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Effects of habitat fragmentation on mammalian species richness in the Republic of Korea

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Road networks cause habitat fragmentation by reducing the patch size and connectivity, threatening wildlife. We assessed the effects of road-induced habitat fragmentation and proximity to roads on mammalian species richness in the Republic of Korea. Habitat patches were delineated to minimize road impact, and patch size and connectivity were quantified. The mammalian species richness was based on nationwide occurrence records. We compared species richness across three consecutive 1-km buffers extending from the roads to evaluate edge effects. In total, 6176 patches were identified, with over 66% being smaller than 1 km^2. Species richness increased significantly with patch size and connectivity, with patch size exerting the strongest effect. Species richness was nearly twice as high in highly connected patches exceeding the connectivity threshold, particularly in landscapes with higher forest cover and lower agricultural land cover. Species richness increased with increasing distance from roads, being lowest at 0–1 km and highest at 2–3 km. These findings indicated that mammalian species richness is highly sensitive to habitat fragmentation and that structurally favorable patches with higher natural cover support substantially greater biodiversity. Pronounced declines in species richness near roads highlight strong edge effects on mammalian species richness in the Republic of Korea.

Keywords Habitat fragmentation, Spatial analysis, Edge effect, Road network, Species richness, Landscape connectivity

There are at least 36 million kilometers of roads worldwide, and an additional 25 million kilometers are expected to be built by 2050[1,2]. Roads divide habitats into multiple patches and act as barriers between them, resulting in a reduced patch size and connectivity, collectively known as habitat fragmentation[3]. Generally, habitat fragmentation hinders an individual's ability to move and reproduce freely, and smaller habitat patches lose their resilience to environmental changes[4]. Roads that disrupt habitat connectivity often force animals to traverse hazardous areas, thereby increasing the likelihood of collisions between wildlife and vehicles. Moreover, the quality of these fragmented habitats has declined, making resources less accessible, disrupting interspecies interactions, and destabilizing the entire ecosystem. Consequently, habitat fragmentation significantly affects ecosystems by threatening population persistence and reducing biodiversity by 13–75%, as shown in a global synthesis of fragmentation experiments[5–9].

Habitat fragmentation caused by road networks negatively affects wildlife population persistence. Fragmented habitats are often characterized by a limited spatial extent, which leads to resource limitation by reducing access to essential resources required for foraging, sheltering, and breeding. This limitation reduces the availability of essential resources and lowers the carrying capacity of each patch[10]. Smaller patches may fail to support the minimum viable population sizes, making the resident species more vulnerable to local extinction. For example, habitat size is the most important factor in determining species diversity, with larger areas supporting more species by providing a greater variety of habitats and sufficient resources to maintain stable populations[11]. The Siberian tiger (*Panthera tigris altaica*) represents a prominent case of this vulnerability, as fragmentation has reduced its population size and range by disrupting access to large, connected territories[12]. Similarly, smaller arboreal mammals exhibit comparable patterns, with species richness and community composition being strongly influenced by patch size and quality in fragmented forests[13]. Consequently, smaller patches produced by fragmentation exhibit lower overall quality, reducing the likelihood of long-term population persistence and ultimately leading to decreased species richness.

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The loss of connectivity between habitat patches is another key consequence of fragmentation that affects wildlife populations. Increased spatial isolation restricts the movement of individuals between patches, thereby reducing opportunities for dispersal and recolonization[3,10]. These constraints hinder gene flow and reduce population viability, ultimately influencing biodiversity across landscapes. For instance, reduced connectivity caused by roads increases genetic differentiation, lowers population viability, and elevates extinction risk, especially in vulnerable or range-restricted mammalian species[14,15]. Over time, the cumulative effects of disrupted connectivity can reduce the metapopulation stability and weaken ecological resilience. Consequently, habitat fragmentation imposes multiple ecological constraints on wildlife populations, leading to a reduction in species richness in fragmented landscapes. Numerous empirical studies have reported consistent patterns across taxa, demonstrating that reduced connectivity and increased isolation lead to declines in mammalian diversity and overall biodiversity in fragmented habitats[16–18].

Another major consequence of fragmentation is the intensification of the edge effect. As the proportion of edge habitats increases relative to interior habitats, animals are exposed to greater levels of human disturbance, making interior-dependent species particularly vulnerable[9,19]. Roads contribute to edge formation in fragmented landscapes by altering habitat structure and introducing continuous sources of disturbance that intensify edge-related impacts. Proximity to roads is frequently associated with decreased species abundance and richness, particularly for disturbance-sensitive species[19,20]. The effects of roads in a fragmented patch, such as noise and light, are typically strongest near the edge and diminish towards the interior[21]. Consequently, species richness and community composition often vary with the distance from roads, resulting in a consistent pattern in which species richness is lower near roads and higher in interior areas[22,23].

The ecological impacts of habitat fragmentation can also be understood using established ecological theories. In particular, the island biogeography theory provides a useful framework for explaining how patch size and connectivity affect species richness[24]. Originally proposed to explain species diversity on oceanic islands, this theory has been widely applied to terrestrial habitat patches functioning as ecological "islands" surrounded by a matrix of inhospitable land cover. This theory posits that species richness in a patch is determined by a dynamic balance between colonization and extinction, both of which are influenced by the patch area and isolation. Larger patches support more species owing to greater habitat heterogeneity and lower extinction probabilities, whereas higher connectivity facilitates species influx and recolonization, reducing local extinction risk[3]. Thus, the species–area relationship (SAR) emerges as a key indicator derived from this theoretical foundation, describing the relationship between habitat area and species richness[25–27]. SAR has been empirically supported across taxa and ecosystems, and remains one of the most robust and widely used tools for predicting biodiversity loss due to habitat fragmentation. These theoretical foundations enable systematic evaluation of the influence of habitat fragmentation on species richness in terrestrial ecosystems.

The negative effects of habitat fragmentation on species richness have contributed to the extinction risk currently faced by 27% of mammalian species worldwide[15]. This global trend is also reflected at the national level. Rapid industrialization and the expansion of dense road networks have profoundly altered natural landscapes in the Republic of Korea, contributing to severe fragmentation at the national level. Among the 83 species of officially recorded terrestrial mammals in the country (National Institute of Biological Resources; species.nibr.go.kr), 18 are classified as threatened by the regional IUCN Red List (5 as regionally Extinct, 1 as Critically Endangered, 3 as Endangered, 8 as Vulnerable, and 1 as Near Threatened). Transportation infrastructure has been identified as the primary cause of population decline in half of these species (https://www.iucnredlist.org/). These figures underscore the significant impact of road infrastructure on the persistence of mammalian populations in the country[28,29].

Several recent studies have examined the effects of habitat fragmentation on mammalian populations in the Republic of Korea. One study reported that patch size positively influenced mammalian species richness, whereas edge length had an adverse effect, underscoring the ecological importance of habitat structure even in urban environments[30]. Another study identified the distance to the forest edge as a the key predictors of regional-scale species richness, highlighting that interior areas tend to support higher mammalian biodiversity than edge areas[31]. A national-level review further emphasized that road infrastructure contributes to habitat loss, edge effects, and population isolation, thereby undermining ecological connectivity, with dense road networks likely intensifying these impacts[32]. Although these studies provide valuable insights, they are largely confined to local contexts or conceptual syntheses. Furthermore, no research has quantitatively assessed how habitat fragmentation influences mammalian populations on a nationwide landscape scale. This study addressed this gap by integrating spatial data across the Republic of Korea to evaluate the combined effects of habitat area, connectivity, and road proximity on mammalian species richness.

The goal of this study was to examine the current status of habitat fragmentation caused by road networks and understand how habitat fragmentation influences mammalian species richness in the Republic of Korea. In this study, we focus on road-induced structural fragmentation, which refers to changes in the spatial configuration of habitats caused by roads. This differs from habitat loss, which involves a reduction in the total amount of habitat area. The analysis therefore isolates the structural effects of fragmentation from the quantitative effects of habitat loss. First, we quantify the patch size and connectivity caused by nationwide road networks. Second, we assessed the effects of patch size and connectivity on mammalian species richness. Accordingly, we hypothesized that mammalian species richness increases with patch size and patch connectivity, as expected from the island biogeography theory. Third, we examined the influence of the distance to roads on species richness. We hypothesized that species richness would be negatively affected by proximity to roads. Given its simplicity and ecological relevance, species richness has been used as a key indicator to assess the effects of habitat fragmentation[33]. We expect that the findings of this study will contribute to the development of effective conservation strategies tailored to the challenges posed by habitat fragmentation in the rapidly changing landscape of the Republic of Korea.

Results

General patch characteristics

We identified a total of 6176 fragmented patches in the Republic of Korea, and the total area with the minimum impact of roads was 83,789 km^2, covering about 83.6% of the country. The patch size ranged from 20.4 m^2 to 2663.6 km^2 with an average (± SD) of 13.6 ± 57.3 km^2 (Fig. 1). Of the total number of patches, the percentages of patches smaller than 1 km^2 were 66.0%, and more than three quarters of the patches (75.9%) had areas less than 5 km^2. Among all patches, only 19.1% were larger than 10 km^2, and 3.1% were larger than 100 km^2.

Patch connectivity ranged from 0 to 2,332,904,566, with an average (± SD) of 47,346,455 ± 247,348,379 (unitless index). The distribution was highly skewed, with most patches showing very low connectivity, and a few exhibiting extremely high connectivity. The high-connectivity patches were mostly concentrated in the Eastern part of the country, along the Baekdu-Daegan range (Fig. 2).

Impact of patch size and patch connectivity on species richness

A total of 52 mammalian species, including 6 threatened species, were recorded in patches across the Republic of Korea. The mean species richness per patch was 1.92 ± 3.97 (± SD; n = 6,178). Patches with very high species richness (≥ 20) had at least 148 km^2 of patch size. The log–log linear regression showed a strong positive relationship between patch size and species richness ($R^2 = 0.55$, $p < 0.001$; log species richness = 0.23 + 0.40 × log patch size) (Fig. 3a). The slope of 0.40 in the SAR represents a rather steep relationship between patch size and species richness. A similar relationship was observed between species richness and patch connectivity, though the effect was weaker ($R^2 = 0.24$, $p < 0.001$; log species richness = − 1.42 + 0.31 × log patch connectivity) (Fig. 3b). The results of the zero-inflated generalized linear model (ZIGLM) showed that species richness was significantly affected by patch size ($p < 0.001$) as well as patch connectivity ($p < 0.001$; Table 1). Multicollinearity diagnostics showed that the variance inflation factors (VIF) values for patch size and connectivity were consistently low (< 1.05), confirming that the predictors were not collinear. The effect of patch size was greater than that of connectivity, as indicated by the standardized regression coefficients (B in Table 1). These results implied that species richness increased with both patch size and connectivity, with patch size being the most influential factor.

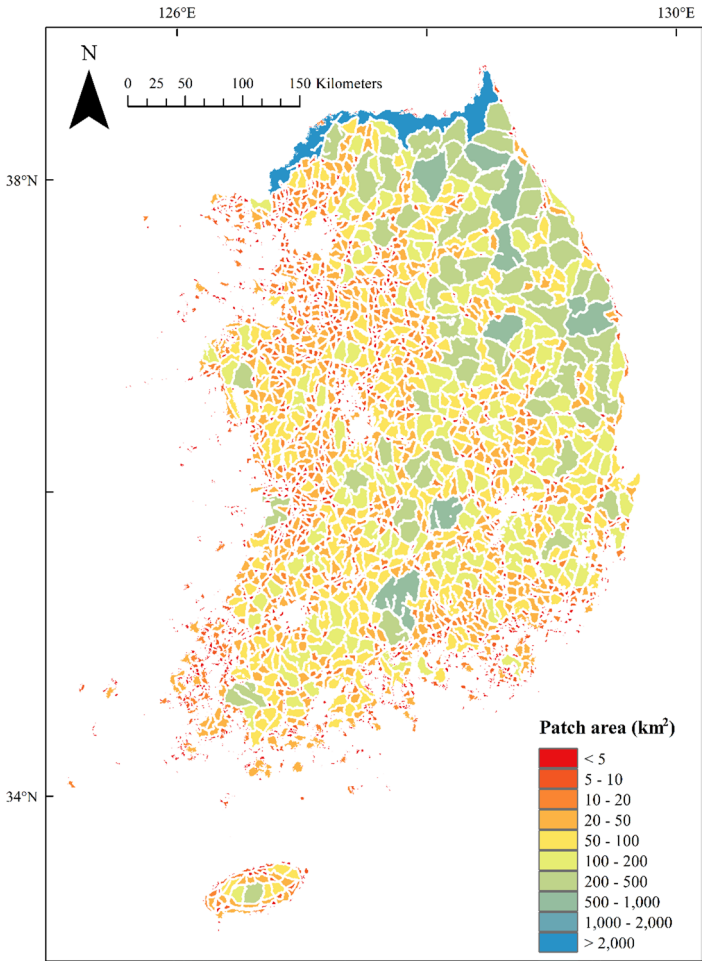


Fig. 1. Distribution of the patches with areas color-coded in the Republic of Korea, as of 2021. A patch was defined as an area with a 1-km buffer from the nearest roads. The map was generated using ArcGIS Desktop 10.8.1.

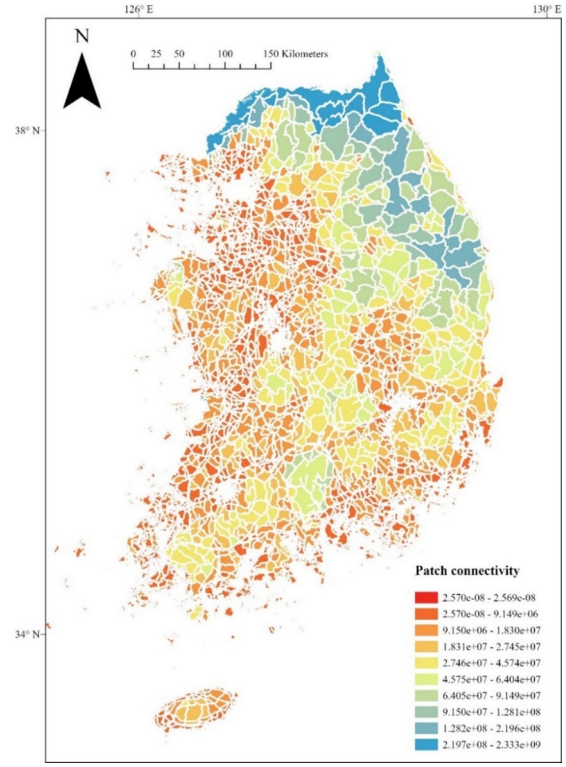


Fig. 2. Distribution of the patches with patch connectivity color-coded in the Republic of Korea, as of 2021. A patch was defined as an area with a 1-km buffer from the nearest roads. The map was generated using ArcGIS Desktop 10.8.1.

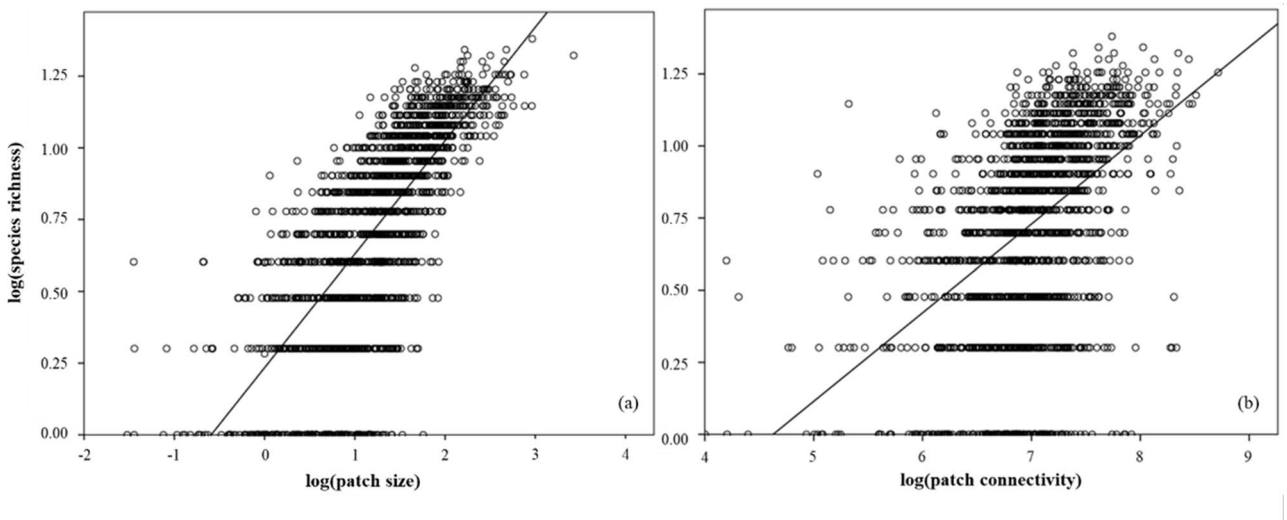


Fig. 3. Regression analyses of patch size (**a**) and patch connectivity (**b**) on species richness. All variables were logarithmically transformed, and outliers were removed.

The contour graph showing the relationship between patch size, connectivity, and species richness revealed that species richness generally increased with patch size and connectivity (Fig. 4). Species richness was the highest in patches that were simultaneously large and well-connected, indicating a clear interaction between the two variables. Species richness was minimum in the patches lower than approximately 1.5 on a log scale of nearly 30 km^2, implying that a certain minimum area is needed to support diverse mammal communities. A similar pattern was observed for connectivity: species richness remained low in patches with connectivity value below 3.0 on a log scale. It gradually increased in patches with higher connectivity values. In addition, species richness notably increased only in patches with connectivity values larger than 2.0 on a log scale, and richness generally

Parameter	B	SE	*P*	
Intercept	0.695	0.010	< 0.001	
Patch size	0.362	0.003	< 0.001	
Patch connectivity	0.307	0.033	< 0.001	

Table 1. The effects of patch size and patch connectivity on mammalian species richness, based on results of the zero-inflated generalized linear model (ZIGLM). Predictor variables were normalized ($n = 6176$).

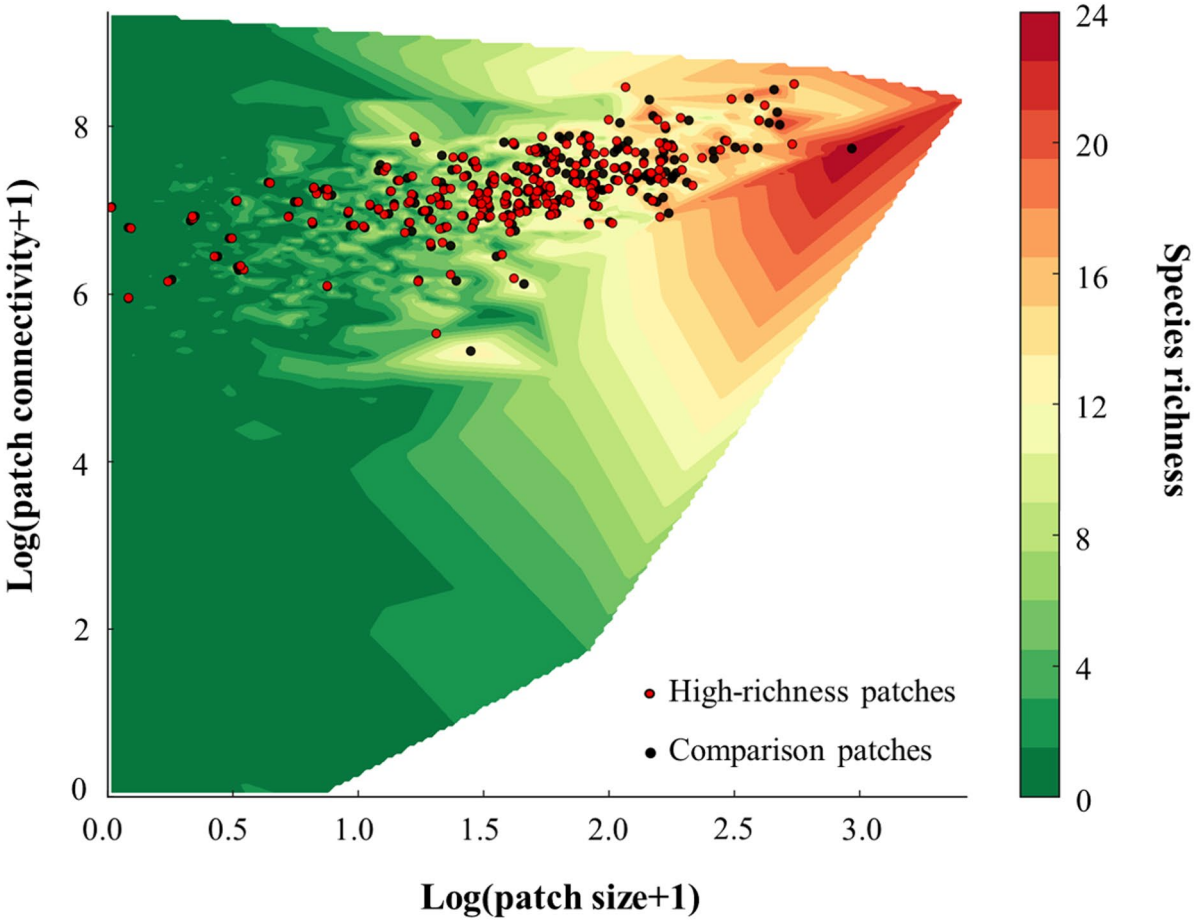


Fig. 4. The contour graph presenting the relationship between patch size, patch connectivity, and species richness. The color bar represents the species richness. Patch size and connectivity were transformed into log(x + 1). Red and black dots indicate high-richness patches and structurally similar comparison patches, respectively. See text for more information.

increased with patch size in patches with connectivity values above 4.0. These patterns highlighted the combined influence of patch size and connectivity in maintaining high species richness.

We identified a total of 269 high species richness patches, relative to structurally similar surrounding patches, located in the upper-middle region of the contour plot, all of which were situated within regions of relatively high patch connectivity. Specifically, patch connectivity values of these patches ranged from 5.32 to 8.13 on a log scale, with an average of 7.05. The mean species richness was 11.43 ± 3.83 in the high-richness patches and 5.92 ± 4.37 in the comparison patches (structurally similar non-outlier patches) (Fig. 4). This difference was statistically significant (Welch's *t*-test, $t = 15.54$, $p < 0.001$). We selected the same number of comparison patches that closely matched the high-richness patches based on the Euclidean distance in these structural attributes to isolate the effect of land-cover composition on species richness, while controlling for the effects of patch area and connectivity. Prior to model fitting, we assessed multicollinearity among the land-cover variables using VIF, confirming that all values had no significant multicollinearity. Logistic regression analysis of land-cover composition revealed that the best predictive model retained the proportions of forests and agriculture with an area under curve (AUC) value of 0.65 (Table 2). The model indicated that patches with a higher proportion of

Land cover	Estimate	SE	Wald	*P*	Odds ratio
Intercept	−0.073	0.381	−0.192	0.848	0.930
Agriculture	−0.118	0.043	−2.730	0.006*	0.888
Forest	0.090	0.035	2.607	0.009*	1.094

Table 2. The best predictive model of logistic regression examining landscape features of high-richness patches compared to other structurally similar patches. Land-cover covariates were transformed into square roots using the proportion of each land-cover type. Asterisks indicate statistically significant relationships.

forests were more likely to exhibit higher species richness. In contrast, higher proportions of agricultural land were associated with lower species richness.

Species richness with distance to roads

We compared species richness in three buffers of varying distances to roads to understand how proximity to roads affects mammalian species richness. In general, the average number of species per unit area (1 km^2) increased with increasing distance from the roads. Species richness was the lowest in the 0–1 km buffer (0.428 ± 0.058), increased in the 1–2 km buffer (0.816 ± 0.067), and was the highest in the 2–3 km buffer (1.043 ± 0.129). The results of the Kruskal–Wallis test showed significant differences in species richness across the three buffer distances ($p < 0.001$). The post hoc Wilcoxon test confirmed that all pairwise comparisons among the three buffer distances were statistically significant ($p < 0.001$ for all comparisons). These results indicate that species richness increases with increasing distance from roads.

Discussion

Our results demonstrate that the Republic of Korea is characterized by an extensively fragmented road network, with the majority of remaining habitats existing as small and isolated patches. This study revealed strong associations between road networks, landscape fragmentation, and reduction in patch size and connectivity, which were linked to lower mammalian species richness in the Republic of Korea. Our results confirm the predictions of the theory of island biogeography, showing higher species richness in larger and more connected habitat patches. In addition, landscape features inside a patch play an important role in preserving high species richness. Moreover, species richness increased significantly with increasing distance from roads, highlighting the negative impact of edge effects associated with increased anthropogenic disturbance and reduced habitat quality near roads. These findings underscore the complexity of habitat fragmentation and highlight the need for comprehensive analyses to guide effective conservation and management strategies.

Our patch-based analysis identified 6178 habitat patches characterized by considerable variations in size and connectivity across the country, with the majority of patches being relatively small and isolated owing to dense road networks. This extensive fragmentation has critical implications for mammalian species, particularly for those that require a large spatial extent[34]. Large patches typically provide abundant food and resources, thereby supporting diverse mammalian communities. Their loss can disproportionately affect species with extensive spatial needs[35]. *Martes flavigula*, a threatened species, has the largest home range size of 32.2 ± 12.9 km^2, among non-reintroduced species in the Republic of Korea[36]. This species represents a typical example of large-ranging mammals constrained by limited patch size and road-induced isolation, illustrating the broader pattern observed across the mammalian community. Considering these extensive spatial requirements, only 10.3% of the habitat patches identified in the country were sufficiently large to accommodate at least a single individual without significant road disturbance. Notably, such large, minimally disturbed patches were predominantly distributed along the Demilitarized Zone and the Baekdu-Daegan mountain range. Supporting this finding, predictive habitat suitability models for *M. flavigula* also identified the Baekdu-Daegan region as the most suitable habitat for this species. Furthermore, the species avoids areas near roads, indicating the effects of fragmentation on habitat use[37,38]. Therefore, our results suggested that only a limited number of habitat patches in Korea effectively meet the requirements of mammalian species with large home ranges, highlighting their vulnerability to habitat fragmentation.

We first focused on patch size using SAR to enable comparisons with the findings of other studies, to better understand how patch characteristics influence species richness. Our findings revealed a relatively steep slope of 0.40. This value exceeds the average SAR slope reported for Eurasian mammals (0.26) across 869 species[39] and typical values observed in non-fragmented continental systems, where slopes often range from 0.15 to 0.25[40]. Relatively steep slopes in SAR curves are often associated with small sampling scales, but more importantly, they are characteristic of fragmented or island-like landscapes, where species richness is particularly sensitive to habitat loss[39–42]. Accordingly, the highly fragmented landscape of the Republic of Korea, marked by large contiguous forested areas in mountainous regions and numerous small isolated patches in urban lowlands, may have intensified the slope. These small and urbanized patches often suffer from rapid declines in habitat quality, increased edge effects, and limited resource availability, all of which restrict population persistence, making species particularly vulnerable to reductions in patch size[10,25,43].

The relationship between patch connectivity and species richness also followed a log–log trend, with a slope of 0.31, indicating a consistent positive effect across the connectivity gradient. Although this increase was gradual rather than abrupt, species richness was clearly higher in patches located within the upper connectivity range, where high-richness patches were strongly concentrated. Similar patterns have been reported in fragmentation studies showing that species richness or occupancy often increases disproportionately once connectivity reaches

ecologically functional levels[44,45]. Highly connected patches facilitate species movement and dispersal, thereby enhancing gene flow and population viability and ensuring the long-term persistence of species in fragmented landscapes[40,41]. Previous studies have further emphasized that connectivity is a primary driver of distribution patterns in arboreal rodents[46] and essential for maintaining the persistence of large mammals and facilitating their movement across fragmented habitats[47]. Collectively, these findings suggest that the connectivity–richness relationship reflects a steadily increasing response with a concentration of high-richness patches at higher connectivity values, consistent with broader evidence that functional connectivity promotes community-level richness.

The findings of the contour graph analysis further clarified how patch size and connectivity jointly shape species richness in fragmented habitats. Species richness increased toward regions where both variables were high, consistent with earlier studies emphasizing the combined importance of these structural attributes in sustaining biodiversity[10,48]. In our results, patches that were larger and more connected supported notably higher richness, indicating that the simultaneous increase in patch size and functional connectivity plays a central role in maintaining mammal assemblages. Species richness declined markedly in patches with low connectivity, a pattern consistent with the classic synthesis showing that fragmentation effects become disproportionately stronger as habitat amount decreases[49]. Conversely, well-connected patches of moderate size exhibited higher species richness, supporting the view that connectivity can mitigate the adverse effects of habitat fragmentation[50]. These patterns suggested that improving connectivity among moderately sized patches can help maintain higher levels of species richness in fragmented landscapes.

In addition to the primary effects of patch size and connectivity, land-cover composition within patches also modulates species richness, highlighting the importance of habitat quality in fragmented landscapes. Our focused analysis of 269 high-richness patches revealed a more refined spatial pattern, all of which were distributed within a high connectivity range and consistently exhibited greater species richness than other structurally similar patches. Importantly, variations in land-cover composition explained the additional differences in mammalian species richness beyond the effects of patch size and connectivity. High-richness patches were characterized by a greater proportion of forested habitats, representing natural habitats, and a lower proportion of agricultural habitats, primarily constituting open and disturbed environments. These results demonstrated that, once a connectivity threshold is surpassed (≥ 5.32 in log scale), variation in land-cover composition plays a key role in shaping local species richness, beyond the effects of patch area and connectivity alone. In patches where connectivity exceeded a certain threshold, the land cover composition within the patch emerged as a key determinant of mammalian species richness. Forested habitats likely provide more stable resources, cover, and microclimatic conditions, whereas agricultural habitats may have increased exposure to edge effects, disturbances, and anthropogenic pressures. This pattern aligns with previous research emphasizing the role of matrix quality in shaping ecological processes, such as movement, foraging, and habitat selection[51,52]. These insights have important implications for landscape management. In highly fragmented areas where securing large habitat patches is difficult, increasing the proportion of natural habitat is beneficial and essential for promoting species persistence and maintaining ecosystem integrity. Our findings underscored that targeted management of habitat composition can play a decisive role in sustaining biodiversity within fragmented landscapes, even when opportunities to expand patch size are limited.

Mammalian species richness in this study critically increased with greater distance from road networks, indicating that road-adjacent environments support simplified assemblages relative to more interior areas. This pattern likely reflects the cumulative impact of various anthropogenic disturbances commonly associated with roads, including noise, artificial lighting, pollution, and vehicular collisions. These effects will likely reduce habitat suitability for disturbance-sensitive species and may contribute to the lower species richness observed near roads. A global meta-analysis similarly showed that mammal abundance and richness decline substantially within several kilometers of major infrastructure and increase with distance, demonstrating the widespread functional footprint of roads across regions[22]. This pattern is also exemplified by a regional-scale study showing that areas near roads consistently supported fewer mammalian species, suggesting the functional degradation of core habitats in road-affected landscapes[30]. Furthermore, another study found that mammalian species richness declines with increasing edge length, suggesting that interior-adapted species are particularly vulnerable to fragmentation and edge exposure in urban areas[31]. These findings indicate that species adapted to core habitat conditions may decline, whereas edge-adapted species may persist, ultimately simplifying species assemblages. Therefore, maintaining sufficient interior habitats is crucial for sustaining mammalian diversity, particularly in landscapes that are increasingly affected by road expansion.

Generally, constructing new roads in areas where the ecological quality is already low and prioritizing the protection of areas with high ecological quality will help minimize the impact of roads and conserve biodiversity[53]. This direction aligns with the goals of the Convention on Biological Diversity (CBD), a multilateral treaty adopted by over 190 countries in 1992 to promote the conservation and sustainable use of biological diversity[54]. Based on the findings of this study, we suggest three practical strategies for promoting the ecological integrity and conservation of wildlife populations. Increasing patch size is a fundamental approach that benefits mammalian species by improving habitat quality and reducing fragmentation effects. However, we recognize that expanding patch size is often constrained in road-dense regions, and thus alternative measures should be considered. Second, enhancing patch connectivity using wildlife corridors can help improve habitat conditions and preserve species persistence where the landscape is highly fragmented and expanding patch size is not feasible. Third, increasing the proportion of natural land cover, such as forests, in the surrounding matrix can support high species richness by reducing anthropogenic disturbances. This study provided a practical and spatially grounded basis for identifying priority conservation areas and avoiding development in ecologically valuable regions. This study provided a practical and spatially grounded basis for identifying conservation priorities and guiding land use decisions in ecologically sensitive areas. Although this research was conducted in the Republic of Korea, the

principles and strategies derived from our findings may be relevant to other regions facing similar challenges of road expansion and landscape fragmentation.

Building on these insights, several limitations and future directions should be considered to improve the applicability and robustness of our findings. First, due to data availability constraints, the analysis did not directly incorporate the actual road network configuration. While structural fragmentation was assessed using patch size and connectivity, road network data derived from public sources substantially underrepresented the extent of linear infrastructure compared to reality. Consequently, the actual degree of fragmentation in the Republic of Korea is likely to be more severe than that estimated in this study. Second, this study focused exclusively on structural fragmentation caused by roads, which represents changes in the spatial configuration of habitats rather than reductions in total habitat area. Future analyses that jointly evaluate habitat amount and configuration provide a more comprehensive understanding of how these processes interact to shape biodiversity patterns[55,56]. In addition, patch delineation in this study was based solely on road influence to quantify structural fragmentation at a national scale. However, in certain regions, particularly in the eastern mountains, patches may appear disconnected due to land cover composition rather than the presence of roads. This limitation underscores the need for future frameworks to integrate land cover-based resistance surfaces to more accurately capture functional aspects of fragmentation. Third, our analysis focused on species richness as a response variable, which captures the number of species present but does not reflect compositional turnover or community structure. Future studies should adopt diversity indices or multivariate approaches to assess the assemblage-level differences between patches, thereby providing deeper ecological insights beyond richness alone. Finally, although the present study aimed to detect structural and compositional predictors of high richness at the community level, a species-specific analysis is essential to inform targeted conservation strategies. Follow-up research should examine how individual species respond to fragmentation and landscape contexts, enabling more tailored and species-specific management plans. Such species-level analyses can also help identify taxa that are particularly sensitive to habitat fragmentation, thereby contributing to developing conservation measures that prioritize vulnerable species. Although this study provided a valuable foundation for understanding biodiversity patterns in fragmented landscapes, future research that addresses these limitations could further enhance their ecological and conservation relevance.

Materials and methods

Study area

Following the Korean War in 1953, the Republic of Korea underwent various stages of infrastructure development to build a competitive economy, one such initiative being the construction of road networks. As of 2021, the country had 113,405 km of roads (Korean Statistical Information Service 2021) (Fig. 5). However, the lengths of all roads, including farm roads and city alleys, are likely to be twice as long as those provided by the Korean Statistical Information Service[57]. The Korean road network comprises seven road types: expressways, national highways, metropolitan roads, provincial roads, municipal roads, county roads, and district roads. Expressways and national highways are considered major roads because they are inter-provincial and have high-speed limits of up to 110 km/h with a wide width. Unlike these two major roads, the rest of the road types extend only within their respective administrative boundaries and generally have lower speed limits and fewer lanes than the major roads.

The geography of the Korean peninsula features the Baekdu-Daegan mountain range, with peaks over 1000 m along the east coast and gentler slopes to the west. The western part of Korea, where major cities are located, has well-developed alluvial plains. Consequently, extensive road networks are predominantly found in the western and southern regions of the Republic of Korea.

Data collection and cleaning

We used mammalian species occurrence data provided by the National Ecosystem Survey of Korea conducted by the National Institute of Ecology[58] as a measure of species richness. This nationwide survey, conducted every 5 years to monitor ecosystems in the Republic of Korea, covers major taxa including vegetation, flora, mammals, birds, amphibians and reptiles, terrestrial insects, freshwater fish, and benthic macroinvertebrates. The location and date were recorded for all observed specimens in the survey. We used occurrence records from 1997 to 2018 to capture the richness of mammalian species across the country. Because national parks were excluded from the National Ecosystem Survey after 2005, earlier records were the only available data for these forested areas. Excluding them would have substantially underestimated the species richness in forests that experience relatively low road development pressure. Therefore, the data were retained to ensure a more representative assessment. Among the 83 terrestrial mammals recorded in the Republic of Korea, the occurrence data included 59 that were recorded during the survey. Of these, four terrestrial species (dhole, *Cuon alpinus*; Manchurian hare, *Lepus mandshuricus*; Eurasian lynx, *Lynx lynx*; and Japanese marten, *Martes melampus*) and one marine species (dolphin, *Delphinus capensis*) were excluded from the analyses because their current presence was uncertain or they were not relevant to the research objectives. In addition, two species without exact scientific names and three domesticated species (dog, *Canis lupus familiaris*; cat, *Felis catus*; and goat, *Capra hircus*) were excluded from the analysis.

Owing to the risk of poaching, information on protected species is not provided in the National Ecosystem Survey of Korea. Thus, we relied on data obtained from the Global Biodiversity Information Facility (GBIF; GBIF.org 2022) for six threatened species: the Eurasian otter *Lutra lutra*, yellow-throated marten *M. flavigula,* reddish-black myotis *Myotis rufoniger*, long-tailed goral *Naemorhedus caudatus*, leopard cat *Prionailurus bengalensis*, and Siberian flying squirrel *Pteromys volans*. Additional observation points for the three protected species (*L. lutra*, *M. flavigula*, and *P. bengalensis*) using georeferenced occurrence maps were extracted from the literature[37,59]. A total of 55 species were used in this study (see Appendix 1 for the total species list).

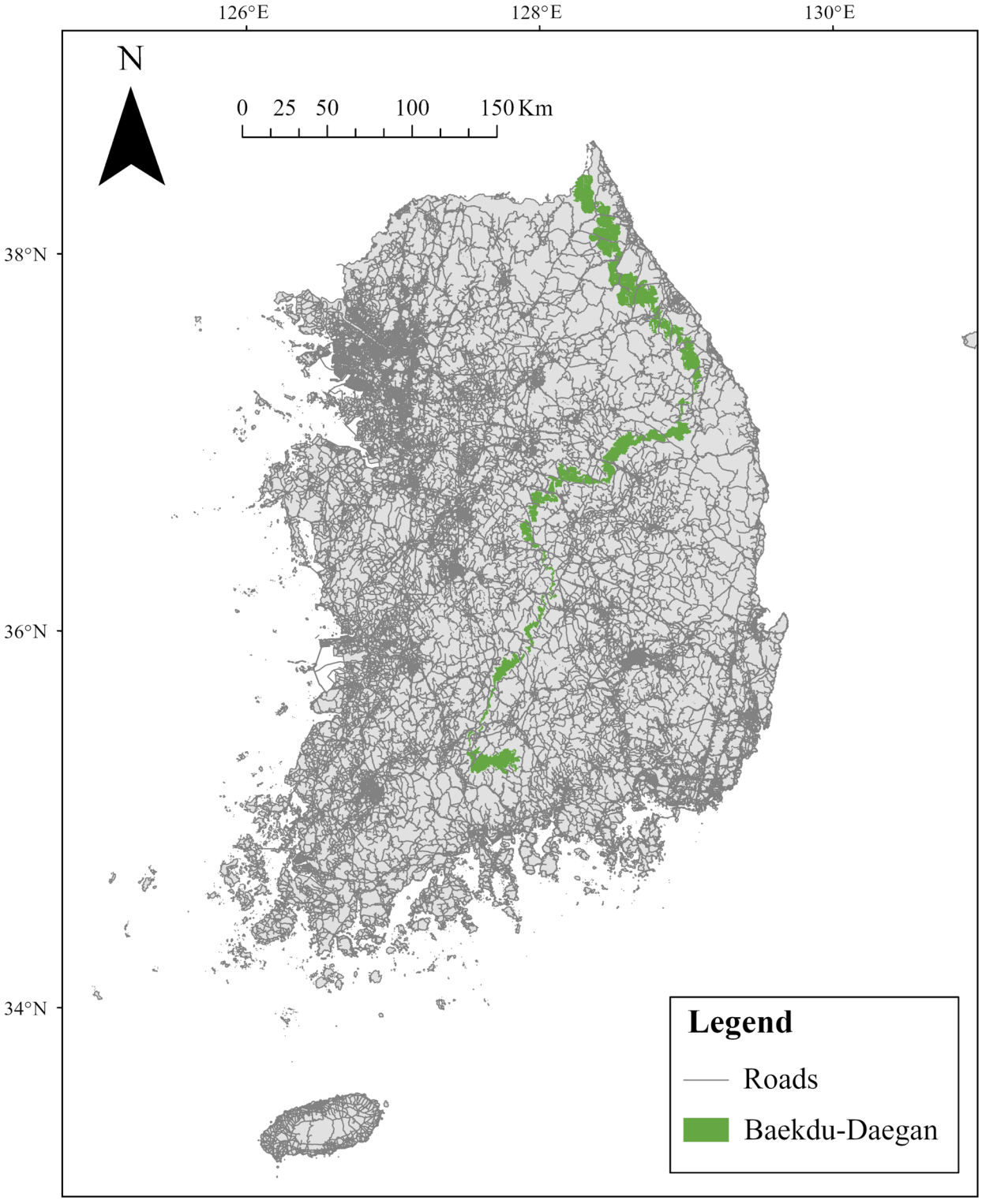


Fig. 5. The road networks of the Republic of Korea presented in grey lines. All road types were combined into a single layer to assess overall fragmentation patterns across the country. The Baekdu-Daegan mountain ranges are indicated in green. Clusters of roads indicate cities.

Analyses

Impact of patch size and patch connectivity on species richness

We first generated patches that could be utilized by mammalian species with minimal disturbance from roads to evaluate the effects of habitat fragmentation on species richness based on patch size and connectivity. Based on a study that reviewed 282 publications, the road impact beyond 1 km from roads was minimal[21]; thus, this

threshold was used to define areas free from road disturbance. Areas within 1 km of roads were excluded, and the resulting patch layer was used to calculate the patch size (km^2) and species richness by counting the number of species present in each patch. Patches were interpreted as potential habitats where wildlife can persist without direct road influence. Because the objective of this study was to evaluate road-induced habitat fragmentation rather than specific habitat types, all land-cover categories were included when delineating patches. Highly urbanized regions were mostly removed during the 1 km buffering process, leaving little remaining area. This approach ensured that the identified patches represent structurally undisturbed spaces that reflect the actual distributional context of mammals across the Republic of Korea. Spatial data on road networks throughout the country were obtained from the National Transport Information Centre (its.go.kr).

We assessed the patch connectivity using a graph-based modeling approach[60]. In graph theory, a landscape is represented as a set of habitat patches (nodes) connected by links representing the potential movement or flow between them. We used the patch layer derived from areas beyond the road impact zone as nodes and constructed a graph using Graphab 2.6.4 software[61]. Patch connectivity was evaluated using the flux (F) metric, which calculates the sum of the capacities of nonfocal patches weighted by their distance from the focal patch. This metric reflects the potential for species dispersal either to or from a focal patch, considering both the size of neighboring patches and their spatial proximity[61–63]. We constructed a landscape graph based on Euclidean distances between habitat patches without applying assumptions about maximum dispersal distances to evaluate structural connectivity rather than species-specific functional connectivity. This approach allowed the analysis to focus on the overall spatial organization of habitat patches at a national scale[60,62].

We then tested the relationship between species richness and patch characteristics using ZIGLM because a large proportion of habitat patches exhibited no recorded mammalian species, resulting in excess zeros that violated standard Poisson assumptions. All variables were log-transformed prior to the analysis to improve normality. Before the statistical analyses, we calculated the VIF to assess the potential multicollinearity between patch size and patch connectivity. In addition, we fitted a log–log linear regression model between the number of species and patch size to evaluate the SAR. Patches with zero species were excluded to allow comparisons with previous studies that assumed the presence of a species. In addition to the area-based relationship, we examined the relationship between patch connectivity and species richness using the same log–log approach. This enabled comparing the relative influences of patch size and connectivity on mammalian diversity patterns.

We generated a contour plot using patch size and connectivity on mammalian species richness, both log-transformed as $\log(x+1)$ to accommodate zero values and improve interpretability and to assess their interactive effects. This plot visualized species richness across the joint gradient of patch size and connectivity and was used to identify the structural conditions under which high richness occurred. To identify potential patterns of species richness, we examined the contour plot depicting the joint gradient of patch size and connectivity. Patches located in regions of high connectivity were then further analyzed to determine whether their richness exceeded structural expectations. Based on this observation, habitat patches in high-connectivity areas were examined to identify those whose richness exceeded expectations given their structural attributes, and determine whether additional landscape factors could explain such deviations. We first fitted a second-degree polynomial regression model, which accurately estimated structural expectations, using the log-transformed patch area and connectivity as predictors, with species richness as the response variable. Residuals were calculated as the difference between the observed and predicted richness. Patches with residuals greater than two standard deviations above the mean were classified as high-residual outliers and defined as high-richness patches. This threshold was selected to identify meaningful outliers that deviated from the expected richness based on the structural attributes alone[64,65]. Comparison patches were selected for each high-richness patch using nearest-neighbor matching in the log-transformed predictor space to enable comparison. Euclidean distance was used to ensure structural similarity in terms of patch size and connectivity, whereas species richness differed across groups.

We extracted the proportions of eight land-cover types (urban area, agriculture, forest, barren, grassland, shrub, wetland, and water) from the World Land Cover 30 m BaseVue 2013 to assess whether differences in landscape composition could explain this variation in richness. All land-cover variables were transformed into square roots to meet the linearity assumptions. Prior to model fitting, multicollinearity among the transformed land-cover variables was assessed using VIF. Then, a stepwise backward logistic regression was conducted using the transformed land-cover variables to identify those that best discriminated between the high-richness and comparison patches.

Species richness with distance to roads

We created three concentric buffer zones (0–1, 1–2, and 2–3 km away from all roads) to understand how mammalian species richness varies with road proximity. Each buffer was ring-shaped with a 1-km interval from the adjacent buffer. The 1 km threshold was adopted based on previous studies showing that the influence of roads on mammal communities typically declines sharply beyond approximately this distance[21]. In this study, the threshold served as an empirical reference to define structurally less disturbed patches and to examine gradients of richness within the ecologically relevant range of road influence. In the buffer analysis, residential areas and water bodies were excluded to focus on land that functions as a suitable habitat for terrestrial mammals, unlike the patch-based analysis, which included all land-cover types for structural assessment at a national landscape scale. The remaining natural areas within each buffer were used as spatial units for analysis. We calculated the species richness within each of the three distance-based buffer zones by counting the number of mammalian species observed. The number of species in each zone was divided by the unit area (km^2) to enable a standardized comparison. We applied the Kruskal–Wallis test to evaluate whether road proximity had a statistically significant effect on mammalian species richness, followed by a post hoc Wilcoxon rank-sum test. All statistical analyses were performed using R version 4.2.1, and IBM SPSS Statistics 21.

Data availability

The species occurrence data used in this study were obtained from publicly accessible databases. The GBIF dataset was downloaded as a DOI-referenced occurrence record (GBIF.org, accessed on 11 December 2022): https://doi.org/10.15468/dl.cxkn7h In addition, occurrence records from the National Ecosystem Survey were accessed through the Ecobank platform operated by the National Institute of Ecology, with the following dataset DOIs: 4th National Ecosystem Survey: https://doi.org/10.22756/NES.20240000000892 3rd National Ecosystem Survey: https://doi.org/10.22756/NES.20240000000891 2nd National Ecosystem Survey: https://doi.org/10.22756/NES.20240000000890

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Author contributions

Material preparation, data collection, and analyses were performed by Kim Kyungmin Kim. Kiyoon Kim contributed to the interpretation of the results and the development of the discussion section. Amaël Borzée provided critical feedback on the manuscript and contributed to manuscript revision. Yikweon Jang supervised the project and contributed to manuscript revision and editing. All the authors have read and approved the final version of the manuscript.

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Declarations

Competing interests

The authors declare no competing interests.

Additional information

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