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the bird of feeding time. Hence, one would expect strong evolutionary pressure to eliminate such misidentification of harmless taxa as harmful. The reason why false-alarm flights are still commonplace is likely to be that birds also face strong selection pressure to avoid misidentifying an attacking predator as something posing no threat. Similar to Type I and Type II errors in statistical testing, cognitive mechanisms that decrease one of these types of identification error will often increase the likelihood of the other. Because the two selection pressures conflict, we would expect prey to evolve cognitive mechanisms that achieve the optimal trade off between the two types of error.

Predators that sometimes encounter unfamiliar stimuli (such as startle signals) experience a similar set of incompatible selection pressures. A startle response (delaying an attack to gather more information before deciding whether to press home the attack) might be the best compromise between the costs of less-efficient foraging (because extra time is taken and because prey might escape during this time) and the costs of mistakenly attacking something that is actually a predatory threat to the attacker.

A logical extension of the arguments above is that startle responses should not be fixed, but should be governed by the shifting trade off between the fitness costs of the two types of error. For example, we would expect startle behaviours to be less extensive in energetically stressed birds and more extensive in birds that perceive their environment to pose a high predation risk to them. Furthermore, we would expect predators to learn about startling displays by innocuous prey through repeated exposure, and so to habituate to these signals; we would expect this learning to be under selection pressure and to be sensitive to the state of the animal as well as to features of the external environment.

Another possible explanation is that the response of the

wild-caught birds in Vallin *et al.*'s experiments stem from generalizations based on previous experience with taxa that show similar signals to *I. io* but are unpalatable or otherwise defended. This could be investigated by measuring the palatability to blue tits of locally found butterflies and moths with eyespot markings, or by repeating the experiment using hand-reared birds whose experience before the experiment can be controlled.

The work of Vallin and colleagues certainly suggests that startling displays by harmless prey are an area richly deserving of renewed attention from evolutionary ecologists. Indeed, there is a wider message that there are several anti-predatory strategies (such as crypsis through countershading or markings that deflect predators away from particularly vulnerable parts of the body of an animal) that have become staples of natural-history books and TV programmes, but that have been unjustly neglected by evolutionary ecologists.

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Letter

The reality of taxonomic change

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In their recent *TREE* paper [1], Isaac *et al.* assert that species numbers are increasing rapidly owing to 'taxonomic inflation', where previously identified species are reclassified under new species concepts into smaller and more numerous new taxa. Using recent phylogenetic concepts (as opposed to classic concepts, notably the biological or isolation concept) will certainly lead to an apparent increase in species number [2–4]. What is unsupported is that such inflation is the dominant force behind the current increase in species

numbers. We argue instead that this increase reflects the underlying nature of species.

Isaac *et al.* point out that researchers use different species concepts for different purposes, suggesting that this is an unrecognized dimension of the species problem, although several publications describe this exact issue (one of which they cite [5], but also see [6]). They then offer two solutions: (i) an ideal world, in which the species concept used for describing taxonomy (and, hence, taxic biodiversity) is the same regardless of whether it is applied to ecological, macroecological or conservation purposes; or (ii) standardized species lists. In our opinion, both solutions are flawed.

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'In an ideal world, each [ecological, macroecological, etc.] hypothesis would be tested using the most appropriate rank in the taxonomic hierarchy.' However, assigning ranks to taxonomic groups above the species level is largely subjective. Thus, ranks are non-comparable and of little use for testing hypotheses. It is this arbitrariness that has provoked proposals for a taxonomy and nomenclature devoid of categorical rankings [7,8]. Even with respect to the rank of species, the ideal world will never materialize. Phylogenetic evolutionists, ecologists and population biologists, for example, have different research goals, focusing on different aspects of biodiversity arising from different evolutionary processes. The phylogenetic evolutionist is interested in the evolution of taxa and, therefore, will use a taxic descriptor of species, such as the phylogenetic species concept (PSC), based on historical patterns that can be objectively recognized in nature [5]. Ecologists and population biologists are more likely to take a contemporaneous 'snapshot', focusing on ongoing processes in restricted areas. It is unlikely that these different views will or can ever agree. Isaac *et al.* also assume that conservationists have only one goal: the preservation of species. But the existence of several species-level entities in nature, described by various species concepts, means that conservationists must also decide, for any given case, which aspect of biodiversity can be diagnosed and then form the focal level of preservation efforts.

The authors' second proposal is to use standardised species lists [9], so that studies based on such lists can at least be consistent, stating that such lists have 'many obvious virtues' and would form 'a useful reference point for *all* species-related issues' [our emphasis]. This ignores huge practical and theoretical difficulties. As argued above, no single species concept can fulfil all of the different requirements posed by the various disciplines. Furthermore, it is doubtful whether any standardized list would be stable for any reasonable period of time. For even some well known taxa, taxonomic lists have been far from stable [10]. For example, in the group of European amphibians and reptiles, of the 63 species recognized in 1996, only 35 had the same taxonomic status in 1960 [11]. If such a small and well-studied group is and continues to be unstable, stability is unlikely for more cryptic taxa. Alternatively, Isaac *et al.* suggest the use of Evolutionary Significant Units (ESUs), which they incorrectly consider to represent a different rank in the taxonomic hierarchy. In any event, the use of ESUs is thwarted by their apparent lack of applicability in the real world [12,13].

Isaac *et al.* assert that taxonomic inflation will lead to an increase in false positives in testing macroevolutionary hypotheses, 'because extra data are effectively pseudo-replicates'. This is true only if these 'extra' species are unreal, echoes of the core data. Application of the PSC might lead to 'splitting', but it is far from clear that either biological or phylogenetic species are more objectively real than the other. Furthermore, because phylogenetic species are diagnosably different from each other, they are not mere replicates, at least as regards the diagnosed

characters. To even call the rise in species numbers 'inflation' is to imply that it is somehow unreal or unnatural, lacking an ontological basis. This implicit assumption is exemplified by the authors' assertion that 'an inflated taxonomy [i.e. one based on the PSC] will therefore have inflated values of endemism', because phylogenetic species generally will have smaller ranges and, thus, hotspots might be more apparent than real. Although they cite Meijaard and Nijman [14] in support of this viewpoint, these workers did not qualify one kind of hotspot as being less 'real' than another (V. Nijman *personal communication*). Instead, Meijaard and Nijman used the terms 'apparent' and 'real' to announce their objective to investigate whether hotspot identification depended on taxonomic classification or on the choice of taxa, a meaning different to that presumed by Isaac *et al.*

Asserting that patterns of global species richness are sensitive to taxonomic inflation, Isaac *et al.* imply that this provides a biased picture of biodiversity. The fact that 'inflated' patterns might be real aside, the only evidence presented concerns the changed patterns in primate species richness. It is debatable whether such a small fraction of global biodiversity in a charismatic and heavily studied group adequately supports such a wide-ranging statement. Certainly, as the PSC will generally diagnose taxa with smaller ranges, more finely grained and numerous hotspots will emerge (*cf.* [14]). However, on the broad scale, it is our impression that studies generally identify similar global hotspots of species richness.

Species are complex things, their identity resting on the methodologies used to diagnose them and on the many different ways that organisms have of belonging to a species. We would do well to embrace plurality, using different species concepts in different circumstances [5], rather than searching for a platonic ideal. It is time to stop over-generalizing and to 'get over it' [15].

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Letter Response

Response to Agapow and Sluys: The reality of taxonomic change

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We agree broadly with many of the points raised by Agapow and Sluys [1]. Indeed, their response seems to have been triggered by observations similar to those that motivated our own article [2]. However, we believe that parts of our paper have been misunderstood, and we welcome the opportunity for clarification.

We disagree with Agapow and Sluys that taxonomic inflation 'reflects the underlying reality of nature'. Our observation was simply that species numbers, especially of charismatic vertebrates, are increasing more or less exponentially, largely as a result of changes in species concepts, rather than because of the discovery of new taxa. Agapow also documented the same trend in a paper that we cited [3]. These changes are unnatural in the sense that they are caused by changes in the definition of species, rather than by new discoveries. Problems arise when these changes are not made explicit, and when species lists contain a mixture of species concepts.

Agapow and Sluys also suggest that we 'point out that researchers use different species concepts for different purposes, although several publications do describe this exact issue'. Our claim was in fact that macroecological hypotheses often assume particular concepts. Therefore, tests of these hypotheses can be strongly affected by taxonomic inflation.

As we acknowledged in our paper [2], the solutions that we offered to the problem of taxonomic inflation are flawed, and we did outline these shortcomings. No solution is infallible or easy: however, we should try to avoid incorrect conclusions in comparative biology, ecology and conservation. Difficulties might be ameliorated by abandoning species altogether [4], by agreeing on standardized lists of species, or by making available complete, synonymic checklists (i.e. including all currently valid taxonomic ranks) and empowering users to choose their own concept. Of these, the last is the most practical.

We did not propose 'an ideal world' with a single rank (species) as a solution; what we said was 'In an

ideal world, each hypothesis would be tested using the most appropriate rank in the taxonomic hierarchy.' In other words, we argued for different absolute ranks for different tests: the more-inclusive biological concept might apply to some tests, the phylogenetic concept to others. Phylogenetic species are often nested within biological species [3], so the concepts specify different taxonomic levels or nodes (ranks in a real sense; although in Linnaean nomenclature, they might all be 'species'). We argued that this is not always apparent to users of species lists, and should be made more explicit. 'Standardized lists' are certainly not stable currently (that was the point of our paper) but it is at least conceivable that international agreement could mandate better stabilization of the rank of species; for other uses, other ranks, say subspecies or subgenera in the same taxonomy, could still be used. Finally, although Agapow and Sluys argue that 'assigning ranks to taxonomic groups above the species level is largely subjective...and of little use for testing hypotheses', we point out that this is also currently true at the species level, owing to taxonomic inflation.

We agree with Agapow and Sluys that phylogenetic species 'are not mere replicates' [1]. However, problems arise in lists containing a mixture of species concepts. Clades where the phylogenetic species concept (PSC) is prevalent will tend to have smaller ranges and more species than will related clades that were classified by other concepts; thus, comparative tests related to these traits will be biased. The problem is exacerbated if the application of species concepts is biased with respect to traits like body size.

Although Agapow and Sluys mention that 'the only evidence [of inflation] presented concerns the changed patterns in primate species richness', primates are an extreme example: bird [5] and amphibian [6] species are also increasing faster than is the rate of new discoveries. Species numbers are increasing in many groups [3], and measures of species richness become less compatible [2] as the PSC gains popularity.

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