

PERSPECTIVE

Cladistic species definitions can lead to under-representation of biodiversity from adaptive radiations.

George F. Turner

School of Environmental & Natural Sciences
Bangor University, Gwynedd LL57 2TH
Wales, UK
bss608@bangor.ac.uk

Abstract: Many species are paraphyletic, but current taxonomic practices often do not recognise this, and attempts are made to apply a monophyletic species concept. While allowing the recognition of ecomorphologically equivalent, or even phenotypically indistinguishable allopatric taxa as species, this often leads to combining distinctive local forms (such as cave-adapted populations) or even whole adaptive radiations (often in lakes) with widespread paraphyletic species to force species monophyly. It is suggested that this has negative consequences for our documentation and understanding of biodiversity, as well as for conservation, through issues such as lack of IUCN redlisting.

Short header: Problems with cladistic species definitions.

Description of new species remains fundamental to many key processes in the documentation of biodiversity, both for academic research, on topics such as ecological correlates of species richness and functional explanations for rates of lineage diversification (Faurby et al. 2007) and for information underlying practical conservation (Garnett & Christidis 2017), for example in obtaining an IUCN red-listing, archiving of range information on the Global Biodiversity Information Facility (GBIF), and for fish, FishBase, etc. Definitions of species remain contentious (e.g. de Queiroz 2007). In practice, many species are now being described based on molecular phylogenetics, either exclusively (e.g. Pons et al. 2006; Limeira Filho et al. 2024) or in combination with morphological traits (e.g. Delicado et al. 2024).

A number of opinion pieces have suggested that adoption of evolutionary or phylogenetic species models in preference to those based around morphology or reproductive isolation have led to ‘taxonomic inflation’ with geographically isolated but ecologically equivalent and morphologically little different populations being described as species, particularly in charismatic taxa of conservation concern (Isaac et al. 2004; Zachos et al. 2013). Other authorities have disputed this, citing improving taxonomic investigation as the cause of increased numbers of recognised species (Sangster 2009). An issue which appears to have generated little discussion is one that I feel is particularly relevant to studies of adaptive radiations, including issues of conservation, namely the reluctance of taxonomists to formally recognise narrowly-distributed endemic taxa as species, even when they are clearly morphologically and ecologically distinct, and often extremely vulnerable. This appears to stem from the belief that taxonomy should be cladistically-based and that this requires all taxa to be monophyletic (de Queiroz 2006; Dubois 2007). However, it seems that this is perhaps a misreading of the basic principles of cladistics, in which it has long been recognised that monophyly really necessarily only applies at the supraspecific level. At the most obvious level, genealogical (or tokogenetic) relationships within a sexually reproducing species do not lead back to a single common ancestor, but to an ever-expanding number of ancestors (Hennig 1966; Wiley 1979). Thus, it has been proposed that non-monophyletic lineages can be accommodated in widely used species definitions, such as that of de Queiroz (2007) which considers monophyly as one of many possible sources of evidence for the existence of the separately evolving metapopulation lineages that constitute species. But, is this how things are currently operational?

I was recently discussing captive breeding programmes and reintroductions of threatened species with staff at Chester Zoo, and was impressed by the lengths to which they had gone to breed the Omani blind cavefish, *Garra barreimiae* Fowler & Steinitz, 1956, which I felt must surely be a very rare and valued species, only to be informed that it was in fact Least Concern on the IUCN red-list (Harrison 2015). A cave-dwelling fish in a desert country, Least Concern? The reason turned out to be that the cave-population is regarded as conspecific with the widely distributed surface population. Indeed, a recent revision of the group (Kirchner et al. 2020) has split the surface population into 5 allopatric species, subtly differentiated in colour pattern and little else (one pair of species differ in gillraker counts). However, this left the cave fish as conspecific with the local surface population, now *Garra longipinnis* Banister & Clarke, 1977 (Kirchner et al. 2020). By contrast, the cave fish are phenotypically highly distinct: unpigmented, blind and showing reduced squamation (Banister 1984), and indeed this is the first taxon separated in the dichotomous key of the Kirchner et al. (2020) paper. The authors do not provide an explicit rationale for their decision to retain the cave populations within *G. longipinnis*. It just seems to be taken for granted. They present a molecular phylogeny based on mitochondrial (mtDNA) COI sequences which places the cave population within an unresolved polytomy with 3 other sequences of *G. longipinnis*, so

distinguishing the cave could potentially make a ‘surface species’ paraphyletic. The tree contains 33 species of *Garra*, of which 15 are shown as monophyletic and the remainder are represented by a single sequence. Of the five monophyletic mtDNA clades in the focal area of Oman, two are assigned to previously described species, one to a former subspecies now raised to species level and two new species are described. It thus seems reasonable to conclude that the authors of this study area largely used mitochondrial monophyly as the main criterion for recognising populations as distinct species. In addition, they also cite a then unpublished companion study (Kirchner et al. 2021): this phylogeographic study used 3 mtDNA loci and 17 microsatellites to investigate population structure, and diagnosed species using Automatic Barcode Gap Discovery and a Bayesian Poisson Tree Process: all 5 Omani species from the 2020 paper were represented as clades (and explicitly discussed in those terms) within the illustrated phylogeny (Kirchner et al. 2021; fig. 2). However, although the cave populations were resolved as a sister clade to the surface *G. longipinnis*, this was still not enough to have them discussed as a potential species. A haplotype network with a larger sample size allowed for the identification of a ‘cave haplogroup’ which had some haplotype sharing with the neighbouring surface populations. Haplotype sharing of this nature is readily explained by incomplete lineage sorting and is commonplace among clearly distinct species in rapid adaptive radiations, such as the African Great Lakes cichlid fishes (Svardal et al. 2021). Another indication of the distinctness of the cave populations comes from the STRUCTURE analysis using microsatellites, where the cave populations were explicitly excluded ‘because differentiation between cave and surface populations produces a stronger signal than any other population structures with the subset Central’ (equal to *G. longipinnis* in Kirchner et al. 2020). It appears that there is little or no gene flow into the cave populations, but cave forms occasionally occur alongside surface forms downstream, and intermediate phenotypes believed to be hybrids are known (Kirchner et al. 2017). There also appears to be some influence of plasticity, even with some eye development in genetically cave-form individuals, perhaps resulting from them having developed from an early stage in the surface habitat (Kirchner et al. 2017). Overall, it seems likely that there is considerable scope for selection to purge the cave-adapted traits from the surface gene pool, although neutral alleles could mix more freely. I feel this is quite consistent with considering the cave form as a distinct species, ecologically, phenotypically and genetically. By contrast, there is also considerable evidence for hybridisation between the phenotypically similar allopatric surface forms, yet they are recognised as distinct species (Kirchner et al. 2021). The discussion of this paper explicitly mentions the de Queiroz (2007) species concept and states that ‘taxa are morphologically similar and delimiting species boundaries based solely on few morphological characters is futile’ but maintains that they [the allopatric surface populations in Oman, raised to species level by Kirchner et al. 2020] can be differentiated using molecular methods. In summary, the cave form although undergoing unidirectional introgression into nearby surface forms, is clearly ecologically and genetically distinct, and easily diagnosed, but it is regarded as an infraspecific variant, while ecologically and morphologically equivalent allopatric populations that also hybridise are regarded as distinct species. The main evidence for this seems to be mitochondrial monophyly and the main species concept cited is that of de Queiroz, both of which seem to be widespread among practicing taxonomists.

Another similar example is the Mexican cave tetra, in which the cave phenotype appears to have evolved several times independently from the surface form. Here, recognising the cave forms as distinct species would render the surface form paraphyletic, or force the creation of a host of essentially indistinguishable allopatric reciprocally monophyletic species. As yet,

the surface forms have not been split, and all – surface and cave forms- are recognised as the single species *Astyanax mexicanus* (De Filippi, 1853) (Garduño-Sánchez et al. 2023; Swaminathan et al. 2024). However, at the time of writing, the IUCN red listing had not yet incorporated this, and the cave forms were still listed as *Astyanax jordani* (Hubbs & Innes, 1936), and as Endangered (Ornelas García 2019). Presumably, if they were placed in the synonymy of *A. mexicanus*, they would inherit its ‘Least Concern’ status (NatureServe 2013)- although it is possible in exceptional cases for subpopulations of a species to be separately assessed (IUCN 2024), this seems rare in practice

Thus, we have clear cases where phenotypically dramatically distinct cave fish are presently not recognised as species, leading to lack of recognition as units of significant conservation value, resulting at least in part, because of their rendering of other taxa as paraphyletic- effectively ‘ancestral’ – taxa. Generally, persistence of ancestral taxa post speciation is held to be prohibited under cladistic principles, where every speciation event necessarily results in the formation of two new sister species (Hennig 1966; Frost & Kluge 1974; Ridley 1989). Although a number of authors have questioned this, both in principle and in practice (e.g. Wilkinson 1990; Funk & Omland 2003; Rieppel 2010; Fraudenstein et al. 2017), this view seems to be widespread among taxonomists and evolutionary biologists. Yet, there are clear examples where paraphyletic species are explicitly recognised, as in the Caribbean anoles, where, for example, *Anolis roquet* (Lacépède, 1788) on Martinique is considered ancestral to *A. extremus* Garman, 1887 on Barbados (Thorpe et al. 2018). In this case, it appears that the colonisation of Barbados took place while Martinique was divided into a number of precursor islands, which have later joined, permitting subsequent gene flow, although there is still a strong signal of differentiation among them, allowing the Western and Central Martinique populations to be more divergent from each other than the Central populations are from the Barbados species (Thorpe et al. 2018).

Similar scenarios may be common for continental species. For example, the separation of the western continental populations of the European Grass snake into a distinct species, *Natrix helvetica* (Lacépède, 1789), is supported by its monophyly and the narrowness of the hybrid zone, suggesting strong selection against hybrids, with the eastern populations retained in *Natrix natrix* (Linnaeus, 1758). However, resulting mitochondrial phylogenies render *N. natrix* paraphyletic (Kindler et al. 2017). Notably, *N. natrix* extends over a much larger geographic area- from the Netherlands to eastern Mongolia (Schöneberg et al. 2023), and it would not be surprising if *N. helvetica* is more closely related to western *N. natrix* than western *N. natrix* is to its distant eastern conspecifics although there may be no actual barriers to gene flow across its ~8,000km west-east range.

The lack of monophyly becomes even more straightforward in the event of hybrid speciation (Funk & Omland 2003) which is increasingly being reported in a variety of taxa (Mallet 2007; Lamichhaney et al. 2018).

How does this affect how we treat adaptive radiations? There seems to be considerable variation in practice. In situations like the African great lake cichlids, vast numbers of species, and indeed genera, are described (Turner 2007), but much less is known about the status of the sister/ancestral taxa, which are often assumed to be long since extinct. Lake Malawi presents an interesting exception to this, with the widespread riverine *Astatotilapia calliptera* (Günther 1894) being resolved by analysis of full genome sequences, as nested within the Lake Malawi radiation (Malinsky et al. 2018). It is hypothesised that this lineage remained in its shallow weedy habitat niche in both rivers and lakes (including Lake

Malawi), with continuing exchange of genes between multiple lake and river systems – presumably intermittently, as some of these water bodies are currently unconnected. During this time, it is estimated to have budded off three species in Lake Malawi which have gone on to diversify into the current 800+ endemics, all currently confined to the Lake Malawi catchment (Malinsky et al. 2018). Similarly, an endemic radiation of catfishes of the genus *Bathyclarias* Jackson, 1959 co-exists in Lake Malawi with its ‘ancestor’, the widely distributed *Clarias gariepinus* (Burchell, 1822), which appears from a mitochondrial phylogeny, both nested inside the endemics and as a sister taxon, depending on geographical proximity (Agnèse & Teugels 2001).

Perhaps a more common situation is where diversification within lakes or islands takes place, while the ancestral species remains allopatric, but persists over a wider geographic range. For example, radiations of mouthbrooding cichlids in Lakes Barombi Mbo and Ejagham both seem to be derived from populations of the widely distributed *Sarotherodon galilaeus* (Linnaeus, 1758), which is thereby rendered paraphyletic (Richards et al. 2018). Likewise, the radiations of *Coptodon* Gervais 1853 species in Lakes Bermin (Stiassny et al. 1992) and Ejagham (Poelstra et al. 2018), may be derived from the widespread and likely paraphyletic *C. guineensis* (Günther, 1862) (but see Dunz et al. 2013).

In general, sympatric species flocks are widely accepted and named as such in tropical lakes, perhaps because of the extreme species richness and phenotypic diversity of headline examples, such as the cichlids of Lakes Malawi, Tanganyika and Victoria. However, this is less clear-cut with temperate lake radiations, where ecomorphologically divergent taxa have traditionally been referred to as ‘sympatric morphs’ (Turner 1999; Skúlason et al. 2019) or ‘ecotypes’ (Lucek et al. 2014). In consequence, local endemic taxa, often forming sympatric species flocks have not been identified as distinct species, but are subsumed into widely distributed ‘least concern’ taxa. To some extent, this may reflect the relative recency of divergence (Lucek et al. 2014; Wund et al. 2008), with similar terminology (ecotypes) used for situations like adaptation of marine sticklebacks to freshwater habitats- which has likely occurred thousands of times, often over very short time-scales, and often showing a major role for phenotypic plasticity, perhaps along with soft sweeps – selection shifting gene frequencies from standing variation (Hu & Barrett 2023). Granting species status to numerous likely ephemeral taxa would seem unwarranted.

By contrast, some taxa, such as the arctic charr morphs in Thingvallavatn, Iceland and Loch Rannoch, Scotland, or the brown trout in Lough Melvin, Ireland are ecomorphologically well-differentiated and these may deserve to be treated as distinct species flocks (Kottelat & Freyhof 2007). Although some old names are available for some of these taxa, they are still not in widespread use and many taxa remain undescribed (Kottelat & Freyhof 2007). However, those taxa lucky enough to have pre-existing older names have sometimes been given an IUCN redlisting, such as *Salvelinus struanensis* (Maitland, 1881), the ‘vulnerable’ Loch Rannoch planktivorous charr (Freyhof & Kottelat 2007; see also Ferguson & Prodöhl 2022 for further discussion of this issue and alternative approaches to conservation). By contrast, whitefish (*Coregonus* Linnaeus, 1758 and relatives) appear to be readily assigned to formal species, with numerous sympatric taxa currently named and more being described recently (Hudson et al. 2011; Selz et al. 2020; Selz & Seehausen 2023). It is not clear why this is (a productive research group that also works on Lake Victoria cichlids?), but it does not seem to have been consistently applied, as, although Hudson et al. (2007) review data from over 200 whitefish radiations (each presumably of more than one taxon), only 95 valid species are listed in FishBase (Froese & Pauly 2024).

So, the Zoological and Botanical communities (prokaryote taxonomists necessarily use molecular-based methods: Meier-Kolthoff et al. 2013) seem to be content with a species concept somewhere between the classic Evolutionary Species Concept (Simpson 1961) and De Queiroz's (2007) separately evolving metapopulation lineages. If we like, we can define reciprocally monophyletic ecologically equivalent allopatric populations as species (e.g. Buckley-Beaton et al. 2006). We can use narrow contact zones as an indication of limited gene flow to support the designation of parapatric species pairs (e.g. Chambers & Hillis 2020)- in general, there seems to be an acceptance that a certain, relatively small, amount of hybridisation both in sympatry and parapatry can be compatible with species distinctness. There is also often an acceptance of paraphyletic species- units which are descended from a single common ancestral taxon, but do not contain all of its descendants. However, this is often unstated, with rare exceptions such as the Martinique Anole (Thorpe et al. 2018). As paraphyletic taxa are prohibited under cladistic principles, some authors have expressed discomfort at the idea of paraphyletic species, mistakenly believing that formal taxonomic codes preclude them (e.g. Grube & Kroken 2000)- in fact there is no requirement for monophyly in any of the generally accepted taxonomic codes (Freudenstein et al. 2017).

There are relatively few explicit discussions of the virtues of recognising paraphyletic species. For example, Rieseberg & Brouillet (1994) believe that paraphyletic species are likely to be common in plants, while Rieppel (2010) proposes that species can never be truly monophyletic. Wiens & Penkrot (2002) discuss how parapatry (or 'non-exclusivity' as they prefer to call it) can be determined in a character set, although in practice using only monophyletic units in species determination. Sukumaran & Knowles (2017) in their critique of multispecies coalescent methods of species delimitation, clearly show a paraphyletic species in their 'correct' speciation tree, without explicitly identifying it as such. Freudenstein et al. (2017) explicitly state that they believe that paraphyletic species exist and can be accommodated in a definition compatible with de Queiroz's (2007) species concept, in which both lineage and ecological role are emphasised. They are, however, clear that they do not propose to accept polyphyletic species, i.e. species comprised of more than one (meta-) population which has evolved similar phenotypes and roles in parallel. Despite these works being generally reasonably well-cited, the concept of paraphyletic species does not seem to have penetrated much into the theoretical literature nor indeed the adaptive radiation literature. I suggest that it is about time that it did.

Paraphyletic species exist: a widely distributed species can colonise isolated islands or lakes, radiate into a number of unique endemics, but continue to exchange genes across its 'mainland' range. In theory, it could do this more than once. For example, *Astatotilapia calliptera*, as well as its role in founding the Malawi cichlid radiation, has also colonised six crater lakes to the north of Lake Malawi, where unique populations have evolved, several of which have clearly divergent male breeding colours (dark grey / black in lakes v yellow in the rivers: Malinsky et al. 2015; Turner et al. 2019). These male breeding colours are associated with mate preferences (Tyers & Turner 2013). In one lake, the colonising species has split into deepwater 'benthic' and inshore 'littoral' taxa which probably justifies species status, differing in habitat preference, trophic morphology and male breeding dress (Malinsky et al. 2015). What holds for *A. calliptera*, holds equally for brown trout, arctic charr and 3-spined sticklebacks: we can recognise and name taxa in lacustrine species flocks, alongside widespread parapatric species. And it also holds for subterranean forms, such as the Omani cavefish and the Mexican blind tetra: these are clearly distinctive separately evolving lineages, diagnosable, worthy of conservation efforts. In the case of the tetra, each cave form

would be a separate monophyletic species- evolved in parallel, but the wide-ranging surface form would be a single paraphyletic species.

Coda: The Limits of Cladistics.

The gist of the previous set of discussions is that I believe that evolution is not necessarily always best described by the cladistic model, and that over-rigorous employment of this model has negative repercussions for taxonomy, evolutionary biology and conservation. I agree that cladistics is a terrific clean, calculable null model, and an excellent way of constructing phylogenies, but it is basically just a set of proposals made by Willi Hennig (1966) - it is neither a set of laws deduced by the logic of mathematics, nor has it been induced from empirical observation to be a set of principles invariable in the natural world.

At the beginning of this piece, I said that cladistic theory from Hennig (1966) onwards did not consider (sexual) species to be monophyletic, because they did not comprise a clade of descendants from a single common ancestor, itself included, but rather a genealogy in which each individual has numerous ancestors (opaquely termed ‘tokogenetic relationships’). I feel that this is not generally how most practicing taxonomists see it. Rather their underlying idea is rather more like the ‘cladistic species concept’ of Ridley (1989), which explicitly defined species as existing between the nodes of speciation events (or between speciation and extinction events). He proposed that cladistic species are monophyletic in the sense of including all the descendants from a speciation event - in other words ruling out persistent ‘ancestral’ species, which would be paraphyletic. I think this reflects how most workers interpret phylogenies: with the caveats of incomplete lineage sorting in recently diverged species (standing in for Hennig’s tokogenetic issues?), we expect species to show reciprocal monophyly at mtDNA loci (with the additional caveat of recent hybridisation) or equivalent coalescence among individuals averaged across multiple mostly nuclear loci (e.g. Zang & Rannala 2010). Tree structures showing parafyly (or polyphyly) are not routinely interpreted as defining species boundaries. I think this more accurately reflects how the cladistic model is made operational among the taxonomic community.

In contrast, while I believe that the evidence is clear that clades undoubtedly exist, so do some paraphyletic taxa. Evolution often proceeds by dichotomous branching: sometimes the ‘true’ sequence is hard to determine, but sometimes theory suggests that the true sequence may not be dichotomous and hard polytomies may be real (Bolnick 2006), which is consistent with molecular evidence (e.g. Scherz et al. 2022). It may sometimes be convenient to regard a speciation event as producing two new daughter species, with the ancestral species going extinct (as required by most readings of cladistic practice). But sometimes this may be misleading and it might be more useful to consider an ancestral species as persisting largely unchanged under stabilising selection and gene flow (as in *A. calliptera*: or the surface-living relatives of the cave fish), while budding off a number of geographically restricted and isolated daughter species. In addition, there is increasing evidence for introgression across the boundaries of stable and diagnosable species, indeed, often among non-sister species, most rampantly in the case of the cichlid fishes of Lake Victoria and neighbouring lakes (Meier et al. 2023). Conceptually, I feel this really ought to make clear that monophyly and the dichotomously branching cladistic tree is more of null model, often a fuzzy approximation, as is the idea of species as ‘separately evolving lineages’.

Finally, this must inevitably raise the question of whether higher taxa can also be paraphyletic. Siefert et al. (2016) make an explicit plea to retain paraphyletic higher taxa, for example where current genera represent clearly distinctive ecomorphological groups. In the

case of adaptive radiations, some of the lacustrine cichlid species flocks are presently considered to contain endemic genera (e.g. Lakes Victoria, Malawi, Barombi Mbo). So are the cottoid fish of Lake Baikal (Kontula et al. 2003). In theory, two or more lakes containing different endemic genera could be descended from the same ancestral riverine species, although I am not sure there is an example of this yet. At present, many riverine cichlids are assigned to the genus *Astatotilapia* Pellegrin, 1904, including relatives of the endemic cichlids of Lakes Malawi, Victoria, Kivu, Edward, Albert and Turkana (Meier et al. 2023). Not only are there no apparent diagnostic traits to break this genus up into monophyletic lineages, but if this was to be achieved, it would not really resolve the problem. There is clear evidence that prior to the evolution of both the Malawi (Svardal et al. 2019) and Victoria region (Meier et al. 2023) radiations there was massive introgression between distantly related ‘*Astatotilapia*-type’ lineages. So, if an attempt were to be made to break *Astatotilapia* up into a series of monophyletic genera, then the two great radiations would have arisen from inter-generic hybrids. A similar problem arises in the case of the Lake Baikal sculpins, where two endemic families and 11 endemic genera are resolved as being nested with the single widespread genus, *Cottus* L., 1758 (Kontula et al. 2003), and it gets even worse for the Baikalian gammarids (Naumenko et al. 2017).

I thank Mark Wilkinson and an anonymous referee for their helpful comments.

References

- Agnès LF, Teugels GG. The *Bathyclarias-Clarias* species flock. A new model to understand rapid speciation in African Great lakes. *Comptes Rendus De L'académie Des Sciences - Series III - Sciences De La Vie* 2001; 324: 683–688
- Banister KE, A subterranean population of *Garra barreimiae* (Teleostei: Cyprinidae) from Oman, with comments on the concept of regressive evolution, *Journal of Natural History*, 1984; 18: 927-938.
- Bolnick DI Multi-species outcomes in a common model of sympatric speciation. *Journal of Theoretical Biology* 2006; 241: 734-744,
- Buckley-Beason VA, Johnson WE, Nash WG, Molecular evidence for species-level distinctions in Clouded Leopards. *Current Biology* 2006; 16: 2371-2376,
- Chambers EA, Hillis DM, The multispecies coalescent over-splits species in the case of geographically widespread taxa. *Systematic Biology* 2020; 69: 184–193.
- Delicado D, Boulaassaf K, Khalloufi N, et al., A holistic perspective on species delimitation outperforms all methods based on single data types in freshwater gastropods (Caenogastropoda: Hydrobiidae: *Pseudamnicola*), *Zoological Journal of the Linnean Society*, 2024; zlae010.
- de Queiroz K. Species concepts and species delimitation. *Systematic Biology* 2007; 56: 879–886.
- de Queiroz K. The PhyloCode and the distinction between taxonomy and nomenclature, *Systematic Biology* 2006; 55:160–162,
- de Queiroz K, Gauthier J, Toward a phylogenetic system of biological nomenclature. *Trends in Ecology and Evolution* 1994; 9: 27–31.
- Dubois A Naming taxa from cladograms: some confusions, misleading statements, and necessary clarifications. *Cladistics* 2007; 23: 390-402.
- Faurby S, Eiserhardt WL, Svenning JC. Strong effects of variation in taxonomic opinion on diversification analyses. *Methods in Ecology & Evolution*. 2016; 7: 4–13.
- Ferguson A, Prodöhl PA. Identifying and conserving sympatric diversity in trout of the genus *Salmo*, with particular reference to Lough Melvin, Ireland. *Ecology of Freshwater Fish*, 2022; 31: 177–207.
- Freudenstein JV, Broe MB, Folk RA, et al., Biodiversity and the species concept- lineages are not enough. *Systematic Biology* 2017; 66: 644–656.
- Freyhof J, Kottelat M. *Salvelinus struanensis*. The IUCN Red List of Threatened Species 2008: e.T135424A4127677. Accessed on 27 March 2024.

- Froese R, Pauly D. Editors. FishBase. www.fishbase.org, accessed 18 March 2024.
- Frost DR, Kluge AG. A consideration of epistemology in systematic biology, with special reference to species. *Cladistics* 1994; 10: 259–294.
- Funk DJ, Omland KE (2003) Species-level paraphyly and polyphyly: frequency, causes, and consequences, with insights from animal mitochondrial DNA. *Annual Review of Ecology and Systematics* 2003; 34:397–423.
- Garduño-Sánchez M, Hernández-Lozano J, Moran RL et al. Phylogeographic relationships and morphological evolution between cave and surface *Astyanax mexicanus* populations (De Filippi 1853) (Actinopterygii, Characidae). *Molecular Ecology* 2023; 32: 5626–5644.
- Garnett ST, Christidis L. Taxonomy anarchy hampers conservation. *Nature* 2017; 546: 25–27.
- Grube M, Kroken S. 2000. Molecular approaches and the concept of species and species complexes in lichenized fungi. *Mycological Research* 104:1284–1294.
- Harrison IJ. *Garra barreimiae*. The IUCN Red List of Threatened Species 2015: e.T8916A3147989. Accessed 18 March 2024.
- Hennig W. *Phylogenetic Systematics*. University of Illinois Press, Urbana. 1966.
- Hu J, Barrett RDH. 2023. The role of plastic and evolved DNA methylation in parallel adaptation of threespine stickleback (*Gasterosteus aculeatus*). *Mol Ecol*. 32:1581–1591.
- Hudson AG, Vonlanthen P, Müller R, et al. Review: The geography of speciation and adaptive radiation in coregonines. *Advances in Limnology* 2007; 60: 111–146.
- Hudson AG, Vonlanthen P, Seehausen O. Rapid parallel adaptive radiation from a single hybridogenic ancestral population. *Proceedings of the Royal Society B: Biological Sciences* 2011; 278: 58–66.
- Isaac NJB, Mallet J, Mace GM. Taxonomic inflation: its influence on macroecology and conservation. *Trends in Ecology & Evolution* 2004; 19: 464–469.
- IUCN. Guidelines for Using the IUCN Red List Categories and Criteria. 2024; Version 16. Prepared by the Standards and Petitions Committee. Downloadable from <https://www.iucnredlist.org/documents/RedListGuidelines.pdf>.
- Kindler, C., Chèvre, M., Ursenbacher, S. et al. Hybridization patterns in two contact zones of grass snakes reveal a new Central European snake species. *Scientific Reports* 2017; 7: 7378.
- Kirchner S, Kruckenhauser L, Pichler A, et al. Revision of the *Garra* species of the Hajar Mountains in Oman and the United Arab Emirates with the description of two new species (Teleostei: Cyprinidae) 2020; *Zootaxa* 4751: 521–545.
- Kirchner S, Sattmann H, Haring E, et al., Hidden diversity- delimitation of cryptic species and phylogeography of the cyprinid *Garra* species complex in Northern Oman. *Journal of Zoological Systematics and Evolutionary Research* 2021; 59: 411–427.

Kitchener, A.C., Beaumont, M.A., Richardson, D., 2006. Geographical variation in the clouded leopard, *Neofelis nebulosa*, reveals two species. *Curr. Biol.* 16, 2377–2383.

Kontula T, Kirilchik SV, Väinölä R, Endemic diversification of the monophyletic cottoid fish species flock in Lake Baikal explored with mtDNA sequencing. *Molecular Phylogenetics and Evolution* 2003; 27: 143-155,

Kottelat M, Freyhof J Handbook of European Freshwater Fishes, Cornol, Switzerland 2007.

Lamichhaney S, Han F, Webster MT, Andersson L, Grant BR, Grant PR. Rapid hybrid speciation in Darwin's finches. *Science* 2018; 359:224–228.

Limeira Filho D, França ERdR, Costa DKdP, et al., Molecular evidence reveals taxonomic uncertainties and cryptic diversity in the neotropical catfish of the genus *Pimelodus* (Siluriformes: Pimelodidae). *Biology* 2024; 13:162.

Lucek, K., Sivasundar, A., Kristjánsson, B. K., et al., (2014). Quick divergence but slow convergence during ecotype formation in lake and stream stickleback pairs of variable age. *Journal of Evolutionary Biology*, 27, 1878–1892

Malinsky M, Challis R, Tyers AM, Schiffels S, Terai Y, Ngatunga BP, Miska EA, Durbin R, Genner MJ, Turner GF (2015) Genomic islands of speciation separate cichlid ecomorphs in an East African crater lake. *Science* 350: 1493-1498

Malinsky M, Svoldal H, Tyers AM, et al. Whole-genome sequences of Malawi cichlids reveal multiple radiations interconnected by gene flow. *Nature Ecology and Evolution* 2018; 2: 1940-1955.

Mallet J Hybrid speciation. *Nature* 2007; 446: 279-283

Meier JJ, McGee MD, Marques DA, et al. Cycles of fusion and fission enabled rapid parallel adaptive radiations in African cichlids. *Science* 2023; 381: eade2833.

Meier-Kolthoff JP, Auch AF, Klenk H-P, et al. Genome sequence-based species delimitation with confidence intervals and improved distance functions. *BMC Bioinformatics* 2013; 14: 60.

NatureServe. *Astyanax mexicanus*. The IUCN Red List of Threatened Species 2013: e.T62191A3109229. Accessed 18 March 2024.

Naumenko SA, Logacheva MD, Popova NV, et al., Transcriptome-based phylogeny of endemic Lake Baikal amphipod species flock: fast speciation accompanied by frequent episodes of positive selection. *Molecular Ecology* 2017; 26: 536–553.

Neumann D, Stiassny MLJ, Schlieven UK. Two new sympatric *Sarotherodon* species (Pisces: Cichlidae) endemic to Lake Ejagham, Cameroon, west-central Africa, with comments on the *Sarotherodon galilaeus* species complex. *Zootaxa* 2011; 2765:1-20

- Ornelas García P. *Astyanax jordani*. The IUCN Red List of Threatened Species 2019: e.T191201A1972594.
- Poelstra J, Richards E, Martin C. Speciation in sympatry with ongoing secondary gene flow and a potential olfactory trigger in a radiation of Cameroon cichlids. *Molecular Ecology* 2018; 27: 4270–4288.
- Pons J, Barraclough TG, Gomez-Zurita J, et al., Sequence-based species delimitation for the DNA taxonomy of undescribed insects. *Systematic Biology* 2006; 55: 595-609.
- Richards EJ, Poelstra JW, Martin CH. Don't throw out the sympatric speciation with the crater lake water: fine-scale investigation of introgression provides equivocal support for causal role of secondary gene flow in one of the clearest examples of sympatric speciation, *Evolution Letters* 2018; 2: 524–540.
- Rieppel O. Species monophyly. *Journal of Zoological Systematics and Evolutionary Research* 2010; 48: 1-8.
- Rieseberg LH, Brouillet L. Are many plant species paraphyletic? *Taxon* 1994; 43: 21–32.
- Sangster G. Increasing numbers of bird species result from taxonomic progress, not taxonomic inflation. *Proceedings of the Royal Society London B* 2009; 276: 3185–3191.
- Schöneberg Y, Winter S, Arribas O, et al. Genomics reveals broad hybridization in deeply divergent Palearctic grass and water snakes (*Natrix* spp.), *Molecular Phylogenetics and Evolution* 2023; 184: 107787.
- Scherz MD, Masonick P, Meyer A et al. Between a rock and a hard polytomy: phylogenomics of the rock-dwelling mbuna cichlids of Lake Malaŵi. *Systematic Biology* 2022; 71: 741–757.
- Selz OM, Dönz CJ, Vonlanthen P, et al. A taxonomic revision of the whitefish of lakes Brienz and Thun, Switzerland, with descriptions of four new species (Teleostei, Coregonidae). *ZooKeys* 2020; 989: 79-162.
- Selz OM, Seehausen O. A taxonomic revision of ten whitefish species from the lakes Lucerne, Sarnen, Sempach and Zug, Switzerland, with descriptions of seven new species (Teleostei, Coregonidae). *Zookeys* 2023; 1144: 95–169.
- Seifert, B., Buschinger, A., Aldawood, A. et al. Banning paraphyly and executing Linnaean taxonomy is discordant and reduces the evolutionary and semantic information content of biological nomenclature. *Insectes Sociaux* 2016; 63: 237–242.
- Skúlason S, Parsons KJ, Svanbäck R, et al., A way forward with eco evo devo: An extended theory of resource polymorphism with postglacial fishes as model systems. *Biological Reviews* 2019; 94: 1786-1808,
- Stiassny M, Schlieven UK, Dominey WJ. A new species flock of cichlid fishes from Lake Bermin, Cameroon with a description of eight new species of *Tilapia* (Labroidei: Cichlidae). *Ichthyological Explorations of Freshwaters* 1992; 3: 311-346

- Sukumaran J, Knowles LL. Multispecies coalescent delimits structure, not species. *Proceedings of the National Academy of Sciences USA* 2017; 114: 1607–1612
- Svardal H, Quah FX, Malinsky M, et al., Ancestral hybridisation facilitated species diversification in the Lake Malawi cichlid fish adaptive radiation. *Molecular Biology & Evolution* 2019; 37: 1100-1113
- Svardal H, Salzburger W, Malinsky M Genetic variation and hybridization in evolutionary radiations of cichlid fishes. *Annual Review of Animal Biosciences* 2021; 9: 55-79.
- Swaminathan A, Xia F, Rohner N From darkness to discovery: evolutionary, adaptive, and translational genetic insights from cavefish. *Trends in Genetics* 2024; 40: 24-38.
- Thorpe RS, Barlow A, Surget-Groba Y, et al., Multilocus phylogeny, species age and biogeography of the Lesser Antillean anoles. *Molecular Phylogenetics and Evolution* 2018; 127: 682-695
- Turner GF. What is a fish species? *Reviews in Fish Biology & Fisheries* 1999; 9: 281-297.
- Turner GF. Adaptive radiation of cichlid fish. *Current Biology* 2007; 17: R827-R831.
- Turner GF, Ngatunga BP, Genner MJ. The natural history of the satellite lakes of Lake Malawi. *EcoevoRxiv* 2019; <https://ecoevorxiv.org/sehdq/> 131pp.
- Tyers AM, Turner GF Signal and preference divergence among populations of the non-endemic basal Lake Malawi cichlid fish *Astatotilapia calliptera* (Perciformes: Cichlidae). *Biological Journal of the Linnean Society* 2013; 110: 180-188.
- Wiens JJ, Penkrot TA. Delimiting species using DNA and morphological variation and discordant species limits in spiny lizards (*Sceloporus*). *Systematic Biology* 2002; 51:69–91.
- Wilkinson M. A commentary on Ridley's cladistic solution to the species problem. *Biology and Philosophy* 1990 5: 433-446
- Wiley EO An annotated Linnaean hierarchy, with comments on natural taxa and competing systems. *Systematic Zoology* 1979; 28: 308-337.
- Wund MA, Baker JA, Clancy B, et al. A test of the “flexible stem” model of evolution: Ancestral plasticity, genetic accommodation, and morphological divergence in the threespine stickleback radiation. *American Naturalist* 2008; 172: 449–462.
- Yang Z, Rannala B. Bayesian species delimitation using multilocus sequence data. *Proceedings of the National Academy of Sciences USA* 2010; 107: 9264–9269.
- Zachos FE, Apollonio M, Bärmann EV et al., Species inflation and taxonomic artefacts—a critical comment on recent trends in mammalian classification. *Mammalian Biology* 2013; 78:1–6.