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COMMENTARY

Testing Holling's textural-discontinuity hypothesis

Holling (1992) suggested the textural-discontinuity hypothesis (TDH) as an explanation for the clumped body-mass distributions he observed for mammals and birds. The TDH states that the discontinuous structure of a landscape should dictate the sizes of the animals that inhabit it. Holling (1992) characterized landscapes in terms of their hierarchical habitat structure, proceeding from finely textured objects, those that can be measured at small spatial and temporal scales such as shrubs and individual trees, to coarsely textured objects measured in hundreds of kilometres and centuries, such as entire forests. The TDH is based on the idea that differently sized animals perceive the landscape at different spatial and temporal scales and have adapted to exploit the resources at these scales. In the same landscape, small-bodied, short-lived species exploit finely textured habitat structure and large-bodied, long-lived species exploit coarsely textured habitat structure. Thus, if habitat structure in a landscape is discontinuous, the distribution of animal body sizes must also be discontinuous.

The TDH also predicts that landscapes dominated by coarsely textured objects should have a preponderance of large-bodied animals and that landscapes dominated mainly by finely textured objects should have more small-bodied animals. Holling (1992) tested this prediction by comparing bird body-mass distributions from the boreal forest and short-grass prairie ecosystems. He reasoned that more small birds would occur in the boreal forest because this ecosystem has a more finely textured habitat structure (individual leaves, twigs and branches) than the prairie. As predicted, the categories of species with the smallest sizes in the boreal forest were much reduced in or entirely absent from the prairie.

Since Holling's (1992) seminal contribution, support for the TDH has been provided primarily by evidence of clumped body-mass distributions in a wide variety of systems, as well as by reported relationships between vegetation structure and body size, reviewed in Allen & Holling (2002). More recently, model landscapes with more characteristic scales of resource distribution, or more 'scale niches', were found to be host to more co-existing species, a pattern that may help to explain the evolution of discontinuous body-mass distributions (Szabó & Meszéna, 2006). Finally, de la Montana *et al.* (2006) showed that the mean body mass of birds was significantly greater in stands thinned of their understory shrub layer than in unthinned stands in central Spain.

Fischer *et al.*'s (2008) recent contribution tests the TDH over the largest spatial extent to date (with the exception of Holling's 1992 study). Using breeding bird count data collected in five landscapes varying in texture, Fischer *et al.* (2008) found a significant relationship between the ratio of detections in simple versus complex landscapes and body mass. In other words, small birds were detected more frequently in landscapes with complex texture, and larger birds were detected more frequently in landscapes with simple texture. Fischer *et al.* (2008) were able to demonstrate this because their landscapes were dominated by individual habitat scales (Fig. 1). As did Holling (1992), they assumed that landscapes covered by forest are dominated by a more finely textured habitat structure than are landscapes composed mostly of grazed areas interspersed with small remnant woodlands.

However, Fischer *et al.* (2008) assessed landscape texture qualitatively, not quantitatively. The reader of their paper is asked simply to believe the authors' statement that the different landscapes studied have different dominant habitat scales. It is unclear whether what we – or Holling (1992), or Fischer *et al.* (2008) – qualitatively perceive to be landscapes of simple or complex texture are in fact characterized by different dominant structures. Furthermore, the subjective selection of landscapes of varying texture from a human perspective may not represent the main textural differences perceived by animals inhabiting those landscapes (Kotliar & Wiens, 1990). A logical alternative that may circumvent these issues is the objective quantification of texture.

Discontinuous habitat structure within a landscape, in the form of hierarchical texture as defined above or as a structure with more complex interrelationships among components, is in fact very difficult to measure. Quantifying the full hierarchical structure of a landscape necessitates obtaining field measurements over multiple observation scales. Although sophisticated field methods exist to reveal discontinuities in vertical vegetation profiles (e.g. Van Pelt & Franklin, 2000), the extension of such a time-consuming approach to characterizing entire landscapes or ecoregions represents an as yet unrealized task. The study design in Fischer *et al.* (2008) allows us to simplify this task because we only need to quantify the dominant habitat scale in each landscape (Fig. 1). In Fischer *et al.* (2008), landscapes (qualitatively) represented different dominant habitat scales so it should be possible to confirm this difference quantitatively. Plotnick *et al.* (1993) define texture in binary landscapes as 'a measure of the gapiness or hole-iness in a geometric structure'. This definition of texture would correspond to the characteristic length-scale of a landscape pattern (i.e. the spatial extent above which an observed pattern does not change significantly; Habeeb *et al.*, 2005).

One possible way to test the TDH explicitly would be to quantify habitat texture in multiple landscapes within an ecoregion in which data on body sizes of a particular taxon (e.g. birds) are available for each landscape. The characteristic length-scale of each landscape could be obtained using land-cover data and the techniques described by Habeeb *et al.* (2005). Different landscapes will show different characteristic length-scales (some may not show any dominant scale), but the set of these scales across the landscapes represents the hierarchical habitat structure for the ecoregion. The body-size data from the different landscapes could then be combined to give

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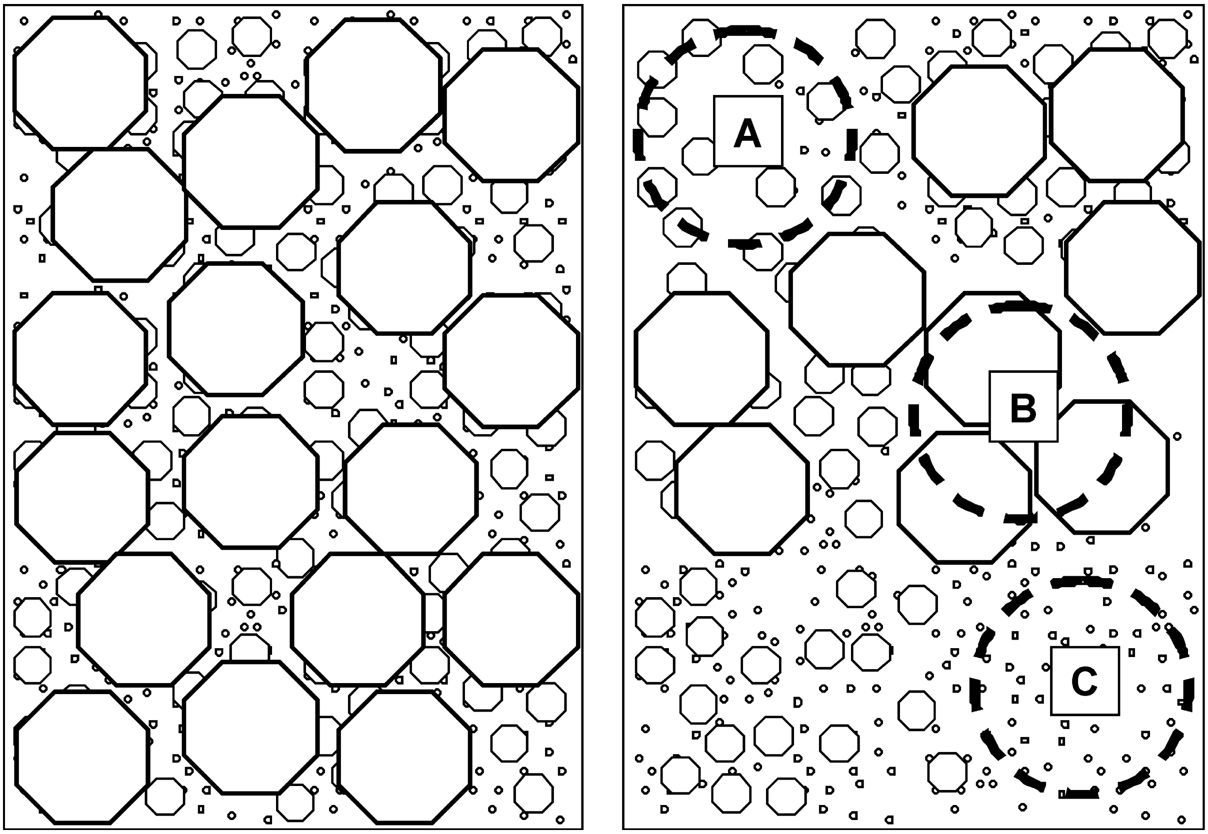

Figure 1 (a) An ecoregion, viewed from above, with three characteristic habitat scales, resulting in three body-size categories according to Holling's textural-discontinuity hypothesis (TDH; Holling, 1992). (b) In this ecoregion the three habitat scales are unevenly distributed over the region. Fischer *et al.* (2008) took advantage of this unevenness to test the TDH. Dashed circles A, B, and C represent landscapes where single habitat scales predominate, so the TDH predicts the predominance of a single body-size category in each.

an overall body-size distribution for the ecoregion. According to the TDH, the number of habitat length-scales in the ecoregion should match the number of body-size clumps. In addition, a positive relationship between mean length-scale and mean body size across landscapes within an ecoregion and/or a positive relationship between length-scale variance and body-size variance would be further evidence in support of the TDH.

In conclusion, Fischer *et al.* (2008) have confirmed the primary prediction of the TDH, namely that landscapes dominated by finely textured habitat structure have more small birds than do landscapes with coarser habitat structure. However, their assessment of habitat structure is purely qualitative; we suggest that the next step is to use the characteristic length-scales of real landscapes to test the TDH quantitatively.

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