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Authors

Cooper, Natalie
Belmaker, Jonathan

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opinion

Habitat data resolution and the detection of species interactions

In a recent paper, Gotelli et al. (2010) presented evidence for competition structuring in the bird assemblages of Denmark at two spatial scales (5 and 10 km grid cells). They used whole-matrix null models to show that ecologically similar species co-occurred less than expected by chance. As these species had similar habitat preferences they concluded that species interactions must have created the mutually exclusive distributions of the birds. This led them to suggest that species interactions should be included in environmental niche models for predicting species occupancy.

Whilst the methodology presented in the paper is sound, we have some doubts about the conclusions. As acknowledged by Gotelli et al. (2010), spatially segregated distributions can be formed either by species interactions, e.g., competitive exclusion, or by species having distinct habitat preferences. The probability of detecting habitat differences is directly related to the resolution of available habitat data; at low resolutions it is unlikely that habitat differences within a guild of similar species will be detected. For example, two species may both live in forests, but if the species require different types of forest they will not overlap. This difference in habitat preference will not be detected unless habitat types are more finely defined than "forest". Gotelli et al. (2010) only recognize 12 habitat types in Denmark, but we believe that birds are likely to have more specific habitat preferences. If so, the spatial segregation of species may reflect the distribution of microhabitats rather than competitive interactions.

Ecologists are increasingly recognizing that the importance of ecological mechanisms changes according to the scale of observation. Similarly, the apparent importance of species interactions at macroecological scales will be contingent on habitat resolution. Broad habitat designations will al-

ways overestimate the importance of species interactions. However, at fine enough resolutions we are bound to conclude that patterns are due to habitat partitioning. Unfortunately, the only way to truly detect competition is to perform manipulative experiments in the field or lab. Even then it is hard to separate the importance of present-day competition from the "ghost of competition past". Given that manipulative experiments are impossible at large scales, should we consider biological interactions in niche models as proposed by Gotelli et al. (2010)? We believe that the resolution of habitat data should influence such decisions. An environmental niche model using coarse habitat designations may indeed need to incorporate species interactions to predict species occupancy. However, a similar model using finer-grained habitat designations may not.

Gotelli N.J., Graves G.R., & Rahbek C. (2010) Macroecological signals of species interactions in the Danish avifauna. *Proceedings of the National Academy of Sciences USA*, 107, 5030-5035.

Natalie Cooper

Department of Ecology and Evolutionary Biology, Yale University, USA

e-mail: natalie.cooper@yale.edu

<http://pantheon.yale.edu/~nc295/home.html>

Jonathan Belmaker

Department of Ecology and Evolutionary Biology, Yale University, USA

e-mail: jonathan.belmaker@yale.edu

<http://sites.google.com/site/jonathanbelmaker/>

Edited by Frank A. La Sorte

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