• A monist would argue that a single concept does exist to recognize that level of organization across all organisms deserving of recognition as species (Analogous to a unified theory of physics).
Monism versus Pluralism

• A pluralist recognizes there might be different concepts, and none of these particular views of organization of organisms is any more fundamental than another, although some may be preferable (But pluralism ≠ anarchy).
Species and Hierarchies

• Nature is not a continuum from one individual to another. It represents a generally discontinuous pattern of diversity being partitioned into generally separate entities that have been termed species.

• To most, the idea of species seems fairly straightforward and simple.

• They are the largest, non-arbitrary unit above the level of the individual (some argue species are individuals).
Primary Concept

- The entities that we envision as species represent fundamental components or “building blocks” in the natural sciences.
- They are the atoms or atomic particles of atomic theory or the celestial bodies of planetary theory.
- In the history of this planet, through selection and drift, speciation has produced entities we call “species”.
Primary Concept of Species

- The ideas abstracted here give us a single primary concept of species. This is a non-operational concept BUT this is a needed quality of a theoretical concept of natural entities. The other concepts of species are operational and restrict one's ability to appreciate diversity. However, together, all of these secondary concepts provide us with the necessary infrastructure to discover species consistent with the primary, theoretical concept of species.
Primary Concept

• The significance of species and our conceptual view of them - as naturally occurring by-products of descent - is noted:

• "the species concept is crucial to the study of biodiversity . . . Not to have a natural unit such as the species would be to abandon a large part of biology into free fall, all the way from the ecosystem down to the organism"

Species

• Fundamental unit of biodiversity, they are natural.
• It is an individual not a class.
Aristotelean naturalness

• This is an essentialists view of the world. Herein, a group is considered natural if the entities placed in the group share or agree in the characteristics that embody the essence of the group. These characters are both necessary and sufficient for group membership (Wiley, 1981). They are also expected to resemble one another in additional characteristics (Crowson, 1970).

• Essential characters were often thought of as those features most important in the functioning of the organisms. For Linnaeus his classification of plants (Species Plantarum 1753) was based largely on the reproductive morphology of the plants.
Phenetetic naturalness

- Groups exhibiting this form of naturalness are composed of members that resemble each other (in overall similarity) more than they resemble any non-member. They are all more similar to each other for the characters examined than any of the members are to a member outside of the group.
- “Essential” characters were no longer considered necessary or sufficient for group membership. Rather, inclusion in a group is based on sharing the maximum of all possible number of characters (or overall similarity).
Phylogenetic naturalness

- Groups exhibiting this form of naturalness are composed of members that share a common ancestor not ancestral to any other group. In other words, members in this group are more closely related to each other than any of them are to members outside of the group.

- With the development of evolutionary thinking and the concept of lineages participating in descent with modification naturalists began thinking of natural groupings being those descended from common ancestors. With this, the natural system became a phylogenetic system.
Natural Taxon?

- Many taxonomist and systematics feel that a natural taxon is one that a competent taxonomist or systematist says it is!
- One might also argue that a natural taxon is one that can be defined and discovered by a set of operations.
- Neither of these philosophies of natural taxa is what an evolutionary biologists or phylogenetic systematists would interpret at being natural. Naturalness connotes “existing in nature, neither artificial nor man-made” (Wiley, 1981).
Natural Taxon (sensu Wiley 1981)

1. Natural taxa exist via descent with modification whether or not there are systematists around to perceive or name them.

2. Because they exist in nature, natural taxa must be discovered, they cannot be invented.

3. Natural taxa originate according to natural processes (=speciation) and thus must be consistent with natural processes.

• When proposing a natural taxon, that is, when hypothesizing that a particular group of organisms is natural, we invoke all of the connotations implied in 1-3.
Classes, Individuals and Historical Taxa

- To fully understand natural groups referable to species or supraspecific taxa we must understand and consider the differences between what philosophers and systematists refer to as Classes, Individuals, and Historical Groups.
Class

• A class is a construct with members. Membership is determined by a class definition or class concept. A class is spatiotemporally unrestricted or unbounded with no unique beginning or ending, it does not participate in natural processes and does not change through time and space, it lacks cohesion and may lack continuity, it possess a general rather than a proper name, there are instances of them, and their constituents are members not parts. Finally, and very importantly, classes have definitions that specify the necessary and sufficient qualities that something must have to be a member.
Individual

- *Individuals* have very distinct qualities. *Individuals* are spatiotemporally restricted with unique beginnings and endings, they participate in natural processes and can change through time and space, they possess cohesion and continuity, they possess proper rather than general names, there are no instances of them, and their constituents are parts not members. Finally, individuals do not have definitions, **they cannot be defined**. Rather, they only have descriptions or diagnoses.
Historical Group

- This term was coined by Wiley (1980, 1981) to refer to natural, supraspecific taxa that are derived from *individuals*. These taxa have qualities of both *individuals* and classes and thus do not really fit into either of these metaphysical categories. Natural taxa are spatiotemporally bounded entities like *individuals*. However, these taxa are distinct from *individuals* in several ways. Thus, natural supraspecific taxa are referred to as either “a special type of individual”, “historical entity”, or “historical group”.
# Individuals vs. Historical Group

<table>
<thead>
<tr>
<th><strong>Cohesion</strong></th>
<th><strong>Individual</strong></th>
<th><strong>Historical Group</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Species have cohesion via sexual reproduction (sexual species), evolutionary stasis (asexual and sexual species), and similar responses of the particular organisms of a species to extrinsic factors of evolution.</td>
<td>No active cohesion because it is composed of individual evolutionary units that have the potential to evolve independently of each other.</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th><strong>Continuity</strong></th>
<th><strong>Individual</strong></th>
<th><strong>Historical Group</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Sexually reproducing species have historical (from ancestral lineage) and ongoing (reproductive ties, etc.) continuity.</td>
<td>Have only historical continuity as all parts have descended from a common ancestral species.</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th><strong>Evolution</strong></th>
<th><strong>Individual</strong></th>
<th><strong>Historical Group</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Units of evolution.</td>
<td>Those containing more than one species are units of history, not evolution. No evolutionary process is known to operate on supraspecific groups together as a unit.</td>
</tr>
</tbody>
</table>
# Terms compared

<table>
<thead>
<tr>
<th></th>
<th>Classes</th>
<th>Individuals</th>
<th>Historical Groups</th>
</tr>
</thead>
<tbody>
<tr>
<td>Space-Time</td>
<td>Unrestricted</td>
<td>Restricted</td>
<td>Restricted</td>
</tr>
<tr>
<td>Participate in Natural Process</td>
<td>No</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>Change through time</td>
<td>No</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>Constituents</td>
<td>Members</td>
<td>Parts</td>
<td>Parts</td>
</tr>
<tr>
<td>Instances</td>
<td>Yes</td>
<td>No</td>
<td>No</td>
</tr>
<tr>
<td>Names</td>
<td>General</td>
<td>Proper</td>
<td>Proper</td>
</tr>
<tr>
<td>Definitions</td>
<td>Yes</td>
<td>No</td>
<td>No</td>
</tr>
<tr>
<td>Descriptions</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>Diagnoses</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>Organization</td>
<td>Only constructs of our mind</td>
<td>Organization and ontogeny</td>
<td>Organization and ontogeny</td>
</tr>
<tr>
<td>Species Concepts</td>
<td>Abbreviations</td>
<td></td>
<td></td>
</tr>
<tr>
<td>------------------</td>
<td>---------------</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. Agamospecies</td>
<td>(ASC)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2. Biological</td>
<td>(BSC)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3. Cohesion</td>
<td>(CSC)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4. Cladistic</td>
<td>(CISC)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>5. Composite</td>
<td>(CpSC)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>6. Ecological</td>
<td>(EcSC)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>7. Evolutionary</td>
<td>(ESC)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>8. Evolutionary Significant Unit</td>
<td>(ESU)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>a. Diagnosable</td>
<td>(PSC1)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>b. Monophyly</td>
<td>(PSC2)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>c. Diagnosable/Monophyly</td>
<td>(PSC3)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>9. Genealogical Concordance</td>
<td>(GCC)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>10. Genetic</td>
<td>(GSC)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>11. Genotypic Cluster Definition</td>
<td>(GCD)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>12. Hennigian</td>
<td>(HSC)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>13. Internodal</td>
<td>(ISC)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>14. Morphological</td>
<td>(MSC)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>15. Nondimensional</td>
<td>(NDSC)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>16. Phenetic</td>
<td>(PhSC)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>17. Phylogenetic</td>
<td>(PSC)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>18. Polythetic</td>
<td>(PtSC)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>19. Recognition</td>
<td>(RSC)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>20. Reproductive</td>
<td>(RCC)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>21. Successional</td>
<td>(SSC)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>22. Taxonomic</td>
<td>(TSC)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Typological Species Concept

- Concept of Plato, Aristotle, Linnaeus.
- Observed diversity consists of a limited number of "universals" or types (eidos of Plato).
- Species consist of similar individuals sharing the same essence.
- Each species is separated from all others by a sharp discontinuity.
- Each is constant through time.
- There are severe limitations to the possible variation of any one species. Variation is an imperfect manifestation of the idea implicit in each species.
Typological Species Concept

• There is no way to determine the essence of a species.
• Individuals of the same species can be very different on the basis of sexual dimorphism, age differences, polymorphisms, and other forms of variation.
• Sibling species differ hardly at all morphologically but are found to represent distinct entities.
• Degree of difference is not the decisive criterion in ranking a taxon as species.
Nominalistic Species Concept

- Popular in the 18th century. Lamark, Buffon
- This concept denies the existence of "real" universals.
- Only individual organisms exist and species are man-made abstractions.
- Thus, we have only names that apply to similar type things.
- “Nature produces individuals and nothing more - species have no actual existence in nature. They are mental concepts and nothing more…. Species have been invented in order that we may refer to great numbers of individuals collectively.”
Nominalistic Species Concept

• Summarized by Mayr (1969) “any naturalist ... knows that this is simply not true.” “Species ... are not human constructs, nor are they types.... They are something for which there is no equivalent in the realm of inanimate objects.”

• It is clear that there are discontinuities in biological diversity, at least in the animal world. Problem is with the plant world, and a number of plant biologists deny the reality of species.
Biological Species Concept

- "groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups" (Mayr 1940).
- This concept provided a solution to an inanimate definition for animate and potentially changing entities that resulted with the advent of evolutionary thought.
- This concept also attempted to solve the paradox caused by the conflict between the fixity of species of the naturalist and the fluidity of the species of the evolutionist. This conflict caused Linnaeus to basically deny a concept of evolution and for Darwin to deny the reality of species.
Biological Species Concept

• The absence of a lineage perspective, its nondimensionality.
• It excludes non-sexually reproducing organisms.
• Indiscriminately uses the reproductive isolation criterion.
• Confusion of isolating mechanisms with isolating effects.
• It is often employed as a typological concept, no different from the frequently criticized morphological species concept.
• Most speciation has been shown to occur in allopatry.
Biological Species Concept

X. alvarezi  X. sp.  X. helleri  X. signum

= evolution of reproductive isolating mechanism

Reproductive Compatibility Inherited
Evolutionary Species Concept

• "a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies" (Simpson 1961:153).

• A lineage concept that avoids many of the problems of the biological species concept without denying that interbreeding among sexually reproducing individuals is an important component in species cohesion. It is compatible with a broader range of reproductive modes and with all speciation models.

• It was proposed by Simpson because of his dissatisfaction with the nondimensionality of the BSC.
Morphological Species Concept

• "Species may be defined as the easily recognized kinds of organisms, and in the case of macroscopic plants and animals their recognition should rest on simple gross observation such as any intelligent person can make with the aid only, let us say, of a good hand-lens" (Shull, 1923:221).

• "A species is a community, or a number of related communities, whose distinctive morphological characters are, in the opinion of a competent systematist, sufficiently definite to entitle it, or them, to a specific name" (Regan, 1926:75).
Phylogenetic Species 1

- "a diagnosable cluster of individuals within which there is a parental pattern of ancestry and descent, beyond which there is not, and which exhibits a pattern of phylogenetic ancestry and descent among units of like kind" (Eldredge and Cracraft, 1980:92).

- It emphasizes the a priori diagnosability of species, irrespective of a criterion of monophyly. There are two purported benefits.
  - First, process is not invoked before pattern is observed (resulting in pattern cladism).
  - Second, phylogenetic methodologies are argued to be applicable only to genealogical relationships of species and supraspecific taxa, not below the level of integration of species wherein tokogenetic relationships of infraspecific entities are the norm.
"a geographically constrained group of individuals with some unique apomorphous character, is the unit of evolutionary significance" (Rosen, 1978:176).

For Rosen (1978, 1979) and de Queiroz and Donoghue (1988, 1990) species have reality if they are monophyletic and supported by autapomorphies. Any biological entity possessing a uniquely derived character, of any type, magnitude, or quantity, qualifies as a species. Those not possessing autapomorphomorphic attributes do not constitute a species, as traditionally viewed, but are referred to as "metaspecies" by some. The application of this concept necessitates a phylogenetic analysis.
Phylogenetic Species 3

• “a species as the smallest diagnosable cluster of individual organisms forming a monophyletic group within which there is a parental pattern of ancestry and descent” (McKitrick and Zink 1988).

• Because in this conceptualization all recognized monophyletic taxa are diagnosable, this definition, the methods for the discovery of species, and any associated practical and theoretical limitations are equivalent to PSC1 and PSC2.
Cohesion species

• “most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms” (Templeton 1989).

• Individuals have to be genetically interchangeable
• Individuals have to be ecologically interchangeable
• Species do not have to be monophyletic
Hierarchy of Species Concepts

Evolutionary Species

Secondary Concepts
- Only Sexual Reproduction
  - No Interspecific Gene Exchange Tolerated
    - GSC
    - HSC
    - RSC
  - Minor Interspecific Gene Exchange Tolerated
    - RCC
    - BSC
    - GSC

Secondary Concepts
- Sexual or Asexual Reproduction
  - Reproduction
    - BSC
  - Monophyly
    - Evidence of Monophyly
      - No Gene Exchange Tolerated
        - CSC
      - Minor Gene Exchange Tolerated
        - CISC
        - GCC
  - Reciprocal Monophyly
    - ASC
    - CISC
    - GCC
  - Difference-Similarity
    - ASC
    - CISC
    - GCC
    - NdSC
    - EcSC
    - PrSC
    - GCD
    - SSC
    - GSC
    - PSC1
    - MSC
    - TSC
Concepts and Operationalism

- Highly operational concepts tend to be least realistic and least inclusive.
- Concepts reflecting species reality as evolutionary individuals often make identification and diagnosis of these individuals very difficult.
- It appears that the more unifying and biologically realistic a concept is, the more difficult it is to implement rigorously and consistently.
Species

• Species are individuals – thus spatially and temporarily restricted.
• Yet they are evolutionary lineages, thus are dynamic.
• Lineages may change though time (anagenesis), or may give rise to daughter lineages (cladogenesis).
Species

• Why cannot species be described?
The floodplain
Symphysodon spp.
Classification of *Symphysodon*

- Schultz 1960 = two species:
  - *S. discus* Heckel 1840
  - *S. d. discus*
  - *S. d. willischwartzi* Burgess 1981
  - *S. aequifasciatus* Pellegrin 1904
    - *S. a. aequifasciatus*
    - *S. a. haraldi* Schultz 1960
    - *S. a. axelrodi* Schultz 1960

- Teton & Allgayer 1986 = only one species:
  - *S. discus* Heckel 1840
    - *S. d. discus*
    - *S. d. aequifasciatus* Pellegrin 1904
    - *S. d. willischwartzi* Burgess 1981

- Kullander 1996 = two species:
  - *S. discus* Heckel 1840
  - *S. aequifasciatus* Pellegrin 1904
Distribution of Symphysodon
Localities of *Symphysodon*

- 358 individuals from 24 populations; ~15 indiv./pop.
Specific questions

- Are phenotypic groups / species monophyletic?
- Population structuring across the Amazon basin?
- What hypotheses best explain the observed patterns?

Materials and Methods

- 358 individuals representing 24 localities
- PCR amplification of the mtDNA control region and of the third exon of RAG1
- Haplotype network reconstruction and testing of association of haplotypes with geography using nested clade analysis, test in Arlequin and the Mantel test
- Basic population genetic characterization
Haplotypenetzwerk - mtDNA

- 358 Individuen
- 24 Lokalitäten
- 471 Nukleotide
- 94 Allele

Haplotypenetzwerk kann nicht parsimonios aufgelöst werden
mtDNA-Allele werden in drei (3) unabhängige Netzwerke gruppiert
- Gruppe grün – S. a. haraldi
- Gruppe blau – S. a. aequifasciatus
- Gruppe braun+heckel+pineapple – S. a. aequifasciatus + S. d. discus + S. d. willischwartzi
• 107 haplotypes
• 23 localities
• 471 nucleotides
• -ln = 2326.13554
• Monophyletic green
• Monophyletic blue
• Monophyletic Xingú
• Non-monophyletic brown, heckel & pineapple
• mtDNA alleles are grouped into three (3) independent networks that are not parsimoniously connected
Haplotype network - green

- Exact Pop. Diff. $P = 1.000$
- $F_{ST} = 0.1285$, $P < 0.001$
- Difference between Tefe+Jupura vs. Jutai+Jurua+Tabatinga
- NCA – restricted gene flow with IBD
- Fu’s $F_s$ $P < 0.001$
Haplotype network - blue

- Exact Pop. Diff. $P = 0.164$
- $F_{ST} = 0.1512$, $P = 0.001$
- Difference between Purus vs. Manacapuru
- NCA – non-significant
- Fu’s $Fs$ $P > 0.05$
Haplotypic network - rest

- Exact Pop. Diff. $P < 0.001$
- $F_{ST} = 0.6427$, $P < 0.001$
- Difference between Xingu vs. rio Negro vs. rest
- IBD
- NCA – restricted gene flow with IBD; allopatric fragmentation
- Fu’s $F_s$ $P > 0.05$
Haplotype network - nuDNA

- 358 individuals genotyped
- 23 localities
- 1443 nucleotides
- 4 segregating sites
- 5 alleles
- Non-random distribution of alleles among color types (Exact Pop. Diff. $P < 0.001$; $F_{ST} = 45.98$, $P < 0.001$)
- NCA – no information
- No signature of population expansion
Results

- Purus Ridge 8 MYA vs. 4% mtDNA
- Junction of Negro and Solimões
- Junction of Xingú and Amazonas
Inference 1

• The green and blue clades have geographic distribution upstream and downstream, respectively, of the Purus ridge. Breach of the ridge varies from 8 to 2 MYBP. Potentially compatible with the observed 4% sequence divergence between the green and blue clades.

• The green clade shows a signature of a demographic expansion.

• Similar patterns are observed in Astronotus ocelatus, Osteoglossum bicirrhosus, Arapaima gigas and Potamotrygon spp.

• The breach of the Purus ridge is potentially a causal event in diversification of some Amazonian fishes.
Inference 2

• The division between the central blue clade and the remaining *Symphysodon* from downstream localities corresponds to the confluence of rio Negro with rio Solimões.
• Restricted gene flow with isolation-by-distance is also inferred for the discus of rio Negro and rio Amazonas.
• Restricted gene flow between rio Negro and rio Amazonas/ Solimões system is also observed in *Melanosuchus niger*, *Caiman crocodilus* and *Trichechus inunguis*.
• The rio Negro is the largest affluent of the Amazon with a radically different chemistry which may present an ecological barrier for many groups of aquatic organisms.
Inference 3

- The divergent Xingú clade is novel.
- The lower Amazon is separated by the Tapajos arch, but no other discus east of the Tapajos arch are differentiated.
- The rio Xingú has a large number of endemics.
- The rio Xingú shares a number of species with the Guyana Shield (e.g. *Prochilodus rubrotaeniatus*).
Specific questions

• What is the genetic architecture of *Symphysodon* spp.?
• What hypotheses best explain this genetic architecture?

Materials and Methods

• 358 individuals representing 23 localities
• PCR amplification and genotyping of 12 microsatellite loci
• Inference of genetic architecture using Structure and IM
• Test of alternate hypotheses
Structure analysis

- Structure (Pritchard et al., 2000) using admixture and unlinked loci.
- Using the ΔK criterion of Evanno et al. (2005), there are four groups.
- Two of the groups are significantly admixed.
Inference 4

- *Symphysodon* spp. is a complex of relatively pure and admixed groups.
- Pure groups correspond to the the green and Xingú groups.
- Some pure groups are introgressed.
- Hybrid groups correspond to the Heckel+abacaxi and blue+brown group upstream of the Tapajos arch – the hybrid groups are in the center of the distribution.

- Patterns of hybridization are also observed in other species of fish (e.g. *Cichla* spp.)
IM analyses

- IM (Hey & Nielsen, 2004) all six parameters allowed to freely vary.
- There is bi-directional geneflow between the Heckel and blue+brown groups but biased towards Heckel, and uni-directional geneflow from green and Xingú to blue+brown.
- Some $Nm$ values are close to 1.
- Coalescent depths were 0.58, 0.62, 0.45, 1.02 and 1.59 million years for the green, Heckel+abacaxi, Xingú, blue+brown groups, and Symphysodon as a whole.
IM analyses

- Effective population sizes vary from 0.5 to 3.8 million individuals.

- Based on Hudson and Coyne (2002), it takes on average $1.8N_{ef}$ and $2.2N_{ef}$ time in generations for at least one or both groups to have a 95% probability of achieving mtDNA monophyly and $7.3N_{ef}$ and $8.7N_{ef}$ for one nuclear gene to achieve monophyly.
Inference 5

- *Symphysodon* spp. is a complex of diversifying groups some of which are experiencing limited gene flow.
- Diversification is a Pleistocene phenomenon.
- Selective processes are contributing to driving and maintaining group differences.
- Because of large effective population sizes, introgression and ongoing geneflow, some groups have not reached monophyly.

- Very large effective population sizes, demographic expansions and haplotype sharing is common in a fish and crocodilians.
Short summary

- Paleo arches and especially the Purus arch have played a role in diversification of freshwater fauna.
- Ecological gradients contribute to diversification of freshwater fauna.
- Diversification through hybridization seems to play a role as well.
- Nearly all groups investigated underwent up to an order of magnitude population expansion since the late Pliocene potentially indicating the presence of ancient refugia.
- Extremely large effective population size result in numerous cases of incomplete lineage sorting.
Taxonomy

• *Symphysodon* most likely contains four evolutionary lineages, however, commonly used operational species concepts are unable to efficiently identify them.
Biodiversity barcoding

- Barcoding aims to identify species through the possession of a unique sequence barcode (COI mtDNA fragment).
- Barcoding using divergence thresholds to discover new species that were previously cryptic.
- Barcoding assumes that species are monophyletic, have diagnostic molecular characters, and intraspecific divergence is smaller than interspecific divergence.
- Barcoding fails in the case of *Symphysodon* spp., and many other Neotropical fish groups.
Summary

- The green and blue groups have geographic distribution roughly upstream and downstream, respectively, of the Purus ridge. It breached approximately 8 MYBP connecting these two regions. This timing, however, appears too old for the observed 4% sequence divergence.
- The division between the central ‘blue’ group and the remaining *Symphysodon* localities corresponds to the confluence of rio Negro with rio Solimões. The rio Negro is the largest affluent of the Amazon with a radically different chemistry which may result in a biogeographic barrier (also observed in *Melanosuchus* and *Caiman*).
- Nested within this group is the divergent Xingú clade. Currently there are no hypotheses for why this clade should be so different, however, this pattern is replicated in other fish species.
Taxonomy

- **One species?**
  - Depends on your species concept

- **Two species?** – *Symphysodon discus* and *S. aequifasciatus*
  - Definitely not! – the main defining character of central bar is commonly found in upper river drainages; also many ‘cruzados’ found; *S. discus* from rio Negro differs in mean lateral line number from *S. aequifasciatus* (not significant)

- **Five species?**
  - Depends on your species concept
Taxonomy

- The green group is defined by two mtDNA apomorphies.
- The blue group by five mtDNA apomorphies.
- The Xingú group by three mtDNA apomorphies.
- But no molecular apomorphies define the brown’ group or the species *Symphysodon discus* or its two subspecies *S. d. discus* and *S. d. willischwartzzi* individually or in any combination.
- Additionally, while the green, the blue and the Xingú groups are monophyletic, they are nested within the remaining *Symphysodon* haplotypes.
Taxonomy

- The PSC does not reject the hypothesis that *Symphysodon* is a single highly variable species with a complex evolutionary history.
- Neither does Mayr’s (1942) biological species concept (BSC) which states that: "a species is a group of potentially or actually interbreeding populations that is reproductively isolated from other such groups" since all forms of *Symphysodon* appear to interbreed under captive or semi-natural conditions, but pre-mating or post-mating isolating mechanisms are difficult to measure in nature.
- Other species concepts such as Templeton’s (1981) cohesion species concept (CSC) also do not reject the hypothesis that *Symphysodon* is just one species.
Conclusion

- Ecological and historical factors seem to have played a role in structuring *Symphysodon* spp. into several groups.
- Only some of these groups are monophyletic.
- Large amount of color pattern variation.

- Consensus of evidence leads to the conclusion that only one evolutionary entity (one species) is present in the genus *Symphysodon*. Phenotypic and genotypic variation is non-exclusive and does not represent the natural kind, a pattern observed in numerous other widely distributed Amazonian species as well. However, what we might be observing is a process of differentiation of one species into several.