

# The roles of extinction and colonization in generating species–energy relationships

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## Summary

1. Positive correlations between energy and species richness are frequently observed, but the causal mechanisms of such species–energy relationships have rarely been identified conclusively.

2. The more individuals hypothesis (MIH) describes one possible cause of positive species–energy relationships. It suggests that greater resource availability in high-energy areas increases population sizes, reducing local extinction rates and promoting species richness. It predicts that extinction rates will be lower in high-energy areas and that, because a given change in population size has a greater influence on extinction risk when initial populations are small, such relationships will be more pronounced in numerically rare species than more abundant ones.

3. Colonization rates may also influence local species richness, and they may respond positively to the greater resource abundance in high-energy areas.

4. We provide the first empirical test of relationships between extinction/colonization rates and energy availability and of the influence of population size on these relationships. We use data on the changing distributions of British birds, in which positive species–energy relationships have previously been documented.

5. We find that extinction rates are lower in high-energy areas, but that such patterns are stronger in more abundant species. Spatial variation in colonization rates is influenced less markedly by energy availability, but such patterns are also more marked in numerically abundant species. While these results provide little overall support for the MIH, nor some of its alternatives, they add to increasing evidence that common species drive much of the spatial variation in species richness.

*Key-words:* abundance, energy availability, more individuals hypothesis, rarity, species richness.

*Journal of Animal Ecology* (2005) **74**, 498–507  
doi: 10.1111/j.1365-2656.2005.0948.x

## Introduction

Relationships between species-richness and energy availability are among the best documented of ecological patterns and almost all include a strong positive phase (Waide *et al.* 1999; Mittelbach *et al.* 2001; Hawkins *et al.* 2003). Most research has focused on describing the nature of species–energy relationships and understanding of causal mechanisms is less complete (Evans, Warren & Gaston 2005). However, it is often suggested that the more individuals hypothesis (MIH), first proposed by Wright (1983), generates positive species–energy relationships (e.g. Rosenzweig & Abramsky

1993). This states that greater resource abundance in high-energy areas enables animals to attain larger population sizes, buffering them from extinction. The resultant lower extinction risk, per species, in high-energy areas may thus elevate species richness. Partial support for the MIH is provided by empirical evidence that energy availability limits population sizes, which have a major negative influence on extinction risk in a wide variety of species (Lande 1993; Forsman & Mönkkönen 2003; Reed *et al.* 2003). Direct evidence for the MIH is, however, scarce and equivocal, with some studies supporting it (Kaspari, Yuan & Alonso 2003; Hurlbert 2004) and others not (Srivastava & Lawton 1998).

The prediction that extinction risk is lower in high-energy areas lies at the core of the MIH, yet this has never been explicitly tested. This may reflect partly the difficulty of

collating data, from numerous sites, over a sufficiently long time period. It may also arise from knowledge that similar predictions may be drawn from other putative mechanisms for species–energy relationships, albeit often under rather limited circumstances (Evans *et al.* 2004).

First, the niche position mechanism (Abrams 1995) suggests that in low-energy areas relatively scarce resources are so rare that the species which utilize them (high niche position species, *sensu* Shugart & Patten 1972) cannot maintain sufficiently large populations to avoid stochastic extinction. Increasing energy availability is thus predicted to increase the number of high niche position species while low niche position species remain largely unaffected, as the relatively more abundant resources that they use can support viable populations even in low-energy environments. Secondly, the dynamic equilibrium mechanism (Huston 1979) suggests that following a population crash greater resource abundance in high-energy areas will enable populations to grow faster, reducing the time during which a population's small size renders it vulnerable to stochastic extinction. The consumer pressure mechanism (Paine 1966; Janzen 1970) argues that in high-energy areas species are exposed to greater rates of predation and parasitism, which reduce population sizes and rates of competitive exclusion, leading to lower extinction rates and greater species richness in high-energy areas.

All these potential explanations for species–energy relationships share the prediction that extinction rates will be lower in high-energy areas, but vary in their secondary predictions regarding which suites of species should exhibit the strongest relationships between extinction and energy. The MIH states that energy availability influences extinction risk solely because of its effect on population size, which is related to extinction risk by a negative decelerating function (Pimm, Jones & Diamond 1988; Lande 1993). It thus predicts that energy–extinction relationships will be weakest among the commonest species, as these have sufficiently high local population sizes for their extinction risk to be relatively uninfluenced by population size and thus energy availability. The niche position mechanism predicts that species that utilize relatively scarce resources, high-niche position species, should exhibit stronger extinction–energy relationships than species with lower niche positions.

The secondary predictions that can be drawn from the dynamic equilibrium and increased consumer pressure mechanisms are more open to interpretation. Under the dynamic equilibrium mechanism, other things being equal, a population crash is more likely to result in extinction if the initial starting population is small; it thus also predicts that extinction–energy relationships will be stronger in rare species. The consumer pressure mechanism relies on the role of competitive exclusion in structuring assemblages and thus predicts that extinction–energy relationships will be stronger for species prone to competitive exclusion, i.e. weak competitors. The abundance of common species suggests, although it need not require, that they are strong

competitors and thus finding that extinction–energy relationships are stronger in rare species may be compatible with the consumer pressure mechanism.

Species richness may also be affected by immigration from an external species pool (Ricklefs 1987; Srivastava 1999). Positive species–energy relationships may thus arise if high-energy areas have higher colonization rates. Such patterns could arise if active dispersers, such as birds, decide to settle in resource rich high-energy areas. Alternatively, greater resource abundance in high-energy areas may increase founder population growth rates and thus increase establishment probability and thus the number of colonizations.

In this paper we present the first test of two key predictions of the MIH: (i) that extinction rates are lower in high-energy areas and (ii) that such relationships are stronger in numerically rare species. We also assess whether other proposed mechanisms for species–energy relationships may contribute to relationships between extinction/colonization rates and energy availability. As a case study we use data on changing distributions of breeding birds in Britain, in which positive species–energy relationships have been described previously (Turner, Lennon & Lawrenson 1988; Lennon, Greenwood & Turner 2000; Evans & Gaston 2005).

## Methods

### DATA

We used the summer (breeding) distribution of the British avifauna recorded during late April to July in 1968–72 (Sharrock 1976) and 1988–91 (Gibbons, Reid & Chapman 1993). These data record species presence/absence at a resolution of 10 km × 10 km quadrats on a continuous grid. We excluded marine species and vagrants, but retained introduced species with self-sustaining populations and more regular sporadic breeders. Eight species that were relatively under-recorded in the second atlas (Gibbons *et al.* 1993) were excluded: *Porzana porzana* (L.), *Rallus aquaticus* (L.), *Scolopax rusticola* (L.), *Tyto alba* (S.), *Strix aluco* (L.), *Asio otus* (L.), *Asio flammeus* (P.) and *Caprimulgus europaeus* (L.), as was *Haliaeetus albicilla* (L.) which was reintroduced between the survey periods. Our final data set retained 183 species. Quadrats that contained less than 50% land were excluded, giving a total of 2262 quadrats. Recording effort for the species that we consider was intensive and relatively consistent between survey periods and extinctions/colonizations recorded by our data reflect real changes in local assemblages, rather than being artefacts of survey techniques (Gibbons *et al.* 1993). The same data have previously been used successfully to investigate spatial variation in extinction/colonization rates (e.g. Thomas & Lennon 1999; Gates & Donald 2000; Donald & Greenwood 2001; Araújo, Williams & Fuller 2002; Gaston & Blackburn 2002).

For each quadrat, we calculated the number of species extinctions/colonizations occurring between the

survey periods and also expressed these as a proportion of species richness during the first survey. We repeated this process with species grouped by their population size, in quartiles, using data from Gaston & Blackburn (2000), and additional data for *Columba livia* (G.) from Greenwood *et al.* (1996). While we group species into abundance quartiles on the basis of their national population size, our analyses assume that this reflects relative local population densities. This assumption is supported by strong positive correlations, within our assemblage, between (i) national population size and local densities (Gaston, Blackburn & Gregory 1997), (ii) national population size and range size (Gregory & Blackburn 1995) and (iii) national range size and local densities (Gaston *et al.* 1998). Correlations between national population size and local densities are likely to be particularly strong at the spatial grain of our analyses (100 km<sup>2</sup>).

Niche position data were derived, for 85 species, from a canonical correspondence analysis based on avian abundance data and environmental variables (Gregory & Gaston 2000). We divided species into those with niche positions below the median, which use relatively common resources (e.g. *Parus caeruleus* L.) and those with high niche positions that use relatively scarce resources (e.g. *Carduelis spinus* L.).

Spatial variation in the type and rate of land-use change may confound extinction–energy relationships, greater rates of habitat alteration in low-energy areas could give rise to higher extinction rates in such localities. Data on avian population trends in the United Kingdom suggest that habitat degradation has been much greater in farmland than woodland or other habitats (Gregory *et al.* 2003). Following Gibbons *et al.* (1993), we classified species by their predominant habitat type (farmland: 27 species, woodland: 47 species and other habitats: 109 species) and analysed extinction–energy relationships for each group. If spatial variation in the magnitude of land-use change confounded relationships between extinction risk and energy we would expect extinction–energy relationships to be strong in farmland species and negligible in other groups. Similarly, extinction rates for threatened species, which are assumed to be particularly sensitive to habitat alteration, should be influenced much more strongly by energy availability than the extinction rates of unthreatened species, which are assumed to be relatively insensitive to habitat modification. Using the classification of Gregory *et al.* (2002) we thus grouped species into highly threatened, moderately threatened and unthreatened categories and calculated extinction/colonization rates for each group.

In Britain and at other high northern latitudes, geographical variation in plant productivity, and thus the energy available to consumers, is related principally to heat and is not markedly influenced by water availability (H-Acevedo & Currie 2003; Hawkins *et al.* 2003). Therefore, following Lennon *et al.* (2000), we measured energy availability as the mean breeding season temperature calculated from the monthly averages for May, June and July. These data were derived from

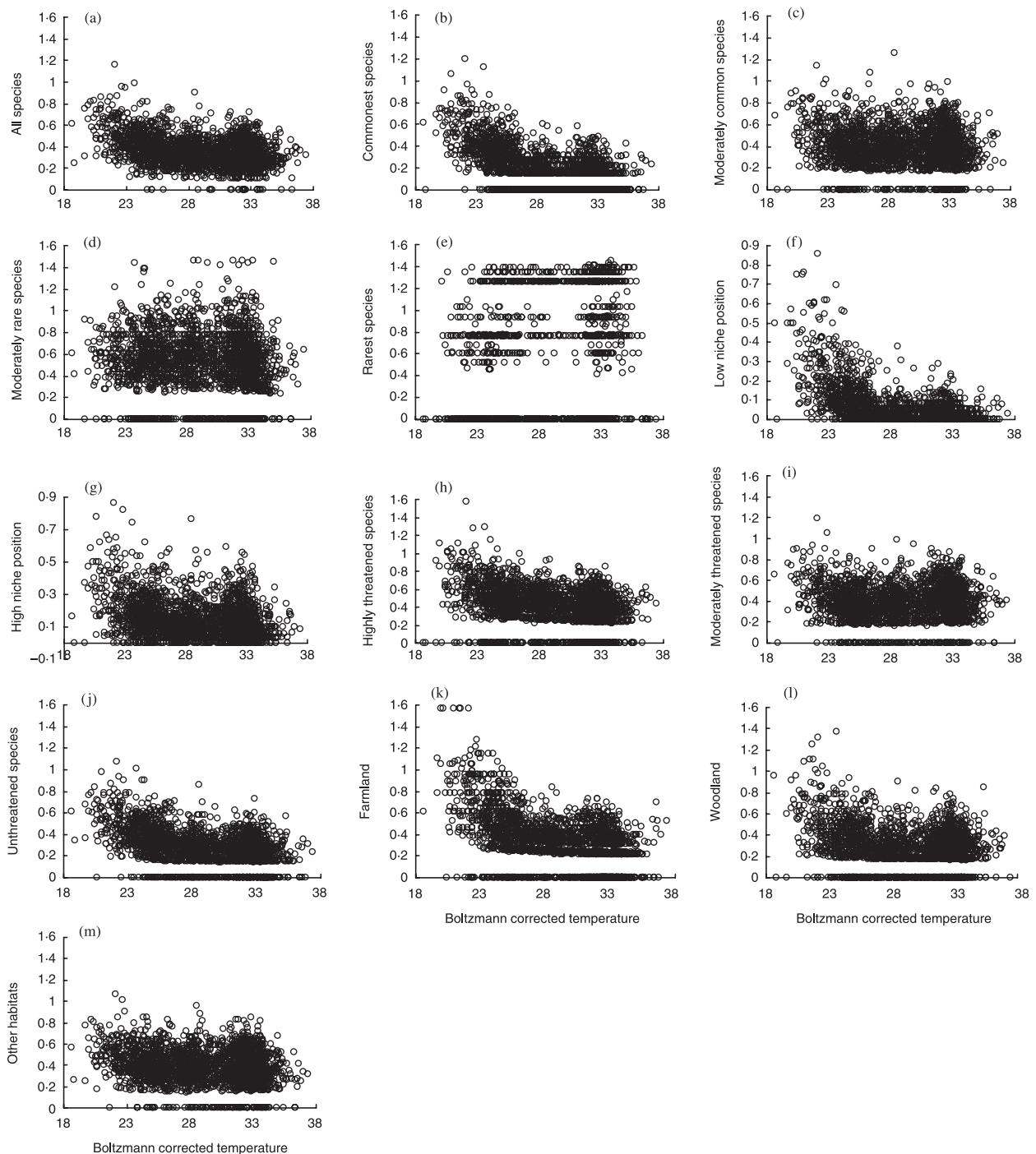
meteorological recording station readings for the period 1961–90 using surface interpolation techniques (Barrow, Hulme & Jiang 1993). The rate of metabolic processes, such as photosynthesis, which controls the amount of energy available to consumers, varies with temperature as  $e^{-E_i/kT}$ , where  $E_i$  is the activation energy (0.6 eV),  $k$  is the Boltzmann's constant for eV ( $8.62 \times 10^{-5}$  eV K<sup>-1</sup>) and  $T$  is absolute temperature in degrees Kelvin (Gillooly *et al.* 2001). We thus used Boltzmann corrected temperatures as a measure of energy availability that was related more closely to resource availability than unmodified temperature data (although in practice this makes little difference to the results).

## ANALYSES

All analyses were conducted in SAS (version 8.2). To reduce the skew in our data the number of extinctions, colonizations and proportion of colonizations were logarithmically transformed (0.1 was added to all values to enable the transformation of zeros). Data on the proportion of extinctions were arcsine square root-transformed. Species distribution data were available from 2262 quadrats, but during the first atlas some of these quadrats did not contain members of some of our species groups. In these cases extinctions and the proportion of colonizations could be calculated for fewer quadrats, first abundance quartile (1422 quadrats), second abundance quartile (2260 quadrats), farmland species (2261 quadrats) and woodland species (2261 quadrats).

We used energy availability, and its squared term, as predictors of extinction/colonization and conducted two sets of analyses. The first assumed independent errors and used the SAS procedure PROC GLM to implement general linear models (GLM), which assume normal errors. Data on extinctions of species with high and low niche positions could not be normalized and although the central limit theorem, combined with our large sample size, suggests that the lack of normality does not invalidate the use of a GLM, we also analysed these data using logistic regression. We used a negative binomial distribution and the SAS procedure PROC GENMOD.

Spatial autocorrelation may systematically invalidate the assumption of independent errors, rendering classical significance tests very misleading (Cressie 1991; Lennon 2000). We thus also analysed our data using the PROC MIXED procedure to implement spatial correlation models that fit a spatial covariance matrix to the data and use this to adjust test statistics accordingly. For technical details of these models see Littell *et al.* (1996). Our spatial models assumed an exponential spatial covariance structure as, for each response variable, this gave a better fit to the null model than five alternative covariance structures: spherical, Gaussian, linear, linear log and power. Comparing null spatial models to ones that assumed independent errors demonstrated that all our response variables were significantly spatially autocorrelated (likelihood ratio tests;  $P < 0.0001$  in all cases).



**Fig. 1.** Relationships between energy availability and extinction risk of British breeding birds in 10-km squares, between 1968 and 1972 and 1988–91. The number of extinctions is expressed as a proportion relative to species richness (arcsine transformed). Note the variation in the y-axis scale.

## Results

### EXTINCTION

Extinction rates, measured across all species, were related to energy availability by a negative decelerating function in independent error models and spatial ones (Table 1, Fig. 1a). Energy consistently explained a greater amount of variance in the proportion of extinction events than the number of extinctions (note that all

measures of explanatory power refer to the former). Extinction rates of the most common species were negatively related to energy availability in both independent error models and spatial ones (Fig. 1b, Table 1). Extinction rates of moderately common (Fig. 1c) and moderately rare (Fig. 1d) species were also negatively related to energy, but much more weakly ( $r^2 = 0.01$  in both cases) than for the most common species ( $r^2 = 0.42$ ; Z-test of  $r^2$  values  $P < 0.0001$ ). Extinction rates of the rarest species exhibited a positive,



**Table 1.** The influence of energy availability on the local extinction risk of British breeding birds, in 10 km squares, between 1968 and 72 and 1988–91. Smaller Akaike's information criteria (AIC) values indicate a better model fit

Response	Test	Linear model			Non-linear model	
		$F_{1,2260}$ -energy	$F_{1,2259}$ -energy	$F_{1,2259}$ -energy <sup>2</sup>	Linear model fit	Non-linear model fit
Total number	GLM	114.1	114.6	10.9+++	$r^2 = 0.048$	$r^2 = 0.053$
	Spatial	40.2	9.7	7.1++	AIC = 1512	AIC = 1517
Total proportion	GLM	344.0	128.6	103.9++++	$r^2 = 0.132$	$r^2 = 0.170$
	Spatial	122.2	77.9	64.4++++	AIC = -3219	AIC = -3267
Rarest spp. number†	GLM	56.8++++	NS	NS	$r^2 = 0.040$	N/A
	Spatial	29.1++++	NS	NS	AIC = 2350	N/A
Rarest spp. proportion†	GLM	81.4++++	17.5++++	-13.3	$r^2 = 0.054$	$r^2 = 0.063$
	Spatial	33.6++++	10.9++	-8.5	AIC = 2199	AIC = 2202
Mod. rare spp. number††	GLM	14.4	NS	NS	$r^2 = 0.006$	N/A
	Spatial	4.9	NS	NS	AIC = 3305	N/A
Mod. rare spp. proportion††	GLM	13.4	9.8++	11.4	$r^2 = 0.006$	$r^2 = 0.011$
	Spatial	4.9	5.7+	6.5	AIC = 347	AIC = 354
Mod. common spp. number	GLM	NS	NS	NS	N/A	N/A
	Spatial	NS	NS	NS	N/A	N/A
Mod. common spp. proportion	GLM	17.7	12.7	10.9++	$r^2 = 0.008$	$r^2 = 0.013$
	Spatial	7.7	25.3	23.4++++	AIC = -1638	AIC = -1648
Common spp. number	GLM	303.9	66.8	42.0++++	$r^2 = 0.250$	$r^2 = 0.264$
	Spatial	317.5	33.4	20.7++++	AIC = 4210	AIC = 4201
Common spp. proportion	GLM	1241.0	340.4	262.2++++	$r^2 = 0.355$	$r^2 = 0.421$
	Spatial	423.1	173.6	133.6++++	AIC = -2478	AIC = -2585
Low niche position number	GLM	612.6	107.4	78.0++++	$r^2 = 0.213$	$r^2 = 0.240$
	Spatial	246.1	54.1	39.0++++	AIC = 4177	AIC = 4151
Low niche position proportion	GLM	1011.8	395.0	317.5++++	$r^2 = 0.309$	$r^2 = 0.394$
	Spatial	344.6	201.9	162.1++++	AIC = -2440	AIC = -2573
High niche position number	GLM	45.1	NS	NS	$r^2 = 0.02$	N/A
	Spatial	17.7	NS	NS	AIC = 3203	N/A
High niche position proportion	GLM	210.2	38.3	28.1++++	$r^2 = 0.085$	$r^2 = 0.096$
	Spatial	82.6	38.4	31.0++++	AIC = -1736	AIC = -1753
Highly threatened number	GLM	34.3	NS	NS	$r^2 = 0.015$	N/A
	Spatial	9.0	NS	NS	AIC = 3253	N/A
Highly threatened proportion	GLM	16.7	19.2	11.3+++	$r^2 = 0.109$	$r^2 = 0.114$
	Spatial	88.8	11.5	7.5++	AIC = -1038	AIC = -1027
Mod. threatened number	GLM	4.7	20.3	19.2++++	$r^2 = 0.002$	$r^2 = 0.010$
	Spatial	NS	13.5	12.8+++	N/A	AIC = 2957
Mod. threatened proportion	GLM	NS	50.0	49.5++++	N/A	$r^2 = 0.020$
	Spatial	NS	36.7	35.9++++	N/A	AIC = -1654
Unthreatened number	GLM	261.7	19.0	11.3++++	$r^2 = 0.104$	$r^2 = 0.108$
	Spatial	128.9	12.5	7.8++	AIC = 3863	AIC = 3867
Unthreatened proportion	GLM	643.0	152.5	16.1++++	$r^2 = 0.221$	$r^2 = 0.260$
	Spatial	269.4	91.7	70.7++++	AIC = -2262	AIC = -2315
Farmland spp. number†††	GLM	192.0	NS	NS	$r^2 = 0.078$	N/A
	Spatial	65.4	NS	NS	N/A	N/A
Farmland spp. proportion†††	GLM	803.4	163.8	121.9++++	$r^2 = 0.260$	$r^2 = 0.300$
	Spatial	238.2	75.6	56.4++++	AIC = -1088	AIC = -1129
Woodland spp. number†††	GLM	NS	60.2	58.7++++	N/A	$r^2 = 0.027$
	Spatial	NS	40.3	39.7++++	N/A	AIC = 3986
Woodland spp. proportion†††	GLM	118.5	179.7	162.2++++	$r^2 = 0.050$	$r^2 = 0.114$
	Spatial	45.7	118.1	108.++++	AIC = -1330	AIC = -1420
Other species number	GLM	95.5	NS	NS	$r^2 = 0.041$	N/A
	Spatial	47.3	NS	NS	AIC = 2610	N/A
Other species proportion	GLM	53.9	20.7	16.8++++	$r^2 = 0.023$	$r^2 = 0.031$
	Spatial	26.2	14.0	11.5+++	AIC = -2117	AIC = -2114

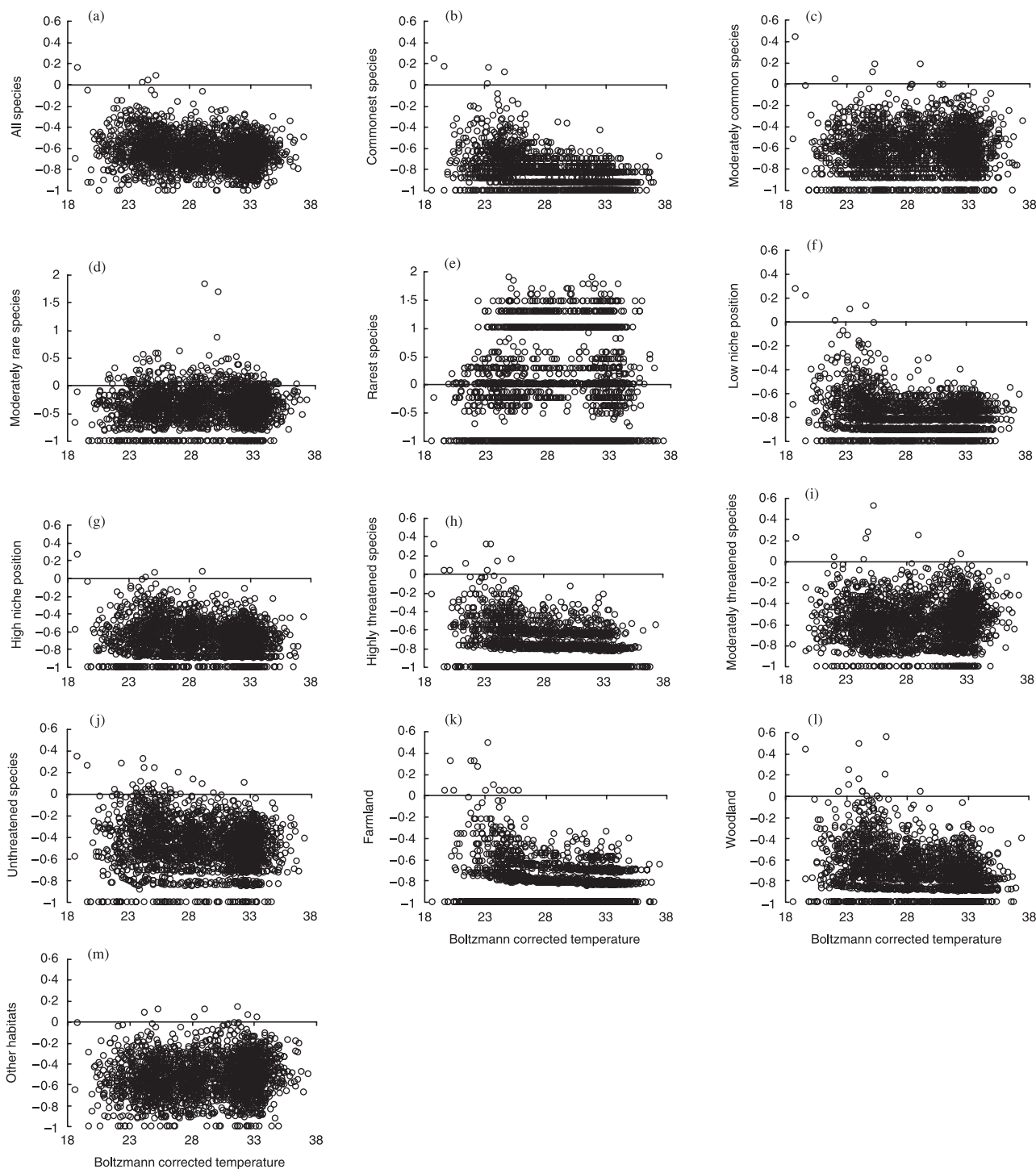
*F* ratio denominators are, in linear and quadratic models, respectively, †1419 and 1418, ††2258 and 2257 and †††2259 and 2258. Significance levels, signs indicate direction +++++  $P < 0.0001$ , ++++  $P < 0.001$ , +++  $P < 0.01$ , ++  $P < 0.05$ , NS  $P > 0.05$ .

but weak, relationship with energy availability (Fig. 1e, Table 1).

Extinction rates of both low and high niche position species were negatively related to energy availability (Fig. 1f,g) in independent error models, including logistic regressions, and spatial ones (Table 1). Energy could explain more of the variance in extinction risk of low-

niche position species ( $r^2 = 0.39$ ) than ones with high-niche positions ( $r^2 = 0.10$ ,  $P < 0.0001$ , *Z*-test of  $r^2$  values).

The extinction risk of highly threatened (Fig. 1h) and unthreatened species (Fig. 1j) were negatively related to energy availability, but such patterns were stronger in the latter ( $r^2 = 0.26$  vs. 0.11; *Z*-test of  $r^2$  values  $P < 0.0001$ ). Extinction rates of moderately



**Fig. 2.** Relationships between energy availability and colonization probability of British breeding birds in 10-km squares, between 1968 and 1972 and 1988–91. The number of colonizations is expressed as a proportion relative to species richness ( $\log_{10}$ -transformed). Note the variation in the y-axis scale.

threatened species were only very weakly related to energy availability ( $r^2 = 0.02$ , Fig. 1i, Table 1). Extinction rates of species grouped by their dominant habitat type were consistently negatively related to energy (Fig. 1k–m) in both independent error models and spatial ones (Table 1). Energy explained more of the variance in extinction rates of farmland species ( $r^2 = 0.30$ ) than woodland ones ( $r^2 = 0.11$ ), or those from other habitats ( $r^2 = 0.03$ ; Z-test of  $r^2$  values,  $P < 0.0001$  in both cases).

## COLONIZATION

Colonization rates, measured across all species, were weakly related to energy availability by a negative decelerating function in both independent error and spatial models; in the latter this relationship was only significant when data were analysed as a proportion of original species richness (Table 2, Fig. 2a). Most species groups exhibited either non-significant or very

**Table 2.** The influence of energy availability on the probability of colonization, of British 10-km squares, by breeding birds between 1968 and 72 and 1988–91. Smaller Akaike's information criteria (AIC) values indicate a better model fit

Response	Test	Linear model		Non-linear model		Non-linear model	
			$F_{1,2260}$ -energy	$F_{1,2259}$ -energy	$F_{1,2259}$ -energy <sup>2</sup>	Linear model fit	Non-linear model fit
Total number	GLM		4.5	4.4+	5.0	$r^2 = 0.002$	$r^2 = 0.004$
	Spatial		NS	NS	NS	N/A	N/A
Total proportion	GLM		93.4	7.6	4.7+	$r^2 = 0.040$	$r^2 = 0.042$
	Spatial		30.5	5.9	4.1+	AIC = -2529	AIC = -2519
Rarest spp. number	GLM		11.1	NS	NS	$r^2 = 0.005$	N/A
	Spatial		NS	NS	NS	N/A	N/A
Rarest spp. proportion†	GLM		NS	36.0++++	36.9	N/A	$r^2 = 0.017$
	Spatial		NS	24.1++++	24.6	N/A	AIC = 5617
Mod. rare spp. number	GLM		8.9++	5.0+	4.24	$r^2 = 0.004$	$r^2 = 0.006$
	Spatial		5.4+	NS	NS	AIC = 2703	N/A
Mod. rare spp. proportion††	GLM		NS	14.7+++	14.2	N/A	$r^2 = 0.008$
	Spatial		NS	5.4+	5.2	N/A	AIC = 815
Mod. common spp. number	GLM		4.8++++	22.5++++	19.8	$r^2 = 0.010$	$r^2 = 0.019$
	Spatial		14.7++++	5.7+	5.5	AIC = 2626	AIC = 2634
Mod. common spp. proportion	GLM		NS	NS	NS	N/A	N/A
	Spatial		NS	NS	NS	N/A	N/A
Common spp. number	GLM		309.6	NS (+ ve 2.2)	6.6	$r^2 = 0.120$	$r^2 = 0.123$
	Spatial		162.7	NS	NS	AIC = 3576	N/A
Common spp. proportion	GLM		728.6	34.3	17.6++++	$r^2 = 0.244$	$r^2 = 0.250$
	Spatial		290.4	20.1	10.8++++	AIC = -2966	AIC = -2963
Low niche position number	GLM		7.6	8.1	7.2++	$r^2 = 0.003$	$r^2 = 0.007$
	Spatial		5.2	6.1	5.4+	AIC = 3198	AIC = 3205
Low niche position proportion	GLM		125.4	91.6	79.0++++	$r^2 = 0.053$	$r^2 = 0.085$
	Spatial		58.8	51.3	43.8++++	AIC = -2584	AIC = -2613
High niche position number	GLM		NS	81.0++++	79.9	N/A	$r^2 = 0.040$
	Spatial		NS	31.7++++	30.8	N/A	AIC = 3041
High niche position proportion	GLM		53.7	18.3	22.4++++	$r^2 = 0.023$	$r^2 = 0.033$
	Spatial		19.0	NS	NS	AIC = -1389.2	N/A
Highly threatened number	GLM		170.3	NS	NS	$r^2 = 0.07$	N/A
	Spatial		84.4	NS	NS	AIC = 3982.6	N/A
Highly threatened proportion	GLM		414.8	21.7	11.6+++	$r^2 = 0.155$	$r^2 = 0.159$
	Spatial		188.1	NS	NS	AIC = -1021	N/A
Mod. threatened number	GLM		NS	NS	NS	N/A	N/A
	Spatial		NS	NS	NS	N/A	N/A
Mod. threatened proportion	GLM		NS	8.9	9.3++	N/A	$r^2 = 0.004$
	Spatial		NS	5.5	5.8+	N/A	AIC = -952
Unthreatened number	GLM		7.6++	37.6++++	35.7	$r^2 = 0.003$	$r^2 = 0.019$
	Spatial		NS	15.7++++	14.8	N/A	AIC = 2419
Unthreatened proportion	GLM		48.7	NS	NS	$r^2 = 0.021$	N/A
	Spatial		22.5	NS	NS	AIC = -761	N/A
Farmland spp. number	GLM		NS	NS	NS	N/A	N/A
	Spatial		NS	NS	NS	N/A	N/A
Farmland spp. proportion†††	GLM		90.3	22.6	17.5++++	$r^2 = 0.038$	$r^2 = 0.046$
	Spatial		51.3	11.5	8.5++	AIC = -1247	AIC = 1241
Woodland spp. number	GLM		68.0	18.3++++	23.1	$r^2 = 0.029$	$r^2 = 0.039$
	Spatial		31.6	11.6+++	14.4	AIC = 3620.8	AIC = 3618
Woodland spp. proportion†††	GLM		304.5	NS	NS	$r^2 = 0.119$	N/A
	Spatial		118.0	NS	NS	AIC = -1040.0	N/A
Other species number	GLM		NS	NS	NS	N/A	N/A
	Spatial		NS	NS	NS	N/A	N/A
Other species proportion	GLM		30.6++++	NS	NS	$r^2 = 0.013$	N/A
	Spatial		15.3++++	NS	NS	AIC = -1302.8	N/A

*F* ratio denominators are, in linear and quadratic models, respectively, †1419 and 1418, ††2258 and 2257 and †††2259 and 2258. Significance levels, signs indicate direction +++++ $P < 0.0001$ , +++ $P < 0.001$ , ++ $P < 0.01$ , + $P < 0.05$ , NS  $P > 0.05$ .

weak colonization–energy relationships, the exceptions being the most common (Fig. 2b,  $r^2 = 0.25$ ), highly threatened (Fig. 2h,  $r^2 = 0.16$ ), low niche position (Fig. 2f,  $r^2 = 0.09$ ) and woodland species (Fig. 2l,  $r^2 = 0.12$ ).

Only in the case of the most common species did relationships remain significant when analysed using the number of colonization events rather than their proportion (Table 2).

## Discussion

We find that extinction risk is related to energy availability by a negative decelerating function. That such a relationship occurs in the highly modified British environment, in which human activities influence extinction risk, is particularly noteworthy and suggests that such relationships may be more general. While this finding is consistent with the MIH, we do not find evidence for the latter's prediction that such relationships will be stronger in rare species, and our results thus provide little overall support for the MIH.

We also find little support for some of the other potential causes of species–energy relationships. Contrary to the predictions of the niche position mechanism we find that extinction–energy relationships are stronger for species with low niche positions that use relatively common resources. Although we lack niche position data for many of the species that we consider, our data incorporate a wide range of values and there is no evidence that our conclusions are influenced by data availability. The dynamic equilibrium mechanism also predicts that rare species will exhibit the strongest extinction–energy relationships; this is because following a population crash the probability of extinction is, other things being equal, greater when the initial population size is small. The increased consumer pressure mechanism suggests that high resource availability generates increased consumer pressure, reducing population sizes and thus competitive interactions and rates of competitive exclusion. Species vulnerable to competitive exclusion should thus exhibit the most marked decreases in extinction rates with increasing energy. The abundance of common species suggests that they are strong competitors that are unlikely to be susceptible to competitive exclusion, and the consumer pressure mechanism thus also predicts that the rarest species should exhibit the strongest species–energy relationships, a pattern which our data do not support.

The extinction rates of rare species may be unrelated to energy availability because their populations are so small that their extinction rates are consistently high. Such an explanation is unlikely to be complete, however, as it cannot explain why energy availability is not strongly related to extinction rates of moderately common species, such as *Anas platyrhynchos* (L.) and *Garrulus glandarius* (L.), which exhibit a positive species–energy relationship (Evans & Gaston 2005).

Energy availability may be confounded with habitat deterioration, generating an artefactual negative correlation between energy and extinction rates. Energy explains a greater proportion of the variation in extinction risk of species whose dominant habitat types have experienced greater modification (farmland compared to woodland and other habitats). However, the forms of the relationships between energy and extinction rates in farmland and woodland species were statistically indistinguishable (95% confidence intervals, linear terms: farmland  $-0.298$  to  $-0.188$ , woodland  $-0.304$  to

$-0.211$ ; squared terms: farmland  $0.003$ – $0.005$ , woodland  $0.004$ – $0.005$ ). Moreover, there is no clear evidence that low-energy areas have experienced the highest rates of habitat deterioration; there has been serious intensification of farmland in both high-energy (arable south-east) and low-energy areas (pastoral south-west), while very little deterioration has occurred in some low-energy areas (pastoral Scottish highlands). In addition, the decrease in extinction rates in high-energy areas occurs despite higher human population densities in such areas (Evans & Gaston 2005). The finding that when species are classified by threat status energy availability has the strongest influence on the extinction rates of unthreatened species, which are insensitive to habitat modification, adds further support to the conclusion that our findings are not, in the main, the result of confounding habitat degradation with energy availability.

Higher extinction rates in low-energy areas may arise, in part, because such localities are located generally in the north and west, and are thus closer to the species' range boundaries where extinctions may be more frequent (Wilcove & Terborgh 1984; Gaston 2003). Such an explanation is unlikely to be complete as range contractions may exhibit other spatial patterns, including contraction towards their peripheries (Channell & Lomolino 2000), and such patterns have been demonstrated to occur frequently in British birds (30% of 25 cases investigated, Donald & Greenwood 2001). Occupancy may be lower at range boundaries and such patchy distributions may elevate extinction risk through, for example, source–sink effects (Chamberlain & Fuller 2000). Evidence for reduced occupancy at range boundaries in our assemblage is, however, at best equivocal (Blackburn *et al.* 1999) and extinction rates of British birds are not related clearly to the extent to which distributions are patchy (Donald & Greenwood 2001). While factors related to the structure of species ranges may thus contribute to the negative relationship between energy and extinction risk, they are unlikely to be the sole cause.

Across all species, spatial variation in colonization rates is relatively uninfluenced by energy availability and the significant relationships that we find are negative. It is thus highly unlikely that the positive species–energy relationship that occurs in British birds (Turner *et al.* 1988; Lennon *et al.* 2000; Evans & Gaston 2005) is, predominantly, a consequence of higher colonization rates in high-energy areas. Negative relationships between energy availability and colonization may arise because high-energy areas contain more species and thus the number of potential colonists is low, and/or because low-energy areas have more stochastic extinctions and thus more vacant niches available for colonization. Indeed, one expects that, at equilibrium, the number of extinctions will be matched by the number of colonizations and it is not surprising that species groups which exhibit the strongest extinction–energy relationships, such as the most common ones, also



exhibit the strongest colonization–energy relationships. Moreover, the fact that at equilibrium the number of colonizations and extinctions is matched may mask other patterns. Following local extinction events energy availability may exert a positive influence on recolonization, but such patterns may be hidden as few extinctions occur in high-energy areas and thus the potential for observing colonizations in such areas may be low. It is thus plausible that as energy input is elevated extinction rates decline and recolonization probability increases, creating a positive link between species richness and energy.

In summary, we find that extinction rates are lower in high-energy areas. While such patterns may contribute to species–energy relationships the mechanisms promoting them remain unclear as, counter to the MIH and some of its alternatives, the most common species exhibit the strongest relationships between energy and extinction rates. Our results concur with increasing evidence that the most common species drive spatial variation in species richness and species–energy relationships (Jetz & Rahbek 2002; Lennon *et al.* 2004; Ruggiero & Kitzberger 2004; Evans & Gaston, in press).

### Acknowledgements

We thank the numerous volunteers who gathered the atlas data and the British Trust for Ornithology for making them available. J. Lennon provided helpful comments on the manuscript. This work was supported by The Leverhulme Trust.

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Received 25 May 2004; accepted 29 October 2004