

NEWS AND VIEWS

PERSPECTIVE

When taxonomy meets genomics: lessons from a common songbird

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Taxonomy is being increasingly informed by genomics. Traditionally, taxonomy has relied extensively on phenotypic traits for the identification and delimitation of species, though with a growing influence from molecular phylogenetics in recent decades. Now, genomics opens up new and more powerful tools for analysing the evolutionary history and relatedness among species, as well as understanding the genetic basis for phenotypic traits and their role in reproductive isolation. New insights gained from genomics will therefore have major effects on taxonomic classifications and species delimitation. How a genomics approach can inform a flawed taxonomy is nicely exemplified by Mason & Taylor (2015) in this issue of *Molecular Ecology*. They studied redpolls, which comprise a genus (*Acanthis*) of fringillid finches with a wide distribution in the Holarctic region, and whose species taxonomy has been a matter of much controversy for decades (Fig. 1). Current authoritative checklists classify them into one, two or three species, and five or six subspecies, based largely on geographical differences in phenotypic traits. Previous studies, including a recent one of the subspecies on Iceland (Amouret *et al.* 2015), have found no evidence of differentiation between these taxa in conventional molecular markers. The lack of genetic structure has been interpreted as incomplete lineage sorting among rapidly evolving lineages. Now Mason & Taylor (2015), using a large data set of genomewide SNPs, verify that they all belong to a single gene pool with a common evolutionary history, and with little or no geographical structuring. They also show that phenotypic traits used in taxonomic classifications (plumage and bill morphology) are closely associated with polygenic patterns of gene expression, presumably driven by ecological selection on a few regulatory genes. Several lessons can be learned from this study. Perhaps the most important one for taxonomy is the risk of taxonomic inflation resulting from overemphasizing phenotypic traits under local adaptation and ignoring a lack of phylogenetic signal in molecular markers.

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According to authoritative checklists, the global avifauna consists of around 10 500 species. A hundred years ago, the number was nearly 19 000, while 60 years ago, it was below 9000. These large fluctuations in species numbers were caused by significant shifts in the philosophy and practice of species delimitation in avian taxonomy (Haffer 1992; Sangster 2009). During the first half of the 20th century, thousands of allopatric species were downgraded to subspecies level and lumped into polytypic species. This trend was reversed in the latter half of the century when many subspecies were again raised to species rank. This practice continues today, with a steady net addition of 40–50 species per year, according to the frequent updates of the IOC World Bird List (Gill & Donsker 2015). The increase results from more taxonomic splits than lumps, while new species discoveries are rather few. A recent review of taxonomic revisions concluded that taxonomy has improved as a scientific discipline with a more integrative conceptual framework and better empirical evidence underlying species delimitation (Sangster 2014). Despite the debate over species concepts, where proponents of the phylogenetic species concept have been accused of causing taxonomic inflation (Isaac *et al.* 2004), there is a growing consensus that species are cohesive lineages with a distinct evolutionary history and intrinsic barriers to gene flow across their borders. However, there are still serious practical challenges and pitfalls in how to interpret the increasing amount of empirical evidence in a taxonomically sound and consistent way.

The 'redpoll complex' represents a good example of an unresolved taxonomic puzzle. Current checklists disagree over whether one (BirdLife International 2014), two (Dickinson & Christidis 2014; Gill & Donsker 2015) or three (Sangster *et al.* 2013; Clements *et al.* 2014) redpoll species should be recognized. With the new results of Mason & Taylor's (2015) study, which forcefully confirm previous genetic studies, the message is clear: the redpoll complex constitutes a single species. Practically no genetic variation exists among the three predefined species, as 98% of the variation in the 20 000 SNPs belonged within species. A coalescent analysis clearly separated the redpolls from the out group, the white-winged crossbill (*Loxia leucoptera*), and gave strong support for lumping the three redpoll species into one. The three 'species' form a latitudinal gradient in phenotypes (Fig. 1). In the north, birds are large, whitish and short-billed (the *hornemanni* type); in the south, they are smaller, greyish, dark-striped and larger-billed (the *flammea* type). In the western Palearctic

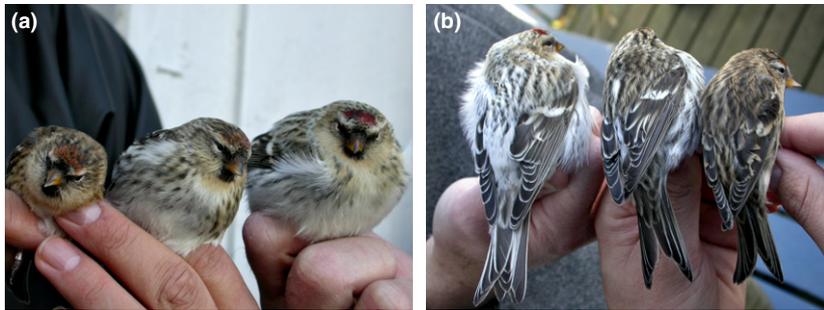


Fig. 1 A bouquet of redpoll phenotypes caught on autumn migration at Titran Bird Observatory, Central Norway. From left (a): the *cabaret*, the *flammea* and the *hornemanni* type, (b): the *hornemanni*, the *flammea* and the *cabaret* type. Photo credit: Ståle Prestøy.

region, the gradient extends further to the south with even smaller and more brownish birds in the British Isles, continental Europe and southern Scandinavia (the *cabaret* type). These phenotypic gradients agree with some classical biogeographical rules in warm-blooded animals: in colder (and drier) climates, organisms tend to be larger-bodied (Bergmann's rule), have smaller extending body parts (Allen's rule) and be less pigmented (Gloger's rule). The phenotypic diversity within the redpoll complex therefore seems to be a result of adaptation to climatic conditions. Mason & Taylor (2015) also performed ecological niche modelling from a large database of breeding records of *hornemanni* and *flammea* in North America and showed considerable overlap in suitable abiotic conditions. Hence, the distribution patterns follow a climatic gradient, not an allopatric/parapatric model or a sympatric niche segregation model.

Another main achievement by Mason & Taylor (2015) is their demonstration, through a principal component approach, of an association between phenotypic diversity (plumage and bill variables) and gene expression profiles. It suggests that phenotypes are shaped by a few key regulatory genes, although many genes may be transcribed. It also provides a possible mechanism for how phenotypic traits in redpolls can rapidly respond to selection and cause local adaptation. This is important from a taxonomy perspective, because traits under environmental selection may not be taxonomically informative in the sense that they also function in reproductive isolation. There is some evidence for assortative mating among *flammea* and *cabaret* types in Norway (Lifjeld & Bjerke 1996), but there are also numerous reports of phenotypic intermediates across their range (e.g. Troy 1985). Therefore, the current genomics evidence of high gene flow provides no support for incipient speciation.

It is tempting to link the redpoll complex to the Darwin's finches. A recent study of Darwin's finches (Lamichhane *et al.* 2015) reported major discrepancies between a genome-based phylogeny and the phenotype-based taxonomy. The taxonomy of this iconic group is largely based on bill size morphology, which has rapidly diversified as adaptations to different food resources. The phylogenomic analysis by Lamichhane *et al.* (2015) revealed extensive evidence for interspecific gene flow, that is hybridization, across the radiation, which calls into question whether the current taxonomy reflects rapid intraspecific diversification of a phenotypic trait under strong environmental selection instead

of separate lineages with intrinsic reproductive isolation. It is an interesting parallel to the redpolls, as taxonomy seems to be inflated for the same reasons in the two cases. Moreover, the Darwin's finches study identified a particular gene that encodes a transcription factor affecting bill development and which seems to have contributed to the diversification of bill shapes in this radiation. It will be interesting to know more about the function of this gene in redpolls.

The redpolls, and presumably also the Darwin's finches, exemplify some important pitfalls in species delimitation. Divergences in phenotypic traits evolving under environmental selection should be used cautiously, and with low weight, unless they clearly reflect barriers to gene flow. Sexual traits that are more directly involved in mate choice and reproductive isolation should have priority. But more importantly in our genomics era, species must be diagnosable from their genomes. In that respect, Mason & Taylor (2015) have carried out an impressive search and arrived at a negative, but robust conclusion. Their analyses nicely confirm that the old conventional markers after all gave a true picture of the evolutionary status of the redpoll complex. That is a comfort for avian taxonomy.

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