



Ecological structures and terrestrial insect diversity across successional stages in abandoned paddy fields

Jaeyeon Kim ^a, Seungwoo Han ^b, Jiweon Yun ^a, Seunghyeon Lee ^a, Youngkeun Song ^{c,*}

^a Interdisciplinary Program in Landscape Architecture, Transdisciplinary Program in Smart City Global Convergence, Seoul National University, Gwanak-ro, Gwanak-gu, Seoul 08826, South Korea

^b Interdisciplinary Program in Landscape Architecture, Seoul National University, Gwanak-ro, Gwanak-gu, Seoul 08826, South Korea

^c Department of Environmental Design, Graduate School of Environmental Studies, Transdisciplinary Program in Smart City Global Convergence, Seoul National University, Gwanak-ro, Gwanak-gu, Seoul 08826, South Korea

ARTICLE INFO

Keywords:

Agroecosystem
Remote-sensing
Arthropods
Management

ABSTRACT

Abandoned paddy fields (APFs) are increasing due to socio-economic changes, but their ecological characteristics across different spatial scales and taxonomic groups remain largely unexplored. Existing studies have primarily focused on single high-value sites or plant communities, limiting our understanding of broader biodiversity patterns and successional stages. This study aims to identify the successional stages of APFs using remote-sensing based ecological indicators and to analyze how these successional stages shape terrestrial insect diversity and community composition. Since APFs exhibit considerable heterogeneity depending on their vegetation structure and moisture conditions, systematic grouping of their successional stages is essential for understanding biodiversity patterns and informing targeted ecological management. The study was conducted in Gyeonggi Province, South Korea, encompassing 2269 sites across approximately 10,171 km², a region where agricultural areas are widely distributed while rapid urbanization is simultaneously occurring. Remote-sensing indices including NDVI, NDWI and Rao's Q diversity index, calculated from Sentinel-2 imagery, were used in principal component analysis and K-means clustering to delineate successional stages. Field surveys were conducted in May 2024 at nine sites representing three successional types. Terrestrial insects were quantitatively sampled using sweep nets. Diversity indices (Shannon and Dominance) were compared among succession stages using ANOVA and community composition was analyzed using NMDS and PERMANOVA. Based on remote-sensing data, principal component analysis and clustering grouped APFs into three ecological types: Cultivated field, Herbaceous-woody mixed APF and Woody-dominated APF. Significant differences in ecological structure were found among clusters (e.g., PC1: $F(2,2266) = 7224, p < 0.001$). Second, significant differences in terrestrial insect diversity were observed between some of the three identified successional types. Herbaceous-woody mixed APF exhibited the highest Shannon index (3.38 ± 0.16), while Cultivated field showed the lowest ($2.58 \pm 0.44, p = 0.02$). The Dominance index was lowest in Herbaceous-woody mixed APF (0.17 ± 0.01) and highest in Cultivated field ($0.34 \pm 0.07, p = 0.01$). NMDS and PERMANOVA ($R^2 = 0.49, p = 0.004$) revealed distinct insect assemblages among successional stages. Cultivated fields were characterized by a higher abundance of Hemiptera and Orthoptera, including pest-associated species, whereas woody-dominated APFs showed greater occurrence of Lepidoptera and Hymenoptera. Herbaceous-woody mixed APFs were strongly associated with predatory taxa such as Mantodea and Odonata, reflecting structurally diverse and moisture-rich environments. These results confirm the feasibility of using remote-sensing to differentiate ecological structures of APFs and show that successional stages significantly shape terrestrial insect biodiversity.

1. Introduction

Agricultural land abandonment is accelerating worldwide

(Macdonald et al., 2000, Serra et al., 2008, García-Ruiz and Lana-Renault, 2011) and presents significant implications for land use, landscapes, biodiversity and ecosystems (Kates et al., 2001, Gellrich

* Corresponding author.

E-mail address: songyoung@snu.ac.kr (Y. Song).

<https://doi.org/10.1016/j.agee.2025.110172>

Received 25 June 2025; Received in revised form 1 December 2025; Accepted 11 December 2025

Available online 17 December 2025

0167-8809/© 2025 Elsevier B.V. All rights are reserved, including those for text and data mining, AI training, and similar technologies.

et al., 2007) Although this abandonment often leads to positive ecological outcomes (Sileika et al., 2006, Orłowski, 2005, Rey Benayas et al., 2007, Plieninger et al., 2014), it necessitates thorough ecological understanding. Among abandoned lands, ‘Abandoned paddy fields (APFs)’ are particularly notable examples of areas undergoing unique secondary succession. This process, driven by vegetation, transforms fields into diverse ecosystems ranging from herbaceous grasslands to woodlands (Lee et al., 2002, Yamada et al., 2013, Tokuoka and Nakagoshi, 2017). As vegetation height and density increase, APFs provide valuable feeding and resting areas for wildlife (Comín et al., 2001) and integrate with surrounding natural ecosystems, ultimately enhancing biodiversity (Orłowski, 2005, Ho et al., 2008, Plieninger et al., 2014, Park et al., 2015). Understanding the biodiversity and ecological structure of APFs is essential, requiring studies that consider different spatial scales and taxonomic groups.

Despite the reported changes in biodiversity across APF succession, most studies have focused on single, high-value sites or concentrated on plant taxa, limiting the generality of findings at the landscape scale. This is a critical issue in rapidly changing landscapes, such as the metropolitan area of South Korea, where rural decline and demographic aging are accelerating agricultural land abandonment (Lee and Choi, 2022). Specifically, in Gyeonggi Province (area of 10,171 km²), where abandonment is most pronounced, identifying the distribution and ecological characteristics of APFs solely through traditional, resource-intensive field surveys is impractical and time-consuming. To overcome these limitations, remote-sensing has emerged as a crucial complementary approach (Petrou et al., 2015). Previous research has used remote-sensing to monitor surface conditions or distinguish abandoned fields from cultivated ones, utilizing indices like NDVI (Normalized Difference Vegetation Index) and NDWI (Normalized Difference Water Index), which reflect vegetation conditions (Alcantara et al., 2012, Löw et al., 2015, Yoon and Kim, 2020, Lee et al., 2020). However, studies that identify and classify APFs based on their secondary succession stages using remote-sensing remain rare.

To fully characterize biodiversity patterns, it is vital to verify remote-sensing based classifications using field-based species occurrence data. While past studies on APF biodiversity primarily focused on vegetation, often considered the main indicator of successional progression (Shimoda, 1996, Lee et al., 2002, Yamada et al., 2007), there is a significant need for research focusing on faunal taxa. Vegetation is not only valuable intrinsically but also fundamentally structures ecosystems by providing essential resources like food and shelter (García et al., 2011). For instance, it is a key determinant of small arthropod distribution (Gunnarsson, 1990, Brose, 2003) and habitat complexity significantly influences invertebrate communities, such as spiders (Greenstone, 1984, Landsman and Bowman, 2017, Baba et al., 2019).

This study, therefore, focuses on terrestrial insects to analyze the ecological structure of APFs. Insects represent one of the most hyper-diverse taxa globally (Stork, 2018) and play crucial ecological roles, including their contributions to key functions in agricultural systems such as nutrient cycling and pest control (Yang and Gratton, 2014, Jankielsohn, 2018). Terrestrial insects are widely recognized as bio-indicators due to their sensitivity to environmental changes (Gerlach et al., 2013) and their community composition is strongly influenced by vegetation structure and habitat complexity (Bonari et al., 2017). Consequently, terrestrial insects are expected to respond sensitively to the vegetation structure and environmental changes that occur during APF secondary succession, making them a promising indicator taxon for characterizing successional stages.

Against this background, this study aims to classify APFs into successional stages at a broad spatial scale using remote-sensing data and investigate the relationship between biodiversity and ecological structure across these stages, with a focus on terrestrial insects. Field-level analyses were conducted on the categorized successional types to examine insect diversity and community composition.

The two main questions addressed in this study are as follows: (1) If

numerous abandoned paddy fields distributed across a broad region are classified based on vegetation changes detected through remote-sensing, how can their successional stages be characterized? (2) How are the patterns of species diversity and community composition of terrestrial insects structured across the successional stages of abandoned paddy fields?

To address these questions, we designed a remote-sensing-based classification of APF successional stages with field validation. Ultimately, this study aims to identify the successional stages of APFs using remote-sensing and to examine how these stages are related to both terrestrial insect biodiversity and the underlying ecological structure of the fields. We hypothesize that APFs undergo distinct vegetation-driven ecological changes during succession, which can be captured through remotely sensed indicators and used to differentiate their successional stages. Additionally, since terrestrial insect communities are known to be highly influenced by vegetation structure and habitat complexity, we hypothesize that species diversity and occurrence patterns of terrestrial insects will differ across successional stages.

2. Materials and methods

2.1. Study area and study sites

The study area is Gyeonggi Province in the midwestern part of the Korean Peninsula, surrounding the capital of South Korea (Fig. 1a, b). It covers approximately 10,171 km², about 10 % of South Korea’s total land area. The agricultural land area in Gyeonggi Province is approximately 1475 km² (Korea, 2024), making it the second-largest land cover type within the province. A total of 2269 sites were utilized for this study, including 1205 APF polygons and 1064 cultivated paddy field polygons. APFs were defined as areas that had been identified as ‘paddy fields’ at any point between 2000 and 2018 but remained uncultivated without the resumption of farming and subsequently transitioned into non-crop vegetated land cover types by 2022.

The identification of APFs was conducted using the thematic ‘Land Cover Map’ provided by the Korean Ministry of Environment, utilizing datasets from four time points: 2000, 2013, 2018 and 2022. As of 2022, approximately 3.49 % of the paddy fields recorded in 2000 had transitioned into APFs. These areas were found to have changed into inland wetlands, natural barren lands, natural grasslands, coniferous forests, mixed forests, or broadleaf forests. Based on land cover classifications, sites that had been converted from paddy fields into urbanized dry lands or artificial land uses—such as golf courses, lawns, cemeteries and park grasslands—were excluded from the study. For comparative analysis, cultivated paddy fields were also included. A total of 1064 cultivated paddy field polygons, including both ‘unleveled’ and ‘leveled’ types, were randomly selected based on attribute data from the 2022 Land Cover Map of Gyeonggi Province using QGIS (version 3.32.3).

2.2. Classification of APFs by secondary succession stages and ecological structure characteristics

2.2.1. Secondary successional patterns in APFs

APFs undergo secondary succession, leading to the formation of wet grasslands (Hakoyama et al., 1977, Matumura et al., 1988, Ohkuro et al., 1996, Comín et al., 2001, Yamada et al., 2007) and eventually wet woodlands (Hayakawa and Takahata, 1975, Shimoda, 1996, Lee et al., 2002). This process begins with the disappearance of crop (*Oryza sativa* L.), triggering a vegetation shift. In the initial stages, herbaceous species such as *Persicaria thunbergii*, *Juncus effusus* var. *decipiens*, *Alopecurus aequalis* var. *amurensis* and *Aneilema keisak* dominate, forming wet grasslands. Over time, woody species like *Salix koriyanagi* or *Salix korensis* grow alongside herbaceous vegetation, creating a transitional habitat between wet grasslands and woodlands. If abandonment continues, species composition gradually shifts toward woody species, eventually forming woodlands dominated by *Salix korensis* or *Alnus*

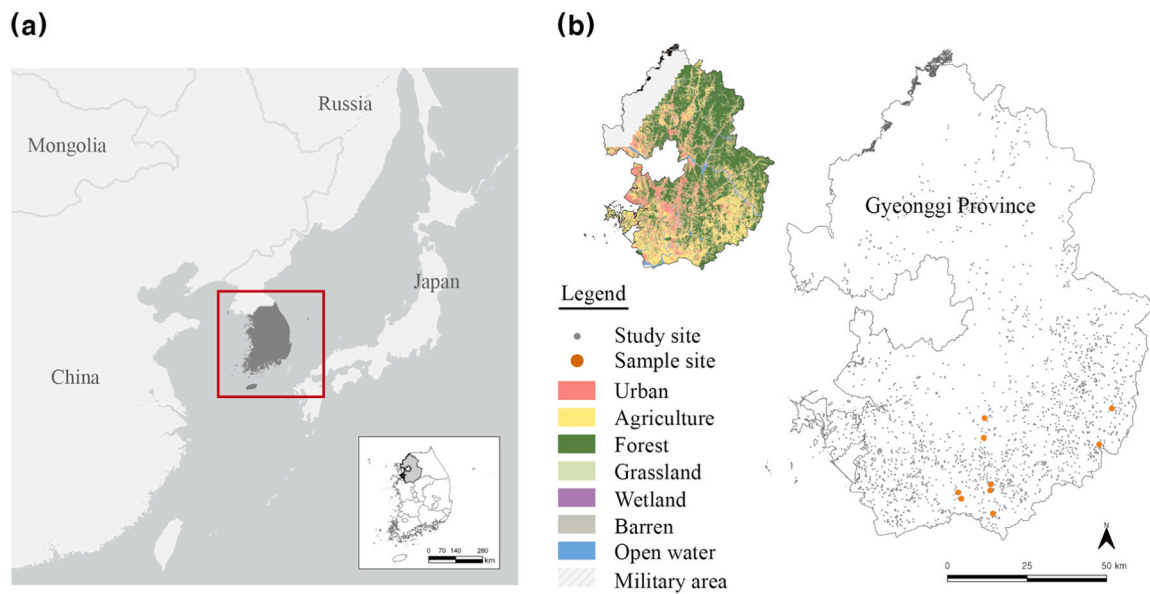


Fig. 1. (a) Locator map showing the position of South Korea in East Asia (red box) and the location of Gyeonggi Province within Korea (bottom right box). (b) Land cover map of Gyeonggi Province (top left) and the map showing the distribution of study sites. Gray dots indicate the study sites, which include both APFs and cultivated paddy fields. Orange dots denote the sampling sites where field surveys were conducted.

japonica (Fig. 2) (Lee et al., 2002, Lim et al., 2022).

However, vegetation succession in APFs does not always follow a uniform trajectory. Complex ecological processes may hinder succession, preventing the transition to woody dominated stage (Tokuoka and Nakagoshi, 2017). Key factors such as soil moisture content (Hakoyama et al., 1977) and the seed bank of surrounding vegetation (Shimoda, 1996, Robinson and Handel, 2000) significantly influence the process. Soil moisture typically increases immediately after abandonment but gradually decreases as succession progresses (Lee et al., 2022). Even after prolonged abandonment, vegetation may fail to develop into the woodland stage if woody plant seeds from the surrounding environment do not reach the site or if species like *Pueraria lobata* are dominant (Baba et al., 2019).

In summary, the key drivers of secondary succession in APFs include not only the length of abandonment but also internal vegetation, soil moisture content and the seed bank of surrounding vegetation. Depending on these factors, APFs transition from wet grasslands to environments where *Salix* spp. coexists, eventually forming wet

woodlands.

2.2.2. Independent variables

As investigated in the earlier studies reviewed above APF succession is influenced by vegetation, soil moisture, seed banks from surrounding vegetation and abandonment duration. These factors drive transitions from wet grasslands to woodlands (Yabe and Numata, 1984, Duelli, 1997, Lee et al., 2002). Based on prior studies and in consideration of large-scale spatial coverage and the applicability of remote-sensing data, eight independent variables were selected to analyze ecological structures in the study sites (Table 1).

To identify the successional stages of APFs and quantify their characteristics at a broad spatial scale using remote-sensing, we explicitly targeted three ecological properties that vary along the successional trajectory: vegetation vigor, soil moisture, and spatial heterogeneity. These properties track transitions from herbaceous to woody vegetation, terrestrialization-driven changes in moisture and increasing canopy complexity. We operationalized these properties with three remote-

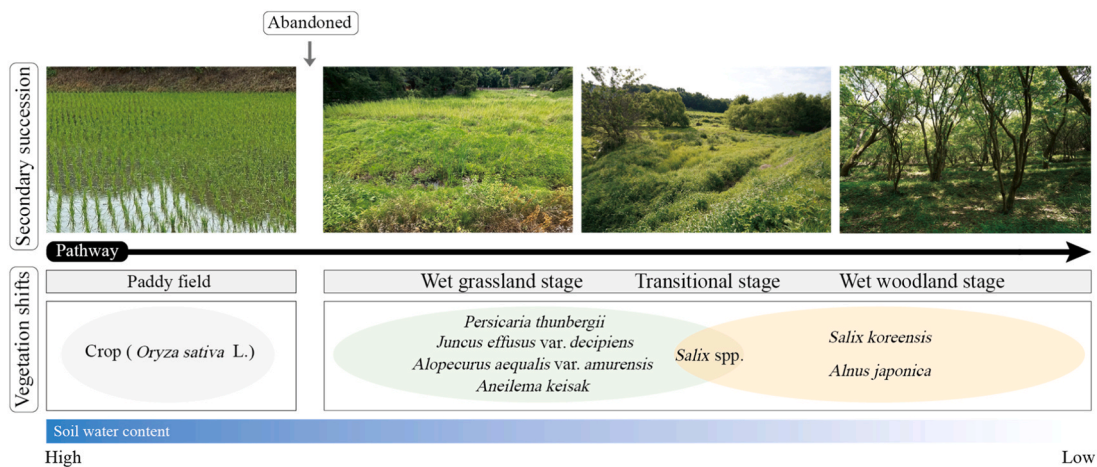


Fig. 2. A diagram illustrating the secondary succession process and stages of APFs. When paddy fields are abandoned, they transition into wet grasslands (Comin et al., 2001; Hakoyama et al., 1977; Matumura et al., 1988; Ohkuro et al., 1996; Yamada et al., 2007). As woody plants grow, a transitional habitat stage forms, eventually developing into the wet woodland stage (Hayakawa and Takahata, 1975; Lee et al., 2002; Shimoda, 1996).

Table 1

Eight independent variables for distinguishing the ecological structural characteristics of secondary succession in the study sites. ¹Seasonal windows: annual = Mar–Oct, spring = Mar–May.

Factor	Metric (code)	What it captures
Vegetation vigor	NDVI_mean, SpNDVI_mean	Mean NDVI (annual ¹ , spring ¹)
Structural heterogeneity	RaoQ_mean, SpRaoQ_mean	Mean Rao's Q from NDVI (annual ¹ , spring ¹)
Moisture status	NDWI_mean	Mean NDWI (spring ¹)
Seed source proximity	Forest_dist	Euclidean distance (centroid → nearest forest) (meter)
Patch size	Area	Polygon area (square meter)
Abandonment duration	Age	Years since cultivation ceased

sensing indices (Table 2) and detail below the rationale and computation for each.

NDVI measures photosynthetic vigor, with higher values indicating greater photosynthetic activity and biomass (Bannari et al., 1995, Xue and Su, 2017). Since woody plants typically have larger leaf area and higher chlorophyll content than herbaceous plants, NDVI values tend to be higher in woody-dominated vegetation (Cristiano et al., 2014, Gamon et al., 1995). These properties make NDVI suitable for identifying changes in vegetation composition during secondary succession (Caughlin et al., 2021). Given that APF successional stages also include grassland dominated by herbaceous plants and woodland dominated by woody plants, NDVI was deemed appropriate for this study. NDVI was calculated using Sentinel-2 MSI imagery (10 m resolution), selecting cloud-free scenes (<5 % cloud cover) from the spring (March–May) and the full growing season (March–October) via Google Earth Engine (Gorelick et al., 2017).

NDWI quantifies vegetation water content and is more sensitive to canopy moisture than NDVI (Gao, 1996, Xiao et al., 2002). In particular, NDWI is a key index for detecting the presence of moisture and terrestrialization in wetland ecosystems (Finger Higgins et al., 2019, Pastick et al., 2019). APFs have been reported to transition from wet to drier conditions during succession (Lee et al., 2002) and species composition patterns in seed banks also suggest a shift away from moisture-dependent species (Yamada et al., 2013). NDWI is considered suitable for differentiating successional stages. NDWI was calculated for the spring season (March–May), when moisture contrast is most pronounced, using Sentinel-2 MSI imagery (10 m resolution) and cloud-free scenes (<5 % cloud cover) via Google Earth Engine (Gorelick et al., 2017).

Rao's Q diversity index differs from the Shannon index (H'), which only considers class proportions, in that it integrates both the relative frequency and dissimilarity of spectral values between pixels, enabling a more sensitive detection of spatial heterogeneity (Rocchini and Neteler,

Table 2

Indices used in the study and their descriptions about formulas.

Indices	Formulas	Descriptions
NDVI	$NDVI = \frac{NIR - Red}{NIR + Red}$	NIR (Near-Infrared): Strongly reflected by healthy vegetation. Red: Absorbed by chlorophyll in plants.
NDWI	$NDWI = \frac{NIR - SWIR}{NIR + SWIR}$	NIR (Near-Infrared): Reflected by vegetation and soil. SWIR (Shortwave Infrared): Absorbed by water, making it useful for detecting moisture.
Rao's Q diversity index	$Qrs = \sum_{i,j=1}^N d_{ij} \times p_i \times p_j$	Qrs = Rao's Q applied to remote-sensing data pi = pj = 1/N = relative abundance of pixel i, j in a selected area composed of N pixels (buffer areas) dij = spectral (distance/dissimilarity) between pixel i and j (dij = dji and dii = 0)

2012, Rocchini et al., 2017). This index is particularly useful for detecting structural diversity in transitional habitats where herbaceous and woody plants coexist (Rocchini et al., 2017, Perrone et al., 2023). As the vegetation structure of APFs varies by successional stage and often features a mosaic of herbaceous and woody plants (Lee et al., 2002, Lim et al., 2022), Rao's Q diversity index is well-suited to identifying such ecological variation. Rao's Q diversity index was calculated in QGIS 3.32.3 using NDVI raster values as input. In this process, the Rao's Q Diversity Index algorithm from the SAGA GIS toolbox integrated within QGIS was employed (Conrad et al., 2015).

Successional patterns in APFs are also shaped by proximity to woody vegetation and habitat size. Forest edges function as seed sources and habitat area influences edge effects and species inflow. Therefore, two additional variables were included: distance to forest and patch area. Distance from forests was measured as the Euclidean distance from the polygon centroid to the nearest forest polygon using QGIS (3.32.3) and patch area was calculated based on land cover maps. Forests provide propagule sources for species such as *Salix* spp. and *Alnus japonica* (Lee et al., 2002), while smaller habitat patches may experience stronger edge effects and reduced species recruitment (Horváth et al., 2002). In addition, abandonment duration was determined using annual land cover maps up to the year 2022.

2.2.3. Classification of APF successional types and ecological structure using PCA and clustering

Principal Component Analysis (PCA) and K-means clustering were performed using R (4.1.0) (R Core Team, 2021) on 2269 study sites, including paddy fields and APFs. PCA conducted with the R package 'stats' reduced correlations among independent variables and identified key variability for quantitative spatial analysis. The eight independent variables were standardized using the R package 'base' and Bartlett's test performed with the R package 'psych' confirmed data suitability. All variables were z-standardized and PCA was performed on the correlation matrix; loadings represent the Pearson correlation between each standardized variable and the PC score (range -1 to +1).

Based on Kaiser's Rule (eigenvalues >1), three principal components (PC1–PC3) were selected, explaining 74.08 % of the variance. A heatmap generated using the R package 'ggplot2' visualized loading values of each variable on the principal components, highlighting their influence. K-means clustering, implemented in the R package 'stats', identified secondary succession stages based on these components. The optimal number of clusters was determined using the Elbow Method, where the within-cluster sum of squares (WCSS) reduction plateaued beyond three clusters. Clusters were formed by iteratively updating centers and results were visualized in three dimensions using the R package 'plotly'.

To statistically assess whether the derived clusters reflect ecological differences across secondary succession stages, both multivariate and univariate statistical analyses were performed. To ensure the reliability of comparisons among principal components, outliers in PC1, PC2 and PC3 were independently removed based on the interquartile range (IQR) method. The analysis was based on a common subset of the data from which outliers had been independently removed using the IQR method for each component (n ≈ 2100). Additionally, analyses of variance (ANOVA) were performed for each principal component using the 'stats' package in R(4.1.0) and post hoc comparisons were carried out using the Tukey HSD function from the 'agricolae' package in R(4.1.0) to identify statistically significant pairwise differences. To assess loading stability and significance, we computed 95 % bootstrap confidence intervals (10,000 resamples) and aligned component signs to the reference PCA solution at each resample; loadings whose 95 % CI excluded 0 were considered significant. For interpretation, we prioritized loading magnitude, treating |loading| ≥ 0.40 as a substantively salient threshold.

Analyses employed the following R packages: 'stats' and 'base' (R Core Team, 2021), 'psych' (Revelle, 2020), 'ggplot2' (Wickham, 2011),

‘plotly’ (Sievert, 2020), ‘agricolae’ (Mendiburu, 2019). For bootstrap CI calculations and data handling, ‘purrr’ (Wickham and Henry, 2023), ‘tidyr’ (Wickham and Henry, 2020) and ‘tibble’ (Müller and Wickham, 2021).

2.3. Analysis of terrestrial insect characteristics based on the ecological structures of APFs

2.3.1. Field survey design and sampling protocol

To analyze terrestrial insect diversity across secondary succession stages, sampling sites were selected based on K-means clustering results (Fig. 1b). For each cluster, sites closest to the cluster center were prioritized and nine sites (three per cluster) were finalized after considering landowner access permissions and logistical constraints. Sampling was conducted on May 17 and 18, 2024. To minimize temporal confounding, all sites were surveyed within a two-day window and during a consistent daytime period (08:00–17:00). All surveys were rain-free and mean air temperature was 17–19 °C across sites. Terrestrial insects were collected using sweep nets (120 cm in length, 42 cm in diameter, 70 cm in depth). One “sweep” was defined as a single 180° arc at chest height through the vegetation while walking at an even pace (~1 m·s⁻¹); the same trained collector performed all sweeps to minimize observer effects. At each site, five sampling points were selected based on vegetation structure representative of the site’s successional stage. The five points were spaced ~10–30 m apart and placed ≥ 10 m inward from the outermost paddy bund trace to reduce edge effects. At each point, a 10 m linear transect was walked while performing ten consecutive sweep-net passes, yielding 50 sweeps in total (50 m of sampled vegetation) per site. This approach was intended to capture within-site variation in insect diversity. Collected specimens were preserved in 70 % ethanol and transported to the laboratory for identification. Taxonomic identification followed the 2023 National Species List provided by the National Institute of Biological Resources (NIBR). When genus-level identification was not possible, individuals exhibiting consistent external morphological differences were classified into distinct morphotypes.

2.3.2. Analyzing species diversity and dominance

To analyze whether the diversity of terrestrial insects in APFs varies across secondary succession stages, a Shannon index and Dominance index were applied based on the species list obtained from the collected samples (Table 3). The Shannon index evaluates the richness and evenness of species within a habitat, reflecting how well a particular habitat supports a variety of species (Shannon, 1948). The Dominance Index was used to determine whether a habitat favors certain terrestrial insect species by assessing the proportion of a specific species within a community. This index measures the degree to which one or a few species dominate the community, helping identify whether a habitat provides conditions advantageous to specific species or whether excessive dominance reduces overall species diversity (Mcnaughton, 1967).

Both the Shannon index and Dominance index were calculated using R(4.1.0) (R Core Team, 2021). To assess whether there are significant differences in biodiversity values across succession stages, an Analysis of Variance (ANOVA) was conducted using the ‘aov’ function in R(4.1.0) (R Core Team, 2021). When significant differences were identified

Table 3
Two indices used in the study and their descriptions about formulas.

Indices	Formulas	Descriptions
Shannon index (Shannon, 1948)	$H' = -\sum[(ni/N) * \ln(ni/N)]$	ni: i Number of individuals of Species N: Total Number of individuals
Dominance index (Mcnaughton, 1967)	$DI = (n1 + n2)/N$	n1, n2: 1, 2 Number of individuals Dominant Species N: Number of individuals in the sample

through ANOVA, a Tukey HSD post hoc test was performed using the ‘TukeyHSD’ function in R(4.1.0) (R Core Team, 2021) to determine which specific pairs of succession stages exhibited differences. Pairwise 95 % confidence intervals (95 % CIs) for mean differences were computed with ‘TukeyHSD’ function in R(4.1.0) and are reported in Supplementary Table S3. Compact letter displays used in figures were derived with ‘agricolae’ package (Mendiburu, 2019) in R(4.1.0) (R Core Team, 2021).

2.3.3. Analysis of occurrence patterns

The order level is known to effectively reflect changes in biological communities in response to environmental variations while reducing the complexity associated with species or family-level analyses (Gaston and Blackburn, 1995). In this study, Non-metric Multidimensional Scaling (NMDS) and Permutational Multivariate Analysis of Variance (PERMANOVA) were used to analyze the differences in the occurrence patterns of terrestrial insects across secondary succession stages at the order level. These methods were employed to identify the occurrence patterns of terrestrial insects that reflect the characteristics of secondary succession in APFs and to examine the differences in insect community structure between succession stages.

Both NMDS and PERMANOVA analyses were performed using the R package ‘vegan’ in R(4.1.0) (R Core Team, 2021). For NMDS, the ‘metaMDS’ function was used with the Bray-Curtis distance to calculate similarities and 100 random starting configurations were employed to find the optimal solution. For PERMANOVA, the ‘adonis2’ function was used, also based on the Bray-Curtis distance. To prevent rare species from distorting the analysis results, orders with fewer than three individuals in the dataset (e.g., Dermaptera, Raphidioptera) were excluded from the analysis. Additionally, to ensure that abundant insect orders did not disproportionately influence the results, the abundance data were transformed using log10(abundance + 1). Analyses employed the following R package: ‘vegan’ (Dixon, 2003).

3. Results

3.1. Classification of successional stages and ecological structure using PCA and K-means clustering

3.1.1. Principal component analysis

A heatmap (Fig. 3) summarizes the correlation structure (loadings)

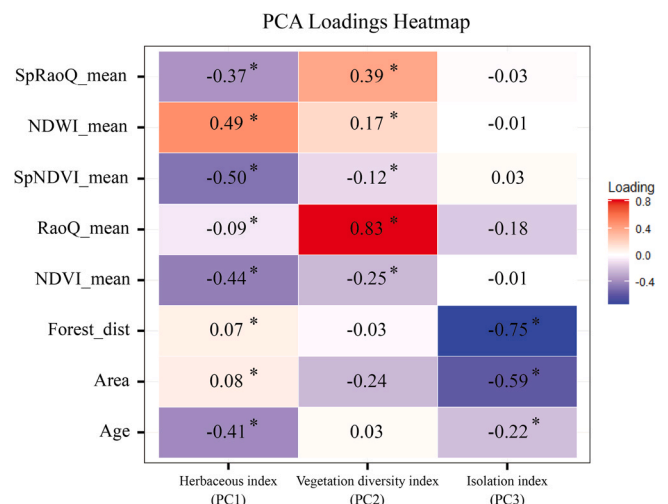


Fig. 3. Heatmap of PCA loadings (Pearson correlations between standardized variables and PC scores). Cells display loading values; asterisks denote statistically significant loadings. Positive correlations are shown in red and negative correlations in blue. Full confidence intervals are provided in Table S1 (Supplementary Material).

between the three principal components and the set of variables, enabling interpretation of ecological structure across successional stages. Asterisks denote statistically significant loadings. (full confidence intervals are provided in Table S1).

PC1 (Herbaceous index). The most pronounced negative loadings are SpNDVI_mean ($\approx -0.50^*$) and NDVI_mean ($\approx -0.44^*$), indicating reduced vegetation vigor in spring and during the growing season. NDWI_mean ($\approx +0.49^*$). shows a strong positive loading, consistent with higher spring moisture. Age (abandonment duration, $\approx -0.41^*$). also loads negatively, indicating that shorter abandonment is associated with higher PC1. Taken together, this pattern reflects conditions of high soil moisture and herbaceous dominance—i.e., cultivated fields or early wet-grassland APFs. Accordingly, higher PC1 scores are interpreted as wetter, herbaceous initial/cultivated stages.

PC2 (Vegetation diversity index). The strongest positive loading is RaoQ_mean ($\approx +0.83^*$) and the seasonal counterpart SpRaoQ_mean is also clearly positive. This indicates that PC2 increases with greater spatial heterogeneity, matching the characteristics of the herbaceous–woody mixed stage, where structural complexity is high. Thus, higher PC2 scores reflect greater vegetation structural heterogeneity and the co-occurrence of diverse microhabitats.

PC3 (Isolation index). Forest_dist, (distance to forest, $\approx -0.75^*$) and Area, (patch area ≈ -0.59). show significant negative loadings, so Lower PC3 scores correspond to smaller sites closer to forests. This is consistent with potential edge effects and seed-source accessibility. Conversely, higher PC3 scores indicate relatively isolated sites that are larger and farther from forests.

In summary, PC1 captures a moisture–herbaceous gradient linked to initial/cultivated stages, PC2 captures structural heterogeneity associated with herbaceous–woody mixing, and PC3 captures an isolation gradient driven by forest proximity and patch size. These component interpretations align with subsequent cluster comparisons (e.g., high PC1 in cultivated/wet grassland stages; high PC2 in transitional stages; low PC3 near-forest, small patches) and quantitatively support ecological differences among successional stages. (In Fig. 3, asterisks denote loadings whose 95 % bootstrap confidence interval excludes 0; full confidence intervals are provided in Table S1, Supplementary.)

3.1.2. Classification of APF successional stages via clustering

K-means clustering grouped the 2269 study sites into three successional clusters (BSS/TSS = 0.56; Fig. 4). MANOVA results indicated statistically significant multivariate differences among clusters based on Wilks' Lambda (Wilks' $\Lambda = 0.096$, approx. $F(6, 4190) = 1560.4$, $p < 0.001$). The Pillai's Trace test also confirmed significant differences (Pillai's Trace = 1.100, approx. $F(6, 4192) = 853.25$, $p < 0.001$).

Univariate ANOVAs with Tukey's HSD confirmed significant differences for all components (Fig. 5; Table S2). Cluster-wise means (μ) indicated the following ordering: PC1 (Herbaceous index) ranked $C1 > C3 > C2$; PC2 (Vegetation diversity index) ranked $C3 > C1 > C2$; PC3 (Isolation index) ranked $C1 > C3 > C2$. Full pairwise contrasts are provided in Table S2.

3.1.3. Ecological characteristics and successional stages of each clusters

Cluster 1 had the highest Herbaceous index (PC1) score (1.73), indicating dominance by herbaceous vegetation with low vegetation vigor. The Herbaceous index was negatively correlated with the vegetation index (SpNDVI_mean, -0.5) and the growing season vegetation index (NDVI_mean, -0.44) and positively correlated with the moisture index (NDWI_mean, $+0.49$), suggesting relatively high moisture content compared to other clusters. The Vegetation diversity index (PC2) score was relatively low (-0.20), indicating a lower Rao's Q diversity index (RaoQ_mean, $+0.83$) and a more uniform vegetation composition. The Isolation index (PC3) score was relatively high (0.03), reflecting greater values for variables negatively correlated with the Isolation index, such as distance from forests (Forest_dist, -0.75) and area (Area, -0.59). This suggests that Cluster 1 sites are generally farther from forests and cover larger areas. Based on these characteristics, Cluster 1 was interpreted as representing either cultivated fields or the early stage of secondary succession, classified as the wet grassland stage. However, aerial imagery and land cover map confirmed that most sites in Cluster 1 were 'Cultivated fields'.

Cluster 2 had the lowest Herbaceous index (PC1) score (-2.45), indicating high vegetation vigor and dominance by woody vegetation. The Herbaceous index was negatively correlated with the spring (SpNDVI_mean, -0.5) and growing season vegetation indices (NDVI_mean, -0.44), while positively correlated with the moisture index

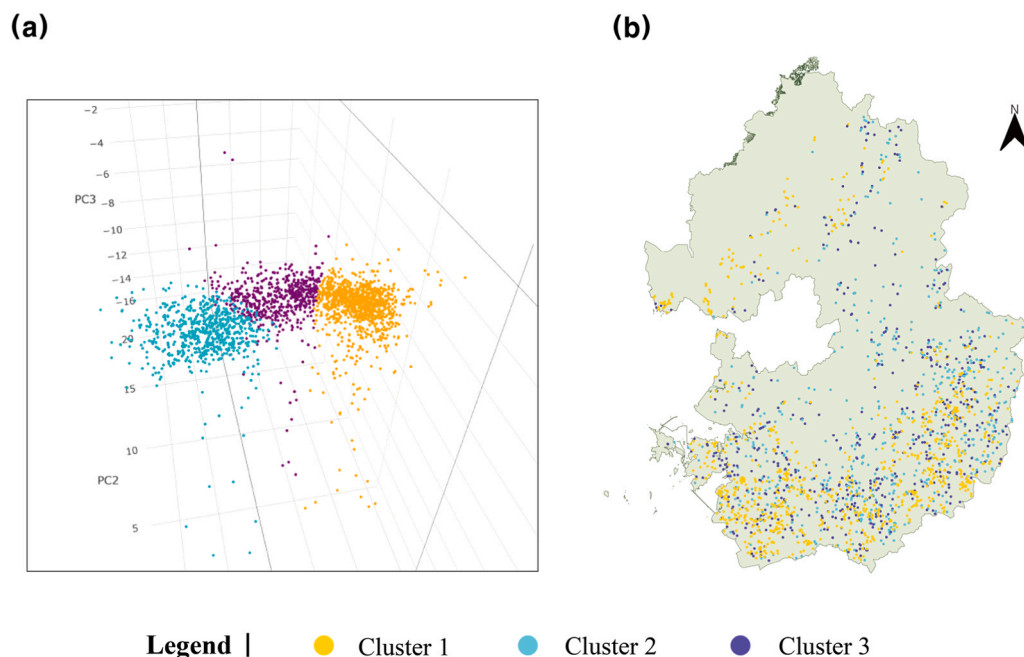


Fig. 4. (a) Visualization of the K-means clustering analysis. Each axis in the three-dimensional space represents one of the three principal components. Based on differences in cluster centroids, yellow, light blue and purple represent Cluster 1, Cluster 2 and Cluster 3. (b) A successional stage map of the entire Gyeonggi Province.

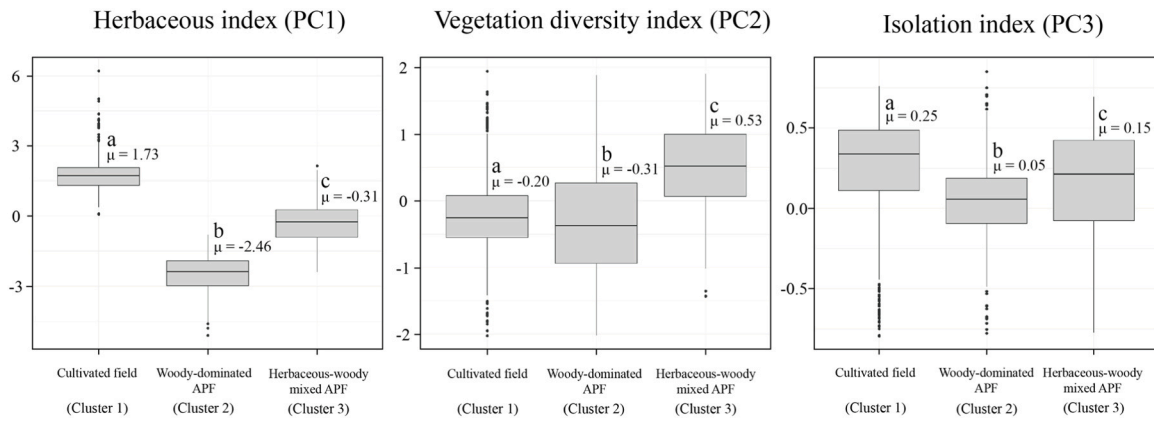


Fig. 5. Boxplots showing the distribution of three principal components across successional types—Cultivated field (Cluster 1), Woody-dominated APF (Cluster 2) and Herbaceous-woody mixed APF (Cluster 3). Each vertical axis represents the standardized principal component scores derived from the PCA. The central horizontal line within each box indicates the median, while the upper and lower bounds correspond to the first and third quartiles, respectively. Whiskers extend to 1.5 times the interquartile range (IQR) and data points beyond this range are plotted as outliers. Letters above boxes denote Tukey HSD groupings (identical letters indicate no significant difference at $\alpha=0.05$) and annotated values (μ) indicate means. One-way ANOVA detected significant among-group differences for all PCs; full pairwise post-hoc results are provided in [Table S2 \(Supplementary Material\)](#).

(NDWI_mean, +0.49), suggesting that Cluster 2 sites had lower moisture levels than other clusters. The Vegetation diversity index (PC2) score was the lowest (-0.28), corresponding to a lower Rao’s Q diversity index (RaoQ_mean, +0.83), indicating relatively uniform vegetation. Cluster 2 was the only cluster with a negative Isolation index (PC3) score (-0.07), reflecting smaller values for variables negatively correlated with the Isolation index, such as distance from forests (Forest_dist, -0.75) and area (Area, -0.59). These findings suggest that Cluster 2 sites are closer to forests and have smaller areas than the other clusters. Based on these characteristics, Cluster 2 was interpreted as ‘Woody-dominated APF’, corresponding to the wet woodland stage.

Cluster 3 had a Herbaceous index (PC1) score of -0.31, a mid-range value among the clusters. The Herbaceous index was negatively correlated with the spring (SpNDVI_mean, -0.5) and growing season vegetation indices (NDVI_mean, -0.44), while positively correlated with the moisture index (NDWI_mean, +0.49). This suggests that both vegetation and moisture indices were relatively high, possibly indicating conflicting trends and transitional characteristics. Cluster 3 had the highest

Vegetation diversity index (PC2) score (0.74), corresponding to a high Rao’s Q diversity index (RaoQ_mean, +0.83), indicating highly diverse vegetation. The Isolation index (PC3) score was relatively high (0.02), suggesting larger values for variables negatively correlated with this index, such as distance from forests (Forest_dist, -0.75) and area (Area, -0.59). This implies that Cluster 3 sites are farther from forests and cover larger areas. Based on these characteristics, Cluster 3 was interpreted as ‘Herbaceous-woody mixed APF’, representing the transitional stage of secondary succession.

3.2. Terrestrial insect characteristics across secondary succession stages in APFs

3.2.1. Species diversity and dominance

Significant differences among succession stages were observed in both the Diversity Index ($p = 0.03$) and Dominance Index ($p = 0.01$), as revealed by ANOVA ([Fig. 6](#)). Post hoc Tukey HSD tests indicated that Herbaceous-woody mixed APF had significantly higher species diversity

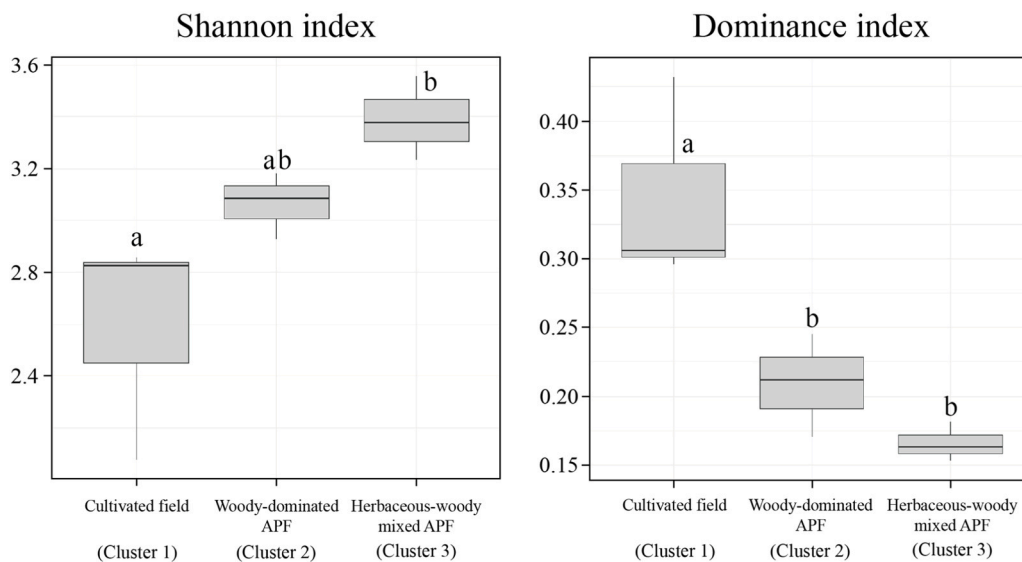


Fig. 6. Boxplots showing the distribution of species diversity(Shannon index) and species dominance (Dominance index) across the three clusters grouped by successional stage. The y-axis in each panel represents the observed index value, while the x-axis indicates cluster membership based on K-means clustering of abandoned paddy fields according to succession stages. The boxes represent the interquartile range (IQR), with the central line indicating the median. Letters above boxes (a, ab, b) denote Tukey HSD groupings; identical letters indicate no significant difference at $\alpha = 0.05$.

compared to Cultivated field ($p = 0.02$). In contrast, the Dominance index was significantly higher in Cultivated field than in Woody-dominated APF ($p = 0.03$) and Herbaceous-woody mixed APF ($p = 0.01$), while no significant difference was found between Woody-dominated APF and Herbaceous-woody mixed APF.

Among the three clusters, Herbaceous-woody mixed APF exhibited the highest species diversity whereas Cultivated field showed the lowest diversity and the highest dominance (Table 4). Woody-dominated APF presented intermediate values (Diversity index: 3.06 ± 0.12). These patterns are consistent with Tukey HSD 95 % CIs (significant contrasts exclude zero); full pairwise values are provided in Supplementary Table S3. A total of 157 species and 497 individuals were recorded across the nine study sites: 48 species (139 individuals) in Cultivated field, 59 species (131 individuals) in Woody-dominated APF and 85 species (227 individuals) in Herbaceous-woody mixed APF.

3.2.2. Occurrence patterns

A significant difference in terrestrial insect occurrence patterns across clusters was indicated by PERMANOVA results ($R^2 = 0.49$, $p = 0.004$), while NMDS analysis showed a stress value of 0.1 [indicating good ordination and interpretability; common guidelines: < 0.05 excellent, $0.05-0.10$ good, $0.10-0.20$ acceptable, > 0.20 poor]. Analyzing the Euclidean distance between cluster centroids and insect orders revealed both commonly abundant orders across all clusters and those with varying abundance among clusters (Table 5).

In Cultivated field, NMDS results showed the highest association with Hemiptera (distance = 0.18), Orthoptera (distance = 0.21) and Diptera (distance = 0.22). In terms of abundance, Diptera was the most dominant order (55 individuals, 39.5 %), followed by Hemiptera (33 individuals, 23.7 %) and Orthoptera (25 individuals, 17.9 %).

In Woody-dominated APF, NMDS results indicated the highest association with Hymenoptera (distance = 0.02) and a strong association with Lepidoptera (distance = 0.10), Diptera (distance = 0.13) and Coleoptera (distance = 0.17). Diptera was the most abundant order with 74 individuals (56.4 %), followed by Coleoptera (19 individuals, 14.5 %) and Hemiptera (18 individuals, 13.7 %) (Table 5). Odonata was represented by a single individual (0.7 %), while Mantodea was absent.

In Herbaceous-woody mixed APF, NMDS results showed the highest association with Hemiptera (distance = 0.10) and a strong association with Coleoptera (distance = 0.17), Diptera (distance = 0.23), Odonata (distance = 0.24) and Mantodea (distance = 0.36). Diptera was the most abundant order with 86 individuals (37.8 %), followed by Hemiptera (77 individuals, 33.9 %) and Coleoptera (23 individuals, 10.1 %). Rare orders such as Odonata (9 individuals, 3.9 %) and Mantodea (7 individuals, 3.0 %) were more frequently observed in this stage.

4. Discussion

4.1. Classification of APF types by successional stage using remote-sensing data

As abandonment persists, APFs exhibit various successional stages, each forming a unique ecological structure that positively influences biodiversity (Orłowski, 2005, Ho et al., 2008, Plieninger et al., 2014, Park et al., 2015). Increasingly, studies have demonstrated that remote-sensing data can aid in detecting and mapping abandoned paddy fields (Yoon and Kim, 2020, Lee et al., 2020, Löw et al., 2015). However,

Table 4

Mean diversity index and Dominance index values of terrestrial insects by succession stage. Values are presented as mean \pm standard deviation.

Stage	Diversity Index (H')	Dominance Index (DI)
Cultivated field	2.58 (± 0.44)	0.34 (± 0.07)
Woody-dominated APF	3.06 (± 0.12)	0.20 (± 0.03)
Herbaceous-woody mixed APF	3.38 (± 0.16)	0.16 (± 0.01)

Table 5

Euclidean distance, individual count and percentage of terrestrial insect orders across the three successional stages (Cultivated field, Woody-dominated APF, Herbaceous-woody mixed APF). Each cell presents values in the format: distance / count / percentage. Lower distance values indicate stronger association with a given stage. A dash(-) denotes orders excluded from NMDS analysis due to low occurrence.

Order	Cultivated field (Dist / Count / %)	Woody-dominated APF (Dist / Count / %)	Herbaceous-woody mixed APF (Dist / Count / %)
Diptera	0.22 / 55 / 39.5 %	0.13 / 74 / 56.4 %	0.23 / 86 / 37.8 %
Hemiptera	0.18 / 33 / 23.7 %	0.27 / 18 / 13.7 %	0.10 / 77 / 33.9 %
Orthoptera	0.21 / 25 / 17.9 %	0.54 / 1 / 0.7 %	0.41 / 13 / 5.7 %
Hymenoptera	0.31 / 11 / 7.9 %	0.02 / 13 / 9.9 %	0.33 / 7 / 3.0 %
Coleoptera	0.26 / 9 / 6.4 %	0.17 / 19 / 14.5 %	0.17 / 23 / 10.1 %
Odonata	0.46 / 3 / 2.1 %	0.59 / 1 / 0.7 %	0.24 / 9 / 3.9 %
Mantodea	0.55 / 1 / 0.7 %	0.71 / 0 / 0.0 %	0.36 / 7 / 3.0 %
Lepidoptera	0.27 / 1 / 0.7 %	0.10 / 4 / 3.0 %	0.37 / 4 / 1.7 %
Dermoptera	- / 1 / 0.7 %	- / 0 / 0.0 %	- / 1 / 0.4 %
Megaloptera	- / 0 / 0.0 %	- / 1 / 0.7 %	- / 0 / 0.0 %

few attempts have been made thus far to identify and classify distinct secondary successional stages within APFs using remote-sensing.

In this study, we first reviewed the literature to define the secondary successional stages in abandoned paddy fields. We then acquired remote-sensing data that could reflect these stages and applied it to identify and group distinct successional stages of abandoned paddy fields across the large area (10,171 km²). This provides ecological insights for managing abandoned paddy fields scattered across large areas. Our study demonstrates that data obtained through remote-sensing can be used to classify secondary successional stages of APFs by reflecting their ecological structures.

According to our clustering results, the successional stages of abandoned paddy fields in Gyeonggi Province were divided into three types, including currently cultivated fields. Each stage exhibited distinct ecological structures. Notably, differences in the herbaceous index and vegetation diversity index were observed between the woody-dominated APFs (Cluster 2), interpreted as the late wet woodland stage of secondary succession and the herbaceous-woody mixed APFs (Cluster 3), corresponding to a transitional stage. These differences align with findings from previous field-based studies on APF succession, which reported trends such as a decrease in herbaceous cover, reduction in moisture content and increase in woody plant cover during secondary succession (Lee et al., 2002; Lim et al., 2022).

4.2. Reasons for differences in species diversity and dominance across successional stages

In herbaceous-woody mixed APF, species diversity was significantly higher than in cultivated field (Shannon's H = 3.38 vs. 2.58; Table 4). This pattern is likely linked to greater habitat complexity (Rocchini et al., 2010). The coexistence of herbaceous and woody vegetation enhanced structural heterogeneity (Fig. S1, Supplementary Material), promoting a more even distribution of terrestrial insect species. In contrast, cultivated fields, dominated by herbaceous vegetation provided a simpler habitat structure with lower species diversity. The positive relationship between species diversity and the complexity of physical habitat structure is well-studied in spiders, which are closely related to terrestrial insects (Hatley and Macmahon, 1980, Greenstone, 1984, Diehl et al., 2013, Baba et al., 2019).

Cultivated fields also showed the highest dominance index (0.34), indicating that their uniform habitat structure favored a few dominant species (Fig. S1, Supplementary Material). Although woody-dominated APFs had vegetation diversity comparable to cultivated fields, their lower dominance likely reflected forest proximity, which facilitated species influx (edge effects) and reduced the prevalence of single dominant taxa (Fig. S1, Supplementary Material) (Horváth et al., 2002).

4.3. Ecological structure and terrestrial insect occurrence patterns across successional stages

Differences in the occurrence patterns of terrestrial insects were observed even among succession stages with no statistically significant differences in species diversity and dominance indices. Conversely, common terrestrial insect groups were identified across succession stages that exhibited significant statistical differences in these indices, as confirmed by the NMDS analysis (Fig. S2, Supplementary Material).

Hemiptera, Coleoptera and Diptera were the groups that showed strong associations across at least two different succession stages. These groups either included species that adapted to a wide range of habitats (Coleoptera, Diptera) or exhibited diverse feeding strategies from extreme carnivory to high specialization on specific host plants (Hemiptera) (Schaefer and Mitchell, 1983, Little et al., 2020). This adaptability and dietary flexibility likely enabled these insect groups to inhabit various succession stages with distinct ecological structures.

In cultivated field, Orthoptera displayed a notable association compared to other succession stages. Cultivated field was characterized by low NDVI and high NDWI, indicating low vegetation vigor and high soil moisture due to artificial irrigation.

These conditions likely provided a favorable environment for Orthoptera, particularly *Xya japonica* and *Tetrix japonica*, which prefer dense herbaceous vegetation and wetland habitats (Ahn and Park, 2012).

Most Hemiptera species found in cultivated fields belonged to Cicadellidae and Delphacidae, major agricultural pests known to rely on rice as a primary host plant and inhabit paddy fields and surrounding weeds (Kil, 1985).

The dominance of Poaceae plants, shaped by agricultural activities, likely facilitated the presence of Orthoptera and certain Hemiptera species in these fields was reflected in the simple vegetation structure with low Rao's Q diversity values, which likely facilitated the presence of Orthoptera and specific pest-associated Hemiptera species.

In woody-dominated APF, NDVI values were high (reflecting dense woody vegetation), but NDWI values were low, indicating reduced moisture conditions typical of late successional stages. This cluster also had low Rao's Q diversity values, indicating a relatively homogeneous canopy.

Under these structural conditions, Lepidoptera and Hymenoptera showed a strong association. These groups play ecologically significant roles in forest ecosystems, providing essential functions for ecosystem maintenance (Didham et al., 1996). Lepidoptera serve as long-distance foragers, facilitating pollen transfer, while certain Hymenoptera function as both pollinators and parasitoids.

Most of the Hymenopteran species belonged to Ichneumonidae, a family of parasitoid wasps that primarily target herbivorous insect larvae concealed within plant tissues (Gauld, 1988). The abundance of woody vegetation and proximity to external forests likely created favorable conditions for these parasitoid wasps.

Hemiptera showed the weakest association in woody-dominated APF. Predatory Hemiptera species (e.g., *Nabis apicalis* and *Gorpis brevilineatus*) were dominant, exploiting the vegetation structure for ambush predation (Evans, 1982).

Finally, Coleoptera also showed a strong association, particularly leaf-feeding Chrysomelidae (*Chrysomela vigintipunctata* on willows, *Agelastica coerulea* on alders as host plants). This pattern aligns with successional vegetation dominated by willows and alders (Lee et al.,

2002, Lim et al., 2022). The presence of leaf feeding beetles that specialize in these woody plants has also been reported in woodland stage APFs. For example 'Ungok Wetland' a designated Ramsar site in Gochang, South Korea, supports such species (Kim and Kim, 2013).

In herbaceous-woody mixed APFs, Odonata and Mantodea showed a strong association compared to other succession stages. These groups were rarely occurred in cultivated field or woody-dominated APF.

Herbaceous-woody mixed APF contained both herbaceous and woody plants, exhibiting high vegetation diversity. This spatial structure likely provided both food resources and a favorable physical environment for ambush and predation by terrestrial predatory insects such as mantises (Svenson and Whiting, 2004).

Moisture levels were higher in this successional stage than in woody-dominated APF. Field surveys confirmed the presence of numerous small ponds and consistently wet conditions in some areas. Similar findings have been reported in 'Mando Plain' within the Korean Demilitarized Zone (DMZ), which shares ecological characteristics with these fields and is known for its abundance of Odonata species (Ahn and Park, 2012). The wet environment likely favored species such as *Ischnura asiatica* and *Orthetrum albistylum*, which oviposit on aquatic plant stems or open water surfaces.

No predatory Hemiptera species were found in herbaceous-woody mixed APF. All observed Hemiptera species were herbivorous, likely due to the availability of diverse food sources provided by both herbaceous and woody plants. Notably, these fields contained agricultural pest species such as *Riptortus clavatus* and *Plautia stali*.

4.4. Implications for ecological management of abandoned paddy fields

The diversity and occurrence patterns of terrestrial insects differed between cultivated fields and APFs at two different successional stages. Herbaceous-woody mixed APF exhibited the highest diversity index and the lowest dominance index. This suggests that these APFs play a crucial role in maintaining terrestrial insect diversity and ecological functions in agricultural ecosystems through complex habitat structures.

However, the occurrence patterns indicate that herbaceous-woody mixed APFs were not only associated with predatory insects such as Mantodea and Odonata but also showed a strong association with Hemiptera, including major agricultural pests such as *Riptortus clavatus* and *Plautia stali*. While these fields may contribute to increasing overall biodiversity in agricultural ecosystems, they could also pose a risk of pest outbreaks in cultivated fields. Although this was not observed directly in APFs, studies conducted in some orchard systems have shown that abandoned farmlands can serve as a source habitat for pest species such as *Cydia pomonella*, continuously supporting their immigration into adjacent commercial orchards (Mazzi and Dorn, 2012). In such cases, even with regular insecticide applications in managed fields, reinvasion from unmanaged areas can sustain pest populations and cause ongoing damage. Therefore, as has been discussed in previous studies about paddy fields and APFs (Baba et al., 2019), similar precautions should be considered for paddy fields and APFs, where potential pest issues may arise and require careful landscape-level management.

This study also found that woody-dominated APFs were more strongly associated with Lepidoptera and Hymenoptera compared to other successional stages. Woody-dominated APFs were typically located close to forests, especially along forest edges. These edge environments are known to function similarly to natural forests, offering abundant food resources and reduced predation risk and are therefore preferred habitats for Lepidoptera and Hymenoptera (Bragança et al., 1998). Such woody-dominated APFs appear to serve as ecological stepping stones, linking open areas with closed forest habitats. These insect groups provide ecosystem services to humans through pollination. Their strong flight abilities allow them to move between woody-dominated APFs and cultivated fields, contributing to pollination. Additionally, most Hymenoptera species in these fields were parasitoid wasps that use herbivorous insects as hosts. These parasitoids

are expected to play a beneficial role in agricultural ecosystems by regulating herbivore populations (Didham et al., 1996). In fact, it is known that establishing APFs between rice fields is important for enhancing the pest control ecosystem service (Ali et al., 2023). Therefore, effective management of woody-dominated APFs near cultivated fields should be considered to maximize ecosystem services.

4.5. Limitations and future directions

This study has several limitations arising from the research design and the scope of data collection. First, field validation relied on a single sampling method. Sweep-netting efficiently captures taxa active in vegetation, but it may underrepresent ground-dwelling or nocturnal insects. To address this bias, multiple complementary methods such as pitfall traps and Malaise traps should be deployed in parallel. Second, Our field validation involved $n = 3$ sites per successional type, which may limit power to detect modest effects. ANOVA assumptions (normality, homoscedasticity) were checked via residual diagnostics; small- n deviations cannot be ruled out. In particular, several pairwise 95 % confidence intervals for comparisons between APF types were wide and included zero. Although family-wise error was controlled through Tukey's HSD, additional field studies are needed to narrow the confidence intervals and enhance the sensitivity to modest effects. Third, fieldwork was conducted at a single time point in mid-May 2024 and therefore did not fully encompass seasonal or interannual variability across sites. Given time and resource constraints, we sampled in mid-May to cover the emergence of arthropods across two seasons (spring and summer) but insect communities and APF successional signals may differ in autumn; long-term, repeated monitoring including the autumn period is warranted. Lastly, the classification of abandoned paddy fields in this study relied on spectral indices derived from Sentinel-2 imagery. This approach primarily reflects horizontal spectral variation and does not sufficiently capture vegetation vertical structure or stratified complexity. Future work that integrates high-resolution three-dimensional data, such as LiDAR, to retrieve vertical structural information would provide more refined insights into successional stages and biodiversity.

5. Conclusions

Together, our results show that remotely sensed ecological indicators can reliably classify abandoned paddy fields into ecologically meaningful successional types at landscape scale and that these structural differences predict terrestrial insect diversity and community composition. Across the landscape, APFs segregate along coupled gradients of moisture, vegetation vigor and structural heterogeneity that define clear successional stages, with structurally heterogeneous Herbaceous-woody mosaics supporting the richest and most even insect assemblages, consistent with the expectation that greater structural complexity increases niche availability in farmland insects (Martin et al., 2020). By integrating Sentinel-2-derived indices with PCA and k-means clustering, we provide an operational, scalable framework for mapping and monitoring APF succession using open remote-sensing data, which could be further strengthened by incorporating three-dimensional sensors such as LiDAR to better capture vertical vegetation structure. The resulting stage maps offer a practical decision-support tool: maintaining mosaics of Herbaceous-woody mixed APFs and strategically managing forest-adjacent, Woody-dominated APFs as stepping stones for pollinators and natural enemies can help maximize landscape-level insect diversity while informing integrated pest management at APF-field interfaces (Litovska et al., 2025). Overall, this study demonstrates that the ecological functioning of APF is strongly shaped by moisture gradients, structural heterogeneity, and forest adjacency. By showing that these key attributes can be consistently detected and managed at large spatial scales through a reproducible remote-sensing-based analytical framework, we provide a practical methodological bridge connecting

the diagnostic assessment of APF spatial patterns with biodiversity-informed land management.

Funding

This work was supported by Korea Environment Industry & Technology Institute(KEITI) through Technology Development Project for Creation and Management of Ecosystem based Carbon Sinks, funded by Korea Ministry of Climate, Energy and Environment(MCEE)(RS-2023-00218245)

This work is financially supported by Korea Ministry of Land, Infrastructure and Transport(MOLIT) as 「Innovative Talent Education Program for Smart City」.

CRedit authorship contribution statement

Jaeyeon Kim: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Jiweon Yun:** Writing – review & editing, Methodology, Formal analysis, Conceptualization. **Seunghyeon Lee:** Writing – review & editing, Formal analysis. **Youngkeun Song:** Writing – review & editing, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Seungwoo Han:** Writing – review & editing, Methodology, Investigation, Formal analysis.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.agee.2025.110172](https://doi.org/10.1016/j.agee.2025.110172).

Data availability

Data will be made available on request.

References

- Ahn, S.-J., Park, C.-G., 2012. Terrestrial insect fauna of the Junam wetlands area in Korea. *Korean J. Appl. Entomol.* 51, 111–129.
- Alcantara, C., Kuemmerle, T., Prishchepov, A.V., Radeloff, V.C., 2012. Mapping abandoned agriculture with multi-temporal MODIS satellite data. *Remote Sens. Environ.* 124, 334–347.
- Ali, M., Clemente-Orta, G., Kabir, M., Haque, S., Biswas, M., Landis, D.A., 2023. Landscape structure influences natural pest suppression in a rice agroecosystem. *Sci. Rep.* 13, 15726.
- Baba, Y.G., Tanaka, K., Kusumoto, Y., 2019. Changes in spider diversity and community structure along abandonment and vegetation succession in rice paddy ecosystems. *Ecol. Eng.* 127, 235–244.
- Bannari, A., Morin, D., Bonn, F., Huete, A., 1995. A review of vegetation indices. *Remote Sens. Rev.* 13, 95–120.
- Bonari, G., Fajmon, K., Malenovský, I., Zelený, D., Holuša, J., Jongepierová, I., Kocárek, P., Konvička, O., Uříčár, J., Chytrý, M., 2017. Management of semi-natural grasslands benefiting both plant and insect diversity: The importance of heterogeneity and tradition. *Agric. Ecosyst. Environ.* 246, 243–252.
- Bragança, M.A., Zanoncio, J., Picanço, M., Laranjeiro, A.J., 1998. Effects of environmental heterogeneity on Lepidoptera and Hymenoptera populations in Eucalyptus plantations in Brazil. *For. Ecol. Manag.* 103, 287–292.
- Brose, U., 2003. Bottom-up control of carabid beetle communities in early successional wetlands: mediated by vegetation structure or plant diversity? *Oecologia* 135, 407–413.
- Caughlin, T.T., Barber, C., Asner, G.P., Glenn, N.F., Bohlman, S.A., Wilson, C.H., 2021. Monitoring tropical forest succession at landscape scales despite uncertainty in Landsat time series. *Ecol. Appl.* 31, e02208.
- Comín, F.A., Romero, J.A., Hernández, O., Menéndez, M., 2001. Restoration of wetlands from abandoned rice fields for nutrient removal, and biological community and landscape diversity. *Restor. Ecol.* 9, 201–208.

- Conrad, O., Bechtel, B., Bock, M., Dietrich, H., Fischer, E., Gerlitz, L., ... & Böhrner, J., 2015. System for automated geoscientific analyses (SAGA) v. 2.1. 4. *Geoscientific model development*, 8(7), 1991–2007.
- Cristiano, P.M., Madanes, N., Campanello, P.I., Di Francescantonio, D., Rodríguez, S.A., Zhang, Y.-J., Oliva Carrasco, L., Goldstein, G., 2014. High NDVI and potential canopy photosynthesis of South American subtropical forests despite seasonal changes in leaf area index and air temperature. *Forests* 5, 287–308.
- Didham, R.K., Ghazoul, J., Stork, N.E., Davis, A.J., 1996. Insects in fragmented forests: a functional approach. *Trends Ecol. Evol.* 11, 255–260.
- Diehl, E., Mader, V.L., Wolters, V., Birkhofer, K., 2013. Management intensity and vegetation complexity affect web-building spiders and their prey. *Oecologia* 173, 579–589.
- Dixon, P., 2003. VEGAN, a package of R functions for community ecology. *J. Veg. Sci.* 14, 927–930.
- Duelli, P., 1997. Biodiversity evaluation in agricultural landscapes: an approach at two different scales. *Agric. Ecosyst. Environ.* 62, 81–91.
- Evans, E.W., 1982. Feeding specialization in predatory insects: hunting and attack behavior of two stinkbug species (Hemiptera: Pentatomidae). *Am. Midl. Nat.* 96–104.
- Finger Higgins, R., Chipman, J., Lutz, D., Culler, L., Virginia, R., Ogdan, L., 2019. Changing lake dynamics indicate a drier Arctic in Western Greenland. *J. Geophys. Res. Biogeosciences* 124, 870–883.
- Gamon, J.A., Field, C.B., Goulden, M.L., Griffin, K.L., Hartley, A.E., Joel, G., Penuelas, J., Valentini, R., 1995. Relationships between NDVI, canopy structure, and photosynthesis in three Californian vegetation types. *Ecol. Appl.* 5, 28–41.
- Gao, B.-C., 1996. NDWI—A normalized difference water index for remote sensing of vegetation liquid water from space. *Remote Sens. Environ.* 58, 257–266.
- García, D., Zamora, R., Amico, G.C., 2011. The spatial scale of plant–animal interactions: effects of resource availability and habitat structure. *Ecol. Monogr.* 81, 103–121.
- garcía-Ruiz, J.M., Lana-Renault, N., 2011. Hydrological and erosive consequences of farmland abandonment in Europe, with special reference to the Mediterranean region—A review. *Agric. Ecosyst. Environ.* 140, 317–338.
- Gaston, K.J., Blackburn, T.M., 1995. Mapping biodiversity using surrogates for species richness: macro-scales and New World birds. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 262 (1365), 335–341.
- Gauld, I.D., 1988. Evolutionary patterns of host utilization by ichneumonoid parasitoids (Hymenoptera: Ichneumonidae and Braconidae). *Biol. J. Linn. Soc.* 35, 351–377.
- Gellich, M., Baur, P., Koch, B., Zimmermann, N.E., 2007. Agricultural land abandonment and natural forest re-growth in the Swiss mountains: a spatially explicit economic analysis. *Agric. Ecosyst. Environ.* 118, 93–108.
- Gerlach, J., Samways, M., Pryke, J., 2013. Terrestrial invertebrates as bioindicators: an overview of available taxonomic groups. *J. Insect Conserv.* 17, 831–850.
- Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., Moore, R., 2017. Google earth engine: planetary-scale geospatial analysis for everyone. *Remote Sens. Environ.* 202, 18–27.
- Greenstone, M.H., 1984. Determinants of web spider species diversity: vegetation structural diversity vs. prey availability. *Oecologia* 62, 299–304.
- Gunnarsson, B., 1990. Vegetation structure and the abundance and size distribution of spruce-living spiders. *J. Anim. Ecol.* 743–752.
- Hakoyama, S., Tanaka, H., Agata, W., Takeda, T., 1977. Studies on weed vegetation in non-cultivated paddy fields: I. The vegetation of non-cultivated paddy fields in the north-western parts of Fukuoka Prefecture. *Jpn. J. Crop Sci.* 46, 219–227.
- Hatley, C.L., Macmahon, J.A., 1980. Spider community organization: seasonal variation and the role of vegetation architecture. *Environ. Entomol.* 9, 632–639.
- Hayakawa, Y. & Takahata, S. 1975. Studies on the landscape management of pastureland using the plant succession theory. 4. The comparison of plant succession and soil fertility on abandoned pastures and paddy fields.
- Ho, B.C., Wojdak, J.M., Kim, J.G., Kwon, G.J., 2008. Report: ecological assessment of plant succession and water quality in abandoned rice fields. *J. Ecol. Environ.* 31, 213–223.
- Horváth, R., Magura, T., Péter, G., Tóthmérész, B., 2002. Edge effect on weevils and spiders. *Web Ecol.* 3, 43–47.
- Jankielsohn, A., 2018. The importance of insects in agricultural ecosystems. *Adv. Entomol.* 6, 62–73.
- Kates, R.W., Clark, W.C., Corell, R., Hall, J.M., Jaeger, C.C., Lowe, I., McCarthy, J.J., Schellnhuber, H.J., Bolin, B., Dickson, N.M., 2001. Sustainability. *Sci Sci* 292, 641–642.
- Kil, K.D., 1985. Effect of transplanting dates on the occurrence of rice stripe and black-streaked dwarf virus diseases in Yeongnam district. *Korean J. Plant Pathol.* 1, 109–114.
- Kim, D.-E., Kim, J.-M., 2013. Insect fauna of Ungok wetland in Gochang, Jeonbuk, Korea, designated as a wetland protection area at Ramsar convention. *J. Environ. Sci. Int.* 22, 1141–1152.
- Korea, S. 2024. 2023 Cultivated Area Survey.
- Landsman, A.P., Bowman, J.L., 2017. Discordant response of spider communities to forests disturbed by deer herbivory and changes in prey availability. *Ecosphere* 8, e01703.
- Lee, C.S., You, Y.H., Robinson, G.R., 2002. Secondary succession and natural habitat restoration in abandoned rice fields of central Korea. *Restor. Ecol.* 10, 306–314.
- Lee, J., Choi, W., 2022. Vulnerability assessment of idleness in rural areas from multiple perspectives. *J. Korean Soc. Agric. Eng.* 64, 15–25.
- Lee, S., Kim, S., Yoon, H., 2020. Analysis of differences in vegetation phenology cycle of abandoned farmland, using harmonic analysis of time-series vegetation indices data: the case of Gwangyang City, South Korea. *GIScience Remote Sens.* 57, 338–351.
- Lim, B.S., Seol, J., Kim, A.R., An, J.H., Lim, C.H., Lee, C.S., 2022. Succession of the abandoned rice fields restores the riparian forest. *Int. J. Environ. Res. Public Health* 19, 10416.
- Litovska, I., Van Der Plas, F., Kleijn, D., 2025. Arthropod abundance is most strongly driven by crop and semi-natural habitat type rather than management in an intensive agricultural landscape in the Netherlands. *Agric. Ecosyst. Environ.* 378, 109298.
- Little, C.M., Chapman, T.W., Hillier, N.K., 2020. Plasticity is key to success of *Drosophila suzukii* (Diptera: Drosophilidae) invasion. *J. Insect Sci.* 20, 5.
- Löw, F., Fliemann, E., Abdullaev, I., Conrad, C., Lamers, J.P., 2015. Mapping abandoned agricultural land in Kyzyl-Orda, Kazakhstan using satellite remote sensing. *Appl. Geogr.* 62, 377–390.
- Macdonald, D., Crabtree, J.R., Wiesinger, G., Dax, T., Stamou, N., Fleury, P., Lazpita, J. G., Gibon, A., 2000. Agricultural abandonment in mountain areas of Europe: environmental consequences and policy response. *J. Environ. Manag.* 59, 47–69.
- Martin, A.E., Collins, S.J., Crowe, S., Girard, J., Naujokaitis-Lewis, I., Smith, A.C., Lindsay, K., Mitchell, S., Fahrig, L., 2020. Effects of farmland heterogeneity on biodiversity are similar to—or even larger than—the effects of farming practices. *Agric. Ecosyst. Environ.* 288, 106698.
- Matsumura, M., Nishimura, N. & Saijoh, Y. 1988. Plant succession in paddy fields lying fallow in Hida mountainous regions, Gifu Prefecture.
- Mazzi, D., Dorn, S., 2012. Movement of insect pests in agricultural landscapes. *Ann. Appl. Biol.* 160, 97–113.
- Mcnaughton, S.J., 1967. Relationships among functional properties of Californian grassland. *Nature* 216, 168–169.
- Mendiburu, F.D. 2019. *Agricolae: statistical procedures for agricultural research. (No Title).*
- Müller, K. & Wickham, H. 2021. *Tibble: Simple data frames.*
- Ohkuro, T., Matsuo, K. & Nemoto, M. 1996. Vegetation dynamics of abandoned paddy fields and their levee slopes in mountainous regions of central Japan.
- ortowski, G., 2005. Endangered and declining bird species of abandoned farmland in south-western Poland. *Agric. Ecosyst. Environ.* 111, 231–236.
- Park, H.C., Lee, G.G., Lee, J.H., 2015. Analysis of vegetation recovery trend in abandoned paddy wetland-Focused on flora and vegetation changes of clear zone surrounding Pyeongtaek K-55 Air Force Base. *KSCE J. Civ. Eng.* 19, 864–872.
- Pastick, N.J., Jorgenson, M.T., Goetz, S.J., Jones, B.M., Wylie, B.K., Minsley, B.J., Genet, H., Knight, J.F., Swanson, D.K., Jorgenson, J.C., 2019. Spatiotemporal remote sensing of ecosystem change and causation across Alaska. *Glob. Change Biol.* 25, 1171–1189.
- Perrone, M., Di Febraro, M., Conti, L., Divíšek, J., Chytrý, M., Keil, P., Carranza, M.L., Rocchini, D., Torresani, M., Moudrý, V., 2023. The relationship between spectral and plant diversity: disentangling the influence of metrics and habitat types at the landscape scale. *Remote Sens. Environ.* 293, 113591.
- Petrou, Z.I., Manakos, I., Stathaki, T., 2015. Remote sensing for biodiversity monitoring: a review of methods for biodiversity indicator extraction and assessment of progress towards international targets. *Biodivers. Conserv.* 24, 2333–2363.
- Plieninger, T., Hui, C., Gaertner, M., Huntsinger, L., 2014. The impact of land abandonment on species richness and abundance in the Mediterranean Basin: a meta-analysis. *PLoS One* 9, e98355.
- R Core Team 2021. *R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria.*
- Revelle, W., 2020. *psych: procedures for psychological, psychometric, and personality research. R. Package Version 2.*
- Rey Benayas, J.M., Martins, A., Nicolau, J.M., Schulz, J.J., 2007. Abandonment of agricultural land: an overview of drivers and consequences. *CABI Rev.* 14.
- Robinson, G.R., Handel, S.N., 2000. Directing spatial patterns of recruitment during an experimental urban woodland reclamation. *Ecol. Appl.* 10, 174–188.
- Rocchini, D., Neteler, M., 2012. Let the four freedoms paradigm apply to ecology. *Trends Ecol. Evol.* 27, 310–311.
- Rocchini, D., Balkenhol, N., Carter, G.A., Foody, G.M., Gillespie, T.W., He, K.S., Kark, S., Levin, N., Lucas, K., Luoto, M., 2010. Remotely sensed spectral heterogeneity as a proxy of species diversity: recent advances and open challenges. *Ecol. Inform.* 5, 318–329.
- Rocchini, D., Marcantonio, M., Ricotta, C., 2017. Measuring Rao's Q diversity index from remote sensing: an open source solution. *Ecol. Indic.* 72, 234–238.
- Schaefer, C.W., Mitchell, P.L., 1983. Food plants of the Coreoidea (Hemiptera: Heteroptera). *Ann. Entomol. Soc. Am.* 76, 591–615.
- Serra, P., Pons, X., Sauri, D., 2008. Land-cover and land-use change in a Mediterranean landscape: a spatial analysis of driving forces integrating biophysical and human factors. *Appl. Geogr.* 28, 189–209.
- Shannon, C.E., 1948. A mathematical theory of communication. *Bell Syst. Tech. J.* 27, 379–423.
- Shimoda, M., 1996. Abandoned rice field vegetation and its evaluation, A case study of wet abandoned rice field vegetation in Hiroshima Prefecture. *Veg. Sci.* 13, 37–50.
- Sievert, C., 2020. Interactive web-based data visualization with R, plotly, and shiny. Chapman and Hall/CRC.
- Sileika, A.S., Stålnacke, P., Kutra, S., Gaigalis, K., Berankiene, L., 2006. Temporal and spatial variation of nutrient levels in the Nemunas River (Lithuania and Belarus). *Environ. Monit. Assess.* 122, 335–354.
- Stork, N.E., 2018. How many species of insects and other terrestrial arthropods are there on Earth? *Annu. Rev. Entomol.* 63, 31–45.
- Svenson, G.J., Whiting, M.F., 2004. Phylogeny of Mantodea based on molecular data: evolution of a charismatic predator. *Syst. Entomol.* 29, 359–370.
- Tokuoka, Y., Nakagoshi, N., 2017. Diverse patterns of vegetation change after upland field abandonment in Japan. *Landsc. Ecol. Sustain. Soc.* 123–137.
- Wickham, H., 2011. *ggplot2. Wiley Interdiscip. Rev. Comput. Stat.* 3, 180–185.

- Wickham, H., Henry, L., 2020. Tidy: Tidy messy data. R. Package Version 1, 397.
- Wickham, H., Henry, L., 2023. Purrr: functional programming tools. R. Package Version 1.
- Xiao, X., Boles, S., Froking, S., Salas, W., Moore iii, B., Li, C., He, L., Zhao, R., 2002. Observation of flooding and rice transplanting of paddy rice fields at the site to landscape scales in China using VEGETATION sensor data. *Int. J. Remote Sens.* 23, 3009–3022.
- Xue, J., Su, B., 2017. Significant remote sensing vegetation indices: a review of developments and applications. *J. Sens.* 2017, 1353691.
- Yabe, K., Numata, M., 1984. Ecological studies of the mobara-yatsumi marsh.: main physical and chemical factors controlling the marsh ecosystem. *Jpn. J. Ecol.* 34, 173–186.
- Yamada, S., Okubo, S., Kitagawa, Y., Takeuchi, K., 2007. Restoration of weed communities in abandoned rice paddy fields in the Tama Hills, central Japan. *Agric. Ecosyst. Environ.* 119, 88–102.
- Yamada, S., Kitagawa, Y., Okubo, S., 2013. A comparative study of the seed banks of abandoned paddy fields along a chronosequence in Japan. *Agric. Ecosyst. Environ.* 176, 70–78.
- Yang, L.H., Gratton, C., 2014. Insects as drivers of ecosystem processes. *Curr. Opin. Insect Sci.* 2, 26–32.
- Yoon, H., Kim, S., 2020. Detecting abandoned farmland using harmonic analysis and machine learning. *ISPRS J. Photogramm. Remote Sens.* 166, 201–212.