Journal of Biogeography (*J. Biogeogr.*) (2004) **31**, 307–314

ORIGINAL ARTICLE

Breeding bird species richness in Taiwan: distribution on gradients of elevation, primary productivity and urbanization

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ABSTRACT

Aim To examine the richness of breeding bird species in relation to elevation, primary productivity and urbanization.

Location The island of Taiwan (120°–122° E, 22°–25° N).

Methods We arranged bird species richness (BSR) data from 288 bird censuses undertaken in Taiwan into a 2×2 km quadrat system and calculated average values of elevation, primary productivity [surrogated by normalized difference vegetation index (NDVI)], and urbanization (surrogated by road density and percentage of built area) for each 2×2 km quadrat.

Results Bird species richness showed a hump-shaped relationship with elevation. It increased with elevation from sea level (10–64 species per 2×2 km quadrat), peaked around 2000 m (43–76 species), and then decreased with elevation towards its minimum at the highest elevation. Road density and percentage of built area decreased with elevation, and NDVI showed a hump-shaped relationship with elevation and inverse relationships with road density and percentage of built area. BSR increased with NDVI and decreased with road density and percentage of built area. Linear and cubic terms of elevation together explained 31.3% of the variance in BSR, and road density explained additional 3.4%. The explanatory power of NDVI on BSR was insignificant after the effects of elevation and road density had been justified.

Main conclusions We argue that urbanization plays an important role in the BSR of Taiwan. Urbanization might indirectly decrease BSR through decreasing primary productivity and therefore change the hypothetical inverse relationship between BSR and elevation into a hump-shaped relationship. We also propose a time hypothesis that the biotic communities in the mid-elevation zone of Taiwan had relatively longer periods of existence during the Pleistocene glacial cycles, which might be one underlying process of the observed hump-shaped relationship between species diversity and elevation.

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Keywords

Species richness, elevation, primary productivity, urbanization, energy limitation theory, time theory, landbridge, macroecology.

INTRODUCTION

Describing and explaining spatial patterns of species diversity are crucial steps in conserving global biodiversity and long-standing research topics for biogeographers. Species diversity has been found correlated with many environmental factors that are often interacting with each other. In this study, we studied the distribution of bird species richness (BSR) in Taiwan and focused on three often-cited environmental gradients: elevation, primary productivity and urbanization.

With highest peak around 4000 m, elevation plays an important role in governing temperature, precipitation, and consequently distribution of species and natural vegetation in Taiwan. Traditionally, species richness is expected to be inversely correlated with elevation as higher mountains are generally smaller in land area, more isolated and simpler in vegetation structure (MacArthur, 1972). However, recent studies have revealed that hump-shaped pattern of species richness in relation to elevational gradient actually is more common than the inverse relationship (Rahbek, 1995; Brown, 2001; Lomolino, 2001).

In Taiwan, there are several environmental variables that change consistently with elevation. Their trends, together with current ecological theories of species diversity, provide some predictions on the distribution pattern of BSR on the elevation gradient. First, land area decreases with elevation. The higher elevation areas have less land area in Taiwan (Lee *et al.*, 1997). Assuming other factors kept constant, the area theory (Terborgh, 1973; Rosenzweig, 1992, 1995) would predict BSR to be inversely correlated with elevation. Secondly, air temperature monotonically decreases with elevation in Taiwan (Lee *et al.*, 1997). Birds are endothermic animals with body temperatures *c.* 37 °C. Under that temperature, increasing air temperature would increase physiological performance and efficiency of energy use of birds and thus be more favourable for birds. Thus, based on the favourableness theory (Terborgh, 1973; Brown, 1981), we would expect BSR to inversely correlate with elevation. Besides, species in areas of higher temperature tend to have shorter life spans and that may increase the rates of speciation (Rohde, 1992). Thirdly, although the local annual precipitation in Taiwan varies greatly with region and aspect, the annual precipitation in most of the areas in Taiwan was higher than 2000 mm (Lee *et al.*, 1997). Assuming other factors kept constant, this high precipitation would make temperature the main factor in governing primary productivity along the elevation gradient in Taiwan. Therefore, we would speculate that primary productivity of natural vegetation decreases with elevation in Taiwan. Assuming all the habitats were not disturbed by human activities, we would also expect BSR to inversely correlate with elevation – based on the energy limitation theory (Hutchinson, 1959; Connell & Orias, 1964; Wright, 1983).

In spite of the predictions of the theories mentioned above, many study conducted at local scale in Taiwan had found hump-shaped relationship between BSR and elevation (Kano, 1940; Jai, 1977; Lin, 1989). Taking advantage of more than 400 bird censuses that has been taken in Taiwan in the last 20 years, the first aim of this study was to transform suitable bird censuses into an equal area quadrat system to analyse the relationship between BSR and elevation at the regional scale. Specifically, we intended to examine whether if BSR decreases with elevation or has a hump-shaped relationship with elevation within the whole-island extent.

The absolute amount of life on earth cannot exceed the amount that can be supported by the total solar energy it receives (Gaston & Blackburn, 2000). Thus the energy limitation theory suggests that energy availability limits the carrying capacity of a community and an increase of primary productivity would increase species richness through increased population sizes and decreased local extinction rates (Hutchinson, 1959; Connell & Orias, 1964; MacArthur, 1972; Wright, 1983). Many studies have shown positive monotonic relationship between primary productivity and species richness of various plant and animal groups (Brown & Lomolino, 1998; Gaston, 2000). Many hypotheses have been proposed to explain, if it is the case, the hump-shaped pattern of species richness on elevational gradient (examples in Heaney, 2001). One of the often-discussed hypotheses is that primary productivity is often higher at intermediate elevation (McCoy, 1990; Md. Nor, 2001). However, many studies reported a hump-shaped relationship between primary productivity and species richness, in which species richness peaks at intermediate level of primary productivity or energy availability (Rosenzweig, 1992, 1995; Waide *et al.*, 1999; Mittelbach *et al.*, 2001). Although the pattern has been widely reported on a variety of organisms, ecosystems, and scales and has been suggested as more common than the positive monotonic relationship (Waide *et al.*, 1999; Mittelbach *et al.*, 2001), its underlying mechanisms are still not clear (Rosenzweig, 1995). In this study, using remote sensing information, we examined the pattern of primary productivity on elevational gradient and tested the energy limitation theory, which predicts BSR has positive monotonic relationship with primary productivity.

Humans have been changing the earth, including modification, degradation, reduction and fragmentation of natural habitats. Urbanization, which replaces the extant natural habitats (e.g. forests, wetlands) with an infrastructure that is capable of supporting humans, is arguably the most dramatic and long-lasting form of land transformation that profoundly affects biological communities (Czech *et al.*, 2000). Urbanization typically decreases the area of natural habitats, increases the vegetation types of early successional stages, increases habitat edges, and often decreases primary productivity (in arid areas, urbanization might increase water supplies and thus increase primary productivity) (McDonnell & Pickett, 1990; McKinney, 2002). Extreme urbanization may decrease all of these factors when the vegetations are all replaced with pavements and structures (Whitney & Adams, 1980). Studies have showed that urbanization dramatically changed composition of bird communities and BSR generally decreases with urbanization (Clergeau *et al.*, 1998; Boren *et al.*, 1999; Rottenborn, 1999; Cam *et al.*, 2000; Jokimäki *et al.*, 2002) with some exceptions that peaked at moderately developed sites (Jokimäki & Suhonen, 1993; Blair, 1996; Allen & O'Connor, 2000). This suburban peak was often attributed to the intermediate disturbance hypothesis (Connell, 1978) or high subsidization of scarce resources (e.g. water or nutrients), which usually increase productivity of those suburban sites (Falk, 1976). In this study, we studied the pattern of BSR along urban gradient in Taiwan, a highly urbanized island. Specifically we intended to examine whether if BSR decreases with urbanization or peaks at intermediate level of urbanization.

In short, this study examined the distribution of BSR on gradients of elevation, primary productivity, and urbanization within the extent of whole Taiwan Island and studied the interrelationships among elevation, primary productivity, urbanization and BSR.

STUDY AREA

Taiwan is an orogenic island of 36,000 km^2 that started to emerge above sea level *c.* 5 Ma and is still rising and tectonically active (Ho, 1986; Teng, 1990). The Taiwan Strait is *c.* 140 km at its narrowest width and if sea level dropped more than 70 m Taiwan would connect to mainland Asia. It is reasonable to estimate that Taiwan had frequently connected with mainland Asia during the Pleistocene (Voris, 2000) and the last landbridge might be connected till *c.* 12 ka (estimated from Fairbanks, 1989). The frequent landbridge connections provided critical dispersal routes for terrestrial biota in Taiwan. Pollen records in central Taiwan (Tsukada, 1966, 1967) revealed that dominant trees changed dramatically during the Pleistocene and at certain times temperature might have been 11 °C lower than present. With the climatic fluctuations and frequent landbridge connections, together with the lofty mountains (highest elevation at 3952 m), many Palearctic and Himalayan species colonized and were trapped in the mountains of Taiwan, creating discontinuous distributions in East Asia (Kano, 1940; Hachisuka & Udagawa, 1950).

The climate of Taiwan is greatly influenced by the lofty mountains and the alternating monsoons. The temperature on Taiwan's mountains generally decreases with elevation, with a lapse rate of -5.43 °C km^{-1} (Su, 1984a). Most of the plains have *c.* 1500–2500 mm annual precipitation. Mountain areas generally receive *c.* 2000–3500 mm. Due to the high precipitation, the natural vegetation types in Taiwan are mostly forests (Su, 1984b). Broadleaf and conifer forests, respectively, dominate lower and higher elevation areas in Taiwan, with a wide transition zone between 1500 and 2500 m. The canopy tree species of broadleaf forests are principally Moraceae and Euphorbiaceae in areas below 500 m and Lauraceae and Fagaceae between 500 and 2500 m. The conifer forests are mainly distributed from 2000 to 3600 m, with dominant canopy tree of cedars, hemlocks, and firs respectively, from low to high elevations.

The immense population pressure in Taiwan (*c.* 619 individual km^{-2} in 2001) caused massive forest clearing in the lowlands during the last four centuries. Currently there is no pristine forest left on the plains, where are thickly inhabited, and only few patches remain on the foothills. Commercial logging during the last century has also eliminated some temperate old-growth forests in the mid-elevation zone (1500–2500 m). Although there is no record of resident bird species being extinct in Taiwan, many lowland species have limited distributions.

METHODS

Quadrat system

An equal-area quadrat system was used as a measurement and an analysis unit in this study. Area size has been found as an important factor in controlling species diversity and is often ignored or fudged in species diversity studies. Whittaker *et al.* (2001) suggested that area size should be held constant and equal area quadrats should be used if a study focuses on examining the relative roles of different environmental variables on species diversity. In this study, BSR and environmental factors were summarized and arranged by the same quadrat system.

The size of quadrats in this study was 2 × 2 km. This quadrat size was chosen as most of the bird censuses in Taiwan employed transect sampling and results were compiled in transects, usually 2–4 km in length. Ideally the quadrat size should not be smaller than the spatial resolution of input data (transect). Therefore, we designed a 2 × 2 km quadrat system. In total, there were 9388 quadrats covering the whole island.

Bird species richness

Only the number of breeding bird species richness was calculated in this study. In Taiwan, contrasting to wintering and vagrant species, the breeding bird species are easier to detect and consequently their richness is more robust to census effort (Hsu *et al.*, 2001). There are 155 breeding bird species in Taiwan. Among them, owls were not included as they are mainly nocturnal and often missed in censuses. Pelagic birds (Laridae and Sulidae) were also excluded as they primarily feed on marine food sources. In total, there were 147 species covered, including waterfowls and waders.

The selection criteria of bird census reports were: (1) published from 1980 to 2000, (2) had six to 12 field counts within a census period between 1 and 2 years, (3) arranged results in a spatial resolution < 10 km^2, and (4) had balanced efforts towards all diurnal avian groups. Totally there were 288 bird census reports selected. We studied the locations of transects or stations in each bird census and find out corresponding grid of each transect. In case that some transects spanned over more than one grid, we chose the grid that covered more than 75% of the transect length as the location of transect. Transects that spanned more than two grids were dropped. In total, 674 quadrats were covered, each representing one transect or sampling station (Fig. 1).

There are some quantitative methods, such as rarefaction method, proposed to justify the effect of unbalanced census efforts on species richness. Nevertheless, the methods are best applied to the same or similar habitats as different habitats usually have different census effort – species richness curves (Sanders, 1968). In Taiwan, it has been shown that the accumulation curves of resident bird species were significantly different among different elevation classes (Hsu *et al.*, 2001) and vegetation types (Shiu & Lee, 2003). In four censuses that had continuously conducted for 59 months, 83% of the resident species had been registered during the first six field counts and 89% registered during the first 12 field counts (Hsu *et al.*, 2001). The bird censuses adapted in this study were conducted in a wide spectrum of habitats and therefore it was difficult to apply those justification methods. In order to limit the effect of census efforts, we only included those censuses that had six to 12 field counts within a census period between

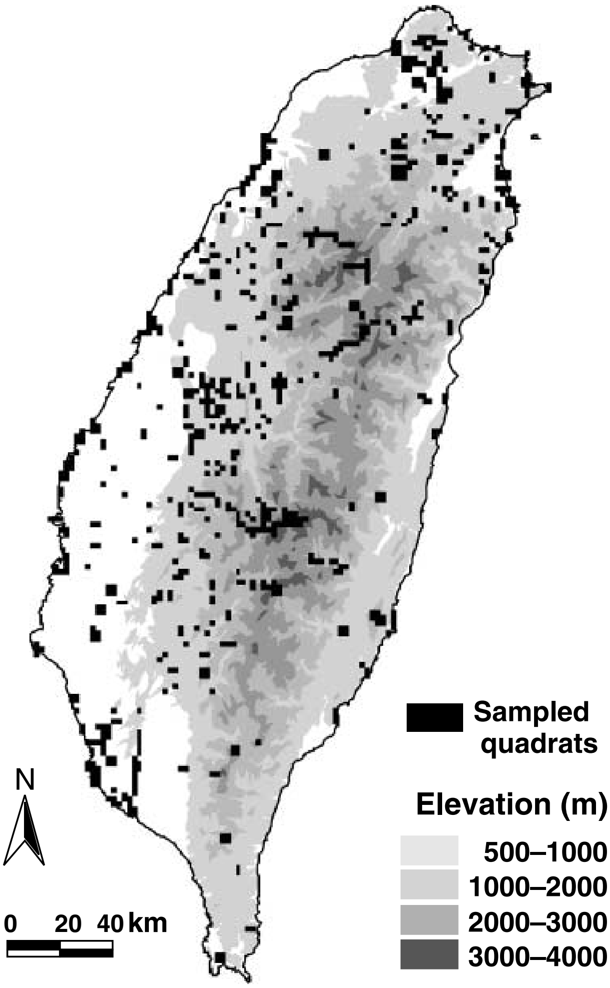

Figure 1 Topography of Taiwan and locations of the 674 sampled quadrats.

1 and 2 years. We argued this census scheme was adequate to record most of breeding bird species in a given location of Taiwan and the effect of unbalanced census efforts should be greatly minimized.

Environmental factors

Elevation of each quadrat was calculated as average of a digital elevation model (DEM) of Taiwan (40 × 40 m in resolution) that was overlaid with the quadrat system.

Primary productivity was estimated by the advanced very high resolution radiometer-normalized difference vegetation index (AVHRR-NDVI). NDVI is a measure (Tucker, 1979) that has been found highly correlated with green-leaf area and absorbed photosynthetically active radiation (APAR) (Curran, 1980; Goward *et al.*, 1985) and has been used as surrogate of primary productivity and vegetative growth of terrestrial ecosystems (Box *et al.*, 1989; Ustin *et al.*, 1991). To minimize cloud contamination, we combined the available NDVI composites from 1992 to 1997 by maximum value composite method (Holben, 1986) into a set of monthly NDVI composites. Each month was combined from 90 to 120 daily NDVI composites. The NDVI data, with original resolution of *c.* 1 × 1 km, were downloaded from the website: http://daac.gsfc.nasa.gov/data/dataset/AVHRR/01_Data_Products/06_Images/03_Asia/.

We used road density and percentage of built area to surrogate urbanization. Both indices were obtained from a 1 : 25,000 digital map created by the Ministry of the Interior of Taiwan in 2000. Road density was calculated as total length of all levels of paved roads divided by land area of each quadrat. Percentage of built areas was calculated as total area of residential, commercial, and industrial buildings divided by land area of each quadrat. We argued that road density and percentage of built area were fair surrogates of urbanization as both indices were accurate, precise, and adequately represented level of human activities.

Data analysis

Beside simple linear correlation, forward stepwise multiple regression was used to evaluate the effects of the environmental variables on BSR. Several procedures were taken during the multiple regression. First, we selected only one environmental variable among those that were highly inter-correlated. Secondly, a stepwise approach was used in response to presumed causal relationships among environmental factors. Thirdly, road density was logarithmic transformed to make the shape of its distribution symmetric and stabilize variances across classes.

RESULTS

General patterns

Bird species richness ranged from seven to 76 species per 2 × 2 km quadrat and showed a hump-shaped relationship with elevation (Fig. 2). BSR increased with elevation from sea level (10–64 species), peaked around 2000 m (43–76 species),

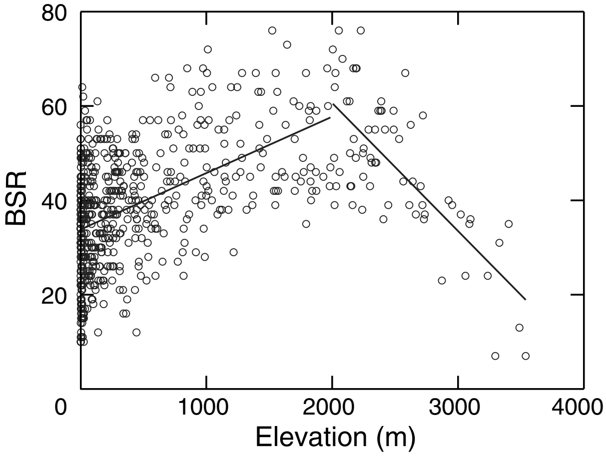

Figure 2 Bird species richness (BSR) showed a hump-shaped relationship with elevation. The fit lines were piecewise linear regression functions that corresponded to the ranges of elevation below 2000 m and above 2000 m.

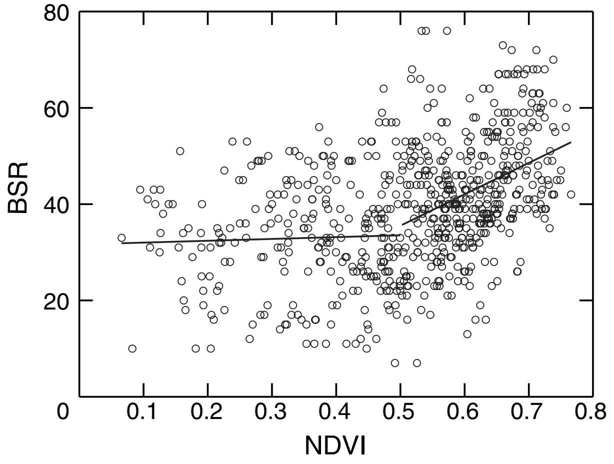

Figure 3 Bird species richness (BSR) generally increased with NDVI. It slightly increased with NDVI in the range of NDVI below 0.5 and positively correlated with NDVI in the range above 0.5.

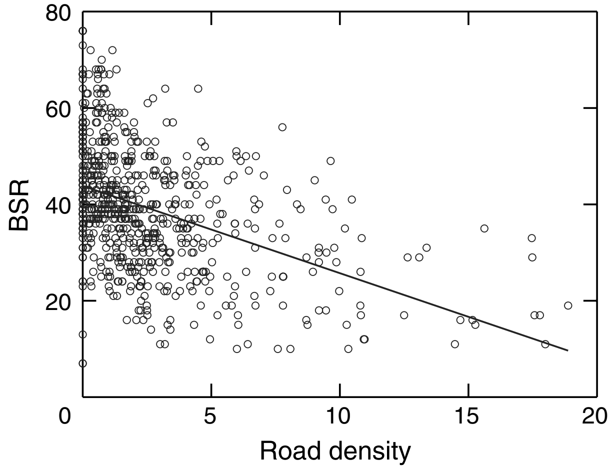

Figure 4 Bird species richness (BSR) decreased with road density (km^{-1}).

then decreased with elevation and reached its minimum at the highest elevation (3538 m). The slope of decreasing phase (slope = -0.027, $r = -0.73$, $P < 0.001$) was steeper than increasing phase (slope = 0.012, $r = 0.48$, $P < 0.001$).

Bird species richness generally increased with NDVI ($r = 0.40$, $P < 0.001$). However, in the range of NDVI < 0.5, BSR did not significantly increase with NDVI (slope = 3.42, $r = 0.03$, $P = 0.57$) (Fig. 3). In the range of NDVI > 0.5, BSR showed a significantly positive relationship with NDVI (slope = 65.29, $r = 0.34$, $P < 0.001$) (Fig. 3). BSR generally decreased with road density ($r = -0.43$, $P < 0.001$) (Fig. 4) and percentage of built area ($r = -0.39$, $P < 0.001$) (Fig. 5).

Collinearity among environmental factors

The four environmental variables were plotted against each other to investigate the patterns of collinearity among them (Fig. 6). The percentage of built area and road density showed inverse relationships with elevation (Fig. 6b,c). There was a strong and positive correlation between percentage of built area and road density ($r = 0.82$, $P < 0.001$) (Fig. 6f). NDVI showed a hump-shaped relationship with elevation (Fig. 6d) and negative relationships with percentage of built area ($r = -0.37$, $P < 0.001$) (Fig. 6g) and road density ($r = -0.52$, $P < 0.001$) (Fig. 6i).

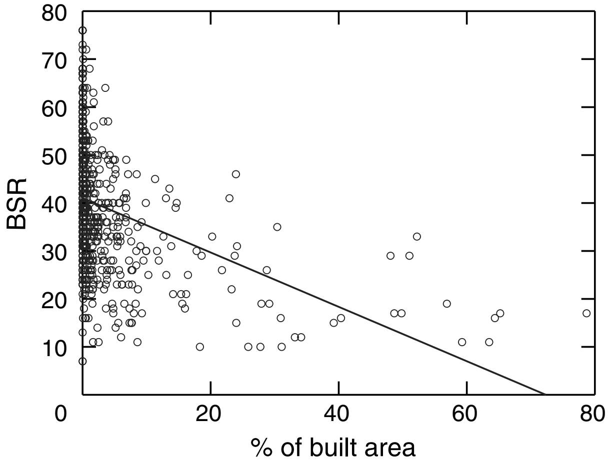

Figure 5 Bird species richness (BSR) decreased with percentage of built area.

Stepwise multiple regressions

Only one variable, road density, was chosen to represent urbanization as road density highly correlated with percentage of built area, had a better spread of data, and had higher degree of correlation with BSR. As BSR showed curvilinear relationships with elevation and NDVI, the quadratic and cubic terms of elevation and quadratic term of NDVI were added into the regression analyses.

In this study, elevation might affect both primary productivity and urbanization; and urbanization might affect primary productivity. Thus, variables of elevation were first entered in the multiple regression models before other variables were admitted, and then road density was entered before variables of NDVI. Linear and cubic terms of elevation were added in the first round of multiple regression analysis (criteria for input: $P > 0.05$) and together explained 31.3% of the variance in BSR (Table 1). Road density added in the second round and explained additional 3.4% of the variance in BSR (Table 1). Linear and quadratic terms of NDVI did not add in the third round for their insignificant explanatory powers. The final model (criteria for input: $P > 0.05$) explained 34.7% of the variance in BSR (Table 1).

DISCUSSION

Bird species richness showed a hump-shaped relationship with elevation in this study. This finding was consistent with previous studies in Taiwan (Kano, 1940; Jai, 1977; Lin, 1989)

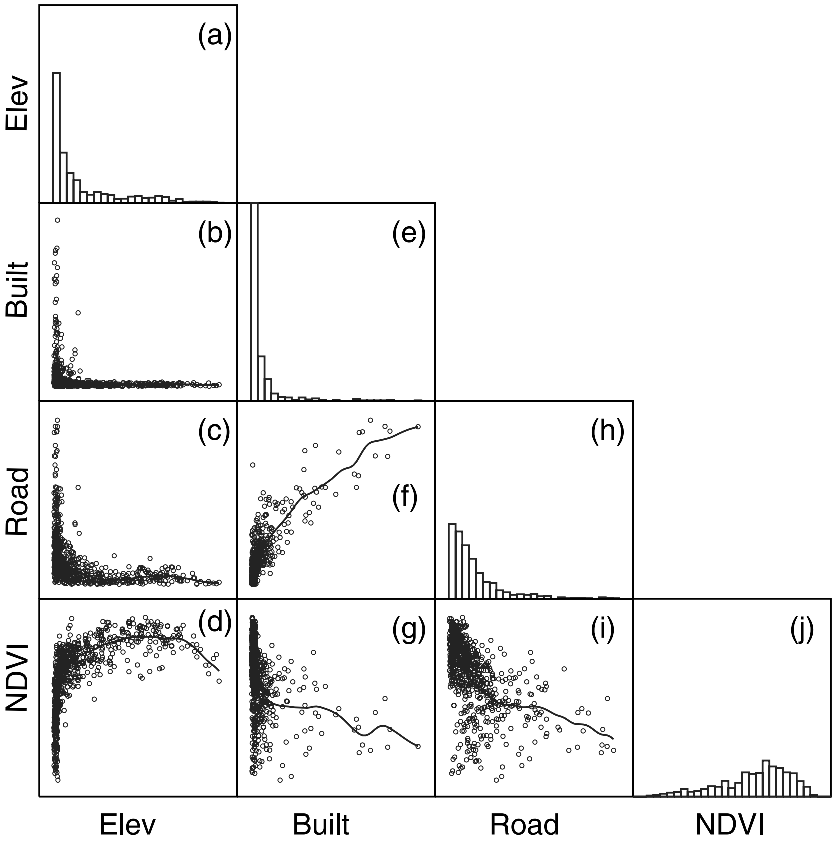

Figure 6 Scatterplot matrices of the four environmental variables: (a) most of the sampled quadrats were in lowlands, (b) percentage of built area (BUILT) showed inverse relationship with elevation (ELEV), (c) road density (ROAD) showed inverse relationship with elevation, (d) NDVI showed a hump-shaped relationship with elevation, (e) most of the sampled quadrats had low percentage of built area, (f) percentage of built area positively correlated with road density, (g) NDVI inversely correlated with percentage of built area, (h) most of the sampled quadrats had low values of road density, (i) NDVI inversely correlated with road density, (j) most of the sampled quadrats were located at intermediate levels of NDVI.

Table 1 Stepwise regression model applied to bird species richness in Taiwan

Variables	Order entered	Standard coefficient	Partial r^2	Model r^2	t	P
Elevation	1	0.83	0.147	0.147	11.5	< 0.001
Elevation^3	2	−0.68	0.166	0.313	−10.6	< 0.001
Log(road density + 1)	3	−0.24	0.034	0.347	−6.0	< 0.001

although they were conducted in different methods, times and spatial scales. This finding supports Rahbek's (1995) argument that the monotonically inverse relationship between species richness and elevation is not as universal as ecologists generally assumed.

Nevertheless, the hump-shaped relationship between elevation and BSR contradicted the predictions of the area theory and favourableness theory. One obvious explanation for this is human disturbance (Jai, 1977). In this study, we tested one important aspect of human disturbance – urbanization, using road density and percentage of built area as surrogates. Urbanization may decrease species diversity through decreasing primary productivity and reducing or degrading original habitats. Taiwan is one of the most densely populated areas in the world and most of the pristine forests have been eliminated on the lowlands. In this study, we found urbanization decreased with elevation, NDVI decreased with urbanization, and BSR decreased with urbanization and increased with NDVI. The results strongly support this human disturbance hypothesis. The human disturbance was extensive on the plains and mostly occurred in the lowlands, it may therefore have changed the hypothetical inverse relationship between BSR and elevation into a hump-shaped relationship.

One way to test this human disturbance hypothesis is to study literature that documents the biotic communities before massive human disturbance. Unfortunately, when Robert Swinhoe undertook the first ornithological collection in Taiwan in 1856, most of the forests in the plains and foothills had already been logged (Swinhoe, 1863; Jai, 1977). There is no reliable information for the BSR in the lowlands of Taiwan before the massive human disturbance started in the seventeenth century.

Beside human disturbance, time is another possible explanation for the hump-shaped relationship between elevation and BSR. During the Pleistocene glacial cycles, dramatic climatic fluctuations occurred in Taiwan and biotic communities shifted up and down along the elevational gradient (Tsukada, 1967). During the maximum of the Tali Glaciation (60,000–50,000 years ago), temperature might have been 11 °C cooler than present (Tsukada, 1966, 1967) and the air temperature of the lowlands should be similar to the air temperature at the current 2000 m elevation in Taiwan. The biotic communities that currently occupy the mid-elevation zone in Taiwan should have had a longer period of existence and the biotic communities adapted to the ends of the elevational gradient might have been totally eliminated by the extreme climates in the Pleistocene glacial periods. Although the avifauna might be enriched by frequent landbridge connections between Taiwan and mainland Asia, the landbridge connections were associated with cold climates. Those bird species that adapted to warm climates had to overcome the dispersal filter of the Taiwan Strait to colonize the lowlands of Taiwan. Many bird species that are widely distributed in the lowlands of south-eastern China are not found in Taiwan. Several bird species introduced from south-eastern China have quickly established stable populations in the lowlands of Taiwan (e.g. *Pica pica*). Besides, most of the endemic bird species in Taiwan are distributed in the mid- and high-elevation zone. All the observations indirectly support this time hypothesis. However, this hypothesis is difficult to test as the observed distribution patterns of species richness along the elevational gradients in Taiwan and nearby south-eastern China are all confounded with human disturbance. Nevertheless, it should be taken under consideration for future studies on the distribution patterns of species diversity of Taiwan and other landbridge islands.

ACKNOWLEDGMENTS

We thank Art Shapiro, Susan Ustin, Bill Rains, and two anonymous reviewers for their helpful comments and suggestions on the earlier drafts. This research was supported by the Council of Agriculture and the National Science Council, Taiwan, Republic of China.

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