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## commentary

## One step closer towards disentangling competing hypotheses in macroecology

Macroecological studies of continental and global gradients are constrained to correlative approaches — including studies of so-called natural experiments — because of their large scale. Even when studies are carefully performed, strong inference may be difficult, since variation and co-variation of potential driving factors are not easily controlled. Often such macroecological data sets are characterized by strong intercorrelations among the predictor variables, so-called multicollinearity. Such problems may cripple the ability to differentiate among competing hypotheses. Nevertheless, new approaches provide greater ability for tackling these problems and progressing our understanding of what determines species diversity. These approaches include analyses that assess spatial variation in relationships, differentiate the components of species diversity, and integrate phylogenetic information into ecological studies. The recent study by Hortal et al. (2011) exemplifies an approach that combines these analytical advances and provides important progress in our understanding of species diversity patterns.

Hortal et al. (2011) are concerned with a complex and controversial, but core, question in ecology and biogeography, namely to what extent current diversity patterns are driven by current environmental conditions, notably current climate, relative to deep-time events and processes, so-called historical factors. Europe was strongly impacted by the Pleistocene glaciations, with large parts of Northern Europe covered by glaciers as late as the Last Glacial Maximum (LGM) just 21 thousand years ago. A number of recent studies have attempted to assess whether these massive past climate changes are still shaping current diversity patterns, e.g. for amphibians and reptiles (Araújo et al., 2007) and mammals (Fløjgaard et al. 2011). However, predictors describing historical factors and current climate are often strongly spatially correlated, making it difficult to tease their respective effects apart.

With their innovative, multifaceted approach, Hortal et al. (2011) have taken an important step towards overcoming such difficulties and present novel insights into the potential drivers of dung beetle diversity patterns across Europe. They used geographically weighted regression (GWR) to show that there is a remarkable geographic variability (non-stationarity) in the association of species diversity to climate variability since the LGM, indicating a stronger influence of past climate on the current diversity pattern of dung beetles in southern Europe than northern Europe. This finding for dung beetles is consistent with what Araújo et al. (2007) previously observed for other ectotherms, namely that the location of the LGM 0°C isotherm of mean annual temperature denotes a change in species composition, from small-ranged amphibians and reptiles south of the isotherm to widespread species north of the isotherm (see also Svenning et al. 2009 for a related GWR-based finding for European plants). GWR is generally useful for investigating macroecological processes where associations between drivers and patterns are likely to change in space, for example, such as in regions where the impact of past glaciations varies strongly across space (e.g. Europe).

Given that traits often show some degree of phylogenetic conservatism, phylogenetic analyses can further help us understand the physiological mechanisms involved in shaping macroecological patterns. Hortal et al. (2011) applied phylogenetic analyses to show that there was a remarkable phylogenetic difference between the southern and northern assemblages, with northern species being phylogenetically clustered, corresponding to particular cold-tolerant clades of species within the dung-beetle family studied. The deconstruction of beta diversity into its components, turnover (change in species composition) and nestedness (species richness differences) (see Baselga 2010), furthermore supported this finding as

northern assemblages also under this perspective were highly nested within the dung-beetle diversity in Southern Europe (Hortal et al. 2011), similar to earlier results for another beetle family, the Cerambycidae (Baselga, 2008). While Hortal et al. (2011) inform their interpretations with the general knowledge of the clade's temperature tolerances, direct incorporation of physiological mechanisms into explanatory analyses could further strengthen inference, as exemplified by Sinervo et al. (2010), who used physiological models to explain recent extinctions and predict future global warming impacts on lizard diversity.

While the conclusions of Hortal et al. (2011) still hinge on the strength of correlations between diversity and hypothesised predictors, investigating the study questions from the different perspectives encompassed by their multifaceted approach has strengthened inference, helping to disentangle the importance of competing hypotheses. Concerning diversity determinants, the study nevertheless has limited geographic and taxonomic scope and how much its findings can be extrapolated to other clades and regions is unknown, although some level of transferability seems likely. However, the approach of Hortal et al. (2011) has general interest to biogeographers and macroecologists because such multifaceted approaches are applicable not only to studies of other clades and regions, but also to other questions across these research fields, notably given the general problem posed by multicollinearity. For the time being, such advances are still somewhat limited by the availability of data, notably full phylogenies, but also databases on species traits needed for the development of phylogenetic and physiological models. With continual new advances in data availability we encourage macroecologists to look for new insights by deconstructing diversity patterns, investigating geographic heterogeneity and considering phylogenetic patterns and physiological mechanisms.

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