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Relative contribution of abundant and rare species to species–energy relationships

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A major goal of ecology is to understand spatial variation in species richness. The latter is markedly influenced by energy availability and appears to be influenced more by common species than rare ones; species–energy relationships should thus be stronger for common species. Species–energy relationships may arise because high-energy areas support more individuals, and these larger populations may buffer species from extinction. As extinction risk is a negative decelerating function of population size, this more-individuals hypothesis (MIH) predicts that rare species should respond more strongly to energy. We investigate these opposing predictions using British breeding bird data and find that, contrary to the MIH, common species contribute more to species–energy relationships than rare ones.

Keywords: abundance; commonness; more-individuals hypothesis; rarity; range size; species richness

1. INTRODUCTION

One of ecology's most important challenges is to explain the marked spatial variation in species richness (Hutchinson 1959; Gaston 2000). Although over 30 hypotheses have been proposed, a consensus is emerging that variation in energy availability can explain much of the variation in biodiversity (Hawkins *et al.* 2003; Pimm & Brown 2004). Identification of the mechanisms promoting species–energy relationships remains elusive, but Wright's (1983) more-individuals hypothesis (MIH) may play a major role (Evans *et al.* 2005). High-energy areas may provide more resources, supporting larger populations that buffer species from extinction, the risk of which is a negative decelerating function of population size (Lande 1993). A given increase in energy should thus disproportionately decrease extinction risk in rare species. The MIH thus predicts that rare species will exhibit the strongest species–energy relationships, contrasting with evidence that common species contribute most to biodiversity patterns (Jetz & Rahbek 2002; Lennon *et al.* 2004) which suggests that these species should exhibit the strongest such relationships.

Determining which of these two opposing predictions is correct is difficult as population size estimates are seldom available for complete assemblages whose spatial variation in species richness has been mapped. Species–energy relationships appear to be stronger in more widespread species (Jetz & Rahbek 2002; Bonn *et al.* 2004) and geographical range size is often positively correlated with abundance, suggesting that this pattern may be general, but the relationship is not perfect and it is often weaker at large spatial scales (Gaston *et al.* 1997). We use data on the breeding avifauna of Britain to test whether numerically rare species or abundant species drive species–energy relationships and also to contrast such patterns between widespread and localized species.

2. METHODS

We used the breeding distribution of the British avifauna (Gibbons *et al.* 1993) but excluded marine species and vagrants, thus leaving 189 species. These data record species presence/absence in a grid of 10 km × 10 km quadrats, those containing less than 50% land were excluded, leaving 2262 quadrats. The size of each species breeding population and breeding range were obtained from Gaston & Blackburn (2000), and for *Columba livia* from Greenwood *et al.* (1996). We ranked species by population size (abundant to numerically rare; numerically rare to abundant) and range size (widespread to localized; localized to widespread), and then calculated the species richness of each quadrat, for increasing numbers of species, along each of these sequences.

In Britain, geographical variation in plant productivity, and thus the energy available to consumers, is related principally to heat alone and is not markedly influenced by water availability (Hawkins *et al.* 2003). Therefore, we calculated the mean summer temperature in each quadrat and used this as a measure of energy availability (for details see Lennon *et al.* (2000)). Metabolic processes such as photosynthesis, which controls plant productivity, vary with temperature in a manner described by the Boltzmann factor $e^{-E_i/kT}$, where E_i is the activation energy (0.6 eV), k is the Boltzmann constant for eV (8.62×10^{-5} eV K^{-1}) and T is absolute temperature in Kelvins (Gillooly *et al.* 2001). We thus used the Boltzmann factor to re-scale mean summer temperature to produce a measure of energy availability that is more compatible with recent advances in investigations of how energy availability influences biodiversity (Allen *et al.* 2002; Meehan *et al.* 2004).

For each sequential step in the cumulative species richness sequences we used SAS (v. 8.2) to regress richness against energy availability, using both linear and quadratic terms. This enabled us to contrast the influence of energy on the richness of the number of most abundant and numerically rare species, with its influence on the full assemblage, and likewise for widespread and localized species. We plot the models' F ratios against the number of species used to calculate richness; thus illustrating the statistical significance of the relationships and their strength. Species that occupy either very few or most of the quadrats are less likely to show strong correlations with environmental variables than species occupying an intermediate number, for purely statistical reasons. Thus, if the frequency distribution of the number of species occupying different numbers of quadrats is not symmetrical about 50% occupancy, this could cause apparent differences between common and rare species in the strength of their correlations with energy. We therefore calculated an 'information index' for each species as $p(1-p)$, where p is the proportion of quadrats it occupies, and characterized each of the groups of n species by the sum of their index values and plotted graphs of F ratios against this index.

Spatial autocorrelation may invalidate the assumption of independent errors, rendering classical statistical tests very misleading (Legendre *et al.* 2002). Therefore, we also analysed our data using the SAS procedure 'PROC MIXED' to implement spatial correlation models that take spatial autocorrelation into account (for details see the Electronic Appendix and Littell *et al.* 1996).

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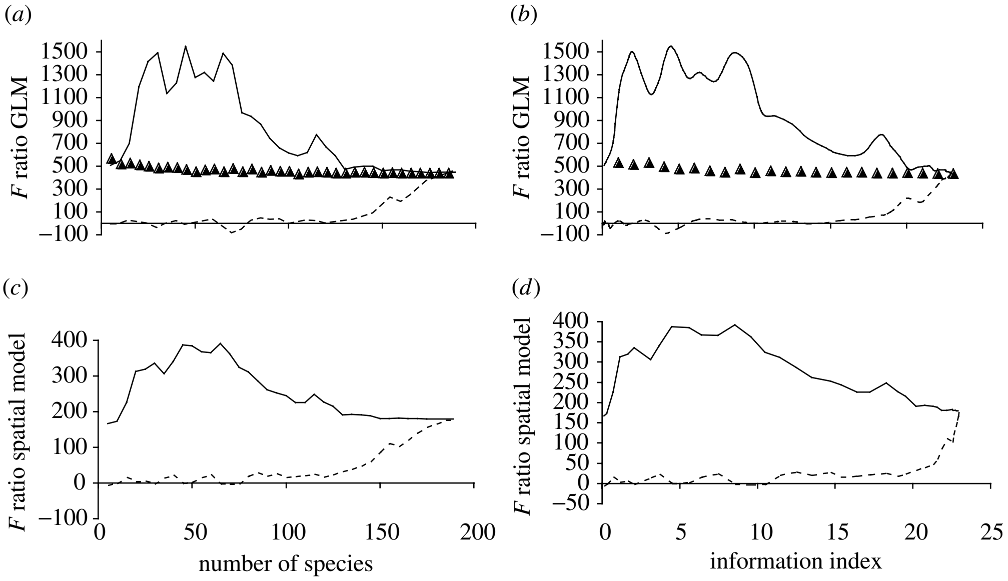

Figure 1. The relative contribution of abundant and numerically rare species to species–energy relationships. Plots show changes in the *F* ratios of linear species–energy relationships of partial assemblages, in which species are added five at a time, along the sequence of abundant to numerically rare species (thick solid line), numerically rare to abundant species (thin dashed line) and in randomly selected assemblages (black triangles, means, standard errors are too small to be illustrated—maximum value ±21.6). Models are constructed assuming independent errors (*a*,*b*), or controlling for spatial autocorrelation (*c*,*d*). Negative *F* ratios indicate a negative species–energy relationship; absolute values greater than 3.84 indicate statistically significant relationships at $p<0.05$ and those greater than 15.19 indicate statistical significance at $p<0.0001$. GLM, general linear model.

When contrasting the species–energy relationships of assemblages containing rare and common species we also compare them with such relationships in assemblages comprising an identical number of randomly selected species. This provides information regarding how the significance of species–energy relationships varies with the number of species in assemblages, rather than their biological attributes (for details see the supplementary materials).

3. RESULTS

In independent error models, partial assemblages comprising numerically abundant species exhibit strong and highly significant ($p<0.0001$) species–energy relationships, which are much stronger than ones restricted to an equal number of numerically rare species (figure 1*a*). Randomly constructed assemblages have stronger species–energy relationships than equivalent ones containing numerically rare species, but weaker relationships than equivalent assemblages containing abundant species (figure 1*a*). Very large random assemblages have species–energy relationships of similar strength to the complete assemblage, as expected given the inevitably very similar species composition. These patterns remain when the information provided by assemblages is taken into account (figure 1*b*). When taking spatial autocorrelation into account, species–energy relationships remain strong and highly significant ($p<0.0001$) across the whole assemblage and in assemblages containing abundant species, but are much weaker in assemblages containing numerically rare species (figure 1*c*, *d*).

Energy availability explained 16.5% of the variance in species richness of the complete assemblage (quadratic models, 23.7%). Explanatory power reached a peak of 40.6% (quadratic models, 57.9%) in assemblages containing the 45 most abundant species, but was much lower in assemblages containing an equal number of numerically rare species (linear model, 0.4%; quadratic model, 4.1%) and randomly selected ones (mean $r^2 \pm 1$ s.e.m.; linear, 16.3±3.8%; quadratic, 22.4±3.7). While the explanatory power of energy availability increased in quadratic models, the relative contributions of common and rare species did not change.

When sequences were based on range size rather than population size, similar patterns emerged with widespread species having strong and highly significant species–energy relationships ($p<0.0001$), localized species having markedly weaker relationships, and randomly constructed assemblages having intermediate ones (figure 2*a*). Taking the information index or spatial autocorrelation into account did not alter these patterns (figure 2*b*–*d*). Explanatory power peaked in assemblages containing the 50 most widespread species (linear r^2 41.0%; quadratic r^2 58.4%) and was much lower in assemblages containing an equal number of numerically rare species (linear r^2 0.8%; quadratic r^2 12.1%) and randomly selected species (mean $r^2 \pm 1$ s.e.m.; linear 15.3±3.6%; quadratic 21.5±3.5). The relative contributions of rare and common species did not change between linear and quadratic species–energy models.

4. DISCUSSION

Common species, defined either by abundance or range size, contribute more to species–energy relationships than rare or randomly selected ones. The explanatory power of energy availability varies

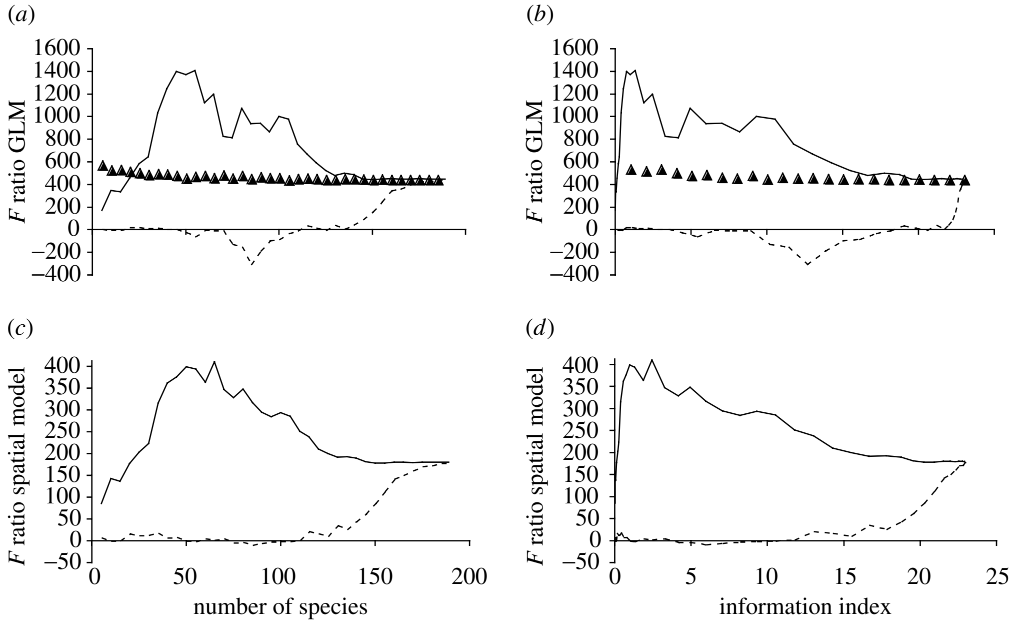

Figure 2. The relative contribution of widespread and localized species to species–energy relationships. Details are as for figure 1 except that the solid line represents the widespread to localized sequence and the dashed line represents the localized to widespread sequence. GLM, general linear model.

from 24%, for the whole assemblage, to 58%. That energy availability cannot fully explain avian species richness is not surprising as the latter is influenced by other abiotic and biotic factors (Lennon *et al.* 2000). Moreover, its explanatory power in this study is comparable to that documented by other macroecological investigations of species–energy relationships (Hawkins *et al.* 2003).

Our results are consistent with evidence that common species contribute most to spatial variation in species richness (Jetz & Rahbek 2002; Lennon *et al.* 2004) and that the latter is primarily influenced by energy availability (Hawkins *et al.* 2003). They also concur with the findings of three other studies. First, widespread African birds exhibit stronger species–energy relationships than localized species (Jetz & Rahbek 2002; Bonn *et al.* 2004). Second, in South American mammals energy availability alone drives the species richness pattern in the widest ranging species, but that of species with the smallest ranges is influenced more strongly by factors other than energy availability (Ruggiero & Kitzberger 2004).

Our findings conflict, however, with the MIH's prediction that the least abundant species will exhibit the strongest species–energy relationships; thus concurring with the observation that extinction risk of British breeding birds, in 10 km × 10 km quadrats, is more strongly influenced by energy availability in common species than rare ones (Evans *et al.* in press). Our findings may contrast with the predictions of the MIH, because most of the species that we consider may have sufficiently large populations so that their extinction risk is low, thus reducing the applicability of the MIH. This appears to be unlikely, as even species with relatively large populations that occupy habitats that have not recently experienced significant loss or deterioration, such as the woodland inhabiting treecreeper, *Certhia familiaris*, and nuthatch, *Sitta europaea*, have experienced a number of local extinctions over recent decades at the spatial scale that we consider (Gibbons *et al.* 1993).

Why does the occurrence of common species, in the assemblages that we consider, respond more strongly to energy than that of rare ones? Rare species, such as snow bunting, *Plectrophenax nivalis*, may be restricted to low-energy environments and thus unable to respond positively to increased energy availability. Such an explanation is unlikely to be complete, as several rare species are restricted to high-energy areas, such as Savi's warbler, *Locustella luscinioides*, and stone-curlew, *Burhinus oedicnemus*, and some relatively abundant species are restricted to low-energy areas, such as red grouse, *Lagopus lagopus*. Alternatively, rare species may be specialists that use restricted or patchily distributed habitats and their richness may thus be constrained by habitat availability rather than by energy. While this may contribute to the patterns that we observe, patchily distributed habitats occur in a relatively large number of quadrats. A more general explanation may be that common species have large populations which acquire a large proportion of the available energy, contrasting with rare species whose small populations may be able to meet their energetic requirements even in low-energy areas.

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The supplementary Electronic Appendix is available at http://dx.doi.org/10.1098/rsbl.2004.0251 or via http://www.journals.royalsoc.ac.uk.