RESEARCH PAPER

Energy availability, abundance, energy-use and species richness in forest bird communities: a test of the species–energy theory

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ABSTRACT

Aim To test the 'more individuals hypothesis' as a mechanism for the positive association between energy availability and species richness. This hypothesis predicts that total density and energy use in communities is linearly related to energy availability, and that species richness is a positive function of increased density. We also evaluate whether similar energy–density patterns apply to different migratory groups (residents, short-distance migrants and tropical migrants) separately.

Location European and North American forest bird communities.

Methods We collected published breeding bird census data from Europe and North America ($n = 187$). From each census data we calculated bird density (pairs 10 ha^{-1}), energy use by the community (the sum of metabolic needs of individuals, Watts 10 ha^{-1}) and geographical location with an accuracy of 0.5°. For each bird census data coordinate we extracted the corresponding monthly values of actual evapotranspiration (AET). From these values we calculated corresponding AET values that we expected to explain the density energy use of forest birds: total annual, breeding season (June) and winter AET. We used general linear modelling to analyse these data controlling for the area of census plots, forest type and census method.

Results Total density and energy use in European and North American forest bird communities were linear functions of annual productivity, and increased density and energy use then translated into more species. Also resident bird density and energy consumption were positive functions of annual productivity, but the relationship between productivity and density as well as between productivity and energy use was weaker for migrants.

Main conclusions Our results are consistent with the more individuals hypothesis that density and energy use in breeding forest bird communities is coupled tightly with the productivity of the environment, and that increased density and energy consumption results in more species. However, not all community members (migratory groups) are limited by productivity on the breeding grounds.

Keywords
Body size, Europe, migrant birds, more individuals hypothesis, North America, productivity, resident birds, spatial autocorrelation, species interactions.

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INTRODUCTION

Geographical variation in species diversity has been studied intensively for almost two centuries (e.g. von Humboldt, 1808; Wallace, 1878). The best-known pattern is a gradient of increasing species richness toward the tropics, which is observed at several spatial scales, from local communities to continental species pools, and in many animal and plant taxa (Hillebrand, 2004). Longitudinal variation among regions at the same latitude has also been well described (Currie & Paquin, 1987; Latham & Ricklefs, 1993; Huntley, 1994; Mönkkönen & Viro, 1997). A plethora of hypotheses exists to explain this variation (e.g. reviewed by Pianka, 1966; Rohde, 1992; Rosenzweig, 1995; Willig *et al.*, 2003) and new ones continue to appear (Ritchie & Olff, 1999; Colwell & Lees, 2000).

Presumably no single factor explains geographical gradients in species richness, but some will be more important than others. Climate-related factors have gained much attention and empirical support as the main determinants of geographical variation in species richness in many groups of animals and plants (Currie & Paquin, 1987; Currie, 1991; Rohde, 1992; Wright *et al.*, 1993; Rosenzweig, 1995; Mittelbach *et al.*, 2001; Rahbek & Graves, 2001; Hawkins *et al.*, 2003a,b; Currie *et al.*, 2004). For example, Hawkins *et al.* (2003a) found that annual actual evapotranspiration (AET) alone explained more than 70% of the variation in global avian species richness. Positive associations between measures of energy availability and species richness support the species–energy theory (SET) as envisaged by Wright (1983). In short, this theory states that where more energy is available, more species will exist. However, surprisingly little is known about the mechanisms involved (Willig *et al.*, 2003): how can increasing energy materialize into more species?

A potential mechanism to translate energy availability into species numbers is provided by the 'more individuals hypothesis' (MIH; Srivastava & Lawton, 1998), which assumes that increasing energy availability leads to increased abundance of consumers, which translates in turn into higher species richness because a larger number of species can obtain a population size that exceeds some minimum viable size (see also Evans *et al.*, 2005a,b). Central to this explanation is the assumption of tight linkage between abundance and energy availability and there is some empirical support for such a relationship (e.g. Kaspari *et al.*, 2000; Hurlbert, 2004; Pautasso & Gaston, 2005). Hubbell's 'unified neutral theory of biodiversity and biogeography' provides an evolutionary explanation for a positive relationship between abundance and species richness by arguing that 'the number of new species arising per unit time is a function of the total number of individuals in the metacommunity' (Hubbell, 2001; p. 236).

The positive relationship between energy availability and abundance of consumers is not a sufficient condition, however, because abundance is not synonymous with energy consumption of the community. Individual energy requirements differ greatly between species according to body size, for example (see, e.g. Peters, 1983), and increased energy availability may be consumed by an equal number of consumers of larger body size. Species diversity examinations that treat each species equally relative to the explaining factor(s) may lead to biased and potentially flawed results. Thus, it is important to study whether increased availability of energy supports more individuals, or larger individuals at a constant density. Testing for this latter alternative would also increase considerably our understanding of factors driving the global diversity gradients. Another potential caveat of the species–energy relationship is that many species escape the lean conditions of the non-reproductive season either in space or time (e.g. migration, winter torpor or dormancy). Therefore, species with different ecologies may not be affected equally by the same measures of productivity and energy availability.

Extra-tropical bird communities provide a useful system to examine the above-mentioned questions, as they consist of species of different body size and with different migratory strategies. The basic pattern is that the proportion of migrant species increases with latitude (MacArthur, 1959; Herrera, 1978; Helle & Fuller, 1988; Newton & Dale, 1996a,b). Species with different migratory habits may not be affected equally by the energy availability on their breeding grounds. Therefore, climatic variables influencing population densities and, ultimately, species richness are not necessarily the same for migrant and sedentary species. Populations of resident species are probably limited by the conditions of the non-breeding season (Lack, 1966; Fretwell, 1972; Forsman & Mönkkönen, 2003), whereas migrant densities and diversity cannot be associated directly with winter climate on their breeding grounds. We argue that better insight into factors affecting abundance and species richness can be achieved if migratory groups are analysed separately.

That the assembly of temperate breeding bird communities is composed of species with different migratory habits, and hierarchical occupation of resources for the reproductive period, invokes the idea of species interactions. Traditional thinking assumes that migrants use the part of energy that is left over from residents that have a prior access to local resources and therefore enjoy a better resource-holding capacity in interactions (MacArthur, 1972; Herrera, 1978). This mechanism has been implicated in the northwards increasing proportion of migrant birds in temperate breeding assemblages. Because of competition, migrant densities and species richness are low in areas where winter climate allows relatively high resident populations in relation to breeding season productivity. Indeed, in a recent geographical analysis Hurlbert and Haskell (2003) examined species numbers of resident and migratory birds in North America relative to the seasonality of the environment and found that resident species seemed to dominate the resources in the most aseasonal environments in which their species richness peaked, whereas the number of migrant species was highest where the difference between summer and winter production was greatest. However, before species interactions manifest themselves in the number of co-existing species in local communities, they first must affect population densities.

In this paper, using published data on European and North American forest bird breeding communities, we test specifically the necessary assumptions of the more individuals hypothesis theory that total density (number of individuals per unit area) by birds is related linearly to energy availability (plant productivity, estimated as actual evapotranspiration), and that species richness is a positive function of increased density. We also study whether energy consumption (amount of energy consumed per unit area) is related to energy availability and whether or not this association is because of changes in average body size with productivity. Energy use by birds is estimated by transforming species body sizes to metabolic rates and multiplying these by the density of each species. We expect that energy use should be related more directly to energy availability than mere densities, as metabolic rate (i.e. energy requirement) is related allometrically to body size and, thus, one pair of thrushes consumes about four times more energy than one pair of warblers. Therefore, increasing energy availability may not result in a linear increase in density if average body size increases with energy availability.

Secondly, we evaluate whether this same pattern applies to different migratory groups (residents, short-distance migrants and tropical migrants) separately. We expect that resident density and energy use will be related more directly to energy availability on their breeding grounds than those of migrants because of prior access to resources by residents. Conversely, density and energy use by migrant birds should be a function of both energy availability and the amount of left-over energy from the residents. Migrant density and energy use are expected to be positive functions of seasonality, i.e. the difference between energy availability in the breeding season and winter.

MATERIALS AND METHODS

Data

We collected breeding bird census data from Europe ($n = 89$) and North America ($n = 98$). A list of the data sources used is available in Appendix S1 (see Supplementary Material). We selected only censuses conducted in mature forests (age > 100 years and/or height > 20 m) to control for the effects of seral (successional) stage. In Europe, the data represent geographical variation from *c.* 42° N (Spain) to 69° N (N. Finland), and from 5° W (Great Britain) to 33° E (western Russia). In North America, the southernmost and the northernmost data points were derived from the latitude of *c.* 31° N and *c.* 63° N, respectively, and longitudinally the data originate from 66° W to 129° W. Therefore, both European and North American data sets represent a corresponding amount of latitudinal (about 30°) variation.

The censuses were categorized into three broad groups according to the composition of the forest. We distinguished deciduous, mixed deciduous–conifer and conifer forests. We acknowledge that this categorization is somewhat crude, but the observation that bird community composition varies among forest types (e.g. Mönkkönen, 1994) indicates that categorization is necessary. These categories represent a gradient from high productivity (deciduous forests) to low productivity sites (conifer forests) and therefore including this factor into the models controls to some extent for local variation in productivity.

From each survey and species we extracted bird density (pairs 10 ha^{-1}; Table 1), area of the census plot (range 2.9–272 ha, mean 31.2 ha) and geographical location with an accuracy of 0.5°. Here, forest birds include woodpeckers (Piciformes), cuckoos (Cuculiformes) and passerines (Passeriformes) but not swallows (Hirundinidae), which were excluded as not being true forest birds. We focused on these bird groups because the standard census methods provide reliable abundance estimates only for these taxa. The three included taxa comprise more than 90% of total abundance and more than 80% of all species in both European and North American survey data.

Bird species were categorized into three migratory habit groups using information in Marshall and Richmond (1992) and Snow and Perrins (1998). Tropical migrants are species whose wintering areas are completely in the tropics or subtropics. Residents include only permanent resident species whose distributions show no difference between summer and winter. All other

Table 1 Mean (range) values of density (pairs 10 ha^{-1}), energy use (Watts 10 ha^{-1}) and energy availability (AET; mm year^{-1}) in European and North American data

	Europe	North America
Total density	49.9 (4.1–146.2)	53.7 (9.7–128.7)
Residents	19.0 (0.7–80.0)	8.2 (0–49.5)
Short-distance migrants	22.4 (1.7–68.9)	14.0 (0–64.5)
Tropical migrants	8.5 (0–46.5)	31.6 (4.3–90.5)
Total energy use	24.7 (1.8–105.7)	23.5 (4.9–88.0)
Residents	5.6 (0.1–37.8)	3.8 (0–18.4)
Short-distance migrants	16.3 (1.0–66.1)	8.2 (0–63.2)
Tropical migrants	2.8 (0–21.8)	11.6 (1.1–36.5)
Annual AET	396 (173–618)	654 (203–1166)
Winter AET	2 (0–13)	17 (0–100)
June AET	84 (54–112)	118 (46–162)

species were treated as short-distance migrants. Species that have both tropical and short-distance migrant populations were considered short-distance migrants. We acknowledge that migratory habit is actually a gradient from truly permanent resident species to highly migratory species, but this categorization makes possible quantifiable comparisons between geographical locations.

We consulted Dunning (1993) to obtain body size estimates for each species. Energy use scales to body size as $E_i = cM_i^b$, where E_i is energy requirement of an individual in species i (Watts), M_i is body mass in kg, and c and b are taxon-specific constants. We used values $c = 4.0$ and $b = 0.73$ for nonpasserine birds, and $c = 7.0$ and $b = 0.72$ for passerine birds (Peters, 1983). Total energy use of a community or migratory group E_{tot} is the sum of metabolic needs of individuals, that is $E_{tot} = \Sigma N_i E_i$ where N_i is the density of the *i*-th species (Watts 10 ha^{-1}; Table 1).

We use actual evapotranspiration, which is a measure of energy–water balance of a location, as the estimate of net primary productivity. Data on actual evapotranspiration (AET, measured in mm time^{-1} units) were obtained from the data set compiled by Ahn and Tateishi (1994), which covers the entire globe at the resolution of 0.5°. This data set is available online from the United Nations Environmental Program (UNEP; http://www.grid.unep.ch/data/grid/climate.php). For each bird census data coordinate we extracted the corresponding monthly values of AET. From these values we calculated corresponding AET values that we expected to explain the density and energy use of forest birds: total annual, breeding season (June) and winter AET. Winter AET is the productivity for months from December to February. In most species and areas breeding activities peak in June, and June AET was used in analyses representing breeding season productivity. In many southern temperate areas, however, birds may start their breeding as early as April but because of multicollinearity among AET values, using any combination of breeding season AET from April to June — either alone or summed — yielded similar results. For simplicity, only June AET was used. We estimated seasonality as the difference between June AET and winter AET.

Analyses

We employed general linear modelling to test the hypotheses. We entered region (Europe vs. North America) into the models. The two continents provide independent tests for the consistency of the proposed energy availability–consumption associations derived from the species–energy theory. We also entered the forest type (three categories) and the area of survey plot (log-transformed), and retained them in the model if significant. It is well known that species richness increases linearly with the area on log-scale (e.g. Rosenzweig, 1995). Density tends to decrease with the area over which populations are censused (Gaston *et al.*, 1999). We also included census method (three categories: territory mapping, point count, line transect) into the models but in no case was this term significant, and therefore it was excluded from the final models to keep the models as simple as possible.

We then tested which — if any — AET variables could be included into the models. We entered annual AET, winter AET and June AET one by one. We used Akaike's information criterion (AIC; see Burnham & Anderson, 2002) to select the best-fitting model that minimizes AIC among the models with alternative AET estimates. We also included the interaction between the region and productivity (AET) to check whether the effect of productivity on body size, density, energy use or species richness is consistent between the two continents. The interaction term was retained in the model if significant.

To test the idea that migrant density and energy use are determined by the amount of energy not consumed by residents, we examined whether the density and energy use of migrants is a function of seasonality [log(June AET–winter AET)]. We fitted models including region, forest type, census plot area and June AET together with seasonality as a covariate. We also included two interaction terms, region × seasonality and June AET × seasonality. The former interaction term tests for consistency of the seasonality effects on the two continents. The latter controls for the possibility that the effects of seasonality differ at different levels of breeding season productivity, e.g. stronger dependence on seasonality at low levels of breeding season productivity. Interaction terms were retained in the models if significant. Finally, all model residuals were tested for normality, and no deviations from normality were observed.

Density, energy use, body size, species richness and productivity (AET) values were log-transformed. The hypotheses we tested predict linear or at least monotonic increase in density and energy use with productivity, and linear or monotonic increase in species richness with density and energy use. When back-transformed to linear scale, slopes significantly less than unity indicate asymptotic and larger than unity exponential relationships.

Spatial autocorrelation potentially biases the analyses of these geographical data because of the inflated number of degrees of freedom in statistical tests resulting from non-independence of observations. We therefore adjusted sample sizes using the method of Clifford *et al.* (1989; see also Fortin & Dale, 2005) to avoid Type I errors. We estimated the effective sample sizes using the equation:

$$N' = \frac{N^2}{N + 2\sum_{d=1}^{N-1}(N-d)r(d)}, \qquad \text{eqn 1}$$

where N is the original sample size and r is correlation calculated for each lag, d. We used 10 lags with 300 km increments for both continents. Lag increment was selected to equalize the number of connections among lags. Degrees of freedom of the error term (d.f.2) was subsequently adjusted as $N'-k$, where $N' =$ adjusted number of observations and k is the number of parameters (including constant) in the model. These adjusted values were used in assessing the significance of the models and their parameters, and are reported below.

Assumptions

We have made some assumptions in the process of selecting appropriate explaining variables, in statistical analyses and in estimating the effect of explanatory factors on response variables that affect the reliability of the results. First, we assume that annual and seasonal productivity as measured by AET determines the energy available that is important to a bird community. AET has been the best explanatory variable of bird species diversity in earlier studies (Hawkins *et al.*, 2003a,b), and therefore for evaluating the species–energy theory it is reasonable to test whether density and energy use is also a function of AET.

The second assumption is that the proportion of total energy supply in the environment that birds can use is related directly to plant productivity. This assumption is difficult to test, but the result by Meehan *et al.* (2004) that total abundance in North American winter bird communities is related positively to annual productivity suggests that the assumption is probably valid. In addition, avian energy consumption of the net primary production apparently varies very little (0.12–0.18%) among different geographical locations and communities (Holmes & Sturges, 1975; Weiner & Glowacinski, 1975; Alatalo, 1978), suggesting that this assumption does not bias the results.

Thirdly, we used AET as the estimate of net primary productivity. This may not be the most accurate estimate of energy actually available to consumers (Jetz & Rahbek, 2002), but still correlates strongly with plant productivity of the location (Rosenzweig, 1968). AET data are available at 0.5° resolution and we assumed that these data are representative for the much smaller plot from which the density data come. This is not ideal, but is common practice in macroecological studies (see, e.g. Jetz & Rahbek, 2002; Pautasso & Gaston, 2005). This mismatch of scales presumably adds environmental noise to the data, therefore making the analyses conservative, but does not jeopardize any of the conclusions. Including forest type as a categorical variable addresses this problem to some extent.

Fourthly, to estimate avian energy consumption we used coefficients taken from Peters (1983) for field metabolic rate. We controlled only for the difference between passerines and non-passerines in the coefficients but in reality the scaling intercept c, for example, varies considerably with ambient temperature and differs across dietary groups (Anderson & Jetz, 2005). However,

breeding assemblages of birds in the temperate and boreal forests are homogeneous in terms of dietary groups, being composed mainly of insectivores (Helle & Mönkkönen, 1990). Therefore, even though we admit that the estimates we use are crude approximations of true energy consumption by bird assemblages, we believe that our conclusions would not change qualitatively even if species-specific and condition-specific variation in scaling coefficients were taken into account.

RESULTS

Density and energy use

Mean total density and energy use by breeding forest bird communities in Europe and North America is almost identical, but the density and amount of energy used by different migratory groups differs markedly (Table 1). In North America tropical migrants comprise on average more than 50% of breeding density and consume about 50% of the energy. Conversely, in Europe short-distance migrants' and residents' relative share of density and energy consumption is marked. Annual AET for our data points is on average 1.7 higher and winter AET about nine times higher in North America than in Europe (Table 1), showing that our European data originate on average from less productive environments (i.e. more arid and further north).

The final models explained about 40% of the variation in density and energy use by total communities (Table 2). There was a significant regional effect, suggesting that after controlling for other variables in the model, densities and energy use levels were higher in Europe than in North America. Forest type, a proxy for

Table 2 General linear models of density and energy use by the total communities and for migratory groups separately testing the hypothesis that density and energy use in forest bird communities are functions of productivity. Abbreviations: annual AET = annual actual evapotranspiration. Expl. = adjusted coefficient of determination (R^2) for the total model and partial η^2 for individual terms describing the proportion of the total variability that is attributable to each term. Slope and its 95% confidence intervals (95% CI) are given for continuous independent variables. Degrees of freedom of the *F*-statistics: for continuous variables d.f.1 = 1, for region d.f.1 = 1 and for forest type d.f.1 = 2; adjusted degrees of freedom of the error term (d.f.2) is given for each model

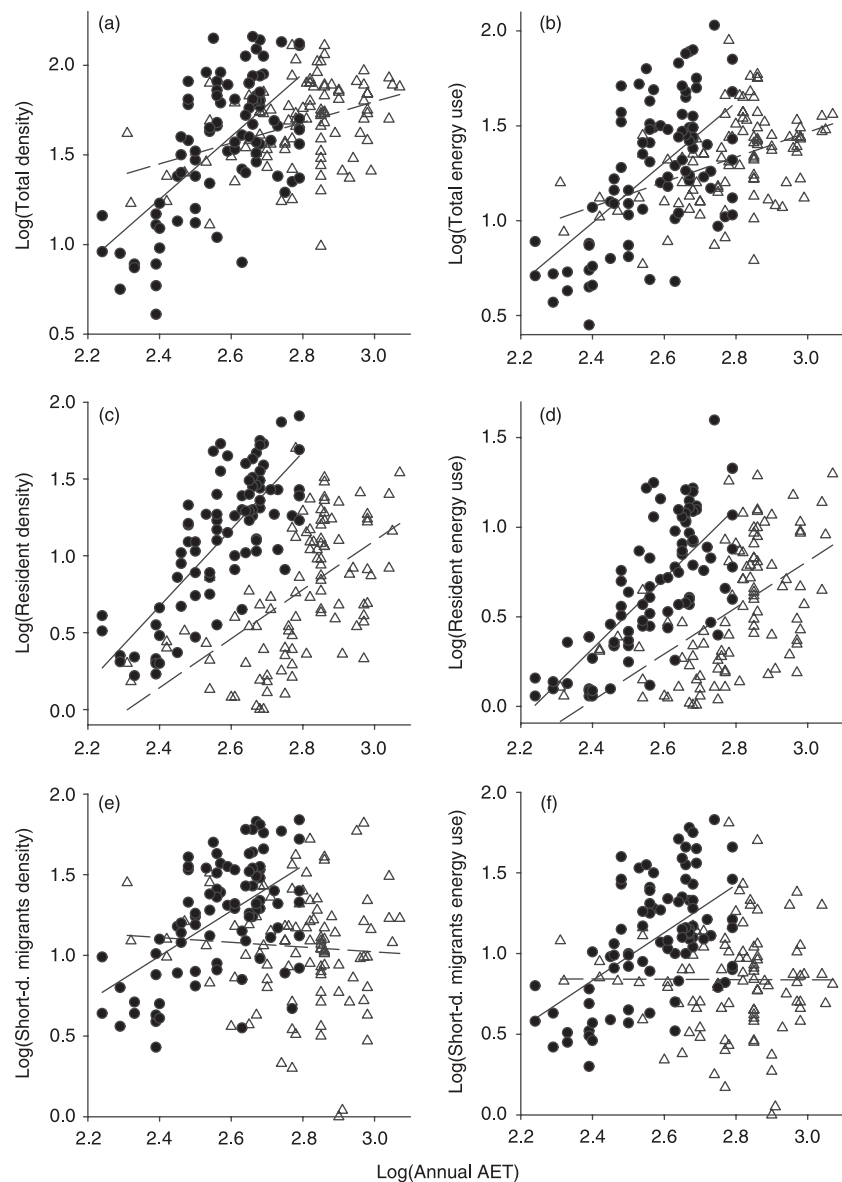|	Density					Energy use				
	F	*P*	Expl.	Slope	95% CI	*F*	*P*	Expl.	Slope	95% CI
All species										
Complete model	23.4	< 0.001	0.42			22.4	< 0.001	0.41		
Region	10.1	0.003	0.05			4.6	0.038	0.03		
Forest type	2.7	0.077	0.03			6.7	0.003	0.07		
Log(plot area)	17.6	< 0.001	0.09	−0.23		17.5	< 0.001	0.09	−0.23	
Log(annual AET)	38.2	< 0.001	0.18	1.27	0.87–1.68	30.1	< 0.001	0.14	1.04	0.64–1.44
Region × log(annual AET)	11.4	0.002	0.06			5.8	0.021	0.03		
		d.f.2 = 42					d.f.2 = 36			
Residents										
Complete model	59.5	< 0.001	0.62			42.6	< 0.001	0.54		
Region	214.8	< 0.001	0.54			104.2	< 0.001	0.37		
Forest type	8.4	0.002	0.09			10.3	0.001	0.10		
Log(plot area)	23.3	< 0.001	0.11	−0.32		18.6	< 0.001	0.09	−0.25	
Log(annual AET)	81.3	< 0.001	0.31	1.48	1.16–1.81	64.0	< 0.001	0.26	1.14	0.86–1.31
		d.f.2 = 22					d.f.2 = 22			
Short-distance migrants										
Complete model	13.1	< 0.001	0.21			19.4	< 0.001	0.28		
Region	13.3	< 0.001	0.07			11.1	0.002	0.06		
Log(plot area)	4.5	0.037	0.02	−0.16		8.0	0.007	0.04	−0.20	
Log(annual AET)	7.7	0.007	0.04	1.18	0.63–1.72	10.9	0.002	0.06	1.19	0.67–1.71
Region × log(annual AET)	15.9	< 0.001	0.08			14.5	< 0.001	0.07		
		d.f.2 = 87					d.f.2 = 50			
Tropical migrants										
Complete model	33.5	< 0.001	0.51			42.1	< 0.001	0.58		
Region	7.1	0.009	0.04			8.9	0.004	0.05		
Forest type	4.0	0.022	0.04			7.5	0.001	0.08		
Log(plot area)	5.7	0.019	0.03	−0.19		5.2	0.027	0.03	−0.14	
Log(annual AET)	2.0	0.162	0.01	−0.87	−1.45 to −0.29	0.06	0.810	0.00	−0.55	−1.01 to −0.10
Region × log(annual AET)	11.0	0.001	0.06			13.2	< 0.001	0.07		
		d.f.2 = 75					d.f.2 = 49			

Figure 1 Relationships between annual AET and density (left panels) and energy use (right panels) for total density (a) and energy use (b), density (c) and energy use (d) by residents, and density (e) and energy use (f) by short-distance migrants. Filled dots and continuous line represent European data while open triangles and dashed line represent North American data.

local productivity, was also significant, the general pattern being that density and energy consumption levels were highest in deciduous forests, lowest in conifer forests and intermediate in mixed forests. Census plot area had a significant negative effect — as expected — on density and energy use.

As predicted by MIH, total density and energy use were related positively to annual evapotranspiration (with annual AET, density model AIC = −223.6, energy use model AIC = −226.5; corresponding AIC values for models with June AET were −215.2 and −221.3, and with winter AET −207.1 and −217.9, respectively). Overall slopes did not differ from unity, indicating a linear relationship between productivity and density (Fig. 1a, Table 2) as well as between productivity and energy use (Fig. 1b, Table 2). Annual AET was a major determinant of total density and energy use (see partial eta squared, η^2, in Table 2). A significant interaction term between region and annual AET indicates that slopes differ between the two continents. When analysed separately the

results showed steeper slopes for Europe (density: slope = 1.11, 95% confidence interval 0.63–1.59; energy use: slope = 0.90, 95% CI 0.42–1.38) than for North America, where the slopes were significantly less than unity (density: slope = 0.53, 95% CI 0.23–0.82; energy use: slope = 0.54, 95% CI 0.25–0.83). This suggests that in North America the relationship between productivity and density and between productivity and energy use is asymptotic. Average body size was related positively to the winter AET (slope 0.04, $F_{1,79}$ = 5.4, P = 0.023; the best fit model also included region and forest type) but not to other measures of productivity. That is, average body size increases about 20% from about 28 g at minimum winter productivity to about 34 g at maximum winter productivity.

Resident density and energy use were best explained by annual AET (AIC = −190.8 and −214.3, with winter AET AIC = 179.8 and −206.3; June AET AIC = −177.2 and −203.0), and the models were able to explain 54–62% of the variation (Table 2). Regional

effect (Table 1) and annual AET were the most important determinants of resident density and energy use. The slope for resident density was similar on both continents (region × annual AET interaction term was not significant) but significantly larger than unity, indicating exponential relationships on a linear scale (Table 2, Fig. 1c). For resident energy use the slope of annual AET was not different from unity (Table 2, Fig. 1d). In other words, at high levels of annual productivity resident density was not limited by energy availability but their energy use was. However, resident body size was not related to any of the productivity estimates.

Models for short-distance migrants included, in addition to region and plot area effects, annual AET (with annual AET, density model AIC = −174.3, energy use model AIC = −180.9; corresponding AIC values for models with June AET were −172.1 and −176.8, and with winter AET −167.4 and −175.3, respectively). Overall coefficients of determination were low compared with the models for other migratory groups, and only about 5% of the variation in the density and energy of short-distance migrants was attributable to annual AET (Table 2). The interaction effect of region and annual AET was significant. In Europe, short-distance migrants' density and energy use were associated with annual AET, but in North America no effect of productivity was found (Fig. 1e,f). In Europe, the regression slopes for density (1.13; 95% CI 0.62–1.64) and energy use (1.12; 95% CI 0.61–1.63) did not deviate from unity, suggesting linear effects of productivity. The body size of short-distance migrants was not related to any of the productivity estimates.

All models for tropical migrants included the interaction term between region and productivity estimates, and an overall negative effect of productivity on density and energy use (see Table 2). Closer inspection of the model parameters clearly indicated opposite effects between the two continents of productivity on the density and energy use of tropical migrants. In Europe the best fit models for tropical migrants' density included census plot size and winter AET and also forest type for energy use (Table 3; density model AIC = −68.6; energy use model AIC = −91.0; corresponding AIC values for models including June AET −61.6 and −86.1, and with annual AET −61.8 and −86.6, respectively).

The models explained about one-fourth of the variation in tropical migrant density and energy use for winter AET, contributing a major share to the explained variation. However, the slopes for winter AET estimates in Europe were negative (Table 3). This is not biologically reasonable, and indicates that some factor other than productivity as measured by AET determines the density and energy use of tropical migrants in their European breeding communities.

In North American data, the best fit models included a positive effect of June AET on density and energy of tropical migrants (density model AIC = −110.7; energy use model AIC = −117.8; corresponding AIC values for models including annual AET were −108.9 and −116.9, and winter AET −105.4 and −113.3, respectively). For density the model included only June AET (Table 3; Fig. 2). The slope (95% CI 0.44–1.45) was not different from unity, and a linear pattern therefore applied. Energy use by North American tropical migrants was affected by forest type and June AET, and the slope of June AET (95% CI 0.35–1.36) indicated a linear relationship with productivity. June AET alone explained more than 10% of the variation in the density and energy use of tropical migrants in North America (Table 3).

The body size of tropical migrants on both continents was related positively to annual AET (slope 0.23, $F_{1,74} = 15.6$, $P < 0.001$; the best fit model included only annual AET). This means that the average body size of a tropical migrant increased by 50% from 14 g to 21 g along the range of annual AET of the data.

Seasonality and species richness

Models testing for the effects of seasonality on the density and energy of migrant birds were similar for short-distance and tropical migrants, and therefore we report here models for combined density and energy use of the two migrant groups. First, the interaction between region and seasonality could be dropped from the best fit model, indicating that the effects of seasonality are consistent on the two continents. The best fit models explained about one-third of the variation in migrant density and energy use, and included seasonality and interaction between

Table 3 Region-specific best fit models testing the hypothesis that tropical migrants' density and energy is a function of productivity; for abbreviations see Table 2

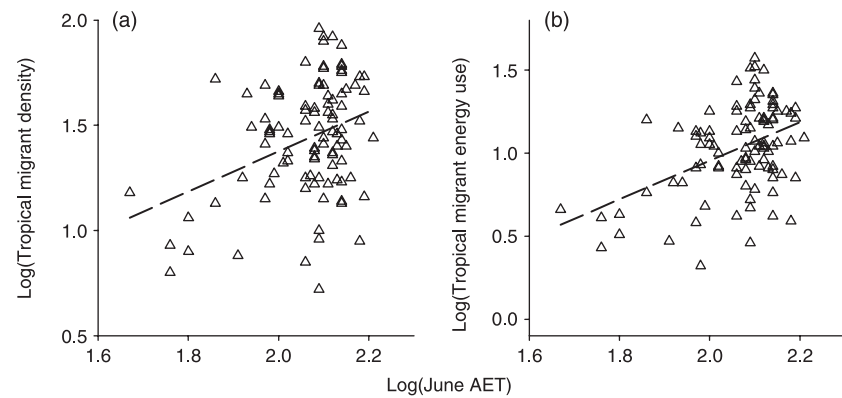|	Density					Energy use			
	F	*P*	Expl.	Slope		*F*	*P*	Expl.	Slope
Europe									
Complete model	12.6	0.001	0.23	−0.27	Complete model	6.5	0.002	0.24	
Log(plot area)	7.7	0.009	0.08	−0.27	Forest type	3.4	0.056	0.07	
Log(winter AET)	21.5	< 0.001	0.20	−0.53	Log(plot size)	4.5	0.048	0.05	−0.16
					Log(winter AET)	15.6	< 0.001	0.16	−0.33
		d.f.2 = 39					d.f.2 = 18		
North America									
					Complete model	10.9	< 0.001	0.26	
					Forest type	3.9	0.032	0.08	
Log(June AET)	13.9	< 0.001	0.13	0.95	Log(June AET)	11.4	0.002	0.11	0.86
		d.f.2 = 40					d.f.2 = 30		

Figure 2 Density (a) and energy use (b) by tropical migrants against June AET in North American forest bird communities.
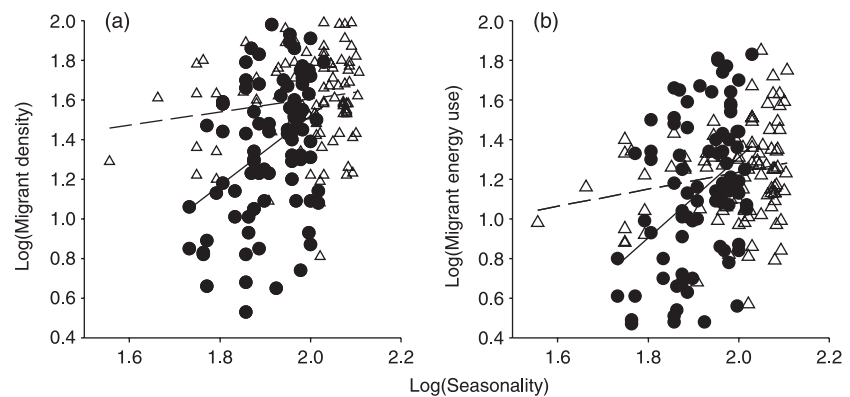

Figure 3 Density (a) and energy use (b) by migrants (short-distance and tropical migrants combined) against seasonality as measured by the difference in June and winter AET. For symbols, see Fig. 1.

Table 4 General linear models testing for seasonality [Log(season.)] effects on density and energy use of migrants; for abbreviations see Table 2

	Density					Energy use			
	F	P	Expl.	Slope		F	P	Expl.	Slope
Complete model	17.4	< 0.001	0.32		Complete model	13.8	< 0.001	0.32	
Region	8.8	0.004	0.05		Forest type	5.9	0.005	0.06	
Log(plot area)	25.3	< 0.001	0.12	−0.29	Log(plot area)	23.5	< 0.001	0.12	−0.29
Log(June AET)	8.4	0.005	0.04	9.3	Log(June AET)	7.0	0.011	0.04	7.9
Log(season.)	8.4	0.005	0.04	10.5	Log(season.)	7.3	0.010	0.04	8.9
Log(season.) × log(June AET)	7.8	0.006	0.04		Log(season.) × log(June AET)	6.0	0.018	0.04	
	d.f.2 = 80					d.f.2 = 48			

seasonality and June AET (Table 4). Migrant density and energy use increased with increasing seasonality (Fig. 3), and this increase was stronger at low levels of June AET. About 4% of the total variability in migrant density and energy use could be attributed to seasonality (Table 4).

Total species richness (Fig. 4) and species richness in migratory groups separately were all related positively to density and energy use (Table 5). In all models, density or energy use was a major determinant of species richness (partial η^2 varied between 24% and 50%; Table 5). For short-distance migrants' energy use and for tropical migrants the models include significant interaction between region and density/energy use, which reflected the pattern that slopes were steeper in Europe than in North America.

All slopes were still positive but significantly less than unity, suggesting asymptotic relationships between density and species richness, and energy use and species richness.

DISCUSSION

Our results are consistent with the 'species–energy theory' (SET; Wright, 1983) and one of its potential mechanisms, the 'more individuals hypothesis' (MIH; Srivastava & Lawton, 1998). First, total density and energy use in European and North American forest bird communities were linear functions of annual productivity. Although a positive correlation between available energy and population densities sounds intuitive, there is surprisingly
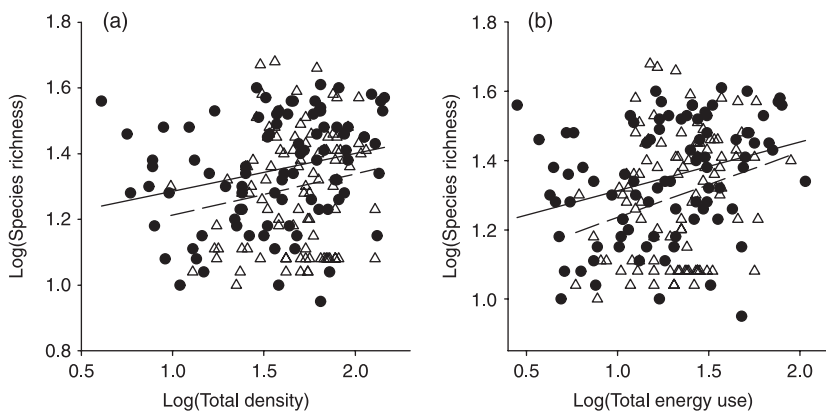
Figure 4 Total species richness plotted against total density (a) and energy use (b) in European and North American forest bird communities. For symbols, see Fig. 1.

Table 5 General linear models for species richness testing in the hypothesis that richness is a function of density and energy use in the bird communities; for abbreviations see Table 2

	Density					Energy use			
	F	*P*	Expl.	Slope		*F*	*P*	Expl.	Slope
Total species richness	38.1	< 0.001	0.44			50.1	< 0.001	0.51	
Forest type	6.2	0.003	0.06		Forest type	6.8	0.002	0.07	
Log(plot area)	130.2	< 0.001	0.42	0.35	Log(plot area)	159.4	< 0.001	0.47	0.35
Log(density)	56.8	< 0.001	0.24	0.28	Log(energy use)	91.4	< 0.001	0.33	0.34
		d.f.2 = 79					d.f.2 = 79		
Resident species richness	120.3	< 0.001	0.76			111.0	< 0.001	0.75	
Region	46.5	< 0.001	0.20		Region	117.17	< 0.001	0.39	
Forest type	5.4	0.008	0.06		Forest type	5.8	0.006	0.06	
Log(plot area)	83.2	< 0.001	0.31	0.29	Log(plot area)	70.5	< 0.001	0.28	0.27
Log(density)	183.5	< 0.001	0.50	0.38	Log(energy use)	161.8	< 0.001	0.47	0.44
		d.f.2 = 46					d.f.2 = 46		
SDM species richness	48.5	< 0.001	0.56			48.9	< 0.001	0.61	
Region	6.6	0.012	0.04		Region	0.15	0.700	0.00	
Forest type	7.0	0.002	0.07		Forest type	7.5	0.001	0.08	
Log(plot area)	111.2	< 0.001	0.38	0.36	Log(plot area)	122.9	< 0.001	0.41	0.37
Log(density)	137.1	< 0.001	0.43	0.39	Log(energy use)	167.7	< 0.001	0.48	0.35
					Log(energy use) × region	4.2	0.044	0.02	
		d.f.2 = 69					d.f.2 = 69		
TRM species richness	110.8	< 0.001	0.70			99.5	< 0.001	0.68	
Region	8.7	0.005	0.05		Region	12.8	0.001	0.07	
Log(plot area)	108.1	< 0.001	0.37	0.35	Log(plot area)	109.5	< 0.001	0.38	0.37
Log(density)	162.1	< 0.001	0.47	0.55	Log(energy use)	173.1	< 0.001	0.49	0.71
Log(density) × region	6.8	0.012	0.04		Log(energy use) × region	11.2	0.002	0.06	
		d.f.2 = 50					d.f.2 = 50		

little empirical evidence of such a pattern from large spatial scales. Many studies have examined the large-scale variation in densities of individual species (Currie & Fritz, 1993; Silva *et al.*, 1997, 2001; Johnson, 1998), but these analyses do not lend themselves to making far-reaching conclusions of the energy use by total communities. Hurlbert (2004) found qualitative support for the relationship between productivity and total abundance in North American grassland bird communities. Pautasso and Gaston (2005) reported that abundance, biomass and energy use increased in forest bird assemblages with increasing energy availability. Meehan *et al.* (2004) were able to show that total

abundance in North American winter bird assemblages increases with annual productivity, and decreases with the ambient winter temperature and with the average body mass of the members of assemblages, indicating energetic constraints on bird density. In our data, which encompassed whole breeding communities of forest-dwelling birds on two continents, strong positive associations between annual energy input and density as well as between annual energy input and energy consumption were clear. Secondly, our results showed that increased density and energy use then translated into more species. This provides support to the argument that energy-related factors are of importance in affecting

geographical patterns of bird species diversity (e.g. Hawkins *et al.*, 2003a,b).

Currie *et al.* (2004) found that in North American Breeding Bird Survey data total abundance is a positive function of productivity (AET) and species richness is a positive function of total abundance. Similar patterns were found in tree species data but not in butterflies. However, Currie *et al.* (2004) showed that species richness of birds (slope = 0.65 over most of the range of the data) and trees (slope = 1.19) accumulated much more quickly than predicted by the MIH. The predicted slope, which is based on Preston's (1948, 1962) 'canonical–log-normal' distribution, is 0.26 for log–log transformed data. We found a slope of 0.28 for density–richness relationship (see Table 5), which is adequately close to the predicted value. Pautasso and Gaston (2005) examined recently global bird census data similar to ours, and found exactly the same slope (0.28) for the total abundance–species richness relationship. Hurlbert (2004) also found slopes in Breeding Bird Survey data rather close to the predicted value (0.18 for forest birds and 0.33 for grassland birds). In sum, extant evidence is largely consistent with the MIH, particularly for birds, but deviations from the expected positive associations exist.

According to the MIH, increasing energy availability results in increased species richness because increased individual density allows a larger number of species to obtain viable population sizes and avoid local extinction (see also Evans *et al.*, 2005a,b). The positive association that we also found between density and species richness is not a unique prediction of MIH, however. If local assemblages are random samples from the regional pool of individuals and species, then species richness is expected to correlate positively with the number of individuals without a linkage to local extinction processes. Random sampling hypothesis and MIH are difficult to disentangle because both also predict that the number of rare species should respond to energy availability more strongly than common ones. Random sampling hypothesis, however, does not make any prediction about association between energy availability and the abundance of consumers. Therefore, the results that density and energy use are positive functions of energy availability require some other explanation than pure random sampling. Our results are also in line with Hubbell's (2001) evolutionary explanation that the number of (new) species is a function of the total number of individuals in the metacommunity, and a critical test among these alternative mechanisms is still missing.

In our data, density is a positive function of productivity and species richness is a positive function of density. Because the MIH assumes a causal pathway from productivity to density to species, a prediction is that proximal linkages (productivity–density; density–richness) are stronger than the distal linkage between productivity and richness (Currie *et al.*, 2004). This is actually the case in our data, where the model for species richness including annual AET together with forest type, region and plot area yields a coefficient of determination of 0.28, which is less than those for proximal models (0.42 and 0.44, see Tables 2 and 5).

The relationship between annual AET and total density as well as between annual AET and total energy consumption of the community was not linear in North American data, but a slope below unity suggests a levelling-off of the increase in density and energy use at high levels of productivity. This pattern may be because at high-energy areas territoriality, not energy, sets a limit to total abundance within species. In Europe, our data showed linear effects of productivity on total density and energy use by birds. On both continents species richness was a positive but asymptotic function of density and energy use. A similar abundance–species richness pattern was found by Hurlbert (2004) for North American forest and grassland bird communities. Combining the asymptotic energy–density/energy use relationship (in North America) and the asymptotic density/energy use–species relationships (both continents) suggests that at high energy areas species richness is not limited by energy availability, and other mechanisms than the MIH must also be involved in determining species richness. This result is in line with findings of nonlinear relationships between productivity and bird, mammal, amphibian and reptile species richness in the Holarctic region (Currie, 1991; Hawkins *et al.*, 2003a).

For resident birds our results were also as predicted by the MIH: resident density and energy consumption were positive functions of annual productivity. Slopes were similar on the two continents, for density significantly larger than unity and for energy use not different from unity. This suggests that at high levels of productivity resident density increases faster (exponentially) than energy use, which increases linearly. This should indicate that at high levels of annual productivity there is a disproportionately high density of residents of smaller body size. Our data, however, did not indicate any decrease in body size of residents with productivity.

Earlier studies have suggested that resident bird populations are limited by energy availability during winter (Lack, 1966; Fretwell, 1972), but our results indicate a larger role of annual productivity. For large parts of the geographical extent of our data, particularly from Europe, the winter AET is zero (50% of data points are zeros). This means that resident birds can survive only on the surplus of energy from the previous growing season(s). Therefore, for residents, winter productivity may not be the most crucial variable for survival but winter temperatures (Forsman & Mönkkönen, 2003) and the amount of total energy in the ecosystem (Meehan *et al.*, 2004). The dependency on the surplus and winter productivity correlate, as it is likely that the role of the surplus energy is higher in low winter productivity.

The overall pattern in our results was that the relationship between productivity and density as well as between productivity and energy use was weaker for migrants than for residents. The amount of variation explained by productivity-based models was lower and the slopes for productivity parameters were less steep. This applied particularly for short-distance migrants in North America, which showed no response to productivity, and for tropical migrants in Europe whose density and energy use were related negatively to large-scale productivity estimates. Apparently, migrants also respond to environmental variation other than primary productivity. The patterns for migrants support the idea that also in migrant birds winter conditions limit breeding season population size (Sherry *et al.*, 2005), and therefore

abundance and energy use in breeding communities is not necessarily a linear function of productivity during the breeding season. These patterns are consistent with our earlier analysis on the geographical density variation of these species groups. Tropical migrants showed little longitudinal variation, but a striking unimodal latitudinal pattern with densities peaking at mid-latitudes. We also found only very little large-scale geographical variation in the density of eastern North American short-distance migrants (Mönkkönen & Forsman, 2005).

Another potential explanation for the weaker relationship between energy availability and density for migrants than residents is the idea that migrants respond primarily to the presence and abundance of other species in the community in addition to productivity of the environment. Hurlbert and Haskell (2003) elaborated further the model developed originally by MacArthur (1972) and Herrera (1978), which suggests that resident populations are limited by the period of lowest productivity while migrant abundance then depends on the production not used by residents. According to these assumptions, Hurlbert and Haskell (2003) showed that the number and proportion of migrant bird species in communities in North America is associated positively with the seasonal pulse in productivity (the ratio of June production minus the minimum monthly production to June production; see also Rabenold, 1993). We found support for this idea, as migrant density and energy use were related positively to seasonality of the geographical location of their breeding communities. This relationship was more pronounced at low levels of breeding season productivity, as expected if interspecific interaction (competition between residents and migrants) is the mechanism. We emphasize, however, that correlative patterns at large geographical scales do not lend themselves to making far-reaching conclusions concerning processes at the local scale. Experimental studies have shown evidence for both competitive (Gustafsson, 1987; Martin & Martin, 2001) and positive interactions (Mönkkönen *et al.*, 1990; Forsman *et al.*, 1998, 2002; Mönkkönen & Forsman, 2002; Thomson *et al.*, 2003) among species in local bird communities.

We found a 50% increase in the average body size of tropical migrants along the annual AET gradient of our data, and a slight increase in overall mean body size with winter AET. This indicates that there is a shift in species composition along the productivity gradient so that larger-bodied (tropical migrant) species are more common in more productive environments. In North America, tropical migrant density was a positive function of June AET, thus increased energy availability in June is consumed by a larger number of tropical migrants of larger body size. Because average body size can vary with productivity, mere density estimates do not reflect fully energy consumption in assemblages, and diversity examinations that treat each species equal in energetic terms may yield considerably biased estimates on species–energy relationships.

To summarize, we found support for the prediction that density and energy use in breeding forest bird communities is coupled tightly with the productivity of the environment, and that increased density and energy consumption result in more species. Moreover, we were able to show that not all community members (migratory groups) are limited by productivity, and

that other mechanisms than the MIH are probably involved in the determination of species richness, particularly at high levels of primary productivity. These results suggest the importance of taking into account species different life history strategies in analyses of large scale species richness and abundance patterns.

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SUPPLEMENTARY MATERIAL

The following material is available online at www.blackwell-synergy.com/loi/geb

Appendix S1 Data sources for the European and North American census results used in this study