

Testing the causal mechanism of the peninsular effect in passerine birds from South Korea

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Abstract

The peninsular effect is a geographical phenomenon that explains patterns of species richness. Hypotheses regarding the peninsular effect in bird taxa should be more focused on testing not only recent deterministic processes but also migrant inflow associated with recent environmental variations. We aimed to identify the latitudinal patterns of passerine species richness and test hypotheses regarding recent deterministic processes (climate, primary productivity, habitat diversity, forest area, and anthropogenic disturbances) and migration influence (ratio of migrant species richness) in the Korean peninsula. We used the distribution data of 147 passerine species from 2006 to 2012. Single regression between passerine species richness and latitude supported the existence of the peninsular effect. Mean temperature induced by latitude gradient negatively affected LAI and forest area, and positively habitat diversity. However, passerine species richness was only influenced by LAI and forest area. Ratio of migrant species richness increased as decreasing habitat diversity and was not influenced by LAI and forest area. And we found that ratio of migrant species richness increased with increasing latitude, and contributed to the increasing in passerine species richness. No. of patches did not influenced passerine species richness. These results support the existence of the peninsular effect in the distribution of passerine birds induced by recent deterministic processes such as primary productivity and habitat area, and migrant species inflow caused by competition.

Introduction

The peninsular effect is one of the geographical hypothesis that explains patterns of species richness. It was proposed by Simpson (1964) and predicts that the number of species declines from a peninsula's base to its tip. Many studies have been conducted using different taxa at various spatial scales and have proposed a variety of hypotheses (Battisti, 2006; Jenkins & Rinne, 2008). The causal mechanisms of the peninsular effect proposed to date may be grouped as follows: (1) recent stochastic processes (equilibrium and derived island biogeography theories); (2) historical events (paleoclimatic and paleogeographic changes); (3) recent deterministic processes with a geographical base-tip gradient; and (4) recent anthropogenic processes (Battisti, 2014).

Recent stochastic processes can be explained by immigration-extinction dynamics, area effect, and isolation effect (Battisti, 2014) in a hypothesis that proposes that inappropriate habitats and isolating conditions for specific taxa may be unevenly distributed throughout a peninsula; consequently, immigration-extinction dynamics may contribute to certain patterns of species richness (Kiester, 1971; Simpson, 1964). Historical processes are the main factors explaining present peninsular patterns in the hypothesis that proposes that species distribution is a result of past climatic or geological events which can determine turnover in species, reduction in genetic diversity, speciation, and genetic differentiation (Battisti, 2014). In contrast, recent deterministic processes are related to patterns of habitat heterogeneity and patchiness, climatic regime,

vegetation structure, and habitat area (Battisti, 2014; Milne & Forman, 1986). Lastly, recent anthropogenic processes are linked to the gradient of human-driven disturbances, such as deforestation, fires, pasture, and fragmentation which might increase or decrease of species richness due to an increase of anthropophilous generalist species (Battisti, 2014; Fahrig, 1997).

According to a study on recent stochastic processes (Simpson, 1964), non-flying taxa (e.g., mammals, amphibians, and plants) are more constrained by geometry features than flying taxa are, which strongly supports the peninsular effect hypothesis. Lawlor (1983) pointed out that this phenomenon was observed only in heteromyd rodents from the Baja California peninsula. However, a recent study proposed that the peninsular effect is more prevalent in flying taxa than in non-flying taxa (Jenkins & Rinne, 2008). For example, according to recent deterministic processes, birds have been identified as the taxonomic group that most supports the peninsular effect hypothesis (Battisti, 2014; Jenkins & Rinne, 2008); these results indicate a higher likelihood of the peninsular effect being attributed to the influence of recent deterministic processes such as habitat, climate, and human disturbances rather than to historical processes or immigration-extinction dynamics (Battisti, 2014). In addition, bird taxa are characterized by dispersal over water, which may exceed dispersal over land, altering the observed peninsular patterns (Battisti, 2014; Taylor, 1987). The observed peninsular patterns could be changed by temporal influx of migrant birds which induced by competition with resident birds. Thus, in the case of bird taxa, the temporal influx of migrant associated with recent environmental variation and competition, rather than recent stochastic processes might be major drivers for the testing of peninsular effect.

In north-south-oriented peninsulas with large climatic range, change of temperature along a gradient is likely the most important factor that explains the distribution pattern of species richness (Battisti, 2014). And change in vegetation (e.g., primary productivity, habitat diversity, and habitat area), induced by climatic gradient, is the main causal factor that determines the bird species richness (Contoli et al., 2000; MacArthur, 1964; Schwartz, 1988). In generally, an increase of the bird species richness can be expected when the primary productivity, habitat diversity, and habitat area increase (MacArthur, 1964; Milne & Forman, 1986). Human-induced habitat heterogeneity and fragmentation might increase or decrease the species richness (Battisti, 2014). If the anthropogenic factors have a base-tip gradient, induced by human-driven disturbances or historical reason, that can influence the distribution of specie richness along the peninsular (Battisti, 2014). Carnicer & Díaz-Delgado (2008) asserted that the convergent response of different migratory (resident and migrant) group on species richness pattern should be considered in determining the distribution pattern of species richness. Herrera (1978) discovered that migrant passerine birds increased with increasing latitude in Europe. Because resident species are generally more specialized with requiring narrower and specific habitat than migrant species (Fuller & Crick, 2008; Smith et al., 2001). Recent stochastic processes merely gives a limited explanation that peninsular geometry may hinder immigration and increase extinction. Thus, to understand the more specific causal mechanism in bird taxa, it is important to identify not only environmental changes but temporal changes in migrant influx caused by competition and habitat changes according to the peninsular effect.

This study aimed to test the peninsular effect on passerine birds in South Korea based on the various aforementioned hypotheses. First, we identified the latitudinal pattern of passerine species richness in South Korea. Then, we tested the hypotheses of the peninsular effect related to recent environmental changes and migrant species inflow: (1) climate; (2) primary productivity; (3) habitat diversity; (4) forest area; (5) anthropogenic disturbances; and (6) migration influence. For testing these hypothesis, we constructed the conceptual scheme of this study and tested hypotheses according to recent deterministic and anthropogenic processes (Fig. 1).

Methods

Bird data

The northern portion of the Korean peninsula is connected to the Asian continent, and its tip is towards the south. Because of the political situation in the Korean peninsula, the present study was limited to South

Korea (34–39°N and 126–130°E) over an area of approximately 95,219 km². Distribution data of passerine species from 2006 to 2012 were extracted from the National Ecosystem Survey (NES) in South Korea. NES has been conducted three consecutive by The South Korean Ministry of Environment since 1986 and the data are available from the EcoBank (website:<http://ecobank.nie.re.kr>).

The NES survey conducted in a grid of 0.041 square decimal degrees (17.3km²) within a 0.125 × 0.125 square decimal degree (Fig 2). The survey points (0.041 square decimal degrees) were randomly selected considering a representative mountain area and accessibility in each grid cell (Fig 2). Within the survey point, a linear path way was walked to count bird data considering geographic status, diversity of habitats, vegetation naturalness (Choe et al., 2019). These transect survey was conducted three times a year from February to November. Species name, number of species, and the geographic location of each species (latitude and longitude) was collected. All data from islands were eliminated from the analysis. Because these islands are used for migratory birds as stopover sites, so species richness might be extremely higher compared with the inland area during migration season (Seo, Lee, Kang, & Kwon, 2015). All birds were classified as resident or migrant (S1 Table). Resident denote a species that spends all season in Korean peninsula and migrant denote a species that stop for a while or visit for the purpose of breeding.

Climate (temperature) and primary productivity (LAI)

To identify the effect of climate and primary productivity on latitudinal distribution, skin surface temperature (TSK) and leaf area index (LAI) were obtained from satellite observation data from the Moderate Resolution Imaging Spectro-radiometer (MODIS). MODIS is operated on two satellite platforms, Terra and Aqua, by the United States National Aeronautics and Space Administration (NASA). TSK was retrieved by a generalized split-window algorithm with thermal infrared detections, and it represents temperature at the soil or canopy surface (Wan, 1999). The TSK data used were monthly-averaged gridded data with a 0.05 decimal degree size for each grid. LAI was defined as the area of a one-sided broad leaf or projected needle leaf per unit ground area. LAI is generally used for quantifying the amount of photosynthetically active leaves. Thus, LAI is considered a key driver of forest productivity (Clark et al., 2007). These data are derived from MODIS surface reflectance with structural and optical characteristics of vegetation types (Tian et al., 2000). The LAI data herein used were 16-day-composed gridded data in 250 m for each grid. For the scale variation of TSK and LAI. The gridded MODIS TSK and LAI data can be obtained via lpdaac.usgs.gov, and all data were averaged from 2006 to 2013, which is the same period of the NES data.

Habitat diversity

A MODIS land cover dataset, which follows the land cover classification from the International Geosphere-Biosphere Programme (IGBP) (Friedl et al., 2002), was used to quantify habitat diversity. The IGBP classification categorizes land covers globally into 17 types (Fig. 3). Among them, land covers in South Korea are classified into 13 IGBP types. Habitat diversity indices were derived from a species diversity index (Kim et al, 2018; Kim et al, 2019). Thus, habitat diversity in a given unit area was defined by the following equation, which is the same as the typical species richness estimation:

$$D = \sum_{i=1}^n \{-A_i/A_{tot} \bullet \ln(A_i/A_{tot})\}(1),$$

where A_i is the covering area of the land cover type i , and A_{tot} is the total area for all land cover types of the given analytical unit. The unit area was set at a 0.125 × 0.125 square decimal degrees, the same unit size of the NES data.

Forest area

The data of forest area were extracted from a 1:25,000 scale land cover map from 2009 from the Korea Ministry of Environment (KME,<http://egis.me.go.kr>). The KME land cover map was produced with a 5 m spatial resolution using satellite imagery (Landsat TM, IRS-1C, SPOT-5, KOMPSAT-2), and it consisted of 22 land cover classes. Among them, the forest area included in a grid of 0.125 × 0.125 square decimal degree was calculated using the ‘calculate geometry’ function of ArcGIS in the land cover map. Then, a grid

of 0.125×0.125 square decimal degree was generated using the fishnet tool in ArcGIS. Spatial data were compiled using the ArcGIS 10.3 and R Studio 1.1.383 software programs.

Anthropogenic disturbances (number of patches)

To identify habitat fragmentation induced by anthropogenic disturbances, we used number of patches. Data on forest patches were extracted from the KME land cover map. An identification number (ID) was assigned to each forest patch and grid. Then, using the union tool in ArcGIS, forest patches were overlapped with grid cells. The number of forest patches was obtained by counting the ID numbers of the forest patches included in a grid of 0.125×0.125 square decimal degree. The number of forest patches was counted using the dplyr package for R Studio 1.1.383.

Data analyses

To identify the peninsular effect on passerine birds, patterns of linear regression between passerine species richness and latitude were verified within a grid of 0.125×0.125 square decimal degree. Species richness was averaged according to resolution scales (0.125×0.125 square decimal degree), to reduce differences in sampling effort (Battisti, 2014). To test the hypotheses of peninsular effect, we settled the conceptual scheme (Fig 1) according to recent deterministic and anthropogenic processes. Latitude was defined as a main factor determining mean temperature and No. of patches. We stipulated mean temperature as a main driver that affects the change in vegetation variables, ratio of migrant species richness, and resident species richness. LAI, forest area, habitat diversity, ratio of migrant species richness, and No. of patches were also stipulated as a main driver affecting passerine species richness. Relationship between variables were identified using linear regression. All statistical analyses were performed using SigmaPlot 13.0 (Systat Software, Inc.) and SPSS statistics 20 (IBM Corp.).

Results

Testing the peninsular effect

A total of 147 passerine species were observed in the 589 regions in lattices of $0.125 \times 0.125^\circ$ resolution (S1 Table). We tested the peninsular effect on 147 passerine species. The linear pattern of single model between passerine species richness and latitude showed that passerine species richness increased with increasing latitude (Table 1, Fig. 4). The linear pattern represented slightly low R^2 but a significant increase ($R^2 = 0.036$, $P < 0.001$).

Testing hypotheses that explain the peninsular effect

To understand the causal mechanism of the peninsular effect, the influence of recent environmental changes and migrant species inflow were identified. Increasing latitude predicted lower mean temperature ($P < 0.001$, Fig. 5(a)). LAI and forest area declined as mean temperature increased ($P < 0.001$, $P < 0.001$, Fig. 5(b) and (c), respectively), whereas habitat diversity increased as mean temperature increased ($P < 0.001$, Fig. 5(d)). Passerine species richness increased with LAI and forest area ($P < 0.001$, $P < 0.001$, Fig. 5(e) and (f), respectively). However, passerine species richness showed no significant relationship with habitat diversity ($P = 0.322$, Fig. 5(g)).

Ratio of migratory species richness showed no significant relationship with LAI and forest area ($P = 0.845$, $P = 0.369$, Fig. 6(a) and (b), respectively), and declined as habitat diversity increased ($P < 0.001$, Fig. 6(c)). Passerine species richness increased with ratio of migrant species richness increased ($P < 0.001$, Fig. 6(d)).

Increasing latitude predicted decreasing No. of patches ($P < 0.001$, Fig. 7(a)). However, there was no relationship between No. of patches and passerine species richness ($P = 0.295$, Fig. 7(b)).

Discussion

Testing the peninsular effect

Our results of the single regression between passerine species richness and latitude support the existence of the peninsular effect (Table 1). However, distribution pattern of passerine species richness showed a decreasing around at $\sim 38^{\circ}\text{N}$ (Fig. 1). We assumed that these effects were caused by the decrease in species richness near the northern border; as many army units and troops are deployed near the Military Demarcation Line, conducting surveys on living organisms in that area is difficult and subject to many restrictions. Moreover, the bird survey data used herein were restricted to South Korea for political reasons; thus, we were unable to consider the richness pattern of the entire peninsula. Nevertheless, the richness decrease from the base towards the tip is shown herein. Considering that our results showed the importance of mean temperature, forest area, and migrant inflow on passerine species richness (Fig. 5 and 6), we expect passerine species richness to increase in North Korea, especially as it is expected containing wider forest areas, LAI, higher migrant inflow, and lower mean temperature.

Testing hypotheses to explain the peninsular effect

Increasing latitude led to decreasing mean temperature. And LAI and forest area, induced by temperature gradient, affected passerine species richness positively (Fig. 8). These results support the existence of the peninsular effect on passerine birds induced by climate, habitat area, and primary productivity. Studies conducted in Baja California (birds) and Iberian peninsula (passerine birds) also showed that change of temperatures along a gradient is likely the most important factor (Battisti, 2014; Telleria & Santos, 1993; Wiggins, 1999). However, in peninsulas with the tip pointing south, the observed decreasing base-tip diversity patterns could not be coherent with the global latitudinal gradient (Battisti, 2014), and against the physiological tolerance hypothesis (Currie et al., 2004). Thus, the hypotheses of the peninsular effect should not directly explain the relationship between temperature and species richness. In our results, LAI and forest area decreased with increasing mean temperature (Fig. 5(b) and (c)). In the global latitudinal gradient generally, species richness of trees decrease monotonically with latitude, and increase with temperature (Currie, 1991). However, according to the peninsular effect explained by landscape ecology, the lack of the available interior habitat, as well as the progressive increase in edge area towards the tip of the peninsular, are the major causal factors explaining the species richness and occurrence (Battisti, 2014; Tubelis et al., 2007). Our results of the mechanism of the peninsular effect relate to habitat (LAI and forest area) were also followed these disciplines.

Many studies suggested that habitat diversity might be the important factor explaining the peninsular effect (Choi, 2004; Wiggins, 1999). Because different climatic and edaphic, induced by topographic heterogeneity (latitude and altitude), can alter habitat diversity (Kocher & Williams, 2000; Tews et al., 2004). In our results, habitat diversity increased with increasing mean temperature, whereas LAI and forest area increased with decreasing mean temperature (Fig. 8), which is presumed to be due to habitat simplification by increased mature forest and forest area towards the base of the peninsular (Fig. 3). These results show primary productivity and forest area are incompatible with habitat diversity. And our results of relationship between passerine species richness and LAI, forest area (Fig. 8) show that primary productivity and habitat area are more important variable than habitat diversity for passerine birds. Meanwhile, ratio of migrant species richness increased as decreasing habitat diversity (Fig. 6(c)) and was not influenced by LAI and forest area (Fig. 6(a) and (b)). In general, vegetation structure and primary productivity are considered an important variable for most passerine bird species (Bailey et al., 2004; Rabinovich & Rapoport, 1975) because they inhabit forest areas to forage, rest, and breed regardless of being resident or migrant. Thus, it is assumed that the reason why the migrant species were distributed in areas with lower habitat diversity without being influenced by LAI and forest area, is that migrant species have the characteristics of generalist due to competition with resident. And we found that the ratio of migrant species richness increased with increasing latitude (Fig. 9(a)), and that contributed to the increase in passerine species richness (Fig. 9(b)). Therefore, these results indicate that migrant species inflow increased passerine species richness and the peninsular effect.

Battisti (2014) argued that if the anthropogenic factors have a base-tip gradient, that can influence the peninsular species richness patterns. Our results show that No. of patches decreased with increasing latitude,

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Tables

Table 1. Results of linear pattern of passerine species richness according to latitudinal gradient.

Independent variable	Number of cells	β	R^2	F	P
Latitude	589	0.991	0.036	22.080	<0.001

Figure legends

Fig. 1. Conceptual scheme of the study to test the peninsular effect according to recent deterministic processes and migrant species inflow.

Fig. 2. Location of the Korean peninsula and NES survey regions and scale.

Fig. 3. Moderate Resolution Imaging Spectro-radiometer (MODIS) land cover map for South Korea with the 17 IGBP classification. The numbers beside the names of land cover types are their percentages to the total land area of South Korea.

Fig. 4. Distribution of passerine species richness in South Korea

Fig. 5. Relationship between (a) latitude and mean temperature, (b) mean temperature and LAI, (c) mean temperature and forest area, (d) mean temperature and habitat diversity, (e) LAI and passerine species richness, (f) forest area and passerine species richness, and (g) habitat diversity and passerine species richness according to the hypotheses of the primary productivity, habitat area, and habitat diversity.

Fig. 6. Relationship between (a) LAI and ratio of migrant species richness, (b) forest area and ratio of migrant species richness, (c) habitat diversity and ratio of migrant species richness, and (d) ratio of migrant species richness and passerine species richness according to the hypotheses of migration influence.

Fig. 7. Relationship between (a) latitude and No. of patches and (b) No. of patches and passerine species richness according to the hypotheses of anthropogenic disturbance.

Fig. 8. Results of testing the causal mechanism of the peninsular effect according to the conceptual scheme. Blue arrows indicate significant relationship between variables and numbers indicate R^2 values.

Fig. 9. . Relationship between (a) latitude and ratio of migrant species richness, (b) ratio of migrant species richness and passerine species richness.









