list will be important not only to facilitate the work of others, but also to enable assessment of progress towards the goal set at the World Summit for Sustainable Development in Johannesburg in 2003, to 'reduce the rate of biodiversity loss by 2010'. But such a list cannot be achieved without the broad participation of the entire community; we must come together to produce such global resources, rather than falling into the trap of endlessly discussing whose fault it is while biodiversity disappears.

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Letters Response

Response to Harris and Froufe, and Knapp *et al.*: Taxonomic inflation

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In their critique of our paper [1], Harris and Froufe [2] point out that species status is sometimes advocated on molecular grounds if genetic divergence is large enough. Typically, mitochondrial DNA (mtDNA) is used for such purposes, and this approach has recently been formalized as 'DNA barcoding' (http://www.barcodinglife.com). According to Harris and Froufe, however, genetic divergence within species has been underestimated, depending too heavily on north-temperate species that recolonized the region after the ice ages. The consequent bottlenecks tended to reduce genetic diversity of more northerly species compared with parent populations further south [3]. In the more-stable tropics, effective population sizes have often remained stable and fairly large. Therefore, Harris and Froufe argue that taxonomic inflation in the tropics will result from overestimation of species diversity from genetic data.

Although this might be true in some cases, most revisions leading to inflation include other factors, such as geographical separation of divergent lineages. Geographically coherent lineages are considered under the phylogenetic species concept to constitute separate species [1], whereas locally mixed mitochondrial lineages with similar levels of divergence would provide evidence for a single species.

In any case, we do not consider a threshold value of divergence at mtDNA to be a useful criterion for delimiting species. Some tropical species have little divergence between them (e.g. $<0.5\%$ at the mitochondrial gene *COI* as found in *Astraptes* skipper butterflies [4], even though DNA barcoders had previously advocated a sixfold higher species level threshold of 3% *COI* divergence [5]). Meanwhile, values of up to 2% *COI* divergence within tropical species are common (e.g. in *Heliconius* butterflies [6] or more in other groups). Time since speciation (τ) and effective population size (θ) jointly determine the level of DNA divergence between species, whereas within-species variability is determined entirely by θ [7]. The coalescence theory underlying these ideas assumes neutral evolution, which is probably approximately correct for most sequence divergence between closely related or sister species. Contrary to what Harris and Froufe suggest, if speciation is rapid and recent in tropical radiations, τ is small and low divergence is expected between species, as in *Astraptes*. However, with effective population sizes generally more stable than at higher latitudes, as Harris and Froufe suggest, θ will be large and high levels of polymorphism are expected within species, so that within- and between-species divergences might overlap. Such effects are found among rapidly diversifying cichlid fish [8], for example. As more data accumulate, it will be interesting to see if a general trend of tropical versus temperate species emerges. In any case, insight from coalescence theory argues against simplistic 'barcoding' or other methods to delimit species depending on genealogical monophyly, especially if based on a single mitochondrial gene [9].

Knapp *et al.* [10] point out that many new species descriptions do not contribute to taxonomic inflation (elevation of already known subspecific taxa to species rank [1]). In our abstract [1], we made a rather misleading statement: 'Species numbers are increasing rapidly. This is due mostly to taxonomic inflation, where known subspecies are raised to species as a result of a change in species concept'. We should have phrased this differently. We intended to refer to the charismatic vertebrates of major conservation and macroecology interest that were the main focus of our argument. We apologise to the many systematists who might feel aggrieved by our unintended slur.

Knapp *et al.* also point out that species-level taxonomy is a living process that inevitably leads to change in scope of species taxa as more data accumulate, regardless of whether a single species concept is applied consistently. Even with excellent knowledge of geographical distributions, morphology and genetics, the activities of 'lumpers' and 'splitters' are unlikely to stop, so that species-level nomenclature will remain unstable; furthermore, the degree of

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splitting will continue to differ across taxonomic groups [1]. Therefore, we agree with Knapp *et al.* that online global taxonomic and nomenclatural resources, with full synonymy and details of currently accepted classification, are for the moment more important than a universal standard for the species taxon. At the same time, we need to re-engineer biodiversity studies, conservation and macroecology to take more account of taxonomic instability.

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