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Independent report by Richard Field on the PhD thesis of Anna Tószögyová

Thesis title: Bird diversity and life-history patterns along gradients of productivity and its variation

First, the formality of fitting requirements: this thesis clearly exceeds the minimum requirements for a PhD in ecology in the faculty. There are five manuscripts in addition to the general introduction, and all are either suitable for international peer-reviewed journals or already published in such journals. All four published papers are in journals with impact factors. While the first paper (Chapter 1) was published in a journal with impact factor below 0.5 at the time (0.43; current IF 0.62), Chapters 2 and 3 were published in *Global Ecology and Biogeography* (GEB), which is a leading subject journal (IF 5.7 and 5.8 in the two cases) and Chapter 4 is also in the leading journal in its specialist area (*Behavioural Ecology*, IF 2.7). Anna is first author of one of the GEB papers, which in itself is a considerable achievement. She is also first author of the unpublished manuscript.

The thesis as a whole sits within the context of the theoretical work recently published by Anna's supervisor, David Storch, and colleagues, most notably in Storch et al (2018, *Ecology Letters*) but perhaps most clearly set out in Storch & Okie (2019, *Global Ecology and Biogeography*). Appropriately, this work is cited frequently throughout the thesis. It makes a theoretical and empirical case for environment setting dynamic limits (or carrying capacity) to biodiversity. One key problem with testing such ideas is the cross-correlation of variables representing different hypothesised influences on biodiversity. Finding ways to disentangle these mechanisms is therefore very important, especially when adopting a macroecological approach (as here, which is highly appropriate for such research), and that is the central theme of Anna's thesis. The research reported in the thesis does this in interesting and quite imaginative ways, as summarised below.

Four of the five chapters (all but Ch3) use the birds of South Africa as the study system, primarily relating important bird traits to environmental productivity. Chapter 3, in contrast, relates species richness to environmental productivity, and is the most ambitious in that it is global in scope and analyses data for mammals and amphibians as well as birds. In all the chapters, environmental productivity was measured using a proxy, the normalised difference vegetation index (NDVI, in most cases obtained from the US Geological Survey). I felt that the **limitations** of using this proxy could have been considered more deeply and thoroughly in the thesis. The traits were quantified as average values of species-level traits in 25 x 25 km grid cells, which is a common and justifiable approach in biogeography and macroecology, but again I would have liked to see more depth in considering the limitations and assumptions involved. These issues can be discussed in the Defence.

The main traits analysed in the four trait-focused chapters were clutch size (commonly considered and clearly important), bird song (as related to territories and breeding) and colour (relevant to both survival and sexual selection). These papers are hypothesis led and I found them largely successful in disentangling at least some of the putative mechanisms involved. Even so, in my judgment there is quite frequent over-conclusion, in the sense that there are many statements of inference that, as written, **claim causal relationships from correlations**. I have the same criticism of Chapter 3.

I found the general introduction to be high-powered and efficiently written. In a few pages, it contains a lot of information, cites a large amount of relevant literature and shows an impressive depth of understanding. I found it quite persuasive and well balanced. My main criticisms of this introduction concern readability. Most strikingly, the paragraphs tend to be very long. For example the third paragraph is more than a page and a half (c.750 words), and pages 5-6 and 12-13 both carry paragraphs longer than a page each. Note: as with Chapters 1-5, I do not see a need to require corrections to address my criticisms within the thesis (I am not identifying fundamental flaws that require correction before the thesis is acceptable).

Chapter 1 is the most limited in scope, and suffers quite severely from a very small sample size of only 5 sites. This probably explains the low ranking of the journal in which it is published, though it should be noted that *Ostrich* is a highly appropriate journal for this sort of work and is a quite a good outlet for the research to reach its core audience. The work is based in part on a field experiment involving artificial nests to measure nest predation pressure, which accounts for the small number of sites. I think the research presented in this paper is interesting and thought provoking, and it is consistent with the main thesis that environmental productivity is key in limiting biodiversity. However, the very low sample size means that **considerable care should be used when inferring from the results**. Mostly, appropriate care is demonstrated within the paper, though the following statement from the first paragraph of the Discussion oversteps the mark in my opinion (despite the caveat two sentences later), being based on a comparison of one site vs four sites: “some threshold seems to exist in environmental productivity/vegetation cover, above which the nest predation rate is rather similar across different levels of environmental variables.” Of more concern to me is the way that most of the later papers in the thesis report conclusions from this first paper: they imply that this paper produced findings that are much more robust than I think they actually were. One example is on p.45 of the thesis: “Also, abundant bird populations and better concealed nests can in fact lower nest predation risk in more complex environments (Horak et al., 2011)”.

The other chapters do not suffer from such sample size limitations. All find patterns in traits or species richness to be consistent with a key role of environmental productivity. Between them, they make a substantial and important contribution to this area of the literature. The two *GEB* papers are to me the most impressive (especially Chapter 3), but chapters 4 and 5 are also nice and I expect the unpublished one (Ch5) to end up in a good journal, probably after major revision.

Chapter 2 is hypothesis led, distinguishing nicely between a hypothesis related to mean resource availability and a variant of it that has more biological meaning, matching resource availability per individual to the timing of breeding. I also like the **subsetting approach** to help disentangle maximum resource availability and resource seasonality. This careful approach led to findings that were not entirely expected: the prediction of Ashmole’s hypothesis that clutch sizes decrease with increasing maximum NDVI at fixed levels of NDVI difference (seasonality), and evidence consistent with it. In this chapter, it would have been nice to see how much of the variance in the spatial GLS was shared between space and the predictors (or at least, have this information more clearly presented), and also to see the actual data on Fig. 4.

Chapter 3 is for me the jewel of this PhD, and it is worth noting here that Anna was the first author. As well as being global in scope and big in taxonomic breadth of the species data, **I found the decomposition of the NDVI time series into seasonal and unpredictable to be an important contribution in itself**. It is very interesting that the unpredictable element of the NDVI variability proved important in the statistical modelling of species richness at this scale. Even more interesting is the perhaps unexpected interaction of unpredictable NDVI variability with mean NDVI to have different modelled effects at different productivity levels. I wonder whether the findings of this paper help to inform us about the long-standing question of whether (or when) the relationship between productivity and species richness is hump-shaped – see for example Mittelbach, et al. (2001, *Ecology* 82: 2381– 2396) and Whittaker (2010, *Ecology* 91: 2522-2533)?

Or the more recent trend towards reversing the presumed causality and assuming that increasing species richness drives increased productivity (biodiversity–ecosystem functioning literature)?

A nice feature of Chapter 4, which exemplifies the general approach to research in the thesis, is the separation of female solo song and duetting, which are typically lumped together in large-scale studies. The findings resulting from this distinction are interesting, and suggest a link to territoriality and ultimately to environment, which fits with the general conclusion about environmental determinism of many aspects of bird biogeography. Even so, I have concerns about bold statements such as “social behavior of birds has inevitably evolved in accordance with environmental conditions” (p.93 of thesis). Such statements make me wonder whether Anna has erred a little towards dogma in interpreting findings, and might benefit from deeper consideration of whether other explanations might be valid, such as some degree of historical contingency. In interpreting the results, I also wonder whether there might be benefit in stepping back and considering basic questions such as ‘why do birds sing’? And how comprehensive the hypotheses are?

Chapter 5, the only unpublished manuscript in the thesis, examines bird colour using a wide range of measures. As with other chapters, the approach of separating different aspects of the phenomenon in question is a nice aspect of the research, in my opinion, allowing some ability to discriminate between different hypotheses or mechanisms. I wonder whether it would be possible to make more sophisticated tests of the various hypotheses, e.g. hypothesising certain combinations of colours, or colour richness to be related to particular causes (such as resource variation)? It would be useful to have a figure or table illustrating the hypotheses and their predictions, in easily digestible form. Currently, it does not help that much of the considerable amount of text on hypotheses in the manuscript is in the Discussion section – to the extent that I feel quite a lot of the material in the rather long Discussion would be better in the Introduction. Overall, then, I think this manuscript would benefit from some reorganisation, before it is submitted to a journal (or at least before it is published).

Even so, the findings of Chapter 5 are interesting, and are consistent with varied roles of colour, including both camouflage (relevant to survival) and signalling (sexual selection). It is not clear to me how much Anna has thought about the colour ranges that the bird species see in, and those of their predators. I would also have liked to know how much agreement there was between the people evaluating colourfulness. More important for the validity of the research is the question of how reliable it is to measure hue, saturation and brightness from book scans? I was surprised this is not addressed in the manuscript. I also note that there is consideration of seasonality in this chapter, but no use of the unpredictability variable from Ch3, which seems like an opportunity missed.

I therefore envisage quite major revisions to Chapter 5 before it is published, but these would be to improve the manuscript, rather than to correct fundamental flaws. So I do not see a need to require corrections for the purpose of the thesis. Similarly, I note that Chapter 5 contains quite a lot of typos and similar minor issues, but none of these obscures the intended meaning enough to require corrections to be made, in my opinion – after all, I hope the work will be published in a journal paper, and that is what people will read.

Overall, there is considerable novelty, depth and competence demonstrated by this thesis. I find the work presented to be more than sufficient for a PhD degree.



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