Species richness can decrease with altitude but not with habitat diversity

In the paper by Allouche et al. (1), the authors suggested that species richness decreases at high levels of habitat diversity because the area available per habitat decreases [area–heterogeneity tradeoff hypothesis (AHTO)]. They showed a hump-shaped relationship between Catalonian bird richness and altitudinal range in grid cells, the authors' surrogate for environmental heterogeneity. However, birds select habitats mainly based on vegetation structure and floristic composition (2). Catalonian high altitudes are dominated by uniform coniferous forests or simple habitats with low vegetation cover (outcrops, grasslands, and scrublands) that are known to be poor in bird richness. Furthermore, high-altitude grid cells have the largest altitudinal ranges but much fewer habitats than lower altitudes (using 48 habitat categories obtained from Inventario Nacional Forestal III, 2007–2008, Spanish Ministerio de Medio Ambiente). Elevation range in Catalonia is tightly correlated with maximum altitude ($r = 0.951$; $P < 0.0001$) and mean elevation ($r = 0.858$; $P < 0.0001$), but poorly correlated with environmental heterogeneity (number of habitats per cell: $r = 0.049$, $P = 0.349$; Shannon index across all habitat categories: $r = 0.119$, $P = 0.024$). When analyzed together (Generalized Additive Model; Fig. 1), bird-species richness shows a hump-shaped relationship with mean elevation [nonlinear P (n-Lp) = 0.003], a negative linear relationship with altitudinal range ($P = 0.001$; n-Lp = 0.426), and a positive, monotonic relationship with habitat diversity ($P < 0.001$; n-Lp = 0.336), as predicted from ecological theory (3). Thus, the unimodal relationship between altitudinal range and richness (1) merely reflects the well-known hump-shaped relationship between species richness and altitude (4), not a tradeoff between richness and environmental heterogeneity.

Hortal et al. (3) demonstrated that AHTO poorly predicts richness–habitat diversity relationships on islands. Allouche et al. (1) claimed that such unimodal relationships remain unsupported so far because previous analyses did not correct for island area. Island area and altitude are often highly correlated (72.75%, on average, in the datasets producing significant richness–elevation models in ref. 1). However, their relationship is not linear (65% of the datasets used in ref. 1), because it typically levels off on large islands. Large islands also host comparatively less habitats per unit area than small islands (5). Correcting for linear effects of area can, thus, promote spurious unimodal relationships because large islands have necessarily less environmental heterogeneity than expected from a linear relationship. This implies that the unimodal relationships between richness and area-corrected environmental heterogeneity found by Allouche et al. (1) cannot be used to support AHTO.

The main drawback of AHTO is that its prediction of decreased richness in heterogenic environments does not appear with realistic values of area, habitat diversity, and niche width (i.e., those present in most natural environments). Following previous suggestions (3), Allouche et al. (1) used larger niche width values than in former versions of AHTO, although keeping high habitat specialism in moderate niche width. Importantly, richness decreases with environmental heterogeneity only for species with very narrow niches (figure S8 in ref. 1; also see ref. 3). Such species are rare in natural environments (see niche width distributions in ref. 3), so local richness will monotonically increase with habitat diversity and level off but not decline when approaching the regional richness.

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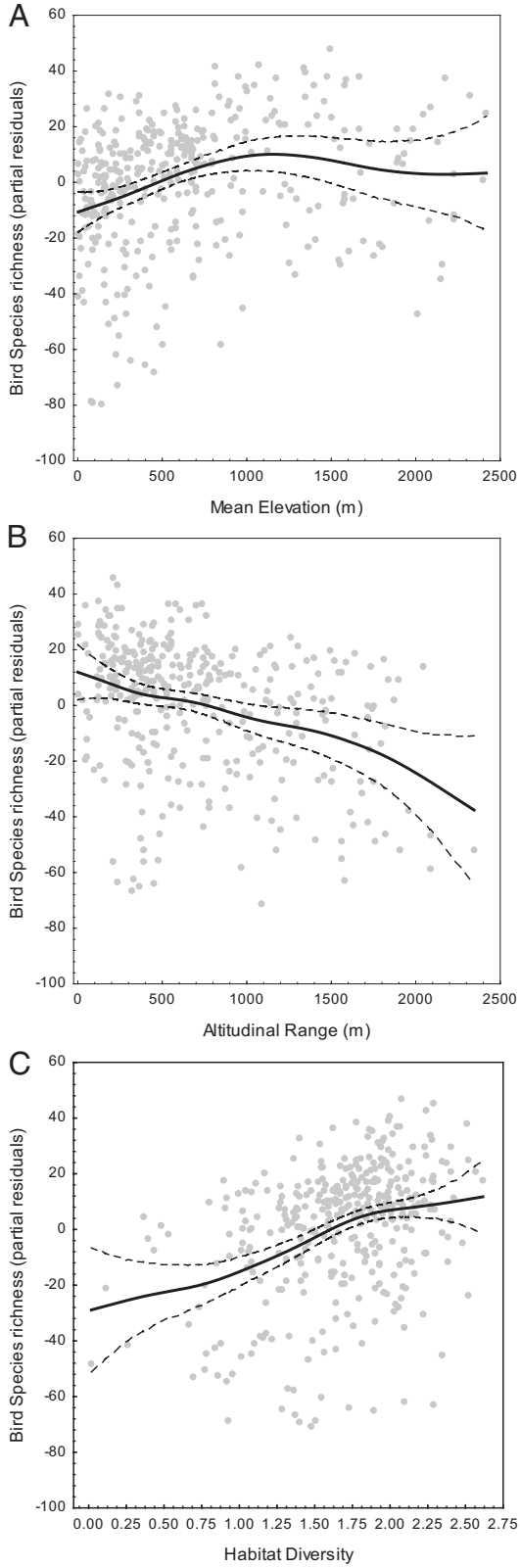

Fig. 1. Partial residual plots derived from Generalized Additive Models illustrating the relationships between bird species richness during the breeding season and mean elevation (*A*), altitudinal range (*B*), and habitat diversity (*C*) in Catalonia (Shannon index of 48 habitat categories). Proportion of deviance accounted by the fitted model: 20.6% ($P < <0.001$). Residual plots show the relationship between a given independent variable and species richness given that the other two independent variables are also in the model, therefore, partialling out their effects (10 × 10 km UTM squares: $N = 363$). Sources: Atlas de las Aves de España 2003 and Inventario Nacional Forestal III 2007–2008, Spanish Ministerio de Medio Ambiente.