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Dissecting the species–energy relationship

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Environmental energy availability can explain much of the spatial variation in species richness. Such species–energy relationships encompass a diverse range of forms, and there is intense debate concerning which of these predominate, and the factors promoting this diversity. Despite this there has been relatively little investigation of whether the form, and relative strength, of species–energy relationships varies with (i) the currency of energy availability that is used, and (ii) the ecological characteristics of the constituent species. Such investigations can, however, shed light on the causal mechanisms underlying species–energy relationships. We illustrate this using the British breeding avifauna. The strength of the species–energy relationship is dependent on the energy metric used, with species richness being more closely correlated with temperature than the Normalized Difference Vegetation Index, which is a strong correlate of net primary productivity. We find little evidence, however, for the thermoregulatory load hypothesis that high temperatures enable individuals to invest in growth and reproduction, rather than thermoregulation, increasing population sizes that buffer species from extinction. High levels of productive energy may also elevate population size, which is related to extinction risk by a negative decelerating function. Therefore, the rarest species should exhibit the strongest species–energy relationship. We find evidence to the contrary, together with little support for suggestions that high-energy availability elevates species richness by increasing the numbers of specialists or predators.

Keywords: NDVI; more individuals hypothesis (MIH); niche breadth; niche position; species–energy relationships; temperature

1. INTRODUCTION

Local and regional species richness vary by orders of magnitude across the globe (Gaston & Spicer 2004). Understanding the factors controlling this variation is one of ecology's most important challenges (Hutchinson 1959; Brown 1981; Rosenzweig 1995; Gaston 2000). There is now a growing consensus that much of the pattern can be explained by differences in environmental energy availability (Hawkins *et al.* 2003; Pimm & Brown 2004); such species–energy relationships have been described for a range of taxa, habitats and, when using latitude as a crude surrogate for energy, geological time periods (e.g. Currie 1991; Roy *et al.* 1998; Crame 2001; Hawkins *et al.* 2003). These relationships exhibit a variety of forms, which has stimulated much debate regarding which predominate and the factors that give rise to this diversity (Waide *et al.* 1999; Mittelbach *et al.* 2001; Mittelbach, Scheiner & Steiner 2003; Whittaker & Heegaard 2003). Much of the debate has focused on the influence of spatial scale on the form of the species–energy relationship. Generally, studies conducted at small spatial grains, the unit of investigation, document unimodal species–energy relationships; studies that use larger grain sizes, scattered across one or more regions, find an increasing proportion of monotonic positive species–energy relationships. Although species–energy relationships are typically strong their relative strengths may vary considerably (see papers reviewed by Waide *et al.* 1999; Mittelbach *et al.* 2001), yet the causes of this variation are seldom discussed.

The form of species–energy relationships, and their underlying causal mechanisms, may depend on how energy availability is measured. Previous studies have used a number of currencies, which can be divided into two main categories (Evans *et al.* 2005*c*). First, solar energy metrics, such as temperature or ultra-violet radiation (UV), record the amount of solar energy falling upon the earth's surface. Broadly speaking, solar energy metrics may give rise to species–energy relationships through two pathways. According to the evolutionary rates hypothesis (Rohde 1978, 1992), high temperatures and/or UV may increase the mutation rate, leading to accelerated rates of evolution and speciation, thus high-energy areas may be species rich because more species evolved there. Alternatively, the thermoregulatory load hypothesis suggests that high temperature may enable endotherms to switch investment from keeping warm to growth and reproduction, thus promoting larger populations that are less vulnerable to extinction (Turner *et al.* 1988). Other things being equal, small bodied endotherm species are more vulnerable to heat loss (James 1970), thus the smallest endotherm species may exhibit the strongest species–energy relationships (Cousins 1989).

Second, productive-energy metrics record the amount of resources available for consumers to turn into biomass. This can be measured as net primary productivity, or its correlates, such as the Normalized Difference Vegetation Index (NDVI), which is a satellite derived measure of the greenness of vegetation (Boelman *et al.* 2003; Kerr &

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Ostrovosky, 2003). The most frequently cited pathway linking productive energy to species richness is the more individuals hypothesis (MIH); this suggests that in areas with high plant productivity consumers may be able to maintain larger populations that reduce their extinction risk, thus elevating species richness (Wright 1983).

Both the evolutionary rates and thermoregulatory load hypotheses predict that solar energy metrics will be a better predictor of species richness than productive energy metrics. A recent review found that this was the case at high northern latitudes, but that the converse was true in other areas (Hawkins *et al.* 2003). In contrast, Kaspari *et al.* (2004) found that solar energy was the superior predictor of ant species richness across a large latitudinal range that spanned the tropics. Relatively few studies have, however, explicitly investigated how the use of different energy metrics influences the shape of the species–energy relationship, or have constructed species–energy relationships that simultaneously use solar and productive energy metrics as predictors (but see Diniz-Filho & Bini 2005).

Discussion of the diversity of forms and relative strengths of species–energy relationships has largely been framed in the context of entire assemblages. Consideration of how the identity and associated characteristics of the species contributing to species–energy relationships influence their form and strength has been relatively muted, despite the fact that this may provide important information on the underlying causal mechanisms. The one exception to this concerns comparisons of species–energy relationships in abundant and widespread species, relative to rarer and more localized ones (Jetz & Rahbek 2002; Ruggiero & Kitzberger 2004; Vázquez & Gaston 2004; Evans *et al.* 2005*c*). Species vary, however, in a number of other traits which, depending on the causal mechanisms that drive species–energy relationships, may influence how species richness responds to energy availability (Evans *et al.* 2005*b*,*c*).

First, in areas with high plant productivity resources may be sufficiently abundant for species to specialize on a few resource types, generating narrower niche breadths that promote coexistence and elevate species richness (see Vázquez & Stevens 2004; Evans *et al.* 2005*b*,*c*). Similarly, high-energy areas may be the only ones that contain relatively scarce resources in sufficient abundance to maintain viable populations of the niche position specialists (sensu Shugart & Patten 1972) that use them (Abrams 1995; Evans *et al.* 2005*b*,*c*). Specialist species, defined in terms of narrow niche breadths and use of scarce resources, may therefore respond more strongly to energy availability than less specialized ones. Second, the transfer of energy between trophic levels is inefficient and thus the number of trophic levels may be regulated by the amount of energy at the base of the food chain (Oksanen *et al.* 1981; Fretwell 1987; but see Post 2002). The longer food chains in highly productive areas may thus enable greater numbers of predatory species to occur. Species–energy relationships, constructed for different trophic levels, may thus vary in their form and strength. Third, migratory species may be able to exploit seasonal flushes in resource availability more fully than residents and thus exhibit stronger species–energy relationships (Rabenold 1979, 1993). Fourth, species–energy relationships comprising taxa that have undergone marked population declines or range contractions in response to human activities, or those that occupy habitats markedly altered by humans, may also differ in their form relative to species that are comparatively uninfluenced by anthropogenic factors (Gaston 2004; Evans & Gaston 2005). More generally, the inheritance of ecological traits through the sharing of common ancestors may introduce taxonomic bias into the form of species–energy relationships.

Here, we provide one of the first comprehensive assessments of how the form and relative strength of the species–energy relationship depends on the type of energy metric used and the characteristics of the constituent species. We use the breeding avifauna of Britain as a case study. We construct species–energy relationships, using annual and seasonal measures of solar and productive energy, across the entire assemblage and groups of species classified by specialization, trophic level, population size, body size, habitat type, threat status (based on population trends), migratory status and taxonomy.

2. MATERIAL AND METHODS

(a) *Avian data*

We used the summer (breeding) distribution of the British avifauna recorded in April–July 1988–1991, shown in the second BTO/SOC/IW atlas of breeding birds (Gibbons *et al.* 1993). These data record species presence/absence at a resolution of 10 km × 10 km quadrats on a continuous grid. Fieldwork was coordinated by a network of regional organisers and undertaken by experienced volunteer ornithologists. Data are based on timed visits, of 2 h duration, to at least eight 2 km × 2 km quadrats within each 10 km quadrat and supplemented with additional records collated over the four survey years. For most quadrats very few species are likely to have been unrecorded and we thus consider our data to be free of significant concerns regarding under-sampling. These constitute one of the best sets of distributional data for any assemblage and have been successfully used in numerous macroecological studies (e.g. Turner *et al.* 1988; Gaston *et al.* 1997; Lennon *et al.* 2000; Donald & Greenwood 2001). We excluded marine species and vagrants (species recorded as a few individuals typically in only one or two quadrats), but retained the more naturalized introductions, giving a total of 189 species. Some initial filtering was performed on the distributional data; 10 km quadrats (100 km^2) that contained less than 50% land were excluded, leaving a total of 2262 quadrats.

Data on breeding population size and body mass were taken from the compilation in Gaston & Blackburn (2000), with additional data, for *Columba livia*, from Greenwood *et al.* (1996), and species were grouped into quartiles of population abundance and body mass. Niche breadth and 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 caerulus*) and those with high niche positions that use relatively scarce resources (e.g. *Carduelis spinus*). Species were classified into two groups of high and low niche breadths in the same manner.

Migratory status was categorized in two ways. First, species were categorized as long-distance migrants if most of their breeding populations wintered outside Britain, in sub-Saharan Africa for most species, with others classed as long-distance residents. Second, species were classed as short-distance migrants if most of their breeding population wintered in an area different to that in which they bred, even if they remained in Britain, with the remainder being classified as short-distance residents. Thus species, such as *Falco columbarius*, that breed on moorland and winter on the coast were classified as residents under the first definition, but migrants according to the second definition.

Data on the major food items in each species' diet were obtained from Cramp *et al.* (1977–1994) and species were classified as herbivores, omnivores, invertebrate predators and vertebrate predators, with 32, 50, 79 and 28 species in each of these respective categories. For a small number of species (for example some grouse, buntings and finches), adults are herbivores whilst chicks feed on invertebrates for the first few days of their life; these species were classified on the basis of both their adult and chick diets, i.e. as omnivores rather than herbivores, but classifying them as the latter does not markedly change our results.

Species were classified by their main habitat type (farmland, woodland, and other) according to the categorization provided in Gibbons *et al.* (1993), with 28, 49 and 112 species in the three habitat types respectively. This classification separates habitats by the extent to which they have been modified in recent decades. Avian population trend data indicate extensive modification of farmland; intermediate levels, on average, of habitat alteration in woodlands (with many species exhibiting stable or increasing population trends, but some having declining population trends); and relatively little modification elsewhere (Crick *et al.* 2004). Finally, species were classified by their threat status based upon Gregory *et al.* (2002). This uses a number of criteria, including population or range declines, extent of European conservation concern for the species, and the extent to which populations are concentrated into a few sites, to list species as red (threatened), amber (moderately threatened) and green (unthreatened). We only used information relating to the magnitude of historic and recent population declines, and range contractions, in assigning species to threat status. Therefore, species that are naturally rare but are listed as moderately threatened on the basis of European conservation concern, such as *Alcedo atthis*, were considered to be unthreatened for the purposes of this analysis.

(b) *Energy metrics*

We used two measures of energy availability in our analyses. First, we used mean monthly temperature data that were derived from meteorological recording station readings for the period 1961-90 using surface interpolation techniques (Barrow *et al.* 1993). Second, we obtained NDVI data from the NOAA/NASA Pathfinder AVHRR Land Data Set (see http://www.ciesin.org/). Note that NDVI and net primary productivity have been found to be strongly positively correlated at latitudes and habitat types similar to those that occur in Britain (Boelman *et al.* 2003; Kerr & Ostrovosky 2003). The NDVI data were collected between 1981 and 2001 at a spatial resolution of a 0.1° latitude/longitude grid, approximately equivalent to an 8 km quadrat (64 km^2) in the UK. Daily readings are converted to maximum values for each 10-day period, which markedly reduces the effects of cloud cover. From these we calculated mean monthly NDVI values and then used GIS to re-project these data at a 10 km resolution which was compatible with our avian distribution data. For both temperature and NDVI we calculated a mean annual measure of energy availability and a mean summer value calculated from the monthly averages for May, June and July.

(c) *Analyses*

All analyses were conducted in SAS (Version 8.2). Spatial autocorrelation may invalidate the assumption of independent errors, distorting classical tests of association and rendering correlation coefficients, regression slopes and associated significance tests misleading (Cressie 1991; Legendre 1993; Lennon 2000; Legendre *et al.* 2002). To avoid this, analyses were conducted 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 (Littell *et al.* 1996). Spatial null models, i.e. ones which lacked predictor variables, which assumed exponential spatial covariance structures fitted the data significantly better than independent error null models (in all cases likelihood ratio tests $p < 0.0001$) and also gave a better fit than spatial models that specified alternative covariance structures (spherical, Gaussian, linear, linear log and power).

We constructed multiple regression models that included both temperature and NDVI, and their square terms, as predictors. We used one measure of temperature, and one of NDVI, selecting the seasonal measure that gave the best fit to our data in models confined to a single measure of energy (see table 1). A full set of models containing all possible combinations of our predictors (temperature, NDVI and their square terms) was constructed and we used Akaike's Information Criteria (AIC) to compare the fit of competing models (Akaike 1973). The use of AIC in ecological research is increasingly recommended (Burnham & Anderson 2001; Ginzburg & Jensen 2004, Johnson & Omland 2004). The AIC estimates the Kullback–Leibler information lost by approximating full reality with the fitted model; computation entails terms representing lack of fit and a bias correction factor related to model complexity. Following Johnson & Omland (2004), we calculated the difference between each model's AIC value and that of the best fitting model, the one with the smallest AIC, and used these data to calculate the weight of each model, the probability that it provides the best fit to the data. In order to investigate the influence of taking spatial autocorrelation into account we also conducted analyses that assumed independent errors by constructing general linear models (GLMs) using a stepwise selection procedure, with $p < 0.05$ being adopted as the threshold for retaining a term in the minimum adequate model (see Electronic Appendix).

3. RESULTS AND DISCUSSION

When predictors are confined to a single seasonal measure of either temperature or NDVI the former is a better predictor of species richness for all our species groups, except that comprising the rarest species (table 1). Species richness generally increases with temperature along a positive decelerating curve, although the rarest and moderately rare species exhibit positive linear relationships these have low explanatory power (tables 1 and 2, figure 1). The general form of the species–temperature relationship remains unchanged when annual, instead of summer, temperature is used as a predictor (table 1). These results confirm those of earlier work (Hawkins *et al.*

Table 1. Akaike Information Criteria (AIC) values for regressions of species richness that use a single seasonal measure of either temperature or the Normalized Difference Vegetation Index (NDVI).

(Summer energy metrics are calculated as the mean value during May, June and July. Smaller AIC values indicate a better model fit. Bold type indicates if summer or annual measures of temperature and NDVI gave the best fit to the data. The best overall single predictor of species richness is indicated by*. Explanatory power is indicated by the r^2 values from general linear models.)

response	summer temperature	summer temperature & summer temperature^2	annual temperature	annual temperature & annual temperature^2	r^2 best temperature model (%)	summer NDVI	summer NDVI & summer NDVI^2	annual NDVI	annual NDVI & annual NDVI^2	r^2 best NDVI model (%)
all species	17522.1	**17396.3***	17545.3	17445.6	24.8	17686.3	17683.4	17684.2	**17673.2**	14.9
non-passerines	15329.2	**15285.6***	15340.5	15300.5	8.2	15435.6	15433.9	15434.9	**15422.3**	9.5
passerines	14382.1	**14185.3***	14409.7	14253.8	37.8	14528.5	14530.5	14526.7	**14523.6**	22.4
long distance resident	16364.8	**16227.8***	16379.3	16275.9	22.1	16514.6	16508.3	16513.1	**16495.6**	14.9
long distance migrant	11888.0	**11834.0***	11930.5	11878.7	26.4	**12022.7**	12031.4	12022.9	12029.4	13.3
partial resident	15776.0	**15650.9***	15809.7	15720.0	40.3	16028.5	16026.4	16025.5	**16016.7**	18.5
partial migrant	13151.1	**13065.3***	13155.5	13069.8	3.2	13165.2	13169.0	13162.1	**13156.7**	4.4
red list	9944.3	**9859.9***	10011.7	9929.0	47.9	10146.3	10153.4	**10146.2**	10149.7	6.9
amber list	11534.7	**11418.1***	11535.9	11423.9	8.5	11531.0	11526.7	11529.6	**11513.2**	6.7
green list	15654.2	**15554.5***	15678.4	15610.6	29.5	15867.2	15868.5	15863.6	**15858.8**	14.3
1st population quartile	12711.3	**12443.5***	12740.8	12532.5	56.0	13077.0	13080.5	13074.5	**13071.1**	27.8
2nd population quartile	13497.9	**13369.3***	13509.8	13403.1	14.6	13538.3	13545.3	13538.9	**13536.9**	11.3
3rd population quartile	**12870.5***	12873.8	12878.5	12879.9	3.5	12911.0	12904.2	12911.1	**12902.0**	4.8
4th population quartile	8405.0	8410.5	**8403.5**	8406.9	0.6	**8378.5***	8383.4	8392.1	8397.6	7.4
1st bodymass quartile	12775.2	**12657.1***	12811.2	12717.5	36.8	12949.7	12952.1	12945.4	**12944.9**	17.3
2nd bodymass quartile	11231.1	**11096.5***	11248.6	11143.2	16.8	11292.2	11295.0	11295.2	**11286.5**	11.9
3rd bodymass quartile	12070.1	**12031.6***	12116.9	12079.1	35.2	12250.9	12257.7	**12250.1**	12252.5	4.2
4th bodymass quartile	11776.0	**11701.7***	11760.5	11709.6	9.6	11790.4	11789.5	11788.4	**11780.8**	2.2
farmland	10064.9	**10007.9***	10114.5	10058.3	69.2	10447.3	10457.7	**10444.2**	10453.7	8.6
woodland	13405.5	**13232.8***	13442.7	13273.8	34.3	13495.8	13499.7	13492.9	**13489.4**	21.3
other habitats	15594.2	**15543.5***	15582.3	15547.5	7.2	15605.0	15604.2	15606.3	**15600.5**	2.8
niche breadth (broad)	12570.2	**12483.4***	12631.8	12559.0	76.0	13180.1	13189.1	**13176.3**	13181.7	13.7
niche breadth (narrow)	12791.7	**12553.4***	12783.9	12614.1	23.4	12793.7	12796.0	12784.2	**12776.1**	6.7
niche position (low)	12145.7	**11924.7***	12179.7	12014.9	56.4	12542.6	12547.0	**12534.0**	12535.4	20.3
niche position (high)	12876.4	**12744.8***	12909.6	12818.3	38.2	**13091.7**	13097.9	13099.9	13097.8	18.5
herbivores	8599.8	**8556.7***	8670.5	8635.9	46.7	8879.9	8886.5	**8877.0**	8879.0	4.4
omnivores	12550.2	**12460.3***	12605.8	12525.2	44.4	12771.8	12770.0	12772.9	**12765.2**	16.8
predators—inverts	14396.1	**14281.2***	14395.9	14312.6	13.9	14494.7	14499.2	14491.8	**14489.6**	8.8
predators—verts	10453.2	**10381.4***	10453.4	10392.6	8.2	10456.3	10460.6	**10450.0**	10450.0	0.04

Table 2. Multiple regression models of species–energy relationships that take spatial autocorrelation into account.

(Model fit was assessed using the Akaike Information Criteria (AIC), smaller values indicate a better fit. The model weight is the probability that the model provides the best fit to the data; we present all models with weights greater than 0.2. Explanatory power is indicated by the r^2 values from general linear models. Models use either summer or annual measures of temperature and NDVI according to which measure provided the best fit to the data in tests that used a single energy metric as a predictor (see table 1). $++++p<0.0001$, $+++p<0.001$, $++p<0.01$, $+p<0.05$; Negative effects $----p<0.0001$, $---p<0.001$, $--p<0.01$, $-p<0.05$.)

number of species	response	temperature	temperature^2	NDVI	NDVI^2	model weight	r^2 (%)
189	all species	$F_{1,2257}=137.9++++$	$F_{1,2257}=111.9----$	$F_{1,2257}=19.7++++$	$F_{1,2257}=17.9----$	0.987	30.4
107	non-passerines	$F_{1,2257}=57.1++++$	$F_{1,2257}=45.2----$	$F_{1,2257}=18.1++++$	$F_{1,2257}=19.2----$	0.946	16.0
82	passerines	$F_{1,2257}=205.8++++$	$F_{1,2257}=170.3----$	$F_{1,2257}=13.4+++$	$F_{1,2257}=9.7--$	0.562	43.1
82	passerines	$F_{1,2258}=219.2++++$		$F_{1,2258}=20.9++++$	$F_{1,2258}=14.0---$	0.438	38.9
141	long distance resident	$F_{1,2257}=151.6++++$	$F_{1,2257}=126.3----$	$F_{1,2257}=26.3++++$	$F_{1,2257}=24.7----$	0.999	28.4
48	long distance migrant	$F_{1,2258}=60.8++++$	$F_{1,2258}=45.1----$	$F_{1,2258}=9.6++$		0.839	29.2
116	partial resident	$F_{1,2257}=144.9++++$	$F_{1,2257}=110.5----$	$F_{1,2257}=24.8++++$	$F_{1,2257}=21.9----$	0.998	45.6
73	partial migrant	$F_{1,2259}=98.3++++$	$F_{1,2259}=91.1----$			0.846	3.2
35	red list	$F_{1,2257}=95.0++++$	$F_{1,2257}=67.6----$	$F_{1,2257}=20.4++++$	$F_{1,2257}=17.8----$	0.896	53.0
35	amber list	$F_{1,2257}=110.6++++$	$F_{1,2257}=169.7----$	$F_{1,2257}=23.2++++$	$F_{1,2257}=22.7----$	0.953	15.1
119	green list	$F_{1,2257}=115.3++++$	$F_{1,2257}=89.6----$	$F_{1,2257}=14.9+++$	$F_{1,2257}=13.3---$	0.857	33.2
47	1st population quartile	$F_{1,2257}=336.0++++$	$F_{1,2257}=262.4----$	$F_{1,2257}=16.8++++$	$F_{1,2257}=12.6---$	0.760	62.2
47	1st population quartile	$F_{1,2258}=340.7++++$	$F_{1,2258}=265.7----$	$F_{1,2258}=26.1++++$		0.241	58.2
47	2nd population quartile	$F_{1,2258}=132.9++++$	$F_{1,2258}=118.8----$	$F_{1,2258}=5.6+$		0.472	15.4
47	2nd population quartile	$F_{1,2259}=156.8++++$	$F_{1,2259}=139.0----$			0.316	14.6
47	2nd population quartile	$F_{1,2257}=130.1++++$	$F_{1,2257}=116.5----$	$F_{1,2257}=9.4+++$	$F_{1,2257}=8.0--$	0.212	18.4
47	3rd population quartile	$F_{1,2258}=39.9++++$		$F_{1,2258}=18.7+++$	$F_{1,2258}=19.9---$	0.782	8.3
48	4th population quartile	$F_{1,2259}=4.9+$		$F_{1,2259}=37.0----$		0.391	7.4
48	4th population quartile	$F_{1,2257}=45.5++++$				0.290	0.7
48	4th population quartile	$F_{1,2258}=6.2+$	$F_{1,2258}=4.8-$	$F_{1,2258}=39.2----$		0.237	7.6
47	1st mass quartile	$F_{1,2258}=127.2++++$	$F_{1,2258}=98.5----$	$F_{1,2258}=24.4++++$		0.599	39.3
47	1st mass quartile	$F_{1,2257}=123.2++++$	$F_{1,2257}=95.1----$	$F_{1,2257}=12.3+++$	$F_{1,2257}=9.0--$	0.401	40.6
47	2nd mass quartile	$F_{1,2259}=165.1++++$	$F_{1,2259}=144.6----$			0.746	16.8
48	3rd mass quartile	$F_{1,2259}=63.6++++$	$F_{1,2259}=42.72----$			0.660	35.2
48	3rd mass quartile	$F_{1,2257}=53.3++++$	$F_{1,2257}=35.3----$	$F_{1,2257}=13.2+++$	$F_{1,2257}=12.4---$	0.231	42.5
47	4th mass quartile	$F_{1,2259}=86.6++++$	$F_{1,2259}=82.0----$			0.508	9.6
47	4th mass quartile	$F_{1,2257}=84.1++++$	$F_{1,2257}=80.7----$	$F_{1,2257}=12.6+++$	$F_{1,2257}=13.8---$	0.416	72.7
28	farmland	$F_{1,2258}=93.3++++$	$F_{1,2258}=52.1----$	$F_{1,2258}=9.3++$		0.841	69.3
49	woodland	$F_{1,2258}=175.8++++$	$F_{1,2258}=145.7----$	$F_{1,2258}=33.9++++$		0.525	39.0
49	woodland	$F_{1,2257}=168.3++++$	$F_{1,2257}=139.0----$	$F_{1,2257}=13.7+++$	$F_{1,2257}=9.4--$	0.475	40.8
112	other habitats	$F_{1,2257}=63.3++++$	$F_{1,2257}=60.7----$	$F_{1,2257}=9.8++$	$F_{1,2257}=11.5---$	0.757	10.8
43	niche breadth (broad)	$F_{1,2258}=141.2++++$	$F_{1,2258}=76.3----$	$F_{1,2258}=20.0++++$		0.954	76.7
42	niche breadth (narrow)	$F_{1,2257}=245.5++++$	$F_{1,2257}=244.9----$	$F_{1,2257}=15.9+++$	$F_{1,2257}=14.5--$	0.743	27.2
43	niche position (low)	$F_{1,2258}=288.8++++$	$F_{1,2258}=218.8----$	$F_{1,2258}=20.8++++$		0.785	58.7
43	niche position (low)	$F_{1,2257}=284.8++++$	$F_{1,2257}=215.9----$	$F_{1,2257}=10.7++++$	$F_{1,2257}=7.7----$	0.214	62.3
42	niche position (high)	$F_{1,2258}=148.0++++$	$F_{1,2258}=117.1----$	$F_{1,2258}=15.5++++$		0.869	40.4
16	herbivores	$F_{1,2257}=64.7++++$	$F_{1,2257}=40.8----$	$F_{1,2257}=27.5++++$	$F_{1,2257}=26.7----$	0.958	52.1
64	Omnivores	$F_{1,2257}=102.7++++$	$F_{1,2257}=73.3----$	$F_{1,2257}=27.4++++$	$F_{1,2257}=24.2----$	0.998	49.7
81	Predators—inverts	$F_{1,2259}=148.4++++$	$F_{1,2259}=126.4----$			0.770	13.9
28	Predators—verts	$F_{1,2259}=76.0++++$	$F_{1,2259}=77.9----$			0.968	8.2

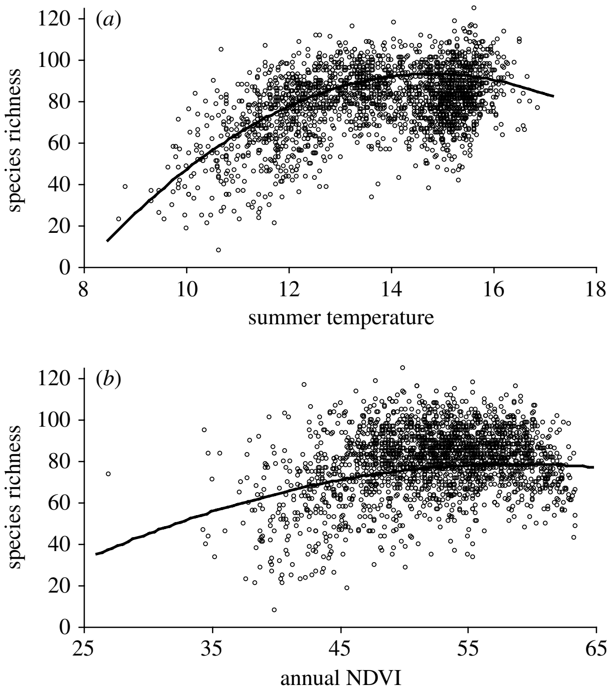

Figure 1. Relationships between species richness and (*a*) temperature (*b*) NDVI across the entire assemblage of British breeding birds. Open circles represent raw data and lines represent the predicted relationship from models that take into account spatial autocorrelation and use a single measure of energy, the seasonal measure that gives the best fit to the data (see table 1).

2003) that at high northern latitudes, such as Britain, temperature is a better predictor of species richness than metrics that combine temperature and water availability, such as measures of plant productivity.

Kaspari *et al.* (2004) also found that the species richness of ant assemblages was more closely related to temperature than to plant productivity and suggested that such a pattern provided support for Rohde's (1978, 1992) evolutionary rates hypothesis. This states that higher levels of solar radiation increase mutation rates, promoting faster molecular evolution and greater speciation, so more species occur in high-energy areas because more evolve there. The British avifauna contains one endemic bird species, *Loxia scotica*, although its taxonomic status is debated (Summers *et al.* 2002). We are not aware of any other suggestions that species of birds breeding in Britain evolved there. Indeed, this seems highly unlikely. First, Britain has been subject to frequent glaciation periods during which most species would have been displaced further south. Moreover, speciation in Britain could only have occurred during the interglacial periods and these were typically much shorter, approximately 25,000 years (Adams *et al.* 1999), than the time typically required for avian speciation, which has been estimated at between 250,000 and two million years (Avise *et al.* 1998; Johnson & Cicero 2004). Second, most species breeding in Britain have large geographic ranges covering Europe, and often parts of Asia and/or Africa (Gregory & Blackburn 1998); it would be rather remarkable if the majority of these species evolved in the same small area of their distribution. In addition, established exotic avian species in Britain exhibit a strong–species energy relationship (Evans *et al.* 2005*d*), which cannot arise through a relationship between energy and speciation rates, suggesting that other mechanisms must play a role. It thus seems highly unlikely that the evolutionary rates mechanism can explain the species–energy relationship in British birds.

The thermoregulatory load hypothesis (Turner *et al.* 1988) also predicts that species richness will respond more strongly to temperature than NDVI. Limited support for this hypothesis is provided by the fact that breeding species richness responds to summer, rather than annual, temperature (table 1); these two variables are, however, strongly correlated ($r^2=92\%$). Small bodied species are more vulnerable to heat loss than larger ones (James 1970), thus the thermoregulatory load hypothesis predicts that smaller bodied species will exhibit the strongest species–temperature relationships, as is the case in our data (table 1). The strength of the species–temperature relationship does not, however, decline consistently across species grouped into quartiles of increasing mass. Therefore, whilst our data are partly consistent with the thermoregulatory load hypothesis they do not provide conclusive support for it. Lennon *et al.* (2000) found that seasonal changes in temperature gradients across Britain are not reflected in seasonal changes in gradients of species richness, and also concluded that the thermoregulatory load hypothesis does not generate species–energy relationships in the avifauna.

Given the lack of support for causal pathways that link species richness to temperature it is unclear why the latter is a better predictor of species richness than NDVI. One possibility is that in highly modified regions such as Britain, which are dominated by intensive agriculture, NDVI is an imperfect measure of the amount of plant productivity that is available to free-living consumers. It has been estimated that in developed countries the proportion of net primary productivity that is acquired by humans (HANPP) may reach 50% (Haberl *et al.* 2002; Imhoff *et al.* 2004). If this proportion varies spatially then this may disrupt the apparent relationship between productive energy and species richness. Unfortunately, data on spatial variation in HANPP across Britain are not available and thus this hypothesis cannot yet be tested. Whilst temperature is a better predictor of species richness than NDVI in models restricted to a single measure of energy availability, it is important to note that temperature and NDVI are correlated (in GLMs summer $\text{NDVI}=-132.79+28.49$ summer $\text{temp}-1.03$ summer temp^2, $r^2=31.6\%$; annual $\text{NDVI}=-20.96+7.10$ annual $\text{temp}-0.39$ annual temp^2, $r^2=10.2\%$). Moreover, NDVI measures are retained in most of the best fitting multiple spatial regression models (table 2), the exceptions being models of predator species richness and those of all but the smallest species, and all their non-spatial equivalents (Electronic Appendix). This indicates that species richness does respond to productive energy availability. This comparison is also compatible with the suggestion that GLS is more sensitive to correlation between predictor variables than OLS (Diniz-Filho *et al.* 2003), but a full investigation of this issue is beyond the scope of this paper.

For most groups of the British avifauna, species richness is related to NDVI along a positive decelerating curve (tables 1 and 2, figure 1). However, one third of species groups (10 out of 29) exhibit a positive linear species–NDVI relationship (tables 1 and 2). Similarly, in 11 of our species groups, assessment of whether linear models provide a better fit to the data than ones containing a square term depends on whether annual or summer NDVI measures are used (table 1). The form of the species–energy relationship thus seems to be more sensitive to the seasonal nature of NDVI measures than those of temperature; this is expected given the closer correlation between annual and summer temperature ($r^2=92\%$) than between summer and annual NDVI ($r^2=73\%$).

Across the entire assemblage the species–energy relationship was moderately strong ($r^2=30\%$); however, our species groups exhibited much variation in the strength of their species–energy relationships, with pseudo r^2 values ranging from less than 5% to over 75%, and this variation is not related to differences in the number of species comprising each grouping (table 2). Species–energy relationships were much stronger in passerines than non-passerine orders (tables 1 and 2). The latter comprise a range of evolutionary groups of varying levels of relatedness. Other studies have reported strong species–energy relationships in non-passerines, such as in South American owls (Diniz-Filho *et al.* 2004) and established exotic birds in Britain (Evans *et al.* 2005*d*), and a link between taxonomy and the strength of species–energy relationships is unlikely to be simple. The difference that we find does, however, suggest that biases in the distribution of ecological traits between taxonomic groups may result in the latter exhibiting species–energy relationships of varying strength. The dataset that we analyse, however, contains insufficient species to justify analyses conducted on smaller taxonomic groups, such as families.

Long distance migrants and residents exhibited species–energy relationships of similar strengths. In contrast to most species groups, the species richness of long distance migrants was more closely related to summer rather than annual NDVI (table 1), and whilst the difference in fit is relatively small this is compatible with Rabenold's (1979, 1993) suggestion that long-distance migrants may be able to respond better to seasonal flushes of productive energy than long-distance residents. A similar trend was not, however, apparent in short-distance migrants (table 1), a group which had a weak species–energy relationship (table 2). This weak relationship may be, in part, because this group comprised many species that breed in high altitude moorland regions with low temperatures and plant productivity.

Species with relatively broad niches exhibited stronger species–energy relationships than those with narrower ones (tables 1 and 2). There was a similar trend, albeit less noticeable, for species that used more widespread resources, i.e. have low niche positions, to have stronger species–energy relationships than those that used relatively scarce resources (tables 1 and 2). Although we lack niche breadth and position data for many of the species that we consider, our data incorporate a wide range of values and it appears unlikely that the conclusions are influenced by data availability. These patterns are not consistent with suggestions that high-energy areas contain more species because increased energy availability promotes the occurrence of viable populations of specialized species (Abrams 1995; also see Vázquez & Stevens 2004; Evans *et al.* 2005*c*).

Trophic position exerts a marked influence on the strength of the species–energy relationship, with herbivores and omnivores exhibiting similar relationships to each other that were much stronger than those of invertebrate and vertebrate predators (tables 1 and 2). These patterns are not those predicted by the suggestion that high energy levels promote species richness by increasing the number of trophic levels in an assemblage (Oksanen *et al.* 1981; Fretwell 1987).

Species groups that have undergone marked population declines (red-listed species) or occupy highly modified habitats (farmland species) exhibit species–energy relationships that are as strong as those with stable population trends (green listed species) or those occupying moderately modified habitats (such as woodland). However, species characteristic of other even less modified habitats, or that have experienced moderate population declines, have much weaker species–energy relationships. These findings suggest that there is no simple correlation between habitat modification/population trends and the strength of the species–energy relationship.

Species–energy relationships were strongest in the commonest species and their strength declined consistently across quartiles of species abundances. This confirms the results of previous work, which used temperature in isolation as a measure of energy availability, reporting stronger species–energy relationships in the most abundant species (Evans *et al.* 2005*c*). Generally, there is a negative correlation between body-size and population size (Damuth 1981), and such a pattern has been demonstrated in British birds (Blackburn *et al.* 1996); this may contribute to the finding that the smaller bodied species exhibit the strongest species–energy relationship. Similarly, British bird species with a low niche position, but not those with a broad niche breadth, tend to be common (Gregory & Gaston 2000); and, although this correlation is noisy, this may partly explain why species with a low niche position exhibit the strongest species–energy relationships.

The more individuals hypothesis (MIH; Wright 1983) is one of the most frequently cited explanations for species–energy relationships. It states that high-energy availability increases resource abundance enabling species to maintain larger populations, which are thus buffered from extinction, consequentially promoting species richness. Extinction risk is linked to population size by a negative decelerating function (Lande 1993), thus the MIH predicts that the rarest species should exhibit the strongest species–energy relationship. Our data do not support this pattern, concurring with other work that questions the extent to which the MIH acts as a general and sole driver of species–energy relationships in British birds (Evans *et al.* 2005*a*,*b*), and more widely (Currie *et al.* 2004).

In summary, we present the first comprehensive analysis that dissects the species–energy relationship into its component parts, on the basis of the ecological and taxonomic characteristics of its constituent species, whilst using a range of energy metrics. Doing so enables us to test hypotheses relating to the poorly known underlying causal mechanisms of species–energy relationships (Currie *et al.* 2004; Evans *et al.* 2005*b*,*c*). Our data are not compatible with suggestions that high levels of energy availability increase species richness by increasing population sizes, or the numbers of predatory and specialist species. Other causal explanations of species–energy relationships have been proposed. The range limitation hypothesis suggests that more species may occur in high-energy areas, particularly warm ones, as more species are physiologically able to maintain viable populations in such conditions (Kerr *et al.* 1998; Evans *et al.* 2005*b*,*c*). In addition, the dynamic equilibrium hypothesis suggests that high levels of productive energy may enable species populations to recover more rapidly from disturbances which, depending on the frequency of disturbance events, may generate positive species–energy relationships (Huston 1979; Evans *et al.* 2005*c*). These alternative hypotheses would merit testing in future investigations of the mechanisms driving the species–energy relationship amongst British breeding birds.

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