Comment

Sometimes the obvious answer is the right one: a response to ‘Missing the rarest: is the positive interspecific abundance–distribution relationship a truly general macroecological pattern?’

In a recent Opinion piece, *Komonen et al.* (2009) suggested that, contrary to previous assertions, the positive interspecific relationship between abundance and distribution may not be a general macroecological pattern. The basis for this claim was their analysis of a single dataset on the abundance and distribution of butterflies in Finland. The abundance–distribution relationship in these data was negative, albeit not significantly different from zero. However, sequentially removing the rarest 30–50% species from the analysis turned the correlation significantly positive. *Komonen et al.* (2009) argued that the predominance of positive abundance–distribution relationships in the literature may thus derive from inadequate sampling of rare species, which may also explain why abundance–distribution relationships appear to be weakest at large spatial scales. They also argued that the observed form of these relationships may be affected by sampling effort, because rare species may face proportionally higher sampling effort at known occurrence sites than do common species. In their data, controlling for sampling effort produced a significant negative abundance–distribution relationship, as long as not more than the rarest 30 per cent of species were omitted. Here, we critically examine *Komonen et al.*’s results and discuss their contentions in the light of previously published analyses.

Komonen et al. (2009) control for the effect of higher sampling effort at known occurrence sites of rare species by dividing each species’ mean abundance by the total number of observation days in each grid cell that the species occupies (D). Thus, corrected abundance $A = (N/S)/D$, where N is the total number of individuals (across all sites) and S is the number of sites. However, D is a function of the number of sites where a species occurs, meaning essentially that A is calculated by dividing through by something more akin to S^2 than S . Imagine that

there are 10 sites, that each site is observed on just a single day and that species α occurs as a single individual on one site and species β occurs as a single individual on all 10 sites. Then, for species α , $A = 1/1/1 = 1$. For species β , $A = 10/10/10 = 0.1$. Yet, both species occur at exactly the same density and were sampled at each site to the same intensity. Thus, species that occur at low numbers of sites have high mean corrected abundances because these are averaged over few sites and few total sampling days. Even accepting that the sites where rare species occur may be disproportionately well sampled, we would expect a negative abundance–distribution relationship to arise from the method *Komonen et al.* use because the number of sites where a species occurs is a massive multiplier of sampling days. We would also expect that abundance of the rarest species would be most heavily biased by this method, such that deleting them decreases the significance of the negative relationship, as *Komonen et al.* find. Better would have been to divide through by the average number of sampling days per site rather than the summed total number of sampling days (although the assumption that doubling the sampling effort doubles the number of individuals recorded from a site may not be true).

Negative abundance–distribution relationships are rare, but have been documented on previous occasions. *Blackburn et al.* (2006) collated information on 279 such relationships from the literature. The overall mean effect size was 0.655, but there was significant heterogeneity within the sample and 29 were negative.

Rather than attempt to ‘explain away’ (*Komonen et al.* 2009) the negative effects, *Blackburn et al.* (2006) interrogated the complete sample of abundance–distribution relationships to assess potential predictors of the observed variation. One factor assessed was the geographical extent over which the relationship was documented. They showed that abundance–distribution relationships were strongest when both abundance and distribution were assessed at national scales. While studies covering different spatial extents did differ significantly in mean effect size, the pattern of differences was not consistent with a simple increase in effect size from large to small scales and does not support the assertion by *Komonen et al.* (2009; see also *Gaston* 1996) that abundance–distribution relationships are weakest at large spatial scales.

Komonen et al. (2009) also suggest that the predominance of positive abundance–distribution relationships in the literature may be influenced by a bias towards studies of birds, which may have anomalous positive relationships because they are often territorial. *Blackburn et al.* (2006) found that there was indeed heterogeneity in effect sizes across taxa and that birds did have a relatively high mean effect size (0.95, although note that this is not reported in the published paper). Nevertheless, mean effect sizes for all taxonomic groups were significantly positive. Thus, there is no evidence that the predominance of positive abundance–distribution relationships in the literature is the result of a bias towards studies of birds.

Overall, we find nothing in *Komonen et al.* (2009) to alter the widely held view that the relationship between abundance and distribution is likely to be

other than generally positive (see reviews in Gaston 1996; Blackburn *et al.* 2006). Many of the observed relationships come from extremely well-sampled assemblages where issues of missing species are unlikely to be of significance. Of course, ‘generally positive’ does not mean that all relationships are positive, because they clearly are not, and nor does it require that negative relationships need to be explained away. Variation in abundance–distribution patterns provides an opportunity to investigate the mechanism(s) underlying them. Suggesting that the 90 per cent or so of relationships that are positive are artefacts is not helpful in this regard, and nor is it credible.

Tim M. Blackburn^{1,*} and Kevin J. Gaston²
¹*Institute of Zoology, ZSL, Regent’s Park, London NW1 4RY, UK*

²*Biodiversity and Macroecology Group, Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK*

*Author for correspondence (tim.blackburn@ioz.ac.uk).

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