Species Diversity at Different Spatial Scales:

Birds in Yushan, Taiwan, and East Asia

Ph. D. Dissertation

By

Tzung-Su Ding

Graduate Group in Ecology

University of California at Davis
SPECIES DIVERSITY AT DIFFERENT SPATIAL SCALES:
BIRDS IN YUSHAN, TAIWAN, AND EAST ASIA

By

Tzung-Su DING

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Approved:

Shu Geng

Arthur M. Shapiro

Susan L. Ustin

Committee in Charge

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ABSTRACT

Understanding spatial patterns of species diversity is one of the most intriguing questions in ecology. Recently most ecologists have agreed that species diversity is governed by multiple processes and the patterns and processes of species diversity are strongly scale dependent. Nevertheless, few studies have investigated patterns of species diversity across spatial scales or tested multiple processes simultaneously. This dissertation investigated the spatial patterns and tested multiple hypotheses of bird species richness at local (Yushan), regional (Taiwan), and continental (East Asia) scales. Bird species richness showed a plateau-then-decreasing relationship with elevation at the local scale, a hump-shaped relationship with elevation at the regional scale, and an inverse relationship with latitude at the continental scale. The energy limitation theory is strongly supported at all scales, suggesting energy availability is one primary process of species diversity and its effects may be consistent across spatial scales. The spatial heterogeneity theory is evident at the local and continental scales, but its explanatory power is less significant than the energy limitation theory. The evolutionary time theory, area theory, isolation theory, and human disturbance hypothesis are all supportable at certain spatial scales but evidence is not consistent across scales.
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Introduction

Describing and explaining species diversity are long-standing problems in ecology and essential cornerstones in biodiversity conservation. Numerous hypotheses and theories have been proposed and the results have obtained consist of a multitude of patterns and possible processes that mirror the entire range of current ecological theories (Brown 1988, Begon et al. 1990, Ricklefs 1990, Cornell & Lawton 1992, Rosenzweig 1995, Brown and Lomolino 1998, Gaston and Blackburn 2000). Some frequently-discussed hypotheses include the time (Fischer 1960), area (MacArthur and Wilson 1967, Terborgh 1973, Rosenzweig 1992), energy availability (Hutchinson 1958, Wright 1983), spatial heterogeneity (MacArthur and MacArthur 1961, MacArthur 1964), climatic stability (Fischer 1960, Connell and Orians 1964), disturbance (Connell 1978), isolation (MacArthur and Wilson 1967), favorableness (Terborgh 1973), competition (Dobzhansky 1950), and predation hypotheses (Paine 1966). These hypotheses can be categorized into four types of rules: capacity rules, allocation rules, origination rules, and extinction rules. The capacity rules (Brown 1981) define how the physical characteristics of environments determine their capacity, or say resource, to support life. The allocation rules (Brown 1981) describe how the limited energetic resources are subdivided among species. The origination rules describe how the characteristics of environments and organisms affect the ability of species being present through immigration or speciation. The extinction rules describe how the physical characteristics of environments or the inter-specific interactions lead to local extinction of species.
Recently, most ecologists have agreed that species diversity is governed by multiple processes and the patterns and processes of species diversity are strongly scale dependent (MacArthur 1972, Shmida and Wilson 1985, Ricklefs 1987, Wiens 1989, O’Neill 1989, Levin 1992, May 1994, Bohning-Gaese 1997, Gaston and Blackburn 1999, Whittaker et al. 2001). That is, patterns vary with the spatial and temporal scale of observation, and a given pattern is usually determined by multiple processes that function at various scales. Ecological patterns observed at one scale often do not extrapolate to other scales. Therefore, interpretation of species diversity will likely be fully completed only if incorporating observations encompass a variety of scales and testing multiple hypotheses that have been generated for species diversity.

Technological advances and information explosions in last few decades promise to have important effects on the studies of species diversity. Advances in computer hardware and software have allowed the compilation and manipulation of enormous quantities of data on truly geographic scales. Geographic Information Systems (GIS), which compile, store, analyze, and visualize spatial information, have tremendously enabled researchers to explore and analyze species diversity patterns from local to global scale. Satellite imagery and other kinds of remote sensing technology have resulted in tremendous information on the physical, biological, and anthropogenic features of the Earth’s surface. A variety of mapping and censusing programs have accumulated a wealth of reliable information on the occurrence and abundance of species at multiple disparate sites. In addition, Internet communication enables quick dissemination and exchanges of those data sets and information. All of these facilitate studies of species diversity to incorporate observations across a variety of scales.
This dissertation is aimed to study the spatial patterns of bird species richness at local, regional, and continental scales (Table 1). Data of bird richness and environmental factors in chapter one (local scale) were mainly recorded from the field. In chapter two (regional scale) and chapter three (continental scale), data were derived from published literature and data sets. At each scale, multiple hypotheses were tested or assessed (Table 2).

Table 1. The spatial and temporal scale of each chapter.

<table>
<thead>
<tr>
<th>Spatial scale</th>
<th>Extend of study area</th>
<th>Resolution of data</th>
<th>Grain size of analysis</th>
<th>Temporal scale</th>
<th>Extend of study period</th>
<th>Resolution of data</th>
<th>Grain size of analysis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Local</td>
<td>7×10 km</td>
<td>200 m diameter circle</td>
<td>200 m diameter circle</td>
<td>1992 Breeding season</td>
<td>Aggregated</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Regional</td>
<td>200×600 km</td>
<td>2×2 km grid</td>
<td>2×2 km grid</td>
<td>1980-2000 Year</td>
<td>Aggregated</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Continental</td>
<td>110° long. × 100° lat.</td>
<td>100 km</td>
<td>100×100 km grid</td>
<td>1950-2000</td>
<td>Aggregated</td>
<td></td>
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</tr>
</tbody>
</table>

Table 2. The hypotheses of species diversity tested or assessed in each chapter.

<table>
<thead>
<tr>
<th></th>
<th>Evolutionary Time</th>
<th>Area</th>
<th>Isolation</th>
<th>Energy Limitation</th>
<th>Spatial heterogeneity</th>
<th>Human disturbance</th>
</tr>
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<tbody>
<tr>
<td>Local</td>
<td>+</td>
<td>+</td>
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<td>Regional</td>
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1. The plus and minus signs (+,-) represent hypothetical positive or inverse effects of each hypothesis on species diversity.

* : the hypotheses that were supported by the results in each chapter.
The relationship between bird species richness (BSR) and elevation was a plateau-then-decreasing relationship at the local scale and a hump-shaped relationship at the regional scale. At the continental scale, BSR generally declined from the tropics to the arctic. However, there were two minor exceptions in Mainland East Asia. BSR was highest around Tropic of Cancer and it fluctuated between 30º and 50º N. Primary productivity showed positive and strong correlation with BSR at all the spatial scales. Spatial heterogeneity also showed positive correlation with BSR at the local and continental scales. Evolutionary time theory was supported at the regional scale but was rejected at the continental scale. After the sizes of analysis units (grains) were all controlled to be equal at each scale, area only showed significant effect on the BSR of isolated habitats (islands) at the continental scale and area theory was rejected at the local scale, regional scale, and of mainland habitats at the continental scale. The effect of isolation was examined and found significant at the continental scale. The effects of human disturbance were tested at the regional and continental scales but found significant only at the regional scale.

The energy limitation theory (Wright 1983) is strongly supported at all spatial scales, suggesting that energy availability is one primary process of species diversity and its effects may be consistent across spatial scales. The spatial heterogeneity theory (MacArthur 1964) also has significant evidence at the local and continental scales. However, at both scales its explanatory power is less significant than the energy limitation theory. The evolutionary time theory (Fisher 1960), area theory (Rosenzweig 1992), isolation theory (MacArthur and Wilson 1967), and human disturbance hypothesis have gained some support at certain scales but their effects are not consistent across scales.
To search for explanations of species diversity, one needs to use evolutionary arguments and to integrate our knowledge of population dynamics, species interactions, landscape mosaics, and energy fluxes. It is not surprising that ecologists have yet constructed a satisfactory conceptual framework on the processes and mechanisms of species diversity. This dissertation intends to help the studies of species diversity in three aspects. First, by integrating studies from various spatial scales and investigating multiple hypotheses at each scale, it provides a holistic view and understanding of species diversity. Second, it demonstrates how to take advantage of GIS and remotely sensed data, which are respectively powerful tool and promising data source that have not been fully utilized by ecologists. Third, it focuses on East Asia, where a large share of global biodiversity is resided but has been traditionally under-reported and understudied by ecologists.

**Literature cited**


Chapter One

Energy, Spatial Heterogeneity, and Rescue Effect on Bird Species

Richness along an Elevational Gradient in Yushan
Abstract

I examined the relationships of primary productivity, spatial heterogeneity, and rescue effect with breeding bird species richness along a local elevational gradient in Yushan, Taiwan. Bird species richness showed a plateau-then-decreasing relationship with elevation and an increasing-then-plateau relationship with net primary productivity. I further tested three mechanisms of the energy limitation theory and the results were consistent with two of the predictions: bird total biomass was positively correlated with net primary productivity, and bird species richness positively correlated with bird total density. However, bird total density showed a hump-shaped relationship with bird total biomass, which contradicts one prediction from the energy limitation theory. This result implies more energy flux (estimated by bird total biomass) might decrease bird species richness through increasing bird body size and reducing total density. Tree species richness showed a hump-shaped relationship with elevation and was positively correlated with bird species richness, supporting the spatial heterogeneity theory. One-kilometer neighborhood area negatively correlated with bird species richness, indicating the rescue effect is not significant. Results suggest that energy availability is possibly the ultimate factor for bird species richness at this scale. For the decreasing phase of bird species richness along the elevational gradient, the energy limitation theory well explains the species richness. For the plateau phase, energy availability might be expressed through multiple mechanisms in maintaining bird species richness. More energy availability might indirectly decrease bird species richness through reducing bird total density and spatial heterogeneity.
Introduction

Understanding spatial patterns of species richness has been one of the core themes in ecology. Traditionally, species richness is expected to inversely correlate with elevation, just as species richness declines from the tropics to the arctic (MacArthur 1972). That is, patterns of species richness along elevational gradients are considered as mirrors of species richness along latitudinal gradients (Stevens 1992). Many papers indeed report that there exists an inverse relationship between species richness and elevation (e.g., Terborgh 1977, Able and Noon 1976, Patterson et al. 1998). Many researchers (MacArthur 1972, Stevens 1992) think that changes of physical conditions with latitude resemble the variations with elevation, and thus, such similarity drives the similarity of species richness patterns on elevation and latitude. In a review of 90 data sets that contain information on species richness of various taxa and elevational gradients (Rahbek 1995), only 21% reported a monotonic decline of species richness on elevational gradients, 49% reported a hump-shaped relationship, that is, peaking at intermediate elevation range, and 25% showed a plateau-then-decreasing relationship. Rahbek (1995) also suggested that some studies which reported a monotonically decreasing relationship between species richness and elevational gradients actually would be hump-shaped if their sampling efforts were standardized (e.g., Terborgh 1977). Rahbek (1995) further pointed out that the climatic conditions among elevational gradients are not exactly mirrors of latitudinal gradients. For instance, the dramatic seasonal temperature differences in arctic and temperate regions are usually not observed on higher mountains in tropical regions, although they are often referred to as arctic and temperate zones.
Also, most elevational gradients have a "humidity peak" that is not observed on latitudinal gradients (Rahbek 1995). Besides, there is a fundamental difference between these two types of gradients: elevational gradients are at local or regional scales, and latitudinal gradients are at continental scale. Scale has been recognized as an important factor that affects various ecological processes, which in turn determine the spatial patterns of species richness (Shmida and Wilson 1985, Ricklefs 1987, Wiens 1989a, O’Neill 1989, Levin 1992, Böhning-Gaese 1997, Caley and Schluter 1997, Goodwin and Fahrig 1998, Gaston and Blackburn 1999, Lyons and Willig 1999). Therefore, patterns of species richness on elevational gradients do not necessarily mirror latitudinal gradients, and explanations for species richness on latitudes may not be considered applicable to elevation considerations.

Taiwan, a small island, lies on the Tropic of Cancer with its highest elevation near 4000 meters. Steep elevational gradients are found within a short horizontal distance, which makes it very suitable for studying species richness along elevational gradients. Birds appear to be the best taxon for studying species richness in Taiwan because they are diverse and well studied taxonomically. I chose to conduct this study at the local scale rather than at the regional scale. The reasons are to: (1) minimize possible influences of regional factors, (2) allow for a standardized sampling scheme, (3) to estimate bird population densities accurately, and (4) to measure vegetation structure directly. The objectives of this study are to examine the bird species richness patterns along an elevational gradient and evaluate the following three most-discussed explanatory theories: energy availability, spatial heterogeneity, and area size. These factors are
commonly considered as key factors that would define the underlying processes that in
turn determine and shape the species distribution patterns.

Earlier ecologists (Hutchinson 1959, Connell and Orias 1964, MacArthur 1965,
1972) proposed that energy availability limits the carrying capacity of a community to
contain species. Wright (1983) combined the energy concept with the island
biogeography theory (MacArthur and Wilson 1967) and suggested a species-energy
theory by replacing “area” with “energy availability” in the models of MacArthur and
Wilson (1967). This species-energy theory (energy limitation theory) suggests that the
increase of net primary productivity (NPP), i.e. gross primary productivity minus plant
total respiration, should increase the ability of plant community to support more
individuals of a consumer taxon per unit area. As the density of that consumer taxon
increases, population sizes increase, local extinction rates decrease, and thus species
richness of that consumer taxon increases. This energy limitation theory predicts a
positive relationship between NPP and species richness of a consumer taxon. This theory
has gained strong empirical and theoretical supports (Wright et al. 1993, Kaspari 2000).
However, recent evidence support a more complicated hump-shaped relationship (Grime
That is, species richness increases with NPP at low levels of NPP, but decreases after
NPP reaches a certain level. Rosenzweig (1992, 1995) examined nine hypotheses for the
decreasing phase and concluded that there is no single convincing hypothesis that could
completely explain the decreasing phase of species richness on NPP. In this study, I
examined the relationship between NPP and bird species richness (BSR) and tested three
mechanisms of the energy limitation theory: (1) NPP increases bird total biomass, (2) bird total biomass increases bird total density, and (3) bird total density increases BSR.

The spatial heterogeneity theory (MacArthur and MacArthur 1961, MacArthur 1964) has also been extensively studied by ecologists – especially avian ecologists. It proposes that, if the spatial structure of a habitat is more complex, it should provide more niches for more species, therefore species richness increases. The commonly used indices of spatial heterogeneity for terrestrial birds at local are foliage height diversity (MacArthur and MacArthur 1961) and plant species richness (Wiens 1989). The positive relationship between BSR and spatial heterogeneity has been shown to hold within several biogeographic regions (Terborgh 1977) and is often applied to explain patterns of species richness along elevational gradients (MacArthur 1972). In this study, I measured foliage height diversity and tree species richness and examined their relationships with BSR.

The area-species relationship, a positive relationship between area size and species richness, has been viewed as one of the most fundamental theories in ecology (MacArthur 1972, Rosenzweig 1995, Ricklefs and Lovette 1999). If we divided mountains into several equal-range elevational belts, the higher elevational belts would usually have less area and greater isolation than lower elevational belts (Rahbek 1997). Based on the island biogeography theory that a larger area has a lower extinction rate and isolation restricts immigration, an inverse relationship between elevation and species richness is therefore expected (MacArthur 1972). Although the importance of area effect on species richness is widely documented, more than 50% of the studies of species richness on elevational gradients did not justify the effect of area (Rahbek 1995).
Intuitively, taking sampling units of equal size along the elevational gradients could eliminate the area effect. However, there are other area-related effects, especially when animals are considered. A mountain can be viewed as composed of several elevational habitat belts and islands and sampling units within larger habitat belts are generally surrounded by larger area of similar habitats. If local populations of a sampling unit in a larger habitat belt suffered disturbances and were locally extinct or nearly extinct, there would be more individuals in the surrounding areas that could move in to rescue the populations from local extinction and recover the species richness. This type of area-related effect is called “rescue effect” (Brown and Kodric-Brown 1977). This rescue effect is rarely discussed in studies dealing with area and species richness. In this study, I estimated neighborhood area of each station and examined its relationship with BSR. Neighborhood area is defined as area of similar habitats where birds can disperse into each sampling station.
Study site

The study site was located on Mt. Yushan (23°28′30″N, 120°54′00″E) (3952 m above sea level), the highest peak of Taiwan. Fifty sampling stations were selected and ranged from 1400 to 3700 m (Figure 1). The selection criteria of sampling stations were: (1) able to represent the typical climax plant communities along the elevation gradient, (2) at least 100 m away from forest edges, creeks, and waterfalls, (3) at least 200 m away from other sampling stations, (4) at least 200 m away from artificial constructions and human-disturbed vegetation. The climatic variation and biotic communities along this elevation gradient are similar to those from subtropical to sub-arctic climate zones (Table 1).

Weather data of 32 weather stations within or near the study site show that annual average temperature decreases 5.29 °C for every 1000 meter elevation ($r^2 = 0.96$) (Su 1984a). This relationship holds well for different seasons (Su 1984a). In the study site, snow falls frequently above 2000 m and the snow season could last one to four months above 3000 m. Precipitation in the study site is mainly affected by the summer southwestern monsoon. Summer rainfall (April to September) accounts for 80-85% of the annual precipitation and shows a hump-shaped relationship with elevation. From sea level, summer rainfall tends to increase with elevation, usually reaches its maximum around 2200 m, and then decreases with elevation (Su 1984a). Winter precipitation (October to March), brought by the northeastern monsoon, only accounts 10%-15% of annual precipitation and is linearly and positively correlated with elevation (slope = 135.5mm/km, $r = 0.88$) due to rain shadow effect (Su 1984a).
Population density is very high in Taiwan (609 persons per square kilometer as of July, 2000). Most of the old-growth forests below 1300 m have been converted into agricultural farms or sylvicultural plantations. In a previous study (Ding et al. 1997) showed that vegetation succession strongly affects the species richness and composition of bird communities in this area. In order to exclude the effect of disturbance and succession, this study was conducted only in the areas of undisturbed climax plant communities, which form several vegetation zones along the elevational gradient (Table 1). The timberline lies around 3600 m. Shrubs of juniper and rhododendron are most prevalent between the timberline and 3800 m. Pure stands of fir dominate under the timberline down to 3100 m. Hemlock forests are distributed between 3100 and 2700 m. In both forest types, secondary trees are generally absent and dense bamboo shrubs overwhelm the forest floor. Spruce forests dominate between 2700 m and 2500 m. Secondary trees are primarily broadleaf trees. On the forest floor, bamboo shrubs are replaced by ferns and herbs. Between 2500 and 2300 m, conifer trees dominate the canopy layer which account for 30% to 70% of the canopy. The secondary tree layer (5-10 m tall) is closed and dominated by various broadleaf trees. Below 2300 m, coniferous trees disappear and broadleaf evergreen trees (mostly Fagaceae and Lauraceae) become dominant. Based on tree composition and ground vegetation type, the broadleaf forests are divided into three zones: upper Quercus zone, lower Quercus zone, and Machilus-Castanopsis zone (Su 1984b). The canopy, secondary tree, shrub, and herb layers of those zones are well developed and rich in floristic composition.
Methods

Estimation of bird densities and total biomass

Bird species densities were estimated from March to July 1992 by using the variable circular-plot sampling method (Reynolds et al. 1980). A pilot study determined the optimal time of bird count, which is a six-minute counting interval per hour for four hours after sunrise. At each station, I recorded the number, distance, sex (by appearance or song) of all bird individuals seen or heard during the six-minute period of every hour. The timing of field counts was designed to correspond to the time lag of bird breeding seasons along the elevational gradient. Bird counts on stations below 2000m were started in late-March and ended in late-May; on stations between 2000m and 3000m were counted from early-April to late-June; and on stations above 3000m were counted between mid-May and early-July. At each sampling station, I counted 16 times for a total of 96 minutes.

The mean body mass data of all breeding bird species in Taiwan (Lee et al. 1999) were combined with bird densities to calculate the bird total biomass at each sampling station.

Estimation of primary productivity

Net primary productivity (NPP) was estimated from weather data. Monthly mean temperature and precipitation at each sampling station were approximated by using the 1961-1990 average monthly weather data of the weather stations within or close to the study site. These estimates were adjusted by elevation, using the models reported by Su
Evapotranspiration (ET) of each station was estimated by the monthly mean temperature and precipitation, using the tables and equations of Thornthwaite and Mather (1957). ET is the amount of water returned to atmosphere through evaporation and transpiration. It correlates well with the photosynthetic activity of plants and has been used as an estimate of NPP (e.g., Currie 1991, Rosenzweig 1995). I estimated annual net aboveground primary productivity of each sampling station by the model of Rosenzweig (1968), \( \log_{10}\text{NPP} = 1.7003 \cdot \log_{10}\text{ET} - 1.7661 \), which explains 90% of net aboveground primary productivity in undisturbed habitats worldwide.

**Measurement of spatial heterogeneity indices**

In the study site, most of the sampling stations had slopes greater than 30° and the precipitous topography prevented researchers from moving freely in the forests. The original methods used to measure foliage height diversity (FHD) (MacArthur and MacArthur 1961) were therefore difficult in this study. A simplified measurement of foliage volume and FHD was employed. I estimated foliage coverage (0-100%) of four layers (0-0.6m, 0.9-1.8m, 3-6m, and 10-15m) in a 40m diameter circle at each station in the summer of 1992. The four layers represented herb, shrub, sub-canopy, and canopy layers of forests. Foliage height diversity was calculated using the Shannon-Wiener Index (Magurran 1988) of the foliage coverage of the four layers. In addition, I counted trees (diameter at breast height > 1cm) within a 20m diameter circle at each sampling station to calculate tree species richness (TSR).

**Estimation of neighborhood area**
Barrowclough (1980) summarized several field studies and concluded that, exclusive of seasonal migration, non-colonial passerine birds disperse roughly one kilometer per year, with a range of 350 to 1700 meters per year. The available bird banding data in Taiwan were in agreement with Barrowclough’s (1980) estimation. Since this study covered only one breeding season, I chose one kilometer as the buffer distance to test the rescue effect. Using ARC/INFO, I created point coverage of the 50 sampling stations and then established circular buffer zones centered at each of the stations with a diameter of two kilometers. Those circular-shaped buffers were further overlaid with digital elevation model (DEM) coverage of Taiwan (40 × 40m resolution). The neighborhood area of each station was calculated as the area of grids that falls within the corresponding buffer zone and within 100 m elevation difference from the station.
Results

Bird species richness, density, and biomass

I recorded 59 breeding species from 13,716 individual records in the field bird counts. Based on the Sibley-Ahlquist-Monroe avian taxonomy system (Monroe and Sibley 1993), 46 species (78%) were passerines and the largest family (18 species) was Sylviidae (babblers and warblers). All the species recorded were non-colonial and showed some territory behaviors during the period of field bird counts.

Bird species richness (BSR) did not monotonically decline nor show a hump-shaped relationship with elevation. BSR curve was roughly equal across in broadleaf forests with considerable variation (16-29 species), reached its maximum (30 species) in mixed forests, then monotonically declined in conifer forests, and reached minimum in juniper shrubs (5-6 species) (Fig. 2a). Bird total density was high in broadleaf forests, mixed forests, and spruce forests (67.1 - 36.2 No. ha.\(^{-1}\)), then deceased with elevation, and was the lowest in juniper shrubs (7.3 - 10.9 No. ha.\(^{-1}\)) (Fig. 2b). Bird total biomass monotonically declined with elevation (1.43 - 0.22 kg ha.\(^{-1}\)) and had higher variation at lower elevations (Fig. 2c).

ET and NPP

The estimated annual ET linearly and inversely correlated with elevation and ranged from 752 to 407 (mm yr\(^{-1}\)) along the gradient (Fig. 2e). Although summer (April – September) precipitation had a hump-shaped relationship with elevation, the amount of rainfall was never a limiting factor for ET in summer. For instance, the summer
precipitation was greater than 2400 mm in all locations. Temperature, which was linearly and inversely correlated with elevation, was the limiting factor for ET. NPP also linearly and inversely correlated with elevation and ranged from 466 to 1343 (g m\(^{-2}\) yr\(^{-1}\)) along the gradient (Fig. 2f). These estimations were consistent to those reported by Lieth and Whittaker (1975) on similar vegetation types worldwide.

After the double log transformation, BSR positively correlated with NPP (slope = 1.58, \(F = 128.5, p < 0.001, R^2 = 0.73\)) (Fig. 3). In a polynomial regression analysis of NPP and BSR, both quadratic and cubic factors were significant (\(p < 0.01\)), suggesting BSR was not linearly related to NPP. In order to test whether it was hump-shaped or an increasing-then-plateau relationship, I subjected sampling stations 1-22 (station 22 had the highest BSR and stations 1-22 had higher NPP) to a linear regression analysis. The result was not significant (\(F = 0.006, p = 0.94\)), implying an increasing-then-plateau relationship between NPP and BSR.

If the energy limitation theory is correct, the following three relationships should be observed. First, NPP increases bird total biomass. Second, bird total biomass increases bird total density. Third, bird total density increases BSR. In my analysis, bird total biomass was positively and linearly correlated with NPP when both variables were log transformed (\(r^2 = 0.77, F = 158.0, p < 0.001\)) (Fig. 4). However, bird total density showed a humped-shape relationship with bird total biomass (Fig. 5), which contradicted the second prediction from the energy limitation theory. Bird total biomass explained 90% of the variance of bird total density in a quadratic regression model (\(t = -9.01, p < 0.001\), for the quadratic factor) (Fig. 5). The bird mean body weight (bird total biomass divided by bird total density) showed a U-shaped relationship with bird total biomass.
(Fig. 6). In a quadratic polynomial regression, bird total biomass explained 64% of the variance of bird mean body weight ($t = -8.99$, $p < 0.001$, for quadratic factor) (Fig. 6). Thus, on average, birds tended to be smaller at intermediate levels of NPP (elevation). The relationship between density and richness, however, was consistent to the third prediction of the energy limitation theory. Bird total density positively and linearly correlated with BSR after both variables were log transformed ($r^2 = 0.78$, $F = 170.5$, $p < 0.001$) (Fig. 7).

**Parameters of plant communities**

TSR ranged from 1 to 22 species (within a circular area of 314m$^2$) and showed a hump-shaped relationship with elevation ($p < 0.01$, for quadratic and cubic factors of polynomial regression) ($p < 0.05$, for the negative slope of linear regression of sampling stations 1-11) (Fig. 2g). Along the elevational gradient, TSR increased first, peaked around 2000 m, and gradually declined with elevation. FHD was lowest in juniper shrubs and roughly remained constant at a high level in other forests along the gradient (Fig. 2h).

TSR showed a hump-shaped relationship with NPP (Fig. 8). NPP explained 84% of the variation in TSR in the polynomial regression model ($F = 71.4$ for quadratic and cubic factors and $p < 0.001$). BSR significantly and positively correlated with TSR ($r^2 = 0.59$, $F = 69.7$, $p < 0.001$) (Fig. 9) and FHD ($r^2 = 0.35$, $F = 26.2$, $p < 0.001$) (Fig. 10).

**Neighborhood area**

The 1 km neighborhood area did not vary consistently with elevation (Fig. 2d). BSR was significantly but negatively correlated with neighborhood area in a simple
regression after both variables were log transformed (slope = -1.28, \( r^2 = 0.26 \), F = 17.0, p < 0.001). The rescue effect predicts the slope of regression function (z) be significantly greater than zero. Thus the rescue effect hypothesis was rejected at this scale.

*Multiple regressions*

Stepwise multiple regression (criteria for inclusion and exclusion, p < 0.05) was applied to evaluate the effects of NPP, TSR, FHD, and neighborhood area on BSR. NPP, neighborhood area, and BSR were log-transformed to meet the normality and variance homogeneity assumptions of the regression analysis. NPP explained 73% of variance in BSR (p < 0.001), FHD explained additional 4% (p = 0.004), and TSR explained additional 3% (p = 0.014) (Table 2). Neighborhood area was excluded in the final model for its insignificant contribution to the model.
Discussion

In this study, BSR plateaued at lower elevations but then declined at higher elevations. Would the BSR remain a plateau, or decline, or increase if the elevational gradient was extended to sea level? This question is virtually impossible to answer in this study because most of the habitats below 1300 m in this region have been extensively modified by human activities. In another study (chapter two), BSR of 674 localities in Taiwan was compiled from 288 avifauna censuses that covered one or two years of census period. BSR and elevation showed a hump-shaped relationship along the entire elevational gradient in Taiwan. BSR was highest between 1400 to 2200 m. Although the massive agricultural and urban land uses on Taiwan’s lowlands might contribute to this hump-shaped relationship; it was also observed that some lowland old-growth forests had significantly fewer bird species than mid-elevation forests. I thus conclude that BSR would not likely increase if I extended the elevational gradient to the lowlands.

Rahbek (1995) argues that species richness patterns on elevational gradients do not necessary mirror latitudinal gradients. He also pointed out that 79% of the cases did not standardize the effect of area and sampling effort, which might distort the actual relationship between species richness and elevation. I employed a sampling scheme of same area and sampling effort. The observed plateau-then-decreasing relationship supports Rahbek’s (1995) argument that the monotonically inverse relationship of species richness and elevation is not as universal as ecologists generally assume.
Energy availability

BSR showed an increasing-then-plateau relationship with NPP. Testing further, I found the results contradict one of the underlying mechanisms. Here I discuss those mechanisms in detail.

First, if energy availability is a limiting factor for species richness, the energy flux into a consumer taxon or trophic group should be proportional to the available energy. That is, the consumer group must be able to exploit more energy if there are more resources available. I used bird total biomass as the index of energy flux. The high correlation between bird biomass and the estimated NPP suggests that the energy consumed by birds is proportional to NPP. This result is consistent with the prediction of the first mechanism of energy limitation theory.

Bird total biomass is not only a reasonable index of energy flux but also possibly a more accurate estimation of NPP that ET. The primary productivity or the energy fixed by photosynthesis is extremely difficult to measure directly. In this study, I collected weather data to estimate NPP through ET, an approach that is popular among ecologists. The result showed a general trend of NPP along the elevational gradient. However, some on-site variations were not accounted in the smooth NPP line along elevational gradient. Although temperature and precipitation played a predominant role in NPP, other environmental factors such as slope, aspect, and soil properties also affect NPP. Estimating NPP solely from weather data may not sufficiently reflect the variation in NPP that could be caused by other important habitat properties. As a result, I suggest bird total biomass is a better estimator of NPP in this case.
Second, if energy availability is a limiting factor for species richness, total density of a consumer group should be proportional to its energy flux. My results do not support this prediction. Bird total density showed a hump-shaped relationship with bird total biomass. Bird density first increased with bird total biomass and decreased after bird total biomass roughly reached one kilogram per hectare. I also observed a U-shaped relationship between bird mean body weight (per individual) and bird total biomass. It is difficult to determine whether this U-shaped relationship was attributed to energy availability, climate, or a combination of both, since mean air temperature also correlated well with bird total biomass in this study.

The third mechanism of the energy limitation theory predicts that species richness be proportional to total density. That is, higher density reduces the possibility of local extinction and thus increases species richness. I found BSR increased with bird total density, which is consistent with the prediction.

In short, the hump-shaped relationship between BSR and NPP was not observed. However, I found a hump-shaped relationship between bird total biomass and total density, which contradicted to one of the underlying mechanisms of the energy limitation theory.

One intriguing pattern in species richness is the hump-shaped relationship between primary productivity and species richness, which has accumulated considerable empirical support in recent years. However, there is no theoretical model that predicts where the peak of hump-shaped relationship occurs. The positive relationship between primary productivity and species richness has often been explained as part (the increasing phase) of the hump-shaped relationship (e.g., Rosenzweig 1992, 1995, Rosenzweig and
Abramsky 1993, Guo and Berry 1998). The observed relationship between NPP and BSR in this study is also difficult to attribute as whole or part of the pattern. Nevertheless, the observed hump-shaped relationship between bird total biomass and total density hints one possible explanation of the decreasing phase of the hypothetical hump-shaped relationship. That is, once energy availability reaches a certain level, it might decrease species richness through increasing body size and reducing total density. Rosenzweig (1992, 1995) discussed nine hypotheses explained the decreasing phase of species richness on NPP. However, the observed hump-shaped relationship between total biomass and total density can not properly fit any of the nine hypotheses. The relationships among primary productivity, body size, density, and species richness are important topics warranting further investigation.

Spatial heterogeneity

The spatial heterogeneity theory postulates that a more complex habitat provides more niches that would allow more species to inhabit it. In this study, I chose FHD and TSR to represent the degree of spatial heterogeneity of the sampling stations. FHD represents the vertical and structural heterogeneity of vegetation, and plant species richness represents the horizontal and floristic heterogeneity of vegetation. Since all the sampling stations were located within climax vegetation, there was not much variance in FHD. Most of the variation came from structural differences between forests and juniper shrubs. Because of the narrow variation of FHD, I did not find a clear relationship between BSR and FHD.
TSR correlated well with BSR. This result is consistent with former studies (e.g. Karr and Roth 1971, Rice et al. 1983). TSR also showed a significant hump-shaped relationship with elevation and NPP. The hump-shaped relationship of TSR on NPP, along with other factors, might be one of the reasons for the observed plateau-then-decreasing relationship of BSR on elevation. Many papers reported that species richness has a hump-shaped relationship with primary productivity (or energy availability). Rosenzweig (1992, 1995) concluded that environmental heterogeneity (Tilman 1982) is one of the most plausible hypotheses that explain the decreasing phase of species richness on NPP but it is probably tautology because spatial heterogeneity might co-evolve with species richness. I did not design this study to explore the processes of TSR; therefore, it is difficult to speculate on the mechanisms for the hump-shaped relationship between TSR and NPP. However, TSR is a reasonable index for environmental heterogeneity from birds’ standpoint and it correlated well with BSR, which supported the environmental heterogeneity hypothesis. Although birds might facilitate TSR through pollination and seed dispersal, it is not very convincing that BSR plays a prominent role for TSR. Therefore, the concern about tautology might not be important in this case.

*Rescue effect*

Ecologists often view area effect as a primary process for spatial patterns of species richness (e.g., Rosenzweig 1995). In this study, each sampling station had the same area size and the neighborhood area was not a factor for species richness. There is no direct evidence that area size is responsible for the observed species richness patterns in this study.
In summary, I found that: firstly, BSR showed a plateau-then-decreasing relationship with elevation; secondly, area was not a factor at this (local) scale; and thirdly, energy availability played an important role and possibly provided the ultimate explanation for BSR in this study. Energy limitation theory explains well the decreasing phase of BSR on elevation. For the plateau phase of BSR on elevation, more energy availability may have indirectly decreased BSR through the reduction of bird total density and spatial heterogeneity.
Literature cited


Table 1. Main vegetation zones along the elevation gradient within the study area
(modified from Su 1984b)

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

Table 2. Stepwise multiple regression suggests that net primary productivity is the best variable to explain bird species richness.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Order</th>
<th>Standard Coefficient</th>
<th>Partial r²</th>
<th>Model r²</th>
<th>t</th>
<th>Prob. &gt; t</th>
</tr>
</thead>
<tbody>
<tr>
<td>Net primary productivity</td>
<td>1</td>
<td>0.68</td>
<td>0.729</td>
<td>0.729</td>
<td>2.5</td>
<td>0.017</td>
</tr>
<tr>
<td>Foliage height diversity</td>
<td>2</td>
<td>0.36</td>
<td>0.044</td>
<td>0.773</td>
<td>3.5</td>
<td>0.001</td>
</tr>
<tr>
<td>Tree species richness</td>
<td>3</td>
<td>0.01</td>
<td>0.028</td>
<td>0.801</td>
<td>2.5</td>
<td>0.014</td>
</tr>
</tbody>
</table>

* Bird species richness and net primary productivity were log transformed.
Figure 1. Location of study area and sampling stations. The sampling stations were ranked by elevation and labeled as 1 to 50 from low to high. Only the labels of those stations at the ends of transects were shown.
Figure 2. Various variables along elevation gradients: (a) bird species richness, (b) bird total density (No·ha\(^{-1}\)), (c) bird total biomass (kg·ha\(^{-1}\)), (d) one kilometer neighborhood area (km\(^2\)), (e) annual evapotranspiration (mm·yr\(^{-1}\)), (f) annual net aboveground primary productivity (g·m\(^{-2}\)·yr\(^{-1}\)), (g) tree species richness, (h) foliage height diversity.
Figure 3. Bird species richness showed an increasing-then-plateau relationship with annual net aboveground primary productivity (g·m⁻²·yr⁻¹).

Figure 4. Bird total biomass (kg·ha⁻¹) increased with annual net aboveground primary productivity (g·m⁻²·yr⁻¹).
Figure 5. Bird total density (No·ha⁻¹) showed a hump-shaped relationship with bird total biomass (kg·ha⁻¹). The fit line is in quadratic function.

Figure 6. Bird mean body weight (g) showed a U-shaped relationship with bird total biomass (kg·ha⁻¹). The fit line is in quadratic function.
Figure 7. Bird species richness increased with bird total density (No.·ha.\(^{-1}\)).

Figure 8. Tree species richness showed a hump-shaped relationship with annual net aboveground primary productivity (g m\(^2\) yr\(^{-1}\)).
Figure 9. Bird species richness increased with tree species richness.

Figure 10. Bird species richness increased with foliage height diversity.
Chapter Two

Breeding Bird Species Richness on Gradients of Elevation, Primary Productivity, and Human Disturbance in Taiwan
Abstract

I examined the distribution patterns of breeding bird species richness on gradients of elevation, primary productivity, and human disturbance in Taiwan. Bird species richness (BSR) data were compiled from avifauna censuses undertaken in 288 sites in Taiwan from 1980 to 2000. BSR showed a hump-shaped relationship with elevation, increased with primary productivity, and decreased with human disturbance. Further analyses revealed that human disturbance decreased with elevation. In addition, primary productivity showed a hump-shaped relationship with elevation and decreased with human disturbance. Multiple regression analysis showed that linear and cubic terms of elevation explained 31.3% of the variation in BSR and human disturbance explained additional 3.4%. The explanatory power of primary productivity was insignificant after the effects of elevation and human disturbance were justified. Results showed that human disturbance is a main reason that BSR increased with elevation in the lower elevations of Taiwan. Furthermore, the biotic communities in the mid-elevation zone had relatively longer periods of existence than those at the extremes of the elevational gradient in Taiwan during the Pleistocene glacial cycles. This historical perturbation might be one cause behind the observed hump-shaped relationship between bird species richness and elevation.
Introduction

Describing and explaining spatial patterns of species diversity are crucial steps in conservation of global biodiversity and long-standing problems in ecology (Lubchenco et al. 1991). Earlier ecologists presumed that interactions (e.g., competition and predation) among populations within small areas are the fundamental forces that regulate community structure and species diversity (Ricklefs and Schluter 1993). However, this local-process paradigm fails to satisfactorily explain spatial patterns of species diversity at broader scales. Ecologists have found many regional and historical processes that significantly affect species diversity at broader spatial scales (Ricklefs 1987, Ricklefs and Schluter 1993, Cornell and Karlson 1996, Whittaker et al. 2001). Manipulation experiment, an approach widely used at local scale, is either practically impossible or ethically unacceptable at regional or continental scales. As a result, another research approach, namely macroecology, has emerged to fill the void. Macroecology is concerned with the statistical distributions of ecological characters of organisms (e.g., species diversity, abundance, distribution range, and body size) from regional to global scales (Brown 1995). It emerged with the growing availability of reliable information on occurrences of species at multiple disparate sites that have been compiled from a variety of censuses and maps (Blackburn and Gaston 1998). Since it is mostly based on observational data that were compiled from various sources, macroecology studies need special efforts to exclude artifacts embodied in the data and rely heavily on inductive rationale in testing hypotheses (Gaston and Blackburn 1999). As Brown (1995) stated,
macroecology is a complementary approach to traditional experimental population and community ecology rather than an alternative.

This study investigates the spatial patterns of species diversity along various environmental gradients in Taiwan using the approaches of macroecology. Birds are often studied in macroecology since ornithologists and bird watchers have accumulated large sets of occurrence and abundance data over the years. In Taiwan, birds also appear to be the best taxon for macroecological studies for the same reason. There have been more than 400 avifauna censuses undertaken in Taiwan in the last 20 years and the distribution patterns of birds are well documented. Lee et al. (1998) developed a distribution database of vertebrates by compiling more than 1000 reports of fauna censuses that were conducted in Taiwan. Nieh (2000) used that database to study the spatial patterns of bird species richness (BSR) along gradients of 20 environmental factors. However, Nieh (2000) found the environmental factors did not have strong explanatory power of BSR. This study used approaches similar to Lee et al. (1998) and Nieh (2000). I compiled available fauna censuses into an equal area quadrat system and compared them with environmental factors. In order to improve data quality, I adapted stricter criteria for input data and incorporated a data set collected by Taiwan Endemic Species Research Institute. The objectives of this study are to investigate the distribution of breeding bird species richness on gradients of elevation, primary productivity, and human disturbance and to evaluate current theories of species diversity.
Elevation

Taiwan is a small island with a land area of about 36,000 km². However, mountains account for 70% of the area of Taiwan and the highest point is close to 4000 m above sea level, which create a dramatic landscape with environmental gradients analogous to those from the tropics to the subarctic. Thus, elevation plays the primary role in governing temperature, precipitation, and consequently, distribution of species and natural vegetation. Traditionally, species richness is expected to correlate inversely with elevation (MacArthur 1972). In a review of data sets that contain elevational distribution of species richness of various taxa, however, Rahbek (1995) found that only 21% of the data sets showed a monotonic decline of species richness with elevation. He argued that the monotonically inverse relationship between species richness and elevation is not as universal as ecologists generally assumed.

Kano (1940) studied the species distribution of terrestrial vertebrates along the elevational gradient in Tsugitaka Mountains (Shiushan, second highest peak in Taiwan). He divided the elevational gradient into 13 elevational bands that each spanned 300 m and summarized the species distributed in each band. He found the total species richness of mammals, reptiles, and amphibians declined with elevation. However, BSR was highest between 1200 and 1500 m, instead of in the lowlands. Jai (1977) studied the elevational distribution of breeding bird species in Taiwan and concluded that species richness increased upwards from the lowlands, peaked between 1200 and 1500 m, and then decreased with elevation. Lin (1989) reported BSR was highest between 1800 and 2100 m in Shiushan. Those studies were derived by combining the elevational distribution of species, instead of systematic sampling at disparate sites along elevational
gradients. In yet another study at local scale (chapter one) that spanned from 1400 to 3700 m elevation in Yushan, BSR remained at a plateau from 1400 to 2300 m and then decreased with elevation. In this study, BSR data were compiled from available avifauna censuses and compared with elevation to test whether the relationship is hump-shaped or monotonically decreasing at an island-wide scale. The relationships between species richness and other environmental factors on the elevational gradient in Taiwan were also examined to search for possible explanations.

*Primary productivity*

The carrying capacity of life on earth cannot exceed the level that can be supported by energy arriving from the sun (Gaston and Blackburn 2000). The energy limitation theory suggests that energy availability limits the carrying capacity of a community to contain species and the increase of primary productivity should increase the species richness through increasing population sizes and decreasing local extinction rates (Hutchinson 1959, Connell and Orias 1964, Wright 1983). Many studies have found positive monotonic relationships between primary productivity and species richness of various plant and animal groups (Currie and Paquin 1987, Currie 1991, Blackburn and Gaston 1996, Gaston 2000). However, some studies reported hump-shaped relationships between primary productivity and species richness, in which species richness peaks at intermediate levels of primary productivity or energy availability (Tilman 1988, Rosenzweig 1992, 1995, O’Brien 1993). In other studies at local and continental scales (Chapter One and Chapter Three), I found that BSR generally increased with primary productivity. In this study, I investigated the spatial pattern of
BSR along a gradient of primary productivity at regional scale and tested whether the relationship was hump-shaped or monotonically positive between primary productivity and species richness.

*Human disturbance*

Human activities impact the Earth, including modification, degradation, reduction, and fragmentation of natural habitats. Although the changes are profound and extensive, most ecological studies are conducted on reserves and wild areas where effects of human beings have been minimal and therefore the effects of human disturbance on species diversity are rarely discussed. To a large extent, this is due to the widespread view in Western culture that nature is something apart from humanity (Brown and Lomolino1998). Typically, human disturbances (e.g., agricultural practices) increase the number of vegetation types of early or intermediate successional species and decrease the primary productivity and size of habitats. Extreme disturbances (e.g., urbanization) may decrease all of these factors when the natural habitats are permanently replaced by pavements and structures. In a review of 19 studies of bird communities along urban gradients in U.S. and Europe, Blair (1996) found that (1) bird species composition changed in urbanized areas, (2) bird abundance increased with urbanization, and (3) BSR decreased with urbanization.

Taiwan is one of the most densely populated areas on the Earth. Most of the lowlands in Taiwan have been changed to meet people’ needs. In this study, I investigated the spatial pattern of BSR along gradients of human disturbance (estimated by road density and percent of built area) and tested the hypothesis that human disturbance decreases BSR.
Study area

Taiwan (formerly known as Formosa) is an island located offshore of the east fringe of Mainland Asia, lying between 120°02’ – 122°00’ E and 21°53’ – 25°18’ N. Taiwan is an orogenic island that was created by collisions of Philippine Plate and Eurasian Plate (Ho 1986, Aubouin 1990). It emerged above sea level about five MYA (million years ago) and is still rising and tectonically active (Teng 1990). The Taiwan Strait is about 130 km at its narrowest width and a sea level drop of more than 70 m would connect Taiwan to Mainland Asia (Nino and Emery 1961). It is now widely accepted that the sea level fluctuated repeatedly during the Pleistocene and the global changes in sea level might drop by well over 160 m lower than present (Shackleton 1987, Brown and Lomolino 1998). Consequently it is reasonable to estimate that Taiwan has had frequent and long connection with Mainland Asia during the Pleistocene (1.6 – 0.01 MYA). From 250 KYA (thousand years ago) to now, in about 17% of time has the sea level in Southeast Asia been 75 m below the present sea level (Voris 2000). Based on a 17,000-year eustatic (global) sea level record from the Caribbean (Fairbanks 1989), the last landbridge connection between Taiwan and Mainland Asia might have lasted until about 12 KYA. The frequent landbridge connections provided dispersal routes for terrestrial organisms and created waves of terrestrial biotic exchange between Mainland Asia and Taiwan.

The glacial periods in the Pleistocene also coupled with dramatic climatic fluctuations. Pollen records taken from Sun-Moon Lake (750 m in elevation) in Central Taiwan (Tsukada 1966, 1967) showed that the dominant trees during the maximum of
Dali Glaciation (60-50 KYA) (the last glaciation in China, counterpart of Early Wisconsin in North America and Würm I in Europe) were largely boreal conifers and pines. At that period, temperature was about 8-11°C cooler than present and winter temperature probably dropped to freezing in the lowlands of Taiwan. During the late Dali Glaciation (50 – 10 KYA), dominant trees were cool temperate species and the temperature fluctuated between about 0 to 8°C cooler than present. In the Holocene (10 KYA to present), those cool-temperate species were rapidly replaced by warm temperate and subtropical species. During the hypsithermal period (about 8-4 KYA), the temperature might have been 2-3°C warmer than at present.

With the climatic fluctuations and frequent landbridge connections during the Pleistocene, together with the lofty mountains in Taiwan, many Palearctic and Himalayan species colonized Taiwan but were then trapped in the mountains. The avifaunas in the higher-elevation zone (> 2500 m) of Taiwan have been reported to be mainly composed of the Palearctic elements and those in mid-elevation zone (1500-2500 m) are strongly affiliated with species in the Eastern Himalayas (Kano 1940, Hachisuka and Udagawa 1950). Only the avifaunas in the plains and foothills of Taiwan have strong affinity with nearby Southeastern China and the Indochina Peninsula. The isolated nature of the island impoverished the total number of breeding bird species in Taiwan (discussed in Chapter three), however it increased the endemism of avifauna. About 10% of the 152 resident bird species in Taiwan are endemic species and about 40% are endemic subspecies. Cursorial birds (e.g., pheasants) and weak fliers (e.g., babblers and bulbuls) have the highest proportion of endemism (Severinghaus 1994).
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 $-5.43^\circ$C/km (Su 1984a). Precipitation can be grouped into winter and summer phases. The winter precipitation (October to March) is brought by the northeast prevailing winds and mostly falls on the northern and eastern part of Taiwan. The summer precipitation (April to September) is mainly brought by typhoons and southwest prevailing winds. In general, mountains receive more precipitation than the lowlands and plains. The rainy belt of SW monsoons is much higher in elevation than that of NE monsoons. The maximum winter precipitation occurs at 300-400 m and summer precipitation reaches a maximum around 2200 m in elevation (Su 1984a). The western and southern parts of Taiwan experience a significant dry season during winter since the NE monsoons are mostly intercepted by the mountain ranges in the north and east. On average, most the plains have about 1500-2500 mm annual precipitation. Mountain areas generally have about 2000-3500 mm annual precipitation but may be up to 7700 mm, depending on the location, aspect, and elevation.

Due to the abundant precipitation, the natural vegetation types in Taiwan are mostly forests (Su 1984b). Broadleaf and conifer forests dominate respectively lower and higher elevation areas in Taiwan, with a wide transition zone between 1500 and 2500 m. The broadleaf forests are dominated by Moraceae and Euphorbiaceae in areas below 500 m and by Lauraceae and Fagaceae between 500 and 2500 m. The conifer forests dominate from 2000 to 3600 m. The dominant canopy tree species of the conifer forests are cedars, hemlocks, and firs from low to high elevation respectively.
Evidence of prehistoric human habitation in Taiwan dated back 12 to 15 KYA. However, the indigenous peoples of Taiwan did not cause extensive landscape changes. In the 17th century, Chinese (Han people) started to immigrate and quickly colonized Taiwan (now 22 million population). The immense population pressure caused massive forest clearing in the lowlands during the last several hundreds of years. Currently there is no pristine forest left on the plains and only few patches remain on the foothills. Extensive logging during the last one hundred years has also eliminated many 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 bird species have limited distribution.
Methods

Quadrat system

An equal-area quadrat system was used for the measurement and analysis unit of species richness and environmental factors. Area has been found to be an important factor in determining species diversity and yet is often ignored or confounded in species diversity studies at coarse scales. Whittaker et al. (2001) suggested that area should be held constant and equal area grid cells should be used if a study intends to examine the relative roles of different environmental variables on species diversity. In this study, the locations of avifauna censuses were carefully analyzed and converted into equal-area quadrats. Based on the census reports, a species was assigned as present, absent, or no data per quadrat. Species richness in this study was defined per quadrat as the number of species occurred in the quadrat. Environmental factors were also summarized and arranged by the quadrat system.

The size of the quadrat was 2×2 km (grain of quadrat system) in this study. This quadrat size was determined by (1) the variability of bird movement, (2) spatial extent and resolution of avifauna censuses, and (3) spatial heterogeneity of environment. First, birds are animals that usually move several hundred meters to several kilometers in a day. The resolution of its distribution data is therefore inherently limited and cannot be as precise as for organisms having fixed location, such as plants. Second, most avifauna censuses in Taiwan employed transect sampling and results were usually compiled by transects. Those transects were usually 2-4 km in length and ideally the quadrat size should not be smaller than the spatial resolution of input data. Third, the mountains in Taiwan are generally steep and one can find high landscape diversity within a short
distance. Within a few kilometers, the elevation difference might be more than several thousand meters and thus create steep environmental gradients. In order to get a better resolution on environmental gradients, a smaller quadrat size is preferred. Combining all above considerations, 2×2 km is deemed the most appropriate quadrat size. In total, there were 9388 quadrats defined that cover the entire Taiwan Island.

_Bird species richness_

Only breeding bird species were included in species richness calculations in this study. Most of the breeding species in Taiwan have established stable populations and their active singing and displaying behaviors during the breeding seasons make them easy to detect. Consequently the probability of breeding species being missed in avifauna censuses is greatly reduced. Typically year-round avifauna censuses in Taiwan detect most of the breeding species after a few field counts. Comparing to breeding species, migrants and vagrants are not very selective in habitats and usually have nomadic distribution and variable abundance, thus the number of migrant and vagrant species is highly dependent on the census effort. There are 155 breeding bird species in Taiwan. However, Strigidae (owls) and Tytonidae (barn owls) were not included here since they are mainly nocturnal and are often missed in avifauna censuses. Pelagic birds were also excluded since they primarily feed on marine food sources. In total, there are 147 species included in this study.

The bird species richness data were selected from extensive avifauna censuses conducted by Taiwan Endemic Species Research Institute (TESRI) from 1992 to 2000 and published reports of avifauna censuses from 1980 to 2000. The selection criteria
were: (1) census period covered one or two years and had at least six field counts during their census period; (2) location was clearly described; (3) results were arranged in a spatial resolution of less than 10 km², and (4) all avian groups (except owls) were surveyed with equal efforts. There were 143 sites selected from the 192 census sites conducted by TESRI and 145 out of 432 published census reports. The locations of census sites were examined and assigned into the 2×2 km quadrat system. In total, 674 quadrats (about 7% of the total quadrats in Taiwan) were defined. A checklist of the 145 selected census reports is provided on the following web site:

http://www.genglab.ucdavis.edu/ding/aves/dist_r_lit.htm

Environmental factors

Elevation was summarized from a digital elevation model (DEM) coverage of Taiwan (40 × 40m resolution). The DEM was overlaid with the 2×2 km quadrat system and average elevation was calculated for each quadrat.

Primary productivity was estimated by the Advanced Very High Resolution Radiometer – Normalized Difference Vegetation Index (AVHRR-NDVI). NDVI is a measure derived by dividing the difference between near-infrared and red reflectance measurements by their sum (Tucker 1979). NDVI is highly correlated with green-leaf biomass, green-leaf area, and absorbed photosynthetically active radiation (APAR) (Curran 1980, Goward et al. 1985) and has been used as estimate of net primary productivity and vegetative growth of terrestrial ecosystems (Goward et al. 1985, Box et al. 1989, Ustin et al. 1991). To minimize cloud contamination, I combined the available NDVI composites from 1992 to 1997 into a set of monthly NDVI composites by
maximum value composite method (Holben 1986). Each month was combined from 90 to 120 daily NDVI composites. The NDVI data, with original resolution of about 1×1 km, were downloaded from web site (3rd Oct. 2001).

http://daac.gsfc.nasa.gov/data/dataset/AVHRR/01_Data_Products/06_Images/03_Asia

Human disturbance was estimated by road density and percent of built area. Both indices were obtained from a digital atlas established by Department of Interior of Taiwan government in 2000. The atlas has a high resolution and contains all levels of roads and built areas in Taiwan. The coverage of built area and road was overlaid with the 2×2 km quadrat system to calculate the sums of road length and area of built area per quadrat. Both variables were justified by land area of each quadrat to get road density and percentage of built area.
Results

General patterns

BSR ranged from 7 to 76 species per quadrat (Figure 1) and showed a hump-shaped relationship with elevation (Figure 2). BSR increased with elevation from sea level (10 - 64 species), peaked around 2000 m (43 - 76 species), then decreased with elevation and reached its minimum at highest elevation. The slope of the decreasing phase (slope = -0.027, r = -0.73) was steeper than increasing phase (slope = 0.012, r = 0.48) (p < 0.01). BSR generally increased with NDVI (Figure 3). In the range of NDVI below 0.5, there was no relationship between BSR and NDVI (r = 0.03). In the range of NDVI above 0.5, BSR showed a strong positive relationship with NDVI (slope = 65.29, r = 0.34). BSR was negatively correlated with road density (r = -0.43) (Figure 4) and percentage of built area (r = -0.39) (Figure 5).

Colinearity among environmental factors

The four environmental variables were plotted against each other to investigate the patterns of colinearity (Figure 6). Percent of built area and road density showed inverse relationships with elevation (Figure 6b, 6c). There is a strong positive correlation between percent of built area and road density (r = 0.821) (Figure 6f). NDVI showed a hump-shaped relationship with elevation (Figure 6d) and inverse relationships with percent of built area (r = -0.369) (Figure 6g) and road density (r = -0.521) (Figure 6i).
Multiple regressions

Stepwise multiple regression analyses were conducted to evaluate the effects of environmental factors on BSR. Several procedures were undertaken before the regression analyses. First, only one index, road density, was chosen as the estimate for human disturbance since there was a high degree of correlation between road density and percent of built area. The reasons to choose road density were that road density had a better spread of data and higher degree of correlation with BSR. Second, the quadratic and cubic terms of elevation and quadratic term of NDVI were added into the regression analyses since BSR showed curvilinear relationships with elevation and NDVI. Third, hierarchical models were used since there were causal relationships among environmental factors. In this study, elevation might affect both primary productivity and human disturbance but should not be affected by those. In addition, human disturbance might affect primary productivity but was less likely affected by primary productivity. Therefore, variables of elevation were first entered into the models before other variables were admitted, and then road density was introduced before variables of NDVI. Fourth, road density was logarithmic transformed to make the shape of its distribution symmetric and variances stabilized.

Since the quadratic term of elevation did not have significant explanatory power, it was eliminated from further multiple regression analyses. Linear and cubic terms of elevation explained 31.3% of the variation in BSR and were kept in the model (Table 1). Road density entered in the second step and was kept in the model. Road density explained additional 3.4% of the variation in BSR (Table 1). Linear and quadratic terms of NDVI were introduced in the third step but were both removed from the final model.
since their explanatory powers were not significant. The final model explained 34.7% of the variation in BSR (Table 1).

To test if the explanatory powers of road density and NDVI were different in the increasing and decreasing phases of BSR on elevation, the sampled quadrats were divided into two groups (below or above 2000 m).

In the low elevation group (< 2000 m), road density inversely correlated with BSR \((r = -0.505)\) and NDVI \((r = -0.541)\). However, NDVI was positively correlated with BSR \((r = 0.377)\) (Table 2). Both road density and NDVI were kept in the final regression model (criteria for removal: \(p > 0.05\)) (Table 3). The final regression model explained 27.0% of the variation in BSR.

In the high elevation group (> 2000 m), BSR highly correlated with NDVI \((r = 0.658)\) and weakly correlated with road density \((r = 0.221)\). The two environmental variables, NDVI and road density, were weakly correlated \((r = 0.092)\). Road density was removed from the final regression model (criteria for removal: \(p > 0.05\)). The final regression model only contained one environmental variable, NDVI, and explained 43.3% of the variation in BSR.
Discussion

In this study BSR showed a hump-shaped relationship with elevation. This finding was consistent with previous studies (Kano 1940, Jai 1977, Lin 1989) even though they were conducted with 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.

Taiwan is a small island with high mountains. Elevation plays an important role for the abiotic and biotic environments. There are several environmental variables that change concurrently with elevation in Taiwan. Their trends, together with current ecological theories of species diversity, provide some predictions about the distribution pattern of BSR on the elevation gradient. First, land area decreases with elevation (Lee et al. 1997). The higher elevation areas always have less land area. Assuming other factors were constant, the area theory (Terborgh 1973, Rosenzweig 1992, 1995) would predict that BSR inversely correlates with elevation. Second, air temperature monotonically decreases with elevation (Lee et al. 1997). Birds are endothermic animals with body temperatures about 37°C. Below that temperature, increasing air temperature would increase physiological performance and efficiency of energy use of birds and thus be more favorable for birds. Thus, based on the favorableness theory (Terborgh 1973, Brown 1981), one would expect that BSR inversely correlates with elevation. In addition, species in areas of higher temperature tend to have shorter life spans and this may increase the rates of speciation (Rohde 1992). Third, although the annual
precipitation in Taiwan varies greatly with region and aspect, the annual precipitation in most areas in Taiwan was greater than 2000 mm (Lee et al. 1997). Under the condition that other factors kept constant, this high precipitation would make temperature the main factor in governing primary productivity along the elevation gradient in Taiwan. In this case, primary productivity of natural vegetation would decrease with elevation in Taiwan. This study and another study at local scale in Taiwan (chapter one) both found BSR positively correlated with primary productivity and rejected the empirical patterns of hump-shaped relationship between primary productivity and species diversity. Assuming all the habitats were not disturbed by human activities, one would also expect that BSR inversely correlates with elevation -- based on the energy limitation theory (Hutchinson 1959, Connell and Orias 1964, Wright 1983).

Nevertheless, BSR showed a hump-shaped relationship with elevation in this study. These results contradicted the predictions of the area theory, favorableness theory, and energy limitation theory. Two alternative hypotheses are proposed to explain the observed pattern.

One obvious explanation is human disturbance (Jai 1977). Human disturbance may decrease species diversity not only through decreasing primary productivity but also by reducing and degrading suitable habitats. Taiwan is one of the most densely populated areas on the Earth and most of the pristine forests have been eliminated in the lowlands. In this study, I found human disturbance decreased with elevation, primary productivity decreased with human disturbance, and BSR decreased with human disturbance and increased with primary productivity. These results strongly support this human disturbance hypothesis. Human disturbance was extensive on the plains and mostly
occurred in the lowlands and therefore changed the hypothetical inverse relationship between BSR and elevation into a hump-shaped relationship.

This human disturbance hypothesis could be examined by studying historic documents describing 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 period of massive human disturbance started in the 17th century.

Although previous studies (Kano 1940, Jai 1977, Lin 1989) and this study all found hump-shaped relationships between BSR and elevation, the peaks of hump-shaped relationships are not consistent. Both Kano (1940) and Jai (1977) concluded that the peaks located between 1200 and 1500 m, Lin (1989) reported the peak between 1800 and 2100 m, and this study found it between 1500 – 2200 m. There is a trend reported in these studies which indicates that earlier BSR peaks lower on the elevational gradient. This was not surprising since human disturbances in Taiwan have kept increasing and has extended into mid- and high-elevation zones which were relatively undisturbed before. The increasing human disturbance might force the peak upward in elevation and make the hump-shaped relationship more right-skewed on the elevational gradient.

Besides human disturbance, another explanation for this pattern is time. During the Pleistocene glacial cycles, dramatic climatic fluctuations occurred in Taiwan. Biotic communities that adapt to a certain climatic condition have shifted up and down along the elevational gradient in Taiwan during the last 1.6 million years (Tsukada 1967). The biotic communities that currently occupy the mid-elevation zone in Taiwan should be
older than others. The biotic communities that adapt to the extremes of the elevational
gradient in Taiwan might have been totally eliminated by the climate extremes during the
Pleistocene glacial periods. Although the avifauna in Taiwan 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 were therefore prevented from colonizing the lowlands of Taiwan through
landbridge connections. Many bird species that are widely distributed in the lowlands of
Southeastern China are not found in Taiwan. Several bird species introduced from
Southeastern China have quickly established stable populations in the lowlands of
Taiwan (e.g., *Pica pica*). However, so far no introduced bird species has established a
stable population in the mid- or high-elevation zone of Taiwan. In addition, most of the
endemic bird species in Taiwan are distributed in the mid- and high-elevation zones. All
these observations indirectly support this time hypothesis. However, this hypothesis is
difficult to test since the observed distribution patterns of BSR on the elevational
gradients in Taiwan and nearby Southeastern China are all confounded by human
disturbance. Nevertheless, it should be taken into consideration for future studies on the
distribution of BSR on the elevational gradients in Taiwan and other continental islands.

In conclusion, I found: (1) BSR increased with primary productivity, (2) BSR
decreased with human disturbance, (3) BSR showed a hump-shaped relationship with
elevation. I propose a time hypothesis and suggest it might be one of the reasons behind
the hump-shaped relationship between BSR and elevation in Taiwan. I also argue that
human disturbance is a primary reason that BSR increased with elevation in the lower-
elevation areas of Taiwan.
Literature cited


Kano, T. 1940. *Zoological studies of the Tsugitaka Mountains of Formosa*. The Shibusawa Institute for Ethnographical Researches, Tokyo, Japan.


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

<table>
<thead>
<tr>
<th>Variables</th>
<th>Order entered</th>
<th>Standard Coefficient</th>
<th>Partial r²</th>
<th>Model r²</th>
<th>t</th>
<th>Prob. &gt; t</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elevation</td>
<td>1</td>
<td>0.83</td>
<td>0.147</td>
<td>0.147</td>
<td>11.5</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Elevation^3</td>
<td>2</td>
<td>-0.68</td>
<td>0.166</td>
<td>0.313</td>
<td>-10.6</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Log (Road density +1)</td>
<td>3</td>
<td>-0.24</td>
<td>0.034</td>
<td>0.347</td>
<td>-6.0</td>
<td>&lt; 0.001</td>
</tr>
</tbody>
</table>

Table 2. Pearson correlation coefficients found among environmental variables and bird species richness. The sampled quadrats were divided into two groups by elevation.

<table>
<thead>
<tr>
<th>Variables</th>
<th>&lt; 2000 m</th>
<th>&gt; 2000 m</th>
</tr>
</thead>
<tbody>
<tr>
<td>Log (Road density +1)</td>
<td>NDVI</td>
<td>BSR</td>
</tr>
<tr>
<td>NDVI</td>
<td>-0.541*</td>
<td>-</td>
</tr>
<tr>
<td>BSR</td>
<td>-0.505*</td>
<td>0.377*</td>
</tr>
</tbody>
</table>

* p < 0.01 in simple linear regression.

Table 3. Stepwise regression model applied to bird species richness in the range of elevation below 2000 m.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Order entered</th>
<th>Standard Coefficient</th>
<th>Partial r²</th>
<th>Model r²</th>
<th>t</th>
<th>Prob. &gt; t</th>
</tr>
</thead>
<tbody>
<tr>
<td>Log (Road density +1)</td>
<td>1</td>
<td>-0.43</td>
<td>0.255</td>
<td>0.255</td>
<td>-10.4</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>NDVI</td>
<td>2</td>
<td>0.15</td>
<td>0.015</td>
<td>0.270</td>
<td>3.6</td>
<td>&lt; 0.001</td>
</tr>
</tbody>
</table>
Figure 1. The topography of Taiwan and spatial distribution of the 674 sampled quadrats.
Figure 2. Bird species richness (BSR) showed a hump-shaped relationship with elevation. BSR increased with elevation from sea level, reached its maximum around 2000 m, and then decreased with elevation. The fit lines were piecewise linear regression functions that corresponded to the ranges of elevation below 2000 m (slope = 0.012, r = 0.48) and above 2000 m (slope = -0.027, r = -0.73).
Figure 3. Bird species richness (BSR) generally increased with NDVI. It slightly increased with NDVI in the range of NDVI below 0.5 (slope = 3.42, r = 0.03). In the range of NDVI above 0.5, BSR showed a strong positive relation with NDVI (slope = 71.87, r = 0.40).
Figure 4. Bird species richness (BSR) decreased with road density (km⁻¹) (kilometer per square kilometer) (r = -0.43).
Figure 5. Bird species richness (BSR) decreased with percent of built area ($r = -0.39$).
Figure 6. Scatterplot matrices of the four environmental variables. (a) Most of the sampled quadrats were located in lowlands, (b) percent 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) percent of built area positively correlated with road density, (g) NDVI inversely correlated with percent 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.
Chapter Three

Spatial Patterns of Bird Species Richness in East Asia
Abstract

Spatial patterns of species diversity at continental scale have been a subject of major interest and investigation in ecology. Yet, despite of its distinct geographical setting and large share of global biodiversity, there is lacking of literature that documents species richness of any major taxon in East Asia (Asia east of 70º E longitude, including Wallacea). In this study, I developed maps of bird species richness (BSR) in East Asia by overlaying the breeding ranges of 2,406 terrestrial bird species and also studied the relationship of BSR with primary productivity, area, isolation, topographic heterogeneity, human population density, and historic environmental changes. Generally BSR declined from the tropics to the arctic. However, there were two minor exceptions in Mainland East Asia. BSR was highest around Tropic of Cancer and it fluctuated between 30º and 50º N. Islands had lower BSR than adjacent mainland areas. Normalized Difference Vegetation Index (NDVI) showed strong and positive correlation with BSR in both mainland areas and islands. For mainland areas, NDVI explained 65% of the BSR variation and topographic heterogeneity explained an additional 6%. On islands, BSR significantly correlated with island area but inversely with distance to mainland. NDVI explained 66% of the BSR variation on islands, which island area explained an additional 13%, and distance to mainland accounted for an additional 1%. I argue that energy availability is the primary process for the observed spatial patterns of BSR in East Asia. However, its effect might not be remarkable on isolated regions, where area size and degree of isolation also have significant influences on BSR. Other factors might also affect species diversity but their influences are not as profound as energy availability, isolation, and area.
Introduction

Spatial patterns of species richness are major research topics for ecologists, systematists, and biogeographers. The most acknowledged one is that species diversity peaks in the tropics and declines when one moves away from the equator (Stevens 1989). Although few taxa, such as aphids (Dixon et al. 1987) and Ichneumonidae (Owen and Owen 1974, Jazen 1981), show their highest species richness in temperate regions, most other major taxa display a latitudinal diversity gradient (Rosenzweig 1995). This latitudinal diversity gradient has been widely reported and suggested as one of the most consistent ecological patterns (Gaston and Blackburn 2000).

More than 25 hypotheses have been proposed to explain the latitudinal diversity gradient (examples in Pianka 1966, Rohde 1992, Rosenzweig 1995, Brown and Lomolino 1998). Some hypotheses are circular – assuming higher species diversity in the tropics (Rohde 1992), which include the competition hypothesis, mutualism hypothesis, and predation hypothesis. Some other hypotheses, such as the environmental stability hypothesis, do not have sufficient evidence to support (Rohde 1992). Some authors (Rohde 1992, Rosenzweig 1995, Gaston and Blackburn 2000, Rahbek and Graves 2001) consider the most promising hypotheses are the time theory (Fisher 1960), energy limitation theory (Hutchinson 1959, Connell and Orias 1964, Currie 1991), and area theory (Terborgh 1973, Rosenzweig 1992, 1995). The time theory suggests that lower latitudes are relatively free of Pleistocene glaciations and severe climatic disruptions, thus enabling more species to persist and evolve than higher latitudes (Fischer 1960, Simpson 1964). The energy limitation theory suggests that, since the tropics usually receive higher
solar radiation and precipitation, they therefore have higher primary productivity which provides wider resource base and permits more species to co-occur (Connell and Orias 1964, Currie 1991). The area theory argues that since the Earth is a sphere, the lower latitudes have larger geographical area and this increases species richness through the reduction of extinction rates and increase of allopatric speciation rates (Rosenzweig 1992).

Ideally, studies on the latitudinal diversity gradient should cover spatial extent from the tropics to the arctic. Partial coverage may result in misleading patterns. For example, Currie (1991) found bird species richness of North America (north of 25° N) peaked around 45° N longitude. However, Blackburn and Gaston (1996) found bird species richness of the New World peaked around the equator and monotonically declined toward the poles. On the Earth, North America, South America, and East Asia are the only continents that span from the tropics to the arctic. However, most studies on latitudinal richness gradient were conducted in North and South America, with some in Africa, Australia and Europe. Little if any literature has mapped distributional patterns of species richness of any major taxa in East Asia (Asia east of 70°E longitude), in spite of its large share of global biodiversity.

East Asia has at least four distinct geographical characteristics. First, there is a chain of islands spanning from the tropics to the arctic. These islands display great variation in size and distance to mainland. Second, tropical East Asia is mostly composed of islands. Mainland East Asia is mainly located in the subtropical, temperate, and arctic zones. The extensions of Eurasia in the tropical zone are all peninsulas (such as Malay Peninsula and India Peninsula) and are isolated from the main part of Eurasia.
Third, East Asia has a distinct latitudinal productivity gradient. In West Asia, Africa, Australia, North America, and South America, deserts mainly locate between 20° and 30° latitude. In East Asia, due to the blocking effect of the Tibetan Plateau, the deserts mainly locate from 35° to 45°N latitude and the latitudinal zone between 20° and 30° N in East Asia actually has extremely high precipitation and primary productivity (An et al. 2001). Fourth, East Asia contains half of the world’s population. Cultivation and modification of natural vegetation have been extensive for thousands of years. All these characteristics make East Asia a distinct site for studying spatial patterns of species richness at the continental scale. By comparing with other continents, East Asia provides a unique opportunity to study the processes of the latitudinal diversity gradient.

Because of their well-studied taxonomy and distribution, birds have been frequently used in studies of species diversity at broad spatial scales. Of the total 9,702 bird species on the Earth, 2,466 species breed in East Asia and 1,906 species can only be found in East Asia (summarized from Monroe and Sibley, 1993). The main objectives of this study are to: (1) establish a fine-scale map of bird species richness in East Asia; (2) investigate the relationships of species richness with area, isolation, primary productivity, topographic heterogeneity, human population density, and historic environmental changes.
Historic environment of the study area

The study area was defined as Asia between 70°E and 180°E longitude (Figure 1). In zoogeographic classification, it included the eastern half of Palearctic Region, entire Oriental Region, and entire Wallacea Subregion (part of Australian Region). The Wallacea Subregion (Mayr 1944), defined as the Indonesian Islands between Wallace’s line and Lydekker’s line, was included because of its strong affinity with the Oriental Region. The latitudinal extent of the study area ranged from 10°S to 80°N (Lesser Sunda Islands to Severnaya Zemlya).

The oldest fossils that have primitive characteristics of Class Aves, *Archaeopteryx*, dated back to the Late Jurassic, about 150 million years ago (MYA). All the fossil bird species in the Cretaceous (144 - 65 MYA) were toothed and most of them became extinct at the end of the Mesozoic (65 MYA) (Feduccia 1995). After the mass extinction, birds underwent a dramatic adaptive radiation and all modern orders of birds were found as fossils in Palearctic Region during the ten million year period in the Paleocene and early Eocene (55-65 MYA) (Blondel and Mourer-Chauvire 1998). Among them, Order Passeriformes (passerines or songbirds) experienced an explosive radiation in the Late Oligocene and Miocene (20 - 5 MYA) and now constitute nearly 60% of living bird species. All modern avian families have arisen by the Oligocene (38-26 MYA), and all modern genera by the Miocene (26-5 MYA) (Feduccia 1995). During the Palaeogene (65-26 MYA) the Earth’s climate was subtropical, without marked seasonality, and forests dominated most of the Northern Hemisphere (Blondel and Mourer-Chauvire 1998). The gradual global cooling in the Neogene (26 – 1.6 MYA)
resulted in the appearance of a latitudinal thermal gradient and seasonal climates in higher latitudes.

*Mountain building by tectonic movements*

In the early Jurassic (about 180 MYA), the supercontinent of Pangea began to break into two landmasses: Laurasia and Gondwanaland. At that time, India and Arabia were part of Gondwanaland and most of the rest of present-day Asia was part of Laurasia. During the middle Cretaceous (about 100 MYA), India broke away from Gondwanaland and drifted northwards rapidly. In the middle Eocene (about 50 MYA), the India Plate collided with Eurasia Plate. However, the initial collision was gentle in the Eocene, not accompanied by any massive upheaval of the terrain. A forceful collision between the two plates started in the early Miocene (about 26 MYA) and resulted in the uplift of the Himalayas, Tibetan Plateau, and the N-S trending mountain ranges in Indochina Peninsula (Whitmore 1987). Evidence showed that the Himalayas were probably over 3000 m and the Tibetan Plateau more than 1000 m above sea level at the end of middle Miocene (about 12 MYA) (Xu 1991, Wu et al. 1991). Most of the uplift took place during the Pleistocene (1.6 – 0.01 MYA) and is still continuing. Zhang et al. (1991) showed that the main part of Tibetan Plateau is still rising at a mean rate of 5.8 mm/year, with the highest rate, 10 mm/year, in the northern Himalayas.

Uplifts of the Himalayas and Tibetan Plateau caused a dramatic effect on the climate. By their vast area and very height, the Himalayas and Tibetan Plateau changed the paths of seasonal winds in East Asia and increased the aridity in the central part of East Asia. In summer, the Tibetan Plateau intercepts large quantities of solar radiation.
As the heat rises, it draws in airs from lower altitudes (anabatic winds) and brings moisture from India Ocean and Pacific Ocean. The moisture condenses and is intercepted by the Himalayas and the N-S trending mountains in Indochina Peninsula, creating monsoons, the characteristic climate pattern in East Asia. Evidence from soil carbon isotopes suggests that by the end of Miocene (around 7 MYA) a monsoonal climate was already in place (Quade et al. 1989). The monsoons brought extremely high precipitation to the latitudinal zone between 20° and 30° N in East Asia, where corresponding latitudinal zones in other continents are mostly deserts.

Around the early Pliocene (about 4 – 5 MYA), the Pacific Plate started to rotate and caused collisions with Philippine Plate and Eurasian Plate, and subsequently resulted in the uplifts of Luzon, Taiwan, Ryukyu islands, and Japan (Teng 1990, Aubouin 1990).

Glaciation and sea-level fluctuation in the Pleistocene

During the Pleistocene (1.6 MYA to 0.01 MYA), the Earth experienced several glacial-interglacial cycles during which glaciers advanced and retreated. Unlike North America and Europe, great portions of northern Asia were not glaciated at all during the Pleistocene due to low precipitation (Nilsson 1983). During the greatest glacial maximums, the West Siberian ice sheet only reached southwards to 55° N and eastwards to 120° E. Beyond that region, glaciation was confined to the mountain ranges in East Siberia and Central Asia. The permafrost line, which currently lies around 48° N (Shi 1991), might have extended southwards to 30° N (Pu 1991). The glacial cycles led to significant changes in climatic regime and vegetation in areas north of 30° N. South of 30° N, the climates remained relatively stable, similar to what they are today; therefore
they served as refuges for Tertiary (65 – 1.6 MYA) taxa to survive through the glacial-interglacial cycles (Ferguson 1993). Some authors (Adams and Woodward 1989, Latham and Ricklefs 1993) argued that the distinct paleoenvironment of East Asia contributed to the far greater temperate tree species richness in East Asia – three times more than forests in eastern North America and six times more than those in Europe.

During the glacial maximums, a large volume of water was removed from the ocean and sea levels fluctuated dramatically. The lowering of sea level by some 100 to 160 m below present, resulted in the formation of land bridges among currently isolated landmasses. East Asia was connected with North America through Beringia and most of the major islands in East Asia were connected to Mainland Asia during the glacial maximums (Voris 2000). One exception was Wallacea. While Borneo, Java, and Sumatra were all connected to mainland Asia, the waters surrounding the islands of Wallacea were deep enough to prevent landbridge connection. Thus, islands in Wallacea were never connected by Pleistocene landbridges to either Southeast Asia or Australia-New Guinea. The latest glacial period (Wisconsin Glaciation) reached its maximum around 18 thousand years ago (KYA). By 6 KYA, the sea level in East Asia had risen to its present level or even exceeded it by 1-7 m (Guo 1979, Wang and Wang 1980, Chen and Liu 1996). However, the latest glaciation was relatively mild in comparison to some earlier glacial maximums and resulted in only a 100 m drop in sea level. Many islands in East Asia, such as Philippines, that had past land connections with Mainland Asia were not connected during the latest glaciation (Heaney 1985).
Methods

*Bird distribution ranges and species richness map*

Breeding ranges of bird species were collected from various literature sources published from 1975 to 2000 (64 books in total, detailed in Appendix 1). For those species that lacked overall distribution maps in East Asia, their distribution ranges were combined from sources that cover certain regions or countries. When there were multiple sources for the distribution of one species, the most precisely delineated maps were used.

Pelagic birds, which primarily feed on marine food sources and usually have nomadic distribution on land, were excluded in this study. These pelagic species included Laridae (gulls, terns, auks), Phaethontidae (tropic birds), and Sulidae (boobies). For taxonomic consistency, this study followed the taxonomy system of Monroe and Sibley (1993). A total of 2,406 bird species, whose breeding ranges were within the study area, were included. A checklist of those species and an atlas of their distribution ranges in the study area are detailed on the website:
http://www.genglab.ucdavis.edu/ding/asianbird/

Each species’ breeding range was transcribed onto a Mercator projection map of the study area and was digitized into GIS polygon coverage in ARC/INFO. The error of the transcription process was controlled to be less than 100 km. The breeding ranges of the 2,406 species were overlaid to create the bird species richness layer.
Quadrat system

Many studies on species richness at continental scale used latitude-longitude quadrats (such as $1^\circ \times 1^\circ$, $5^\circ \times 5^\circ$) as analysis units. The real land area of quadrats was either unjustified (Currie and Paquin 1987) or included as one possible factor of the observed spatial patterns of species richness (Currie 1991, Kerr and Packer 1997, Rahbek and Graves 2001). There is a potential pitfall in this strategy: the area of the quadrat correlates with latitude. Except for coastal quadrats, the area of inland quadrats at higher latitudes is always less than those of lower latitudes. Justifying the area of latitude-longitude quadrats before regression analyses could statistically obscure the correlation between species richness and other factors that are dependent on latitude (e.g., primary productivity, temperature). To bypass the confounding effect of area, I used equal-area quadrats as the analysis unit (grain) for regression analyses. The country coverage in the ESRI ArcWorld 1:3M data set (ESRI 1992) was transformed to Lambert-Azimuth equal-area projection and overlaid with a $100 \times 100$ km quadrat system. Those quadrats with land areas less than 3000 km$^2$ were excluded. In total 3,433 quadrats met the criteria and 345 of them were on islands (Figure 2).

Environmental factors

Terrestrial ecosystem productivity was estimated by the Advanced Very High Resolution Radiometer – Normalized Difference Vegetation Index (AVHRR-NDVI). The AVHRR-NDVI was derived from the data collected by National Oceanic and Atmospheric Administration (NOAA) and processed by National Aeronautics and Space Administration (NASA). NDVI is a measure derived by dividing the difference between
near-infrared (0.725 – 1.1µm) and red (0.58-0.68 µm) reflectance measurements by their sum (Tucker 1979).

\[
\text{NDVI} = \frac{\text{Channel}_{\text{infrared}} - \text{Channel}_{\text{red}}}{\text{Channel}_{\text{infrared}} + \text{Channel}_{\text{red}}}
\]

NDVI has been shown to be highly correlated with green-leaf biomass, green-leaf area, and absorbed photosynthetically active radiation (APAR) (Curran 1980, Goward et al. 1985). The NDVI equation reproduces values in the range of –1.0 to 1.0, where increasing positive values indicate increasing green vegetation and negative values indicate non-vegetated surface features such as water, barren land, ice, and snow. Spatial patterns of NDVI have been viewed as reasonable representations of net primary productivity and vegetative growth of terrestrial ecosystems at continental and global scales (Goward et al. 1985, Box et al. 1989, Ustin et al. 1991). The daily NDVI composites usually contain a certain amount of cloud contamination. To minimize the problem, researchers create monthly NDVI composites by maximum value composite method; choosing the maximum daily NDVI value for each individual pixel location (Holben 1986). However, during monsoon seasons, the monthly composites of East Asia were still heavily plagued by cloud contamination. Therefore, the 144 monthly NDVI composites of 12 years (1987-2000) were combined by the maximum value composite method to create historic monthly NDVI composites. The NDVI data, with a resolution of 8×8 km, were downloaded from the website (8th June 2001, http://daac.gsfc.nasa.gov/data/dataset/AVHRR/01_Data_Products/06_Images/03_Asia/).

Landscape heterogeneity could be represented by variation in either topography or land cover. Since there is a lack of accurate land cover map in East Asia and elevation difference has profound influences on abiotic environment and biotic community, I used
elevation range of each quadrat (maximum minus minimum elevation recorded in each quadrat) as an estimate for landscape heterogeneity. The elevation range was calculated from the Global 30 Arc Second Elevation Data Set (GTOPO30), produced by U. S. Geological Survey, EROS Data Center. GTOPO30 is a digital elevation model (DEM) with a resolution of 30 arc seconds (approximately one kilometer). The DEM data set was overlaid with the quadrat system and the elevation range within each 100×100 km quadrat was calculated.

Population density data were obtained from ESRI ArcAtlas data set (ESRI 1996). The data was compiled from various sources including national population censuses and United Nation demographic yearbooks. Most of the databases were established between 1981 and 1994. The population density coverage was overlaid with the quadrat system to calculate average population density of each quadrat.

Island area and distance to mainland were also calculated for the 345 quadrats located on islands. Island area was directly calculated from the land/ocean coverage in the ESRI ArcWorld 1:3M data set (ESRI 1992) that had converted into Lambert-Azimuth equal area projection. Distance to mainland was calculated as the minimum distance from this island to mainland at two-point equidistant projections.

Analyses

The distribution ranges of the 2,406 bird species were overlaid with the quadrat system and the area of each species distribution in each quadrat was calculated. For each species, if its distribution covered more than 25% land area of the quadrat, I assigned it as ‘present’ in that quadrat, otherwise ‘absent’ was recorded. To test if the choice of cut-off
point significantly affected the results, I calculated the species richness of Anseriformes and Sylviidae at cut-off points of 0%, 25%, 50%, and 100%. Results showed that species richness at each cut-off point was highly correlated with each other (r > 0.98 for all of the pair-wise comparisons). The 2,406 binary species distribution matrices were added to create a layer of bird species richness in raster format.

The environmental factor data layers were all transformed to Lambert-Azimuth equal-area projection and overlaid with the 100×100 km quadrat system. The average NDVI (mean of the 1987-200 historic monthly NDVI), elevation range, and average population density of each quadrat were calculated. By using multiple regression analyses, the power of average NDVI, elevation range, and average population density in explaining the variation of BSR were determined. For those quadrats located on islands, island area and distance to mainland were also added into the regression analyses.
Results

Bird species richness

Within the 100×100 km quadrats, BSR ranged from 5 to 510 species. All the island quadrats had lower BSR than adjacent quadrats in Mainland Asia. BSR was highest at the base of Indochina peninsula, specifically the border zones of Myanmar adjacent to India and China (Figure 3). It is the region where the Himalayas spread into tropical lowland and has high topographic variation and low development pressure. These species richness hotspots expanded from 20° to 30°N latitude, with the maximum spots around Tropic of Cancer. Northern Siberia, Gobi Desert, Taklimakan Desert, and Tibetan Plateau had lower BSR.

Along the latitudinal gradient, BSR generally declined from the tropics to the arctic (Figure 4a). However, there are two noticeable exceptions on the mainland. First, although the fitted curve of mainland BSR peaked around the equator, the quadrats that had maximum BSR located around 25°N, instead of around the equator. Second, BSR fluctuated in Mainland Asia from 30°N to 50°N. BSR rapidly decreased from 25°N to 40°N and increased again from 40°N to 50°N.

Area

Within the extent of this study, mainland made 93% of total land area (Figure 4b). The southernmost point of Mainland Asia is located at 2°N. Within the study area, only 1% of Mainland East Asia is located south of 10°N, and only 15% were within the tropical zone (south of Tropic of Cancer). Most of the mainland East Asia is located in
subtropical, temperate, and arctic zones. Islands extended from 10°S to 80°N within the study area. However, 80% of island area is located within tropical zone and 73% between 10°S and 10°N.

On mainland East Asia, BSR did not correspond closely with land area along the latitudinal gradient (Figure 4). In order to test if land area correlated with BSR along the latitudinal gradient, Mainland Asia was divided into equal-range latitudinal bands at 1°, 5°, 10°, and 20° and the land area and BSR of each band were calculated respectively. Results showed BSR did not have any significant correlation with land area (Table 1). For the 5° and 20° bands, land area was independent to BSR. For the 10° bands, land area negatively correlated with BSR and only explained 4% of the variation in BSR.

On island quadrats, however, land area correlated well with BSR. After both log transformed, BSR of island quadrats significantly correlated with island area in a simple linear regression analysis (intercept = 2.19, slope = 0.26, $r^2 = 0.39$, $p<0.001$ for both coefficients). This species-area relationship expressed in the power model is:

$$\text{BSR} = 2.19 \cdot \text{Area}^{0.26}$$

The results suggest the effect of land area is only significant on island BSR, not on the mainland.

**Primary productivity**

There were high spatial and temporal variations among monthly NDVI (Figure 5). In tropical Asia, NDVI remained at a high level all year round. However, in temperate and arctic zones, NDVI had great seasonal variations. Tibetan Plateau, Gobi Desert, and Taklimakan Desert had low NDVI all year round. Average NDVI was highest in tropical
islands (e.g., Borneo, Sumatra, and Sulawesi) and mountain ranges of the Indochina Peninsula and was lowest in Taklimakan Desert, Gobi Desert, and Northern Siberia (Figure 6).

Average NDVI significantly and positively correlated with BSR (slope = 380.0, \( r^2 = 0.59, t = 70.4, p < 0.001 \)). After separating the quadrats into two groups (mainland and islands), NDVI explained 65% of the variation in mainland BSR (slope = 430.67, \( t = 76.4, p < 0.001 \)) (Figure 7a) but only 30% of the variation in island BSR (slope = 423.71, \( t = 12.1, p < 0.001 \)) (Figure 7b) in simple linear regression analyses.

\[
\text{BSR}_{\text{mainland}} = -0.58 + 430.67 \cdot \text{NDVI} \\
\text{BSR}_{\text{island}} = -65.37 + 423.71 \cdot \text{NDVI}
\]

To test if the slopes and intercepts of both regression equations were significantly different, the significance levels of coefficients of following regression model were estimated.

\[
\text{BSR} = \beta_0 + \beta_1 \cdot X + \beta_2 \cdot \text{NDVI} + \beta_3 \cdot X \cdot \text{NDVI}
\]

\( X = 0, \text{if on mainland quadrats,} \)

\( X = 1, \text{if on island quadrats.} \)

The slope of the mainland BSR was not significantly higher than island BSR (\( H_{\text{null}} : \beta_3 = 0, t = -0.28, p = 0.78 \)). However, the intercept of mainland BSR was significantly higher than island BSR (\( H_{\text{null}} : \beta_1 = 0, t = 3.82, p < 0.001 \)). These results confirm that islands have lower BSR than on the mainland and suggest that the increments of primary productivity on BSR are similar on mainland and islands.
Topographic heterogeneity

Elevation range was high in the Himalayas, Tienshan, Kunlunshan, and some islands in Western Pacific Ocean (such as Java, Sumatra, Taiwan, and Sulawesi) (Figure 8). Elevation range positively correlated with BSR (slope = 0.0244, \( t = 16.9, p < 0.001 \)) but only explained small proportion of variation in BSR \( (r^2 = 0.08) \). After separating the quadrats into two groups (mainland and islands), elevation range still positively correlated with BSR of mainland quadrats (slope = 0.0246, \( t = 17.0, p < 0.001, r^2 = 0.09 \)) but did not significantly correlate with BSR of island quadrats (slope = 0.0063, \( t = 1.0, p = 0.32 \)).

Population density

Human populations were unevenly distributed over East Asia (Figure 9). Some areas were densely populated (density > 1000 persons/km\(^2\)), while some vast areas were almost unpopulated (e.g., Tibetan Plateau, Taklimakan Desert) (density < 1 person/km\(^2\)). In a simple linear regression analysis, population density positively correlated with BSR (slope = 0.162, \( t = 11.1, p < 0.001 \)) but only explained 3% of the variation in BSR. After separating the quadrats into two groups (mainland and islands), population density still positively correlated with BSR of mainland quadrats (slope = 0.231, \( t = 11.8, p < 0.001, r^2 = 0.04 \)) but did not significantly correlate with BSR of island quadrats (slope = 0.032, \( t = 0.49, p = 0.63 \)).
Multiple regressions

Stepwise forward multiple regression (criteria for inclusion and exclusion, $p < 0.05$) was applied to evaluate the effects of NDVI, elevation range, and population density on mainland BSR. NDVI explained 65.4% of variance in mainland BSR ($p < 0.001$), Elevation range explained an additional 5.7% ($p < 0.001$), and population density only explained an additional 0.1% ($p = 0.007$) (Table 2). Primary productivity was the best variable in explaining the variation of mainland BSR. The standard coefficients for NDVI, elevation range, and population density were 0.802, 0.237 and –0.028 respectively. Results suggest mainland BSR increases with primary productivity and topographic heterogeneity but decreases with population density. Notably, population density positively correlated with mainland BSR in a simple linear regression but negatively correlated with the residuals of mainland BSR once the effects of NDVI and elevation range had been justified.

For island BSR, island area and distance to mainland were added into the multiple regression analysis. All the variables were log-transformed to fit the normality assumption of regression analysis and fix the problem of inconsistent variance of the errors. NDVI explained 66.2% of variance in island BSR ($p < 0.001$), island area explained an additional 14.9% ($p < 0.001$), and distance to mainland explained an additional 0.8% ($p < 0.001$) (Table 3). Elevation range and population density were excluded in the final model because of their insignificant contribution to the model. The standard coefficients for NDVI, island area, and distance to mainland were 0.718, 0.401 and –0.089 respectively. These results suggest primary productivity is the most influential variable in explaining the
variation of island BSR. Generally, island BSR increases with primary productivity and island area but decreases with distance to mainland.
Discussion

Earlier ecologists (e.g., MacArthur and Connell 1966) believed that the latitudinal diversity gradient should have a general explanation since it is a widespread and consistent ecological pattern. For years, more than 25 hypotheses have been proposed to explain the latitudinal diversity gradient. There are at least three reasons that might answer why there are so many competing hypotheses in explaining latitudinal diversity gradient. First, those hypotheses are not mutually exclusive. Many of the proposed factors could have operated together, either sequentially or concurrently, to affect current latitudinal patterns of species richness (Brown and Lomolino 1998, Whittaker et al. 2001). Second, as wide as the spatial extent of the latitudinal diversity gradient is, ecologists have to rely on comparison studies that do not provide clear cause-effect relationships. Third, most investigators have focused on testing only one single hypothesis, instead of testing multiple processes simultaneously.

Most ecologists now are convinced that species diversity is governed by multiple processes that function at various spatial and temporal scales. Most of the arguments focus on which ones are primary processes of species diversity and which are secondary. Brown and Lomolino (1998) argued the primary hypotheses should relate to some abiotic characteristics of the Earth and those hypotheses (e.g., inter-specific competition begets species diversity) which purely rely on biological characteristics and make no direct reference to the Earth’s abiotic template should be secondary. Here I discuss three theories that are often considered as primary causes of the latitudinal diversity gradient: the time theory, energy limitation theory, and area theory. In addition, the spatial heterogeneity theory and the effect of human population density are also discussed.
**Time theory**

Without dramatic disturbance, the total number of species in biotic communities generally increases with time. The time theory argues that higher latitudes have younger communities than lower latitudes because of the Pleistocene glaciations and severe climatic disruptions in the past. The time theory can be split into ecological time and evolutionary time theories (Pianka 1966). The ecological time theory, dealing with a shorter span of time, proposes that the lower richness in higher latitudes is a consequence of the shorter period available for species to colonize from lower latitudes. The evolutionary time theory proposes that the lower richness at higher latitudes is because species have not had enough time to diversify, focusing on speciation rather than colonization.

If the time theory is correct, the most glaciated areas should have the lowest species richness. That is, higher latitudes and altitudes are expected to have lower species richness. In this study, within the band between 50° and 80° N, BSR declined monotonically with latitude, which is consistent with the prediction of the time theory. However, within the band between 35° and 80° N, a hump-shaped relationship between BSR and latitude was observed. BSR was higher in Tienshan and those mountain ranges in Southern Siberia and Northern Mongolia. These mountain ranges were heavily glaciated in the Pleistocene and even served as centers of glaciation during earlier glacial stages (Nilsson 1983). These mountain ranges should have lower BSR than adjacent regions, as Tibetan Plateau did. Similar patterns have been also observed in Europe and temperate North America. The bird species richness has been reported highest at mid-
latitudes within Europe (Mönkkönen 1994, Gregory et al. 1998) and Rocky Mountains and Sierra Nevada within North America (Simpson 1964, Cook 1969), all of which were heavily glaciated in the Pleistocene.

It is certainly true that historical factors can affect contemporary species diversity. However, these results suggest that the effects of historical glaciation are either not long lasting or insignificant for birds in East Asia. Birds are known as good migrators and many birds have the greatest capability for long distance dispersal. Their strong dispersal ability should, on average, enable birds to colonize newly available habitats within a relatively short temporal scale. The impacts of historic disturbances in the Pleistocene might therefore not be important for contemporary bird species richness. The observed spatial patterns of BSR in East Asia should be regulated primarily by ecological processes (e.g., energy availability, spatial heterogeneity) that function on a relatively short temporal scale.

Energy limitation theory

Most living organisms on Earth either directly or indirectly depend on the energy radiated from the sun. The energy fixed by plants establishes the upper limit for a community to support organisms and species. The energy limitation theory proposes that higher energy availability in a given area can support more species because, in general, species can be more specialized and still be able to maintain sufficiently large population sizes to avoid extinction (MacArthur 1972). At local scales, many studies however show evidence against the energy limitation theory; the relationship between species richness and available energy is often found to be hump-shaped (Tilman 1988, Rosenzweig
However, at continental scale, primary productivity and species richness of various plant and animal groups have shown a positive monotonic relationship (Currie and Paquin 1987, Adams and Woodward 1989, Currie 1991, Blackburn and Gaston 1996, Gaston 2000). My results show a similar pattern. Overall, BSR positively and monotonically correlates with primary productivity in East Asia. This monotonic relationship is especially significant in Mainland East Asia, where BSR corresponded closely to NDVI.

This relationship between energy and BSR was not strong on islands. All the islands had fewer bird species than adjacent regions in Mainland Asia, even though the islands had similar or higher primary productivity and topographic heterogeneity. Some paired examples are Southern Japan to Korea, Taiwan to Southern China, Sri Lanka to Southern India, and Borneo to Malay Peninsula. This impoverishment of island biota can be attributed to the isolated nature of islands. The water barriers surrounding islands reduce immigration possibilities of organisms and make species on islands more vulnerable to regional extinction. The isolation effect explains why the highest BSR is located on the subtropical mountains of the Indochina Peninsula, instead of on the tropical islands, which has the highest primary productivity. Among the tropical islands, it is also significant that larger islands tend to have more bird species than smaller islands, even though they have similar levels of primary productivity.

Nevertheless, primary productivity is an important variable in explaining BSR in East Asia. The results suggest energy availability should be the most important process in regulating BSR in East Asia. Other factors, though they explained in some detail spatial patterns of BSR, can not explain the overall pattern observed.
Area theory

The area-species relationship has been suggested as one of the few rules in community ecology. Most world maps are shown in Mercator projection that gives a false impression that Earth has more land area at higher latitudes. However the Earth actually has more land area at lower latitudes. The area theory extends the area-species relationship and posits that the larger area in lower latitudes increases species richness through reducing the extinction rate of species (Rosenzweig 1992) and increasing the chances for allopatric speciation (Terborgh 1973).

As mentioned before, East Asia has one distinct geographical characteristic: the temperate and subtropical regions have far larger areas than tropical regions. If the area theory is correct, BSR should correspond closely to geographical area along the latitudinal gradient and the vast area in the temperate East Asia should have very high BSR. My results contradict the prediction of the area theory. BSR was higher in Tropical East Asia, where has smaller area but higher primary productivity. The higher BSR observed in Tropical East Asia should be a sequence of higher primary productivity there, rather than the smaller geographical area. The area theory is rejected in this study because of its inability to explain the latitudinal BSR gradient in East Asia.

One might argue that, overall, the Earth still has larger area and higher species diversity in the tropical zone. However, the terrestrial tropical ecosystem on the Earth is separated into three isolated regions: America, Africa, and Asia-Australia. Each is far away from others and the three regions share few common bird species. The vast area
and rich avifauna on the other two tropical regions therefore have little or no effect on reducing extinction rate or increasing colonization rate of bird species in tropical Asia.

Nevertheless, at regional scale, area showed a strong correlation with BSR for isolated habitats. Larger islands tended to have more bird species, which was consistent with the prediction of the island biogeography theory (MacArthur and Wilson 1967). This relationship still held after the effect of primary productivity (NDVI) was adjusted. Although area alone can not explain the overall latitudinal diversity pattern observed in East Asia, it can play an important role for species diversity of isolated areas at regional scale.

*Spatial heterogeneity*

Spatial heterogeneity theory posits that more diverse physical and biotic habitat structure permits finer subdivision of limiting resources and hence promotes greater specialization of species. For terrestrial birds, the heterogeneity of habitat can be split into structural complexity of vegetation and landscape heterogeneity. MacArthur and his associates (MacArthur and MacArthur 1961, MacArthur et al. 1966) studied bird species richness and habitat characteristics in different habitats of North America and found that BSR was highly correlated with foliage height diversity. Since then, structural complexity of vegetation has been referred to as one possible cause of the latitudinal species gradient (e.g., Pianka 1966). However, structural complexity of vegetation might not be a direct cause of species diversity but a property caused by others factors that also affect species diversity. Factors like historic perturbation and productivity might affect both species diversity and structural complexity of vegetation. In addition, structural
complexity of vegetation itself is a product of plants. It might be a consequence of species diversity rather than a cause. Clearly, structural complexity of vegetation is not an adequate explanation for species diversity along a latitudinal gradient.

Landscape heterogeneity has been widely used as estimate of spatial heterogeneity at regional and continental scales. At these broader scales, more habitats (vegetation type, land cover, or ecosystem) will enable more species that specialized in certain habitats to occur together and thus increase species diversity. Landscape heterogeneity has been found to be one important factor of species diversity at broader spatial scales. It also has been found to correlate with island area and is often used as one explanatory mechanism of the area-species relationship. However, landscape heterogeneity does not have a consistent relationship with latitude. Higher latitudes do not necessarily have lower landscape heterogeneity than lower latitudes. Therefore, landscape heterogeneity is often used as a secondary or independent process of species diversity on the latitudinal gradient. In this study, I used topographic heterogeneity as estimate of landscape heterogeneity. Although it only explained a small amount of variation, it significantly correlated with BSR. In addition, topographic heterogeneity was independent of primary productivity in this study. Its explanatory power was not weakened after the effect of primary productivity was statistically controlled.

*Population density*

Higher human population densities usually cause more anthropogenic perturbations and could reduce species diversity of natural ecosystems. Since East Asia contains half of the world population and has been extensively colonized for thousands of
years, I included population density as a possible factor of BSR. Simple linear regression revealed population positively correlated with BSR. However, the positive but weak correlation does not necessarily imply that population density begets species diversity. It might reflect correlation among human population density, BSR, and other factors, such as primary productivity. For example, human beings avoid dwelling in low productivity areas where conditions are not suitable for agricultural cultivation. After the effect of primary productivity was justified, population density did show a significantly negative relationship with BSR.

In conclusion, I argue that bird species richness in East Asia is primarily governed by energy availability. Primary productivity establishes the upper limits of habitats’ capacity to contain species and the number of bird species. The hump-shaped relationship between productivity and species diversity was not observed at continental scale. However, in isolated areas (such as islands and peninsulas), birds might not able to reach the richness limits set up by primary productivity. In that case, degree of isolation and area size might also be influential in determining species diversity. Other factors, such as spatial heterogeneity, biotic interactions, and perturbations, may also affect species diversity. However, their influences are secondary and not strong as energy availability, isolation, and area size.
Literature Cited


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Table 1. Regression analyses at various scales showed that land area did not significantly correlate with BSR along the latitudinal gradient in Mainland East Asia. Land area of and the number of bird species that distributed within each 5°, 10°, 20° latitudinal band in Mainland East Asia were calculated and log transformed to fit the power model, \( \log(\text{BSR}) = c + z \cdot \log(\text{Area}) \).

<table>
<thead>
<tr>
<th>Scale</th>
<th>n</th>
<th>z</th>
<th>( r^2 )</th>
<th>t</th>
<th>Prob. for ( z &gt; 0 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>5° band</td>
<td>15</td>
<td>0.005</td>
<td>0.00</td>
<td>0.028</td>
<td>0.98</td>
</tr>
<tr>
<td>10° band</td>
<td>7</td>
<td>-0.108</td>
<td>0.04</td>
<td>-0.506</td>
<td>0.64</td>
</tr>
<tr>
<td>20° band</td>
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<td>-0.052</td>
<td>0.00</td>
<td>0.067</td>
<td>0.95</td>
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</tbody>
</table>
Table 2. Stepwise multiple regression suggests that NDVI is the best variable to explain mainland bird species richness (d.f. = 3088).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Order</th>
<th>Standard coefficient</th>
<th>Partial $r^2$</th>
<th>Model $r^2$</th>
<th>$t$</th>
<th>Prob. &gt; $t$</th>
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</thead>
<tbody>
<tr>
<td>NDVI</td>
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<td>0.802</td>
<td>0.654</td>
<td>0.654</td>
<td>78.2</td>
<td>&lt; 0.001</td>
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<tr>
<td>Elevation range</td>
<td>2</td>
<td>0.237</td>
<td>0.057</td>
<td>0.711</td>
<td>24.3</td>
<td>&lt; 0.001</td>
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<tr>
<td>Population density</td>
<td>3</td>
<td>-0.028</td>
<td>0.001</td>
<td>0.712</td>
<td>-2.72</td>
<td>0.007</td>
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</tbody>
</table>

* All the variables were log transformed.

Table 3. Stepwise multiple regression suggests that NDVI is the best variable to explain island bird species richness (d.f. = 343).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Order</th>
<th>Standard coefficient</th>
<th>Partial $r^2$</th>
<th>Model $r^2$</th>
<th>$t$</th>
<th>Prob. &gt; $t$</th>
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<tbody>
<tr>
<td>NDVI</td>
<td>1</td>
<td>0.718</td>
<td>0.662</td>
<td>0.662</td>
<td>28.3</td>
<td>&lt; 0.001</td>
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<tr>
<td>Island area</td>
<td>2</td>
<td>0.401</td>
<td>0.149</td>
<td>0.811</td>
<td>16.5</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Distance to mainland</td>
<td>3</td>
<td>-0.089</td>
<td>0.008</td>
<td>0.819</td>
<td>-3.7</td>
<td>&lt; 0.001</td>
</tr>
</tbody>
</table>

* All the variables were log transformed.
Figure 1. This study covered the entire Oriental Region, the eastern part of Palearctic Region, and the entire Wallacea Subregion. The zoogeographic regions and boundaries follow Wallace’s (1876) and Mayr’s (1944) schemes.
Figure 2. The 100×100 km quadrat system served as the analysis unit of this study. The map is in Lambert-Azimuth equal projection.
Figure 3. Bird species richness was highest at the base of the Indochina Peninsula and lowest in northern Siberia, Gobi Desert, Taklimakan Desert and Tibetan Plateau. Islands had lower bird species richness than adjacent areas in Mainland Asia.
Figure 4. Bird species richness (a) and land area (b) showed different distributions along the latitudinal gradient of East Asia. Green circles denote mainland quadrats, and blue triangles denote island quadrats. The lines represent the trends found by DWLS (Distance Weighted Least Squares) fits to the data. The red line represents the mainland quadrats and blue line the island quadrats.
Figure 5: There were high spatial and temporal variations among monthly NDVI (Normalized Difference of Vegetation Index) of East Asia. Increasing positive NDVI values indicate increasing green vegetation and negative NDVI values indicate non-vegetated surface features such as water, barren land, ice, and snow.
Figure 6. Average NDVI (Normalized Difference of Vegetation Index) (1988-2000) was highest in the tropical islands and mountain ranges of the Indochina Peninsula and was lowest in Taklimakan Desert, Gobi Desert, and northern Siberia.
Figure 7. Bird species richness significantly correlated with NDVI (Normalized Difference of Vegetation Index) on both (a) mainland and (b) islands. The slopes of regression functions were not significantly different. However, the intercept of BSR-NDVI regression model on island quadrats was significantly lower than mainland.
Figure 8. Topographic variation was high in Himalayas, Tianshan, Kunlunshan, and on some islands such as Java, Taiwan, Sulawesi, and Sumatra.
Figure 9. Human population density displayed high spatial variation in East Asia. Most of the populations in East Asia dwelled in eastern China, India Subcontinent, Java, and the plains of the Indochina Peninsula.
Appendix 1

(1) By taxa: having global maps of species distribution range


(2) By regions: maps of distribution range of all species within the region or country


(3) textual description of distribution ranges


