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Energy flux, body size and density in relation to bird species richness along an elevational gradient in Taiwan

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ABSTRACT

Aim To examine the species richness of breeding birds along a local elevational gradient and to test the following assumptions of the energy limitation hypothesis: (1) the energy flux through birds is positively correlated with above-ground net primary productivity, (2) bird density is positively correlated with total energy flux, and (3) bird species richness is positively correlated with bird density.

Location An elevational gradient from 1400 to 3700 m on Mt. Yushan, the highest mountain in Taiwan (23°28'30" N, 120°54'00" E), with a peak of 3952 m a.s.l.

Methods We established 50 sampling stations along the elevational gradient. From March to July 1992, we estimated the density of each bird species using the variable circular-plot method. Above-ground net primary productivity was modelled using monthly averages from weather data for the years 1961–90.

Results Bird species richness had a hump-shaped relationship with elevation and with net primary productivity. Bird energy flux was positively correlated with net primary productivity and bird species richness was positively correlated with bird density. The relationship between bird density and energy flux was hump-shaped, which does not support one assumption of the energy limitation hypothesis.

Main conclusions The results supported two essential assumptions of the energy limitation hypothesis. However, when energy availability exceeded a certain level, it could decrease species richness by increasing individual energy consumption, which reduced bird density. Thus, energy availability is a primary factor influencing bird species richness at this scale, but other factors, such as body size, could also play important roles.

Keywords

Altitude, biomass, body size, energy limitation hypothesis, primary productivity, species richness.

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INTRODUCTION

Patterns of species richness along elevational gradients have long been expected to parallel the patterns of species richness along latitudinal gradients (Stevens, 1992; Brown, 2001). Species richness should decrease with increasing elevation, just as it decreases with increasing latitude. Numerous studies have reported an inverse relationship between species richness and elevation (e.g. Able & Noon, 1976; Terborgh, 1977; Navarro, 1992; Patterson *et al.*, 1998). However, Rahbek (1995) reviewed 90 data sets that provided species richness patterns for a variety of taxa along elevational gradients and found that only 21% reported a monotonic decline in species richness with increasing elevation. Nearly half (49%) of the studies found that the rela-

tionship was hump-shaped and 25% reported no change in species richness until it decreased at the upper end of the range. McCoy (1990) reviewed studies on insect species richness along elevational gradients and concluded that a hump-shaped relationship was the most common relationship between elevation and species richness. Rahbek (1995) pointed out that changes in climatic conditions along elevational gradients are not identical to those along latitudinal gradients. The dramatic seasonal temperature differentials in arctic and temperate regions are not characteristic of most high mountains in tropical regions, although, based on vegetation type, areas on the mountains are often called arctic and temperate zones. In addition, most elevational gradients have an intermediate 'humidity peak' that is not typical of latitudinal gradients (Rahbek, 1995). A monotonically

inverse relationship between species richness and elevation may not be as universal as ecologists generally assumed. Explanations for latitudinal patterns of species richness may not apply to elevational patterns (Rahbek, 1995; Brown, 2001).

Numerous hypotheses have been proposed to explain the patterns of species richness along elevational gradients (examples in Heaney, 2001). One of the foremost is the energy limitation (Wright, 1983). Earlier ecologists (e.g. Hutchinson, 1959; MacArthur, 1965, 1972) proposed that energy availability limits the number of species a habitat can support. Wright (1983) combined the idea of energy limitation with island biogeography theory (MacArthur & Wilson, 1967) to develop a species–energy theory in which ‘area’ is replaced with ‘energy availability’ in the models of MacArthur and Wilson (1967). According to the species–energy theory (energy limitation hypothesis), an increase in net primary productivity (NPP) will increase the number of individuals of a consumer taxon that can be supported per unit area. As the density of a consumer taxon increases, population sizes increase, local extinction rates decrease, and thus, species richness of that consumer taxon increases. Many studies (e.g. Janzen *et al.*, 1976; Terborgh, 1977; Heaney, 2001) held that the energy limitation hypothesis could explain the patterns of species richness along elevational gradients. The monotonically inverse relationship (Terborgh, 1977), hump-shaped relationship (Janzen, 1973; Janzen *et al.*, 1976; Scott, 1976; McCoy, 1990; MdNor, 2001) and positive relationship (Sanders *et al.*, 2003) between species richness and elevation are believed to reflect the relationship between NPP and elevation.

Although the energy limitation hypothesis has gained both empirical and theoretical support (Currie, 1991; Wright *et al.*, 1993; Kaspari *et al.*, 2000), in the recent years, numerous empirical studies on a variety of organisms, ecosystems, and scales have found that the relationship between NPP and species richness is hump-shaped. That is, species richness increases with NPP when NPP is low, but decreases after NPP reaches a certain level (Rosenzweig, 1992, 1995; Waide *et al.*, 1999; Mittelbach *et al.*, 2001). Theoretically, in any ecosystem, if no energy was available for living organisms, there would be no species. Therefore, in every ecosystem, near the origin of species richness–productivity relationship, an increase in productivity is expected to increase the species richness, as predicted by the energy limitation hypothesis (Wright, 1983). However, if the species richness–productivity relationship is typically hump-shaped, why does species richness decrease after energy availability exceeds a certain level? Rosenzweig (1992, 1995) examined nine hypotheses and concluded that none of them adequately explained the decrease in species richness with high NPP.

If the energy limitation hypothesis is correct, the following relationships should also hold true. First, the energy flux of a consumer taxon should be positively correlated with the NPP of its habitat. If energy availability limits species richness, the energy flux into a consumer taxon or trophic group should be proportional to the energy available. Consumer groups must be able to exploit more if more resources are available. Second, the density of a consumer taxon should be positively correlated with its total energy flux. Again, if energy is limiting, then the more

energy consumed, the greater the number of individuals produced. Third, the species richness of a consumer taxon should be positively correlated with its density. Thus, more individuals of a taxon should allow more species to coexist because population sizes will be greater, which should decrease the local extinction rate. The relationship between individual abundance and species richness may follow logarithm or power functions (Srivastava & Lawton, 1998).

Few studies have dissected the relationships between energy flux, density and species richness. To test the energy limitation hypothesis, Srivastava and Lawton (1998) studied detritivorous aquatic insect communities in artificial tree holes. In general, they found support for the assumptions of the energy limitation hypothesis, but there were exceptions. Total density was not correlated with productivity in assembling experiments. This led them to conclude that the energy limitation hypothesis is not a sufficient explanation for the observed increase in species richness along the primary productivity gradient. It omits some important processes and factors, including dispersal, colonization, disturbance and body size. Kaspari *et al.* (2000) studied assemblages of ground-dwelling ants along a productivity gradient in the New World and their results also supported the assumptions of the energy limitation hypothesis. Positive decelerating functions were found in (1) above-ground NPP and ant density and (2) ant density and species richness. Kaspari *et al.* (2000) suggest that energy limitation of species richness predominates at finer spatial scales and that the energy limitation hypothesis is a necessary, but insufficient, explanation for the increase in species richness with increasing productivity.

In this study, we examined the pattern of bird species richness (BSR) along an elevational gradient and determined whether the energy limitation hypothesis explained changes in BSR associated with changes in productivity and elevation in Taiwan. Taiwan is a largely mountainous island (32,260 km²) that lies across the Tropic of Cancer and has a maximum elevation just under 4000 m. Steep elevation and primary productivity gradients occur over short horizontal distances, making Taiwan well-suited for the study of species richness along these gradients. Birds are an appropriate taxon for studying species richness in Taiwan because they are diverse and well-studied taxonomically. Above-ground NPP and bird total metabolic rate (an index of energy flux) were modelled using standardized methods. In this study, we determined whether BSR had a monotonically inverse, hump-shaped, or monotonically positive relationship with elevation and NPP. In addition, we tested the three assumptions of the energy limitation hypothesis: (1) increases in NPP increase the energy flux into birds, (2) increases in bird energy flux increase bird density, and (3) increases in bird density increase BSR.

Study site

We established 50 sampling stations on Mt. Yushan (23°28′30″ N, 120°54′00″ E) (3952 m a.s.l.), the highest peak in Taiwan. The sampling stations spanned an elevation range from 1400 to 3700 m and were located in a 10 × 10 km area (Fig. 1). The climate and biotic communities along this elevation gradient

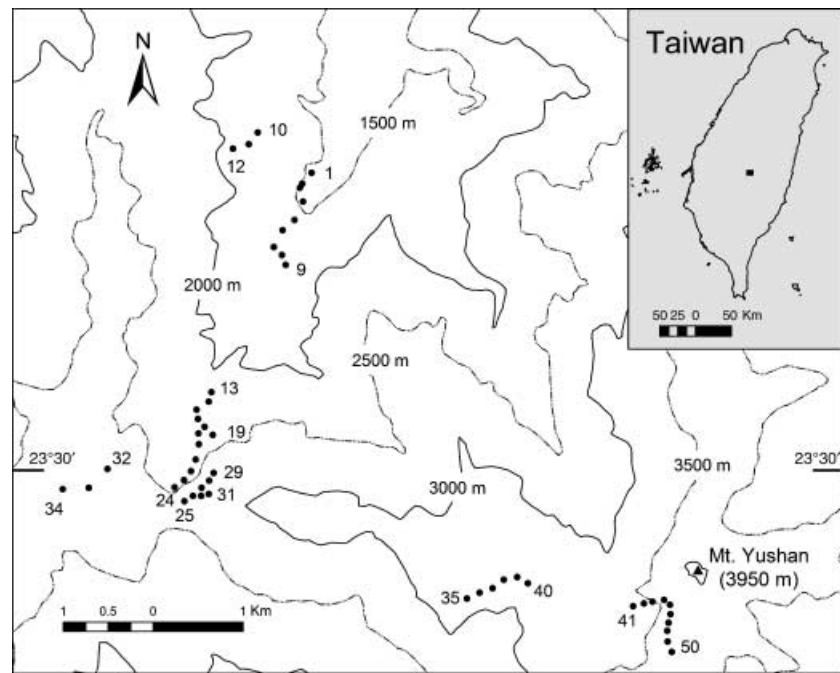


Figure 1 Location of the study area and sampling stations. The sampling stations were ranked by elevation and numbered from lowest (1) to highest (50). The numbers of the stations at each end of each transect are shown.

Table 1 Vegetation zones along the elevation gradient in the study site (modified from Su, 1984b)

Vegetation zone	Approximate elevation range (m)	Climatic zone	Annual mean temperature range (°C)	Canopy height (m)	No. of sampling stations
Alpine zone	3800–3952	Subarctic	< 4	0.1	0
Juniper shrub	3600–3800	Subarctic	4–5	2	5
Fir forests	3100–3600	Cold–temperate	5–8	10–20	8
Hemlock forests	2700–3100	Cool–temperate	8–10	15	6
Spruce forests	2500–2700	Cool–temperate	10–11	35–40	8
Mixed forests	2300–2500	Temperate	11–12	30–40	6
Upper <i>Quercus</i> zone	2000–2300	Temperate	12–14	20–25	5
Lower <i>Quercus</i> zone	1500–2000	Warm–temperate	14–17	25–30	6
<i>Machilus–Castanopsis</i> zone	500–1500	Subtropical	17–23	25–35	6

are equivalent to those found in subtropical to subarctic climate zones (Table 1). The criteria for selecting sampling stations were: (1) the vegetation should be representative of typical climax plant communities in the study area; and that the station should be (2) at least 100 m away from forest edges, creeks, and waterfalls, (3) at least 200 m away from other sampling stations, and (4) at least 200 m away from man-made structures and vegetation disturbed by humans.

Weather data from 32 weather stations within or near the study site show that the annual average temperature decreases linearly with elevation, by $-5.29\text{ }^{\circ}\text{C km}^{-1}$ ($r = 0.98$) (Su, 1984a). The correlation between temperature and elevation holds for all the seasons (Su, 1984a). In the study site, snow falls frequently above 3000 m and stays on the ground for one to four months. Most precipitation at the study site comes from the southwestern summer monsoon. Summer rainfall (April to September) accounts for 80–85% of annual precipitation. There is a hump-shaped relationship between summer rainfall and

elevation. From sea level to 2200 m in elevation, the amount of rainfall increases. Beyond that height, however, the amount of rainfall decreases (Su, 1984a). Winter precipitation (October to March) comes from the northeastern monsoon and accounts for only 10–15% of total annual precipitation. Because of the rain shadow effect, winter precipitation is positively linearly correlated with elevation (slope = 135.5 mm km^{-1} , $r = 0.88$) (Su, 1984a).

Taiwan is densely populated (about 619 people km^{-2} in the year 2001) and most old-growth forests below 1300 m have been converted to agricultural or silvicultural plantations. In previous studies (Ding *et al.*, 1997; Lee *et al.*, 2004), we showed that the stage of succession of vegetation strongly affected the species richness and composition of bird communities in the study area. Hurlbert (2004) suggested that higher primary productivity might lead to greater habitat complexity and indirectly increase species richness. To exclude the effects of anthropogenic disturbance and succession, we conducted this study only in areas of late successional stage of vegetation, which

forms discrete vegetation zones along the elevational gradient (Table 1). Shrubs of juniper (*Juniperus squamata*) and rhododendron (*Rhododendron pseudochrysanthum*) dominate from the timberline (3600 m) to 3800 m. Pure stands of fir (*Abies kawakamii*) and hemlock (*Tsuga formosana*) forests dominate forests near the timberline. In both forest types, secondary trees are generally absent and dense bamboo shrubs overwhelm the forest floor. In spruce (*Picea morrisonicola*) forests, secondary trees are common and most are broadleaved trees. In mixed forests, a variety of conifers forms the canopy layer and covers 30–70% of the canopy. Broadleaved trees dominate the dense, secondary tree layer (5–10 m tall). Conifers do not grow below 2300 m. Forests below this elevation are dominated by broadleaf evergreen trees (mostly Fagaceae and Lauraceae). Based on dominant tree species and ground vegetation, broadleaf forests are divided into three zones: the upper *Quercus*, the lower *Quercus*, and the *Machilus–Castanopsis* zones (Su, 1984b). The canopy, secondary tree, shrub, and herb layers of those zones are well-developed and floristically rich.

Among the 45 sampling stations located in the forests, tree species richness was inversely correlated with elevation, but foliage height and the effective distance at which different bird species could be detected did not change significantly with elevation (T.-S. Ding, unpublished).

METHODS

Estimating bird density and total energy flux

From March to July 1992, the density of each bird species was estimated using the variable circular-plot method (Reynolds *et al.*, 1980). In a pilot study, we determined that the optimal time to count birds was during the four hours after sunrise and that the time spent in counting birds at each station should be 6 minutes each hour. At each station, we recorded the number, distance and sex (by appearance or song if possible) of all birds seen or heard within 6 minutes. We excluded migrant species and individuals of breeding species that simply flew past the station. During this study, we counted birds 16 times, resulting in a total sampling time of 96 minutes at each sampling station.

We estimated the bird total metabolic rate and used it as an index of energy flux. Within the thermoneutral zone, the metabolic rate of birds is proportional to individual body mass to the 0.75 power (Peters, 1983; Marquet, 2002; Meehan *et al.*, 2004). We used the allometric equation for passerines reported in Nagy (1987):

$$\text{Field metabolic rate (Kj d}^{-1}\text{)} = 8.88 \times \text{body mass}^{0.749}\text{(g)}$$

We obtained the average body mass of individual birds of each species from Lee *et al.* (1999) (see Appendix S1 in Supplementary Material). We calculated the metabolic rate of each bird species using the above equation and then calculated the total energy flux of all birds at each station by multiplying the field metabolic rate with the density of each species. The average energy consumption of an individual bird at each station was calculated using the method described in Meehan *et al.* (2004).

Estimation of net primary productivity

We modelled NPP using weather data. Mean monthly temperature and precipitation at each sampling station were estimated using the 1961–90 average monthly weather data from weather stations in or close to the study site. Estimates were adjusted for elevation using the models in Su (1984a). Actual evapotranspiration (AET) at each station was estimated from the monthly mean temperature and precipitation, using the tables and equations of Thornthwaite and Mather (1957). AET is the amount of water returned to atmosphere through evaporation and transpiration. AET is strongly correlated with photosynthesis and is frequently used as a surrogate for NPP (e.g. Currie, 1991; Rosenzweig, 1995). During the breeding season, birds might use NPP produced during the non-breeding season, directly or indirectly. Therefore, our analyses used annual above-ground net primary productivity rather than summer above-ground net primary productivity. We estimated the above-ground net primary productivity of each sampling station using the model in Rosenzweig (1968): $\log_{10} \text{NPP(g m}^{-2}\text{)} = 1.7003 \times \log_{10} \text{AET(mm)} - 1.7661$.

The model explained 90% of above-ground net primary productivity in undisturbed habitats worldwide (Rosenzweig, 1968).

We classified the relationships among NPP, bird energy flux, bird density, and bird species richness as positive, negative, hump-shaped, U-shaped, or random. Earlier studies relied heavily on visual approximations to determine the form of relationship (examples in Rosenzweig, 1995). Waide *et al.* (1999) used the significance level of the quadratic term in a polynomial regression model to classify a relationship as hump-shaped or U-shaped. However, although a significant quadratic term indicates that the relationship is curvilinear, it does not always result in an internal peak. Therefore, recent studies (e.g. Mittelbach *et al.*, 2001; Chase & Leibold, 2002; Fukami & Morin, 2003) have classified the relationships as hump-shaped or U-shaped based on the test of Mitchell-Olds and Shaw (1987) (the MOS test). The MOS test was developed originally to detect stabilizing or disruptive selection. In this study, we used a general linear model with the equation: $Y = a + bX + cX^2$. If the quadratic term of the polynomial regression model was significant ($P < 0.05$) after fitting the linear term, we used the MOS test to determine whether the maximum (when $c > 0$) (hump-shaped) or minimum (when $c < 0$) (U-shaped) of the relationship significantly fell within the observed range of independent variable. If the quadratic term of regression was not significant ($P > 0.05$), we used a linear model to determine whether the relationship was positive, negative or not significant.

RESULTS

Bird species richness, density and energy flux

We counted 13,716 birds belonging to 59 breeding species (see Appendix S1 in Supplementary Material). Based on the Sibley-Ahlquist-Monroe (SAM) avian taxonomy system (Monroe & Sibley, 1993), 46 species (78%) were passerines and the family with the largest number of species was the Sylviidae (babblers and warblers; 18 species).

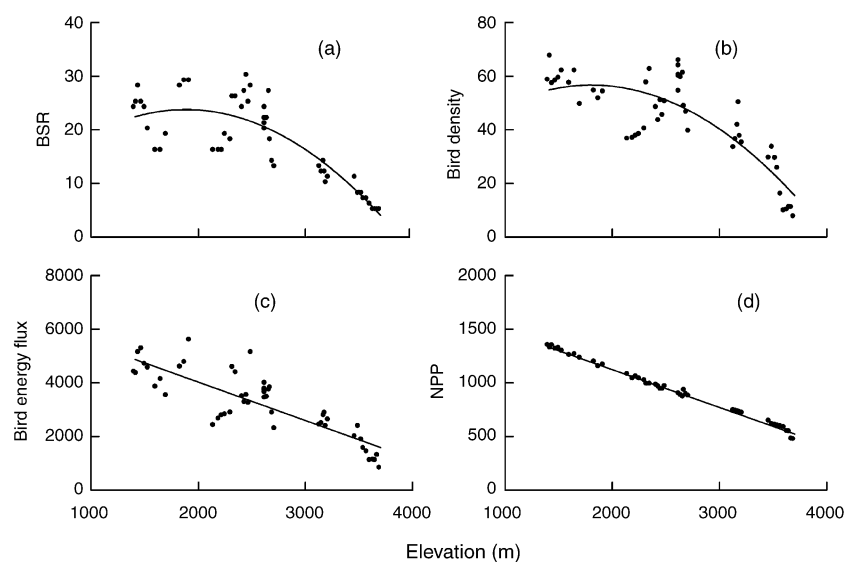


Figure 2 Changes in four variables along an elevational gradient: (a) bird species richness (BSR), (b) bird density (No. ha⁻¹), (c) bird energy flux (kJ ha⁻¹ day⁻¹), and (d) annual aboveground net primary productivity (NPP, g m⁻² yr⁻¹). In (a) and (b) the lines are fitted with a quadratic function.

The relationship between (BSR) and elevation was hump-shaped (MOS test, $P < 0.01$). BSR varied considerably in broadleaf forests (16–29 species), was highest in mixed forests (30 species), and decreased monotonically with elevation in coniferous forests, reaching a minimum in high elevation juniper shrubs (five to six species) (Fig. 2a). The relationship between bird density and elevation was also hump-shaped ($P < 0.01$). Bird density in broadleaved, mixed and spruce forests varied considerably (36.2–67.1 birds ha⁻¹), then decreased monotonically with elevation, reaching a minimum in juniper shrubs (7.3–10.9 birds ha⁻¹) (Fig. 2b). Bird energy flux decreased monotonically with elevation (5566–795 kJ ha⁻¹ day⁻¹), with the greatest variation occurring at low elevations (Fig. 2c).

AET and NPP

Estimated annual AET was inversely correlated with elevation and ranged from 752 to 407 mm per year. The relationship between summer (April to September) precipitation and elevation was hump-shaped. However, summer precipitation was so abundant it was never a limiting factor for AET. For example, stations around 2400 m in elevation received the most summer precipitation, about 3300 mm, whereas the stations at the lower and higher bounds of the elevational gradient received about 2400 mm of summer precipitation. Temperature was inversely correlated with elevation and was the limiting factor for summer AET. Summer AET accounted for 62–74% of the estimated annual AET at the sampling stations. Annual NPP was inversely correlated with elevation and ranged from 1343 to 466 g m⁻² year along the elevational gradient (Fig. 2d). Summer NPP was highly correlated with annual NPP ($r^2 = 0.99$). Our NPP estimates were consistent with those reported for similar vegetation types around the world (Lieth & Whittaker, 1975).

With neither variable transformed, the relationship between BSR and NPP was hump-shaped (MOS test, $P < 0.01$; $R^2 = 0.69$ for the quadratic polynomial regression model) (Fig. 3a). This contradicts the prediction of the energy limitation hypothesis.

The relationship between bird energy flux and NPP was monotonically positive (Fig. 3b), which is consistent with the first assumption of the energy limitation hypothesis. However, we did not find support for the second assumption of the energy limitation hypothesis because the relationship between bird density and bird energy flux was hump-shaped (MOS test, $P < 0.01$; Fig. 3c). Bird energy flux explained 91% of the variance in bird density in the quadratic polynomial regression ($P < 0.01$ for the quadratic term; Fig. 3c). The relationship between the energy consumption of individual birds and bird energy flux was U-shaped (MOS test, $P < 0.01$; Fig. 4). In a quadratic polynomial regression, bird energy flux explained 70% of the variance in the energy consumption of individual birds ($P < 0.01$ for quadratic term) (Fig. 4). On average, birds consumed less energy while energy flux was at an intermediate level. To determine whether the U-shaped relationship between individual energy consumption and total energy flux could be attributed to a few dominant species with extremely low or high body weights, we removed the Formosan firecrest (*Regulus goodfellowi*) (mean body weight: 7 g), the most abundant species at stations with moderate productivity, and the Formosan laughing thrush (*Garrulax morrissonianus*) (mean body weight: 77 g), the most abundant species at stations with low productivity, from the analysis. The relationship remained U-shaped (MOS test, $P < 0.01$). The relationship between bird density and BSR was consistent with the third assumption of the energy limitation hypothesis. BSR exhibited a positive relationship with bird density ($r^2 = 0.67$, $P < 0.01$) (Fig. 3d).

DISCUSSION

In this study, the elevation gradient was not extended to sea level because agriculture and urbanization have disturbed or destroyed most natural habitats below 1300 m. In a previous study, we determined the BSR of 674 sites using avifauna census data and found that the relationship between BSR and elevation was hump-shaped for the entire range of elevations found in Taiwan and that BSR was highest from 1400 to 2200 m (Lee *et al.*,

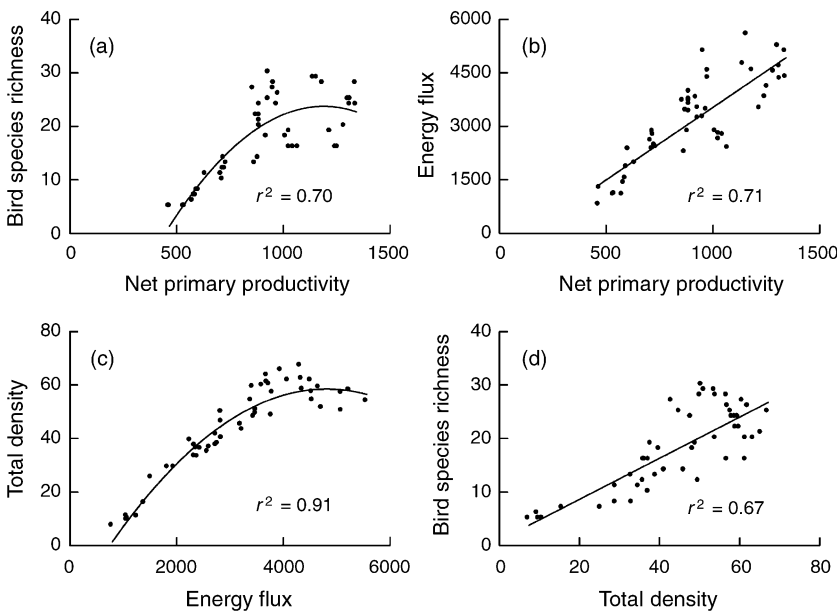


Figure 3 Relationships among four variables examined in this study. (a) The relationship between bird species richness and annual aboveground net primary productivity ($\text{g m}^{-2} \text{yr}^{-1}$) was hump-shaped. The line is fitted with a quadratic function. (b) Bird energy flux ($\text{kJ ha}^{-1} \text{day}^{-1}$) monotonically increased with annual net aboveground primary productivity ($\text{g m}^{-2} \text{yr}^{-1}$). (c) The relationship between bird density (No. ha^{-1}) and bird energy flux ($\text{kJ ha}^{-1} \text{day}^{-1}$) was hump-shaped. The line is fitted with a quadratic function. (d) Bird species richness increased with bird density (No. ha^{-1}).

2004). A study of bird communities in central Taiwan found that the relationship between BSR and elevation was hump-shaped and that BSR peaked between 1500 and 2000 m (Shiu & Lee, 2003). Therefore, we do not think BSR would be greater if we had extended the elevational gradient to lowlands in this study. The observed hump-shaped relationship supports Rahbek's (1995) assertion that a monotonically inverse relationship between species richness and elevation is not as universal as ecologists have generally assumed.

Some researchers have proposed that the mid-domain effect, which predicts that species richness will be greatest near the centre of a bounded range, is an appropriate null model for the distribution of species along spatial gradients (Colwell & Lees, 2000; Jetz & Rahbek, 2001; Colwell *et al.*, 2004). The mid-domain effect predicts that the distribution of species richness along an elevational gradient will be symmetrical and hump-shaped. Because of constraints associated with the study sites, this study did not include the entire range of elevations occurring in Taiwan, which

prevented us from quantitatively testing the predictions and assumptions of the mid-domain effect. However, other studies conducted in Taiwan found that the hump-shaped relationship between BSR and elevation was not symmetrical — the slopes were often less precipitous on the lower elevation sides (Shiu & Lee, 2003; Lee *et al.*, 2004). The mid-domain effect played an important role in the observed hump-shaped relationship, as predicted by Colwell and Lees (2000) and Colwell *et al.* (2004). However, we believe other factors, such as primary productivity and body size, also play a role.

We found that the relationship between BSR and NPP was hump-shaped. This finding refutes one assumption of the energy limitation hypothesis. The hump-shaped relationship between bird energy flux and total density is explained by the U-shaped relationship between bird energy flux and individual energy consumption. Individual birds consume more of the available energy at both ends of the primary productivity gradient, and birds tend to be bigger where energy availability is extremely high or low. Because our findings support the other two assumptions of the energy limitation hypothesis, it appears that changes in body size alone can change the hypothesized positive relationship between species richness and productivity into a hump-shaped one. We are not aware of any other studies that have proposed that body size might be an important factor affecting the shape of the species richness–productivity relationship.

Two processes might act together to produce the uneven distribution of bird individual energy consumption (body size) along the productivity gradient. First, sampling stations with bird energy flux lower than $1500 \text{ kJ ha}^{-1} \text{day}^{-1}$ were located in juniper shrubs. The physiognomy of the vegetation differed greatly from that of the dense forests in which the other sampling stations were located. The air temperature was lower and the wind stronger in juniper shrub habitats than in the forests. Larger body size should be favoured in juniper shrub habitats. Larger individuals have greater fat reserves relative to their metabolic

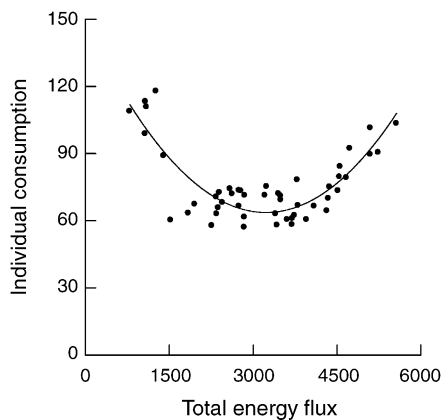


Figure 4 The relationship between individual energy consumption (kJ day^{-1}) and energy flux ($\text{kJ ha}^{-1} \text{day}^{-1}$) was U-shaped. The line is fitted with a quadratic function.

needs, so they are less likely to starve, and they have a smaller surface area to volume ratio, so they use less energy per unit body weight for thermoregulation (Blackburn & Ruggiero, 2001). When results from the stations above the timberline are omitted, the relationship between total energy flux and individual energy consumption is positive. Second, larger species and individuals are associated with habitats having greater resource availability (Thiel, 1975; Coe *et al.*, 1976; Janzen *et al.*, 1976; Ballance *et al.*, 1997; Aava, 2001). The mechanism producing this pattern remains unclear. Greater energy availability may relieve energetic constraints on the body size of animals (Aava, 2001) and larger animals could be better competitors (Ballance *et al.*, 1997). In this study, the average body weight of birds at stations with high energy flux was roughly double the body weight of birds at stations with intermediate energy flux. If body size increases significantly with energy availability, the monotonically positive relationship between energy flux and total density would change to a hump-shaped one. Consequently, we expect the relationship between primary productivity and species richness to be hump-shaped.

In conclusion, energy availability is an important factor affecting bird species richness, but the energy limitation hypothesis does not sufficiently explain the patterns observed in this study. The mechanisms of this hypothesis are multiple-stepped and might be affected by other factors, such as scale (e.g. Jetz & Rahbek, 2002) and an uneven distribution of individual energy consumption, as found in this study. Clearly, further studies are needed to understand how average body size changes along a productivity gradient and how it affects species richness.

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SUPPLEMENTARY MATERIAL

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

Appendix S1. Scientific names, English names, biomass and vegetation zones of bird species recorded in this study.

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