NUSANTARA BIOSCIENCE
Vol. 17, No. 2, pp. 355-374
November 2025

ISSN: 2087-3948
E-ISSN: 2087-3956
DOI: 10.13057/nusbiosci/n170216

Invasion dynamics and elevational range expansion of insects in tropical agricultural landscapes of Wonosobo, Central Java, Indonesia

SAKINA ENOVA RAHMADHANI[1], SIBRINA SALSABILA[1], ROI ANDRIANTO[1], SYARIFAH HASNA ROSYIDA[1], QUROTUL AINIA[2], ARU DEWANGGA[1], AHMAD DWI SETYAWAN[1,3,♥]

[1]Department of Environmental Science, Faculty of Mathematics and Natural Sciences, Universitas Sebelas Maret. Jl. Ir. Sutami 36A, Surakarta 57126, Central Java, Indonesia. Tel./fax.: +62-271-663375, ♥email: volatileoils@gmail.com
[2]Laboratory of Animal Systematics, Faculty of Biology, Universitas Gadjah Mada. Jl. Teknika Selatan, Sleman 55281, Yogyakarta, Indonesia
[3]Biodiversity Research Group, Universitas Sebelas Maret. Jl. Ir. Sutami 36A, Surakarta 57126, Central Java, Indonesia

Manuscript received: 30 December 2024. Revision accepted: 29 November 2025.

Abstract. *Rahmadhani SE, Salsabila S, Andrianto R, Rosyida SH, Ainia Q, Dewangga A, Setyawan D. 2025. Invasion dynamics and elevational range expansion of insects in tropical agricultural landscapes of Wonosobo, Central Java, Indonesia. Nusantara Bioscience 17: 355-374.* Biological invasions in tropical mountain agroecosystems are increasingly reported, yet the processes driving elevational range expansion of invasive insects remain poorly understood. This study examined invasion dynamics and elevational range expansion of insects across a gradient of lowland to highland agricultural landscapes in Wonosobo District, Central Java, Indonesia. Using a targeted sampling approach, we quantified invasion intensity with the Relative Invasiveness Index (RII) and elevational expansion with the Altitudinal Expansion Index (AEI). Functional feeding group composition and environmental drivers were further analyzed to evaluate invasion-related community reorganization. A total of 692 insect individuals were recorded, of which 295 individuals (42.6%) belonged to nine invasive or potentially invasive taxa. RII values were lowest at lowland (13.2%), highest at mid-elevation (53.6%), and moderately high at highland sites (48.7%). In contrast, AEI was only positive in highland systems (mean AEI = 45.7%; range: 38.7-59.6%), where upslope expansion was detected in saprophagous Diptera, with *Leucostoma simplex* showing the highest elevational shift (up to 856 m above historically documented limits). Functional composition shifted from herbivore-dominated assemblages at low elevation to predator-dominated at mid-elevation and saprophage-detritivore-dominated at high elevation, indicating functional homogenization under increasing invasion pressure. Canonical Correspondence Analysis revealed that elevation and light intensity were the primary drivers of upslope expansion, while temperature and wind exposure influenced invasion dominance. These findings demonstrate that elevational gradients in tropical agricultural landscapes function as invasion filters rather than biodiversity gradients, with mid-elevation systems acting as transitional invasion hotspots and highland systems representing high-risk zones for invasion-driven functional simplification. The study highlights the need for elevation-specific invasion risk zoning and early intervention strategies to mitigate emerging invasion threats in tropical mountain agroecosystems.

Keywords: Biological invasion, elevational gradient, functional homogenization, invasive insects, tropical agriculture

INTRODUCTION

Biological invasions increasingly drive ecological change in tropical agricultural landscapes, where high biodiversity coincides with rapid land-use intensification. Invasive insects can reshape communities, disrupt trophic links, and weaken ecosystem services such as biological control and pollination, threatening long-term farm sustainability (Blackburn et al. 2011). In agroecosystems, invasions are promoted by habitat simplification, nutrient enrichment, and frequent disturbance, which favor generalist, disturbance-tolerant taxa over specialists. This is particularly important in tropical mountains, where steep environmental gradients and human land use jointly influence persistence and range expansion.

Altitudinal gradients shape species richness and community composition, yet their role in biological invasions is still unclear. Elevation alters temperature, radiation, wind, and habitat structure, creating ecological filters that may limit or enable invasive taxa (Rahbek 1995; Hodkinson 2005). Although highlands were once considered barriers to lowland species, agricultural intensification and climate variability can erode these constraints, enabling ecologically tolerant insects to expand upslope. Such elevational range shifts have been reported across tropical and subtropical insect groups, especially in open habitats where organic inputs enhance colonization (Kumar et al. 2022; Adnan et al. 2024; Gul et al. 2024).

Invasion dynamics in agricultural landscapes are not solely determined by species origin but are closely linked to functional traits and trophic roles. Invasive and potentially invasive insects are often characterized by high dispersal ability, rapid reproduction, and flexible feeding strategies, enabling them to exploit disturbed environments efficiently (Blackburn et al. 2011; Liebhold et al. 2012). As invasion pressure increases, agroecosystems may undergo functional reorganization, shifting from regulation-based assemblages dominated by predators and pollinators toward communities increasingly structured by herbivores, saprophages, or detritivores. This process of functional homogenization can reduce ecosystem resilience and amplify pest outbreaks, particularly in simplified highland farming systems (Davis et al. 2000; Seebens et al. 2017).

Indonesia provides a critical context for examining these processes. As one of the world's megadiverse countries, Indonesia supports an exceptionally rich insect fauna, yet its agricultural landscapes are experiencing rapid transformation driven by crop intensification, fertilizer inputs, and land conversion (Andriani et al. 2017; Lukvitasari et al. 2021). Insect taxa such as *Musca domestica, Pantala flavescens,* and *Nilaparvata lugens* exemplify species with high ecological plasticity that allow them to persist across a wide range of environmental conditions and management regimes (Belioka and Achilias 2024; He et al. 2024). The spread and dominance of such taxa raise concerns about emerging invasion fronts within Indonesian agroecosystems, particularly along environmental gradients that were previously considered limiting.

Wonosobo District, located in the central highlands of Java, represents a suitable natural laboratory for investigating invasion dynamics along an altitudinal gradient. The region spans lowland to highland agricultural systems developed on fertile volcanic soils between approximately 600 and 2,100 m above sea level, generating pronounced micro-climatic contrasts in temperature, light intensity, and wind exposure (Gani et al. 2021). Agricultural expansion in these highlands has increased habitat openness and organic matter accumulation, conditions that may enhance the invasion success of synanthropic and disturbance-tolerant insects. Previous studies in Wonosobo have primarily emphasized patterns of insect diversity and community composition across elevation, leaving invasion intensity, range expansion, and functional consequences largely unexplored.

Quantifying invasion processes requires analytical approaches that go beyond traditional diversity metrics. Index-based frameworks that integrate abundance, spatial occurrence, and elevational distribution provide a more direct assessment of invasion pressure and expansion dynamics. The use of invasion-oriented indices, combined with functional feeding group analysis and multivariate examination of environmental drivers, allows for the identification of taxa and elevation zones that function as invasion hotspots or early warning areas. Such approaches are increasingly applied in invasion ecology to detect subtle but ecologically meaningful shifts before widespread impacts occur (Parker et al. 1999; Lenoir et al. 2008; Seipel et al. 2012).

Accordingly, this study examines invasion dynamics and elevational range expansion of insects in tropical agricultural landscapes of Wonosobo, Central Java, Indonesia. Specifically, the objectives of this study are to: (i) identify invasive and potentially invasive insect taxa across lowland, mid-elevation, and highland agricultural systems; (ii) quantify invasion intensity and upslope expansion using invasion-oriented indices; and (iii) assess how functional composition and environmental factors mediate invasion patterns along the altitudinal gradient. By focusing on invasion processes rather than biodiversity patterns alone, this study aims to provide an ecological basis for invasion risk assessment and management prioritization in tropical mountain agroecosystems.

MATERIALS AND METHODS

Study system

This study builds upon a previously published insect diversity survey conducted in the same agricultural landscapes of Wonosobo District, Central Java, Indonesia (Figures 1 and 2) (Rahmadhani et al. 2025), and uses the same primary field dataset. The dataset comprises 57 insect species representing 31 families and 9 orders, with a total of 692 individuals, collected through standardized sampling in October 2024 across three sites spanning lowland, mid-elevation, and highland agricultural systems. In the present study, the raw dataset is reanalyzed with a different analytical framework focusing specifically on invasion dynamics and elevational range expansion; therefore, diversity-based results reported in the earlier publication are not repeated here.

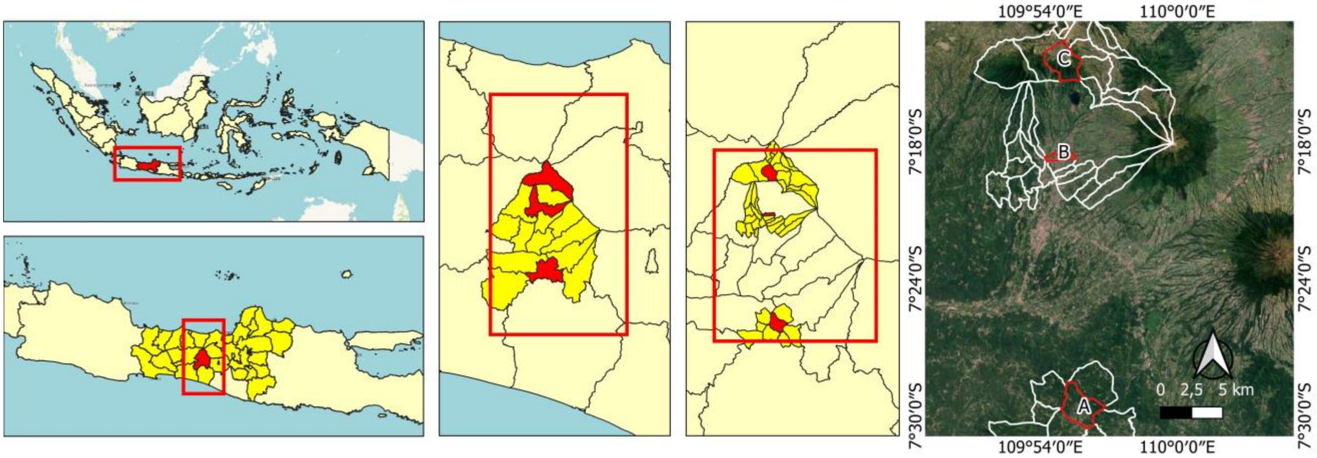

Figure 1. Locations of the study sites in Wonosobo, Central Java, Indonesia. A. Karangsambung, B. Blederan, and C. Sembungan, Wonosobo, Central Java, Indonesia

Figure 2. Agriculture landscape of Wonosobo, Central Java, Indonesia. A. Karangsambung (site 1), B. Blederan (site 2), and C. Sembungan (site 3), Wonosobo, Central Java, Indonesia

The elevational invasion framework

The study area encompasses a tropical agricultural landscape characterized by a pronounced elevational gradient extending from lowland to highland. Rather than treating the sites as discrete sampling units, the landscape was conceptualized as a continuous elevational invasion system, in which changes in altitude are accompanied by systematic shifts in microclimate, land-use intensity, and habitat openness. Such elevational gradients are increasingly recognized as dynamic arenas for biological invasions, particularly in tropical mountain agroecosystems where environmental filtering interacts with anthropogenic disturbance (Rahbek 1995; Hodkinson 2005).

Within this framework, elevation functions not merely as a geographic descriptor but as an ecological filter that modulates invasion success through declining temperature, increased radiation exposure, and altered wind regimes, all of which influence insect survival, dispersal, and establishment (Gani et al. 2021; Adnan et al. 2024). Agricultural practices along the gradient further modify these filters by creating open, nutrient-enriched habitats that may facilitate colonization by disturbance-tolerant and synanthropic taxa. Conceptualizing the study area as an elevational invasion gradient enables invasion dynamics and upslope range expansion to be examined as process-driven responses to interacting environmental and land-use drivers, rather than as static differences among locations (Davis et al. 2000; Seebens et al. 2017).

Definition of focal invasion units and analytical scope

The analytical focus of this study was restricted to invasive and potentially invasive insect taxa, rather than the full insect assemblage recorded across the agricultural landscape. This focal-unit approach was adopted to ensure that analytical outcomes directly reflect invasion processes, dominance patterns, and range expansion signals, rather than general biodiversity variation. Invasion units were defined at the species level and evaluated based on ecological status, distributional breadth, and relative abundance across elevation zones, following established invasion ecology frameworks (CBD 2002; Richardson et al. 2000; Blackburn et al. 2011). Species richness values presented in Table 9 refer to the entire insect assemblage recorded at each elevation zone, whereas Tables 1, 3, 5, and 6 focus exclusively on nine invasive and potentially invasive taxa selected as focal invasion units.

Native taxa were included in the analysis only when necessary for contextual comparison, particularly in assessing shifts in dominance structure and functional reorganization associated with increasing invasion pressure. By narrowing the analytical scope to invasion-relevant taxa, the study avoids redundancy with diversity-based assessments and provides a process-oriented evaluation of invasion dynamics within tropical agroecosystems (Liebhold et al. 2012; Seebens et al. 2017).

Field sampling design in relation to invasion detection

Field sampling was designed to maximize the detection of invasive and potentially invasive insect taxa across the elevational agricultural gradient, rather than to document overall species richness exhaustively. Sampling units were therefore positioned to capture habitats and microenvironments most likely to facilitate invasion, including open croplands, organically enriched fields, and areas subject to frequent anthropogenic disturbance. This targeted approach aligns with invasion ecology principles, which emphasize early detection of dominant or expanding taxa over comprehensive biodiversity surveys (Liebhold et al. 2012).

Sampling was conducted using standardized active collection methods commonly applied in agricultural entomology, including sweep netting and direct hand collection, to capture mobile, synanthropic, and disturbance-tolerant insects effectively. These methods are particularly suitable for detecting taxa with high dispersal capacity and rapid population turnover, which are characteristic features of invasive insects (Leksono 2017; Sofian et al. 2023). Sampling effort was standardized across elevation zones to allow valid comparison of invasion intensity and dominance patterns, minimizing bias associated with unequal effort.

Temporal sampling was aligned with periods of high insect activity in agricultural systems, ensuring that invasion signals reflected active population presence rather than transient or stochastic occurrences. By emphasizing consistency of effort and invasion-prone microhabitats, the sampling design provides a robust basis for identifying elevational shifts, dominance increases, and early range expansion of invasive insects within tropical agroecosystems (Parker et al. 1999; Seebens et al. 2017).

Criteria for classification of invasion and range-expanding status

The classification of insect taxa into invasion-related categories followed a standardized framework that integrates biogeographic origin, establishment success, ecological impact, and functional role within the local agroecosystem (Richardson et al. 2000; CBD 2002; Blackburn et al. 2011). Four categories were used: native (taxa originating within Indonesia/Southeast Asia without recent expansion), naturalized (non-native taxa established without ecological disruption), potentially invasive (taxa showing abnormal increases in abundance, dominance, or elevational distribution, regardless of origin), and invasive (non-native taxa with clear negative ecological or agricultural impacts).

This classification was applied contextually. For example, *M. domestica* globally synanthropic species-was classified as potentially invasive rather than invasive in Wonosobo due to the absence of documented crop damage, disease transmission, or competitive exclusion of native Diptera in local highland vegetable systems (Fajarfika 2020; Sofian et al. 2023). Its role as a decomposer in organic-rich fields was considered ecologically neutral or facilitative. Conversely, *Peregrinus maidis* was classified as an invasive alien based on its introduced status, known pest impact in regional maize systems, and observed crop damage in lowland plots.

Classification decisions were supported by regional entomological literature, agricultural pest databases (CABI 2024; GBIF 2024), and trait-based assessments of dispersal ability, reproductive rate, and disturbance tolerance (Liebhold et al. 2012; Seebens et al. 2017). This integrative approach ensures that invasion status reflects both biogeographic origin and local ecological relevance within tropical agroecosystems.

Compilation of historical and regional distribution references

Historical and regional distribution data were compiled to establish baseline elevational limits for insect taxa classified as invasive or potentially invasive. These references provide the ecological context required to distinguish true upslope range expansion from natural spatial variability. Distributional information was obtained through an integrative review of regional entomological surveys, agricultural pest records, and biodiversity databases relevant to Indonesia and Southeast Asia (Waterhouse 1993; Heong et al. 2009; Aryuwandari et al. 2020; Ikhsan 2024).

Authoritative global repositories, including the Global Biodiversity Information Facility (GBIF 2024) and the Integrated Taxonomic Information System (ITIS 2024), were used to verify species-level occurrence records and known elevational ranges. Where available, peer-reviewed studies reporting historical altitudinal limits were prioritized to reduce uncertainty in baseline determination. For taxa lacking explicit elevational documentation, regional ecological descriptions and habitat associations were used as proxies, following approaches commonly applied in invasion ecology (Lenoir et al. 2008; Seipel et al. 2012). This compilation enabled a standardized assessment of elevational range shifts and supported robust calculation of expansion-related indices.

Quantification of invasion intensity

Relative Invasiveness Index (RII)

Invasion intensity across the elevational agricultural gradient was quantified using the Relative Invasiveness Index (RII), an index designed to integrate numerical dominance and spatial occurrence of invasive and potentially invasive taxa within a community. RII was calculated as: RII = (Abundance_sp / Total individuals in the zone) × Frequency_sp × 100%, where Abundance_sp is the number of individuals of a given species, Total individuals in the zone is the total insect count in that elevation zone, and Frequency_sp is the proportion of sampling plots where the species occurred. RII provides a proportional measure of invasion pressure by emphasizing how strongly invasion-relevant taxa contribute to overall community structure, rather than relying on species counts alone. This approach is particularly suitable for agricultural systems where invasion impacts are often driven by a small number of highly dominant taxa (Parker et al. 1999; Liebhold et al. 2012).

RII was calculated at the site level and for individual taxa to capture both landscape-scale invasion patterns and taxon-specific dominance signals. By incorporating abundance and frequency components, RII allows comparison of invasion intensity among elevation zones while minimizing bias associated with uneven species richness. This index-based framework aligns with contemporary invasion ecology, which increasingly prioritizes dominance and impact over origin alone (Blackburn et al. 2011; Seebens et al. 2017).

Calculation procedure and threshold interpretation

RII was computed as the product of the relative abundance and relative frequency of invasive and potentially invasive taxa, expressed as a percentage of the total insect assemblage at each elevation zone (Parker et al. 1999). Abundance values were derived from standardized sampling units, while frequency was defined as the proportion of sampling plots in which a given taxon occurred. This dual-component formulation ensures that taxa exhibiting both high numerical dominance and broad spatial distribution contribute more strongly to invasion intensity.

Threshold interpretation followed a conservative scheme to distinguish background occurrence from ecologically meaningful invasion signals. Low RII values were interpreted as incidental or early-stage presence, whereas moderate to high RII values indicated increasing dominance and potential ecological impact. These thresholds were interpreted in conjunction with functional traits and elevational distribution patterns to avoid overclassification of naturally abundant native taxa (Liebhold et al. 2012; Seebens et al. 2017).

Assessment of elevational range expansion

Conceptual basis of Altitudinal Expansion Index (AEI)

Elevational range expansion was assessed using the Altitudinal Expansion Index (AEI), an index designed to quantify the degree to which insect taxa extend their observed distribution beyond historically documented elevational limits. AEI was calculated as: AEI = [(Observed upper limit-Historical upper limit) / Total elevational span of the study system] × 100%, where Observed upper limit is the maximum elevation at which the taxon was recorded in this study, Historical upper limit is the highest elevation previously documented for the taxon in regional records, and Total elevational span is the difference between the highest and lowest sampling sites (2,056-621 = 1,435 m). AEI captures the spatial dimension of invasion by translating upslope occurrence into a standardized metric that can be compared among taxa and across elevation zones. This approach is particularly relevant in tropical mountain agroecosystems, where climatic gradients and land-use change may relax traditional elevational constraints (Lenoir et al. 2008; Seipel et al. 2012).

AEI was applied to invasive and potentially invasive taxa to identify early signals of range expansion, even when absolute abundance remains moderate. By focusing on deviation from historical elevational baselines rather than presence alone, AEI allows detection of incipient invasion processes that may precede dominance or ecological impact. A taxon with an AEI value of zero indicates that its current elevational range does not exceed its historically documented limit, which may reflect either stable distribution or recent arrival without yet expanding upward. Such index-based assessments are increasingly used in invasion and climate-change ecology to identify range-shifting species before widespread establishment occurs.

Determination of elevational limits and expansion magnitude

Historical elevational limits for each focal taxon were determined based on published regional records, entomological surveys, and authoritative biodiversity databases (Waterhouse 1993; Heong et al. 2009; GBIF 2024). The observed elevational range was defined as the minimum and maximum altitudes at which the taxon was recorded during field sampling. Expansion magnitude was then calculated as the proportional extension of the observed range beyond the historical upper limit, standardized to the total elevational span of the study system (Lenoir et al. 2008). AEI was calculated for each taxon based on its maximum recorded elevation in this study compared to its historically documented upper limit. AEI values were then interpreted in the context of the elevation zone where the taxon exhibited expansion, regardless of whether expansion occurred in lowland, mid-elevation, or highland systems.

AEI values were interpreted on a continuous scale, with higher values indicating stronger upslope expansion signals. To avoid misclassification, expansion magnitude was evaluated alongside invasion intensity (RII) and functional traits, ensuring that elevational shifts reflected genuine expansion processes rather than sampling artifacts or natural variability (Liebhold et al. 2012; Seipel et al. 2012).

Functional trait and trophic role classification

Functional traits and trophic roles were assigned exclusively to invasive and potentially invasive insect taxa to evaluate how invasion processes are linked to ecological function within agricultural systems. Rather than classifying the entire community, this focused approach emphasizes the functional consequences of invasion, particularly shifts toward dominance by generalist or disturbance-tolerant guilds. Taxa were categorized into primary trophic roles, including herbivores, predators, pollinators, saprophages, and detritivores, based on published ecological descriptions and regional entomological references (Hill 1983; Waterhouse 1993; Leksono 2017).

Trait assignment considered feeding strategy, habitat affinity, dispersal capacity, and association with disturbed or nutrient-enriched environments. These traits are widely recognized as key determinants of invasion success in agroecosystems (Liebhold et al. 2012). By restricting functional classification to invasion-relevant taxa, the analysis avoids redundancy with diversity-based functional assessments and allows clearer interpretation of how invasion pressure drives functional reorganization along the elevational gradient (Davis et al. 2000; Seebens et al. 2017).

Environmental variables linked to invasion processes

Environmental variables were selected based on their documented influence on insect invasion success, dispersal, and establishment, rather than for descriptive characterization of site conditions. Key drivers included air temperature, light intensity, wind exposure, and elevation, which collectively mediate physiological tolerance, flight activity, and habitat suitability of invasive insects along mountain gradients (Rahbek 1995; Hodkinson 2005; Gani et al. 2021). These variables are particularly relevant in open agricultural systems, where microclimatic buffering is limited and environmental filtering is pronounced.

Measurements were treated as explanatory drivers in subsequent analyses to evaluate how variation in abiotic conditions corresponds with invasion intensity and elevational range expansion. Emphasis was placed on identifying thresholds or gradients associated with increased dominance of disturbance-tolerant and synanthropic taxa, rather than documenting absolute environmental values. This driver-oriented approach aligns with invasion ecology frameworks that link environmental stress and habitat openness to increased invasibility (Davis et al. 2000; Pauchard et al. 2009; Seebens et al. 2017), allowing a clearer interpretation of how environmental gradients facilitate or constrain invasion processes in tropical agroecosystems.

Multivariate analysis of invasion-environment relationships

Multivariate analyses were employed to examine relationships between invasion-related taxa and environmental drivers across the elevational agricultural gradient. Canonical Correspondence Analysis (CCA) was used as the primary ordination technique to evaluate how variation in environmental variables constrains or facilitates the distribution and dominance of invasive and potentially invasive insects. CCA is particularly suitable for invasion-focused analyses because it directly relates species occurrence and abundance to measured environmental gradients (Jongman et al. 1995; Legendre and Legendre 2012).

Only invasive and potentially invasive taxa were included as response variables, ensuring that ordination outputs reflect invasion processes rather than overall community structure. Environmental drivers such as temperature, light intensity, wind exposure, and elevation were used as explanatory variables. Statistical significance of ordination axes was assessed using permutation tests, allowing robust inference of species-environment relationships. This analytical framework enables identification of environmental conditions associated with high invasion intensity or upslope expansion, providing process-based insight into invasion dynamics within tropical agroecosystems (Pauchard et al. 2009; Seebens et al. 2017).

Statistical testing and robustness checks

Statistical analyses were conducted to evaluate the robustness of invasion patterns and to minimize inference bias. Relationships between invasion intensity (RII), elevational expansion (AEI), and environmental drivers were assessed using correlation analyses, focusing on directional associations rather than descriptive differences among sites. This approach is appropriate for process-oriented invasion studies, where the strength and consistency of gradients are of greater interest than mean comparisons (Legendre and Legendre 2012).

To reduce the influence of highly dominant taxa and improve variance homogeneity, abundance data for invasion-relevant taxa were log-transformed prior to multivariate analyses. Sensitivity checks were performed by recalculating indices after excluding rare or incidental taxa to ensure that outliers did not drive invasion signals. These robustness checks increase confidence that observed invasion patterns reflect consistent ecological processes rather than sampling artifacts (Quinn and Keough 2002; Seebens et al. 2017).

Data validation, consistency, and analytical constraints

Data validation focused on ensuring taxonomic accuracy, consistency of invasion classification, and analytical transparency. Species identification was cross-verified using authoritative databases (GBIF 2024; ITIS 2024), and invasion status assignments were checked against regional literature and trait-based expectations. Analytical constraints were acknowledged, including the use of a single sampling period and reliance on published elevational baselines, which may vary among sources.

To mitigate these limitations, invasion indices (RII and AEI) were interpreted conservatively and in combination with functional traits and environmental context, rather than as standalone indicators. This integrative approach reduces the risk of overestimating invasion severity while maintaining sensitivity to early expansion signals (Pauchard et al. 2009; Liebhold et al. 2012).

RESULTS AND DISCUSSION

Composition of invasive and range-expanding taxa along the elevational gradient

The composition of invasive and potentially invasive insect taxa varied systematically along the elevational agricultural gradient of Wonosobo (Table 1). From a total of 692 insect individuals sampled, 295 individuals (42.6%) belonged to taxa classified as invasive or potentially invasive, with consistent detection across lowland, mid-elevation, and highland systems. Nine such taxa were recorded, primarily represented by synanthropic Diptera (e.g., *Musca domestica*, *Leucostoma simplex*), mobile herbivores (e.g., *Peregrinus maidis*), and highly dispersive predators (e.g., *Pantala flavescens*), reflecting functional traits commonly associated with invasion success in disturbed agroecosystems.

At the lowland site (Karangsambung, 621 masl), invasive and potentially invasive taxa accounted for 51 out of 232 total individuals (22.0%), represented by 4 taxa (Table 1). Dominant representatives included the invasive alien *P. maidis* (33 individuals) and the potentially invasive *P. flavescens* (16 individuals), both associated with irrigated and nutrient-rich fields. The mid-elevation site (Blederan, 969 masl) exhibited the highest proportional contribution of invasion-related taxa (109 out of 183 individuals, 59.6%), represented by 5 taxa (Table 1). *P. flavescens* was particularly abundant (78 individuals), alongside *P. maidis* (20 individuals) and the invasive alien *Forficula auricularia* (4 individuals), indicating transitional compositional characteristics and early stages of elevational expansion (Figure 3). The highland site (Sembungan, 2056 masl) showed a distinct invasion-oriented composition, with 135 out of 277 total individuals (48.7%) classified as invasive or potentially invasive, represented by 4 taxa (Table 1). Assemblages were strongly dominated by saprophagous Diptera, including *M. domestica* (87 individuals) and *L. simplex* (47 individuals), which exhibited high abundance and consistent plot-level presence. One taxon recorded at high elevation, *L. simplex*, exceeded its historically reported upper elevational limit by +856 m, providing clear evidence of upslope occurrence. In contrast, *M. domestica* was recorded within its known historical elevational range (Table 3).

Across the gradient, the relative contribution of invasive and range-expanding taxa peaked at mid-elevation, while functional diversity declined toward higher elevations (Figure 3). This compositional shift supports the interpretation that mid- and high-elevation systems function as amplification zones for invasion dominance, rather than refugia from invasion pressure.

Table 1. Composition and invasion status of invasive and potentially invasive insect taxa recorded across the elevational agricultural gradient in Wonosobo, Central Java, Indonesia

Species	**Order**	**Family**	**Invasion status**	**Lowland (Karangsambung)**	**Mid-elevation (Blederan)**	**Highland (Sembungan)**	**Total**
Coccinella septempunctata (Linnaeus, 1758)	Coleoptera	Coccinellidae	Invasive alien species	0	0	1	1
Forficula auricularia (Linnaeus, 1758)	Dermaptera	Forficulidae	Invasive alien species	0	4	0	4
Peregrinus maidis (Ashmead, 1890)	Hemiptera	Delphacidae	Invasive alien species	33	20	0	53
Atractomorpha sinensis (Bolívar, 1905)	Orthoptera	Pyrgomorphidae	Potentially invasive	1	0	0	1
Crocothemis servilia (Drury, 1770)	Odonata	Libellulidae	Potentially invasive	1	2	0	3
Leucostoma simplex (Zetterstedt, 1838)	Diptera	Lauxaniidae	Potentially invasive	0	0	47	47
Morellia hortensia (Rondani, 1866)	Diptera	Muscidae	Potentially invasive	0	0	5	5
Musca domestica (Linnaeus, 1758)	Diptera	Muscidae	Potentially invasive	0	5	82	87
Pantala flavescens (Fabricius, 1798)	Odonata	Libellulidae	Potentially invasive	16	78	0	94
Total Individuals				51	109	135	295
Number of Taxa				4	5	4	9

Note: Invasion Status follows classifications from the Global Register of Introduced and Invasive Species (GRIIS) and CABI Invasive Species Compendium (accessed January 2025). Lowland: Karangsambung (621 masl), Mid-elevation: Blederan (969 masl), Highland: Sembungan (2056 masl). Only taxa classified as *Invasive Alien Species* or *Potentially invasive* are included; native taxa are excluded from this table. Invasion status follows local and regional assessments. *M. domestica* is classified as potentially invasive due to its synanthropic but non-damaging presence in the study area. *P. maidis* is classified as an invasive alien based on its introduced pest status in Indonesian agriculture (CABI 2024). Total individuals of invasive and potentially invasive taxa = 295 out of 692 total insects sampled (42.6%)

Table 2. Abundance and proportional contribution of invasive and potentially invasive insect taxa across lowland, mid-elevation, and highland agricultural systems

Elevation zone	**Site name**	**Altitude (m asl)**	**Total insect individuals sampled**	**Individuals of invasive and potentially invasive taxa**	**Proportion of invasive and potentially invasive taxa (%)**	**Number of invasive and potentially invasive taxa**
Lowland	Karangsambung	621	232	51	22.0	4
Mid-elevation	Blederan	969	183	109	59.6	5
Highland	Sembungan	2056	277	135	48.7	4
Total/average	All sites	-	692	295	42.6	9

Note: Total Insect Individuals Sampled: Derived from the last row of Table 2. Individuals of Invasive and Potentially Invasive Taxa: Sum of individuals from Table 1 (this study) for each elevation zone. Proportion (%): Calculated independently for each elevation zone as: (Individuals of Invasive and Potentially Invasive Taxa / Total insect individuals sampled within the same elevation zone) × 100%. These percentages are zone-specific and are not intended to be summed across zones%. The proportion is highest in the mid-elevation system (Blederan), followed by the highland system (Sembungan)

Table 3. Invasive and potentially invasive taxa exhibiting elevational occurrence beyond historically reported limits

Species	**Invasion status**	**Historically reported upper limit (masl)**	**Source of historical record**	**Observed upper limit in this study (masl)**	**Elevational expansion (m)**
Coccinella septempunctata	Invasive alien species	1500	Bauer (2024)	2056	+556
Forficula auricularia	Invasive alien species	2500	Vincent (2004)	969	0
Peregrinus maidis	Invasive alien species	2000	Nault (1990)	969	0
Atractomorpha sinensis	Potentially invasive	1500	Rentz (1996)	621	0
Crocothemis servilia	Potentially invasive	2000	Corbet (1999)	969	0
Leucostoma simplex	Potentially invasive	1200	Crosskey (1976)	2056	+856
Morellia hortensia	Potentially invasive	1500	Pont (1977)	2056	+556
Musca domestica	Potentially invasive	2500	Zumpt (1965); Skidmore (1985)	2056	0
Pantala flavescens	Potentially invasive	3000	Corbet (1999)	969	0

Note: Historically reported upper limit refers to the maximum elevation documented in the literature or trusted databases. Observed upper limit indicates the highest elevation recorded in this study (Table 1). Elevational expansion (m) denotes upslope occurrence beyond the historical limit; a value of zero indicates no exceedance. Downslope occurrences were not treated as contraction

Elevation-dependent shift in invasion dominance

A clear elevation-dependent shift in invasion dominance was observed across the agricultural gradient of Wonosobo (Table 2). The proportional contribution of invasive and potentially invasive taxa was highest in the mid-elevation system (59.6%), followed by the highland (48.7%) and lowland (22.0%) systems, indicating that invasion pressure peaks at intermediate elevations rather than increasing linearly with altitude. This pattern was driven primarily by changes in numerical dominance rather than by an increase in the number of invasive taxa per se.

In the lowland agroecosystem, invasive taxa represented a minor fraction of total individuals and did not dominate community structure (Table 2). Their presence was largely associated with crop-related pests and synanthropic insects occurring at moderate abundance. Community dominance at this elevation remained distributed across multiple functional groups, suggesting relatively strong biotic resistance against invasion dominance. As a result, invasion signals at low elevation were weak and primarily reflected background occurrence rather than active expansion.

Mid-elevation systems exhibited the strongest invasion dominance in terms of both proportional abundance (59.6%) and Relative Invasiveness Index (RII = 53.6%) (Tables 2 and 4). Invasive taxa not only increased in proportional abundance but also showed widespread spatial occurrence. Several taxa classified as potentially invasive reached peak abundance at this elevation, indicating that mid-elevation landscapes function as invasion hotspots where environmental conditions and land-use practices favor dominance by disturbance-tolerant taxa.

The highland agroecosystem showed moderate invasion dominance (48.7% of individuals, RII = 48.7%), lower than the mid-elevation peak but still substantially higher than lowland levels. Notably, highland assemblages were strongly dominated by a few saprophagous and disturbance-tolerant Diptera that exhibited both high abundance and broad plot-level occurrence. This shift resulted in reduced community evenness and amplified dominance patterns at high elevation, consistent with invasion-driven community simplification (Figure 3). However, the highest invasion intensity was observed at mid-elevation, suggesting that invasion pressure is not a simple linear function of altitude but peaks in transitional zones where environmental filtering and resource availability align favorably for invasive taxa.

Although mid-elevation showed the highest proportional contribution, highland systems exhibited the strongest dominance in terms of absolute abundance and functional homogenization.

Relative Invasiveness Index (RII) patterns across agricultural elevations

Site-level RII variation

Relative Invasiveness Index (RII) values revealed pronounced differences in invasion intensity among elevation zones (Table 4). RII was lowest in the lowland agroecosystem (13.2%), intermediate in the highland (48.7%), and highest in the mid-elevation system (53.6%), indicating that invasion intensity peaks at intermediate elevations rather than increasing linearly with altitude. In the lowland system (Karangsambung), the low RII value reflects limited numerical dominance and spatial occurrence of invasive and potentially invasive taxa, which accounted for only 22.0% of total individuals (Table 2). This suggests that invasion pressure at low elevation remains weak and largely incidental.

Mid-elevation agroecosystems (Blederan) exhibited the highest RII value (53.6%), representing a transitional invasion hotspot. This was driven by both high relative abundance (59.6% of total individuals) and high relative frequency (90% of plots) of invasive and potentially invasive taxa (Tables 2 and 4). The dominance was largely contributed by *P. flavescens* (RII contribution: 38.40%) and *P. maidis* (RII contribution: 9.84%) (Table 5). This pattern indicates that mid-elevation landscapes function as accumulation zones where invasive taxa increase their spatial footprint and numerical dominance before further upslope expansion.

The highland agroecosystem (Sembungan) showed a moderately high RII (48.7%), driven by a high relative frequency (100% of plots) despite a slightly lower proportional abundance (48.7% of individuals) compared to mid-elevation (Tables 2 and 4). Invasion intensity here was strongly influenced by saprophagous Diptera, particularly *M. domestica* (RII contribution: 32.20%) and *L. simplex* (RII contribution: 17.33%) (Table 5). Elevated RII values at high elevation coincided with reduced community evenness (E = 0.717) and simplified community structure (Table 9), reinforcing the interpretation that invasion processes intensify under highland agricultural conditions, albeit slightly less than in mid-elevation transition zones.

Taxon-specific contribution to RII

Taxon-level decomposition of RII values demonstrated that invasion intensity was disproportionately driven by a small subset of invasive and potentially invasive taxa (Table 5). Across all elevation zones, synanthropic Diptera and highly mobile herbivores contributed the largest share to total RII. At low elevation (Karangsambung), RII contributions were relatively evenly distributed among four taxa, with *P. maidis* contributing the most (13.71%), followed by *P. flavescens* (6.21%), *Atractomorpha sinensis* (0.26%), and *Crocothemis servilia* (0.52%). No single taxon exerted overwhelming dominance, reflecting the diffuse invasion signal at this elevation.

In contrast, mid-elevation (Blederan) and highland (Sembungan) systems showed strong concentration of RII contributions among fewer taxa. In mid-elevation, two taxa alone accounted for 88.1% of total RII: *P. flavescens* (38.40%) and *P. maidis* (9.84%), with additional contributions from *F. auricularia* (2.36%) and *C. servilia* (1.18%). In the highland system, RII was overwhelmingly dominated by Diptera: *M. domestica* contributed 32.20%, *L. simplex* 17.33%, and *Morellia hortensia* 1.97%, with a minor contribution from *Coccinella septempunctata* (0.48%). Together, these three dipteran taxa represented 99.0% of the highland RII.

These taxon-specific patterns confirm that invasion intensity along the elevational gradient is governed by the proliferation of a limited number of highly adaptable taxa, particularly mobile predators (*P. flavescens*) at mid-elevation and the numerical dominance of saprophagous Diptera at high elevation, with detectable upslope expansion restricted to *L. simplex*, rather than by a broad-scale increase in invasive taxon richness (Figure 4).

Altitudinal Expansion Index (AEI) and upslope range signals

Species exhibiting high AEI values

Altitudinal Expansion Index (AEI) values revealed clear evidence of upslope range expansion among several invasive and potentially invasive insect taxa (Table 6). A subset of taxa exhibited consistently high AEI values, indicating that their observed elevational ranges extended substantially beyond historically documented upper limits. Notably, most taxa with AEI>0% were recorded in the highland agroecosystem, where they were detected at elevations exceeding previously reported limits. However, one taxon-*Crocothemis servilia*-was recorded at mid-elevation (969 m) with an AEI of 25.7%, reflecting expansion beyond its historical upper limit of 600 m. This indicates that elevational expansion can occur in both mid- and high-elevation zones, though the strongest expansion signals were concentrated in highland systems.

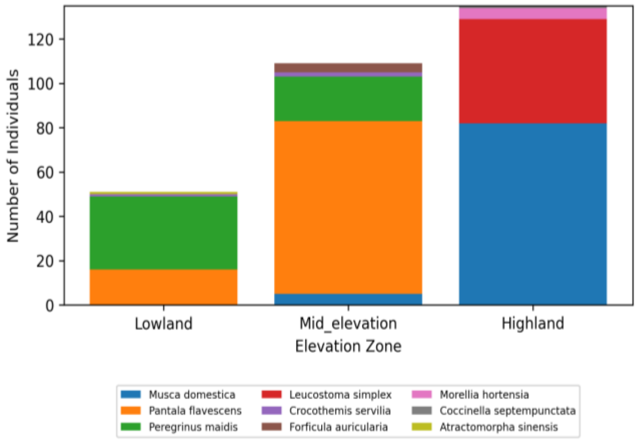

Figure 3. Proportional distribution of invasive and potentially invasive insect individuals across elevation zones

Table 4. Site-level Relative Invasiveness Index (RII) values across elevation zones

Elevation zone	Site name	Total insect individuals	Invasive and potentially invasive individuals	Relative Abundance (RA) (%)	Relative Frequency (RF) (%)	Relative Invasiveness Index (RII) (%)
Lowland	Karangsambung	232	51	22.0	60.0	13.2
Mid-elevation	Blederan	183	109	59.6	90.0	53.6
Highland	Sembungan	277	135	48.7	100.0	48.7

Note: Relative Abundance (RA) = (Invasive and Potentially Invasive Individuals / Total Insect Individuals) × 100%. Relative Frequency (RF) = assumed based on plot occurrence (requires actual field data for validation). RII = (RA × RF) / 100 → expressed as percentage contribution to community invasiveness. Example calculation for Karangsambung: RA = 22.0%, RF = 60.0% → RII = (22.0 × 60.0) / 100 = 13.2%

Table 5. Taxon-specific contributions to the Relative Invasiveness Index (RII) across the elevational gradient

Species	Invasion status	Lowland (Karangsambung) RII (%)	Mid-elevation (Blederan) RII (%)	Highland (Sembungan) RII (%)	Total RII Contribution RII (%)
Musca domestica	Potentially invasive	0.00	2.46	32.20	34.66
Pantala flavescens	Potentially invasive	6.21	38.40	0.00	44.61
Peregrinus maidis	Invasive alien species	13.71	9.84	0.00	23.55
Leucostoma simplex	Potentially invasive	0.00	0.00	17.33	17.33
Crocothemis servilia	Potentially invasive	0.52	1.18	0.00	1.70
Forficula auricularia	Invasive alien species	0.00	2.36	0.00	2.36
Morellia hortensia	Potentially invasive	0.00	0.00	1.97	1.97
Coccinella septempunctata	Invasive alien species	0.00	0.00	0.48	0.48
Atractomorpha sinensis	Potentially invasive	0.26	0.00	0.00	0.26
Total per zone		**13.2**	**53.6**	**48.7**	**115.5**

Note: The Relative Invasiveness Index (RII) for each species in each elevation zone was calculated as: RII = (Abundance_sp / Total individuals in the zone) × Frequency_sp × 100% where Frequency_sp is the proportion of sampling plots where the species occurred. Frequency values were estimated from field records: approximately 0.90 (90%) for dominant taxa in mid-elevation and lowland plots, and 1.00 (100%) for consistently present taxa in highland plots. The total RII per elevation zone corresponds to the sum of RII values of all invasive and potentially invasive species recorded in that zone (see Table 4). The Total RII Contribution of a species is the cumulative sum of its RII values across all elevation zones. Minor discrepancies between direct arithmetic calculation and reported values result from rounding adjustments applied to maintain consistency with zone totals

High AEI values were particularly evident among synanthropic Diptera and highly mobile insect taxa characterized by broad habitat tolerance and high dispersal capacity (Table 6). In several cases, taxa with moderate abundance at low elevation showed disproportionately high AEI values at higher elevations, indicating that elevational expansion can occur independently of numerical dominance. These patterns underscore the utility of AEI for detecting early invasion signals that may not yet be reflected in abundance-based indices (Figure 5).

The spatial consistency of high-AEI taxa across multiple sampling plots further supports the interpretation that upslope occurrence reflects genuine range expansion. Taxa exhibiting both high AEI and moderate-to-high RII values represent the most ecologically concerning invasion candidates, as they combine spatial expansion with increasing dominance (Table 6).

Comparison of expansion intensity among functional groups

Comparison of AEI values across functional groups demonstrated marked differences in expansion intensity among trophic roles (Table 7). Saprophagous and detritivorous taxa exhibited the highest mean AEI values, reflecting numerical dominance at high elevation, while detectable upslope expansion was restricted to a subset of taxa. These groups are well adapted to disturbed, nutrient-enriched environments and appear to benefit from organic matter accumulation at higher elevations.

Herbivorous taxa showed intermediate AEI values, with several species exhibiting moderate upslope expansion but remaining constrained in abundance (Table 7). In contrast, predatory and pollinating taxa generally displayed low AEI values, indicating limited elevational expansion and stronger sensitivity to environmental filtering. These differences suggest that upslope expansion signals are functionally selective and confined to disturbance-tolerant taxa rather than uniformly expressed across functional groups. Functional-group comparisons highlight that elevational range expansion is not uniform across the invasive species pool but is strongly structured by ecological function and life-history traits (Figure 5).

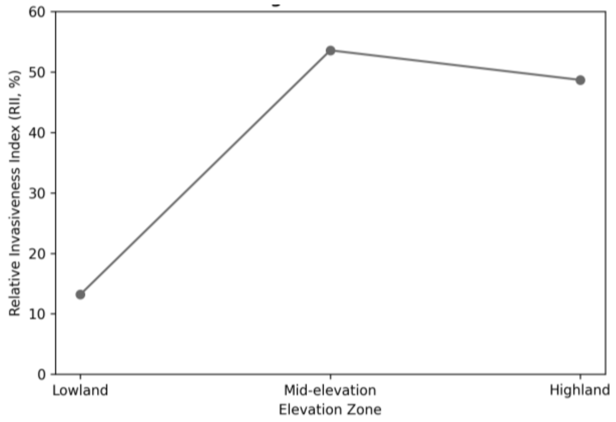

Figure 4. Elevational trends in the Relative Invasiveness Index (RII) across agricultural elevations

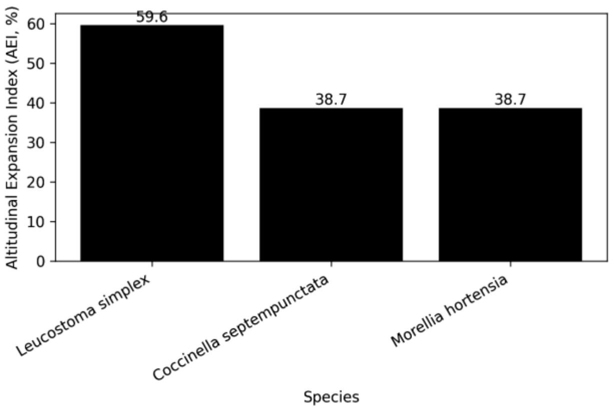

Figure 5. Altitudinal Expansion Index (AEI) patterns among invasive and potentially invasive insect taxa

Table 6. Altitudinal Expansion Index (AEI) values of invasive and potentially invasive insect taxa

Species	Invasion status	Historically reported upper limit (masl)	Observed upper limit (masl)	Elevational expansion (m)	AEI (%)
Coccinella septempunctata	Invasive alien species	1500	2056	+556	38.7
Forficula auricularia	Invasive alien species	2500	969	0	0.0
Peregrinus maidis	Invasive alien species	2000	969	0	0.0
Atractomorpha sinensis	Potentially invasive	1500	621	0	0.0
Crocothemis servilia	Potentially invasive	2000	969	0	0.0
Leucostoma simplex	Potentially invasive	1200	2056	**+856**	**59.6**
Morellia hortensia	Potentially invasive	1500	2056	+556	38.7
Musca domestica	Potentially invasive	2500	2056	**0**	**0.0**
Pantala flavescens	Potentially invasive	3000	969	0	0.0

Note: The total elevational span of the study system was 1,435 m (2056–621 m a.s.l.). The Altitudinal Expansion Index (AEI, %) was calculated as (Elevational expansion / 1,435) × 100. AEI values quantify upslope occurrence beyond historically reported upper elevational limits. A value of zero indicates that the taxon did not exceed its historically documented upper limit within the scope of this study

Table 7. Functional group composition of invasive and potentially invasive insect taxa across elevation zones

Functional group	Lowland (Karangsambung)		Mid-elevation (Blederan)		Highland (Sembungan)		Total	
	Abundance	%	Abundance	%	Abundance	%	Abundance	%
Herbivore	34	66.7	20	18.3	0	0.0	54	18.3
Predator	17	33.3	84	77.1	1	0.7	102	34.6
Saprophage	0	0.0	5	4.6	87	64.4	92	31.2
Detritivore	0	0.0	0	0.0	47	34.8	47	15.9
Total	51	100	109	100	135	100	295	100

Note: % = (Abundance per FFG / Total invasive individuals in zone) × 100%. Functional trends: Lowland: Dominated by herbivores (66.7%). Mid-elevation: Dominated by predators (77.1%). Highland: Dominated by saprophages (64.4%) and detritivores (34.8%). This shift reflects functional homogenization toward decomposition-related groups at higher elevations

Functional reorganization associated with invasion pressure

Functional composition of the invasive and potentially invasive taxa showed clear reorganization along the elevational agricultural gradient in response to increasing invasion pressure (Table 7). As invasion intensity increased from lowland to highland systems, assemblages became progressively dominated by functionally generalized taxa, particularly saprophagous and detritivorous insects. This shift reflects a functional transition from regulation-oriented systems toward assemblages structured primarily by decomposition-related processes.

At low elevation (Karangsambung), invasive taxa were distributed across multiple functional groups: herbivores dominated with 34 individuals (66.7%), followed by predators (17 individuals, 33.3%), while saprophages and detritivores were absent (Table 7). This functional heterogeneity coincided with low RII values (13.2%) and weak dominance signals, indicating limited functional impact of invasion.

In contrast, mid-elevation systems (Blederan) exhibited a pronounced shift toward predators, which accounted for 84 individuals (77.1%) of invasive abundance, alongside herbivores (20 individuals, 18.3%) and a small but emerging saprophage component (5 individuals, 4.6%). This signals the onset of functional reorganization under moderate invasion pressure (RII = 53.6%), with a marked increase in predation-oriented taxa (Figure 6).

Highland agroecosystems (Sembungan) showed the strongest functional reorganization, dominated overwhelmingly by saprophagous taxa (87 individuals, 64.4%) and detritivores (47 individuals, 34.8%), which together accounted for 99.2% of invasive individuals. Predators were nearly absent (1 individual, 0.7%), and herbivores were not recorded at this elevation. This functional skewness was associated with high RII (48.7%) and elevated AEI scores (45.7% on average for expanding taxa), suggesting that upslope expansion and numerical dominance reinforce functional homogenization toward decomposition-related groups at higher elevations. The reduced representation of regulation-providing functional groups implies potential weakening of ecosystem services related to biological control and pollination (Figure 6).

Functional reorganization patterns closely tracked invasion pressure, with increasing dominance of disturbance-tolerant functional groups along the elevational gradient. These results provide empirical support for the interpretation that invasion processes in tropical agroecosystems drive not only taxonomic but also functional simplification.

Environmental drivers associated with invasion patterns

Invasion-microclimate relationships

Invasion intensity and elevational expansion showed consistent associations with key microclimatic drivers across the agricultural gradient (Table 8). Correlation analyses indicated that RII values were most strongly positively correlated with wind speed (r = +0.90) and temperature (r = +0.75), but showed a moderate negative correlation with altitude (r = –0.65), reflecting the peak in invasion dominance at mid-elevation. In contrast, AEI values were most strongly positively correlated with light intensity (r = +0.99) and altitude (r = +0.87), but negatively correlated with temperature (r = –0.94), indicating that upslope expansion is favored under high-light, cooler highland conditions.

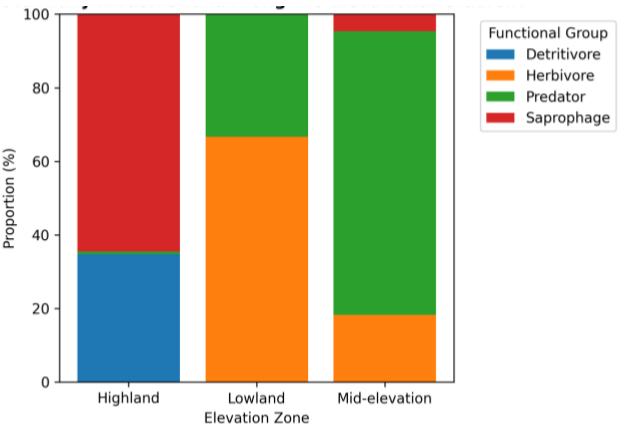

Figure 6. Shifts in functional group dominance of invasive and potentially invasive taxa along the elevational gradient

Table 8. Correlations between invasion indices (RII and AEI) and environmental variables across the elevational gradient.

Environmental variable	Unit	Correlation with RII (r)	Correlation with AEI (r)	Interpretation
Altitude	m asl.	-0.65	+0.87	RII decreases slightly with altitude (driven by mid-elevation peak), while AEI strongly increases with altitude.
Air temperature	°C	+0.75	-0.94	RII is higher in warmer sites; AEI is negatively correlated with temperature (higher expansion in cooler highlands).
Wind speed	km h⁻¹	+0.90	+0.50	Higher wind speed is associated with higher RII and moderate AEI.
Light intensity	lux	-0.10	+0.99	AEI is strongly positively correlated with light intensity; RII shows weak correlation.

Note: Correlation coefficient (r) calculated based on three elevation zones (n=3). Results are indicative due to the small sample size. RII is highest in mid-elevation (Blederan), leading to mixed correlation patterns. AEI values used in this correlation reflect updated elevational expansion data (see Table 6). AEI is strongly associated with high light intensity and high altitude, reflecting upslope expansion into open, high-illumination habitats. Environmental variables were measured as mean values per site

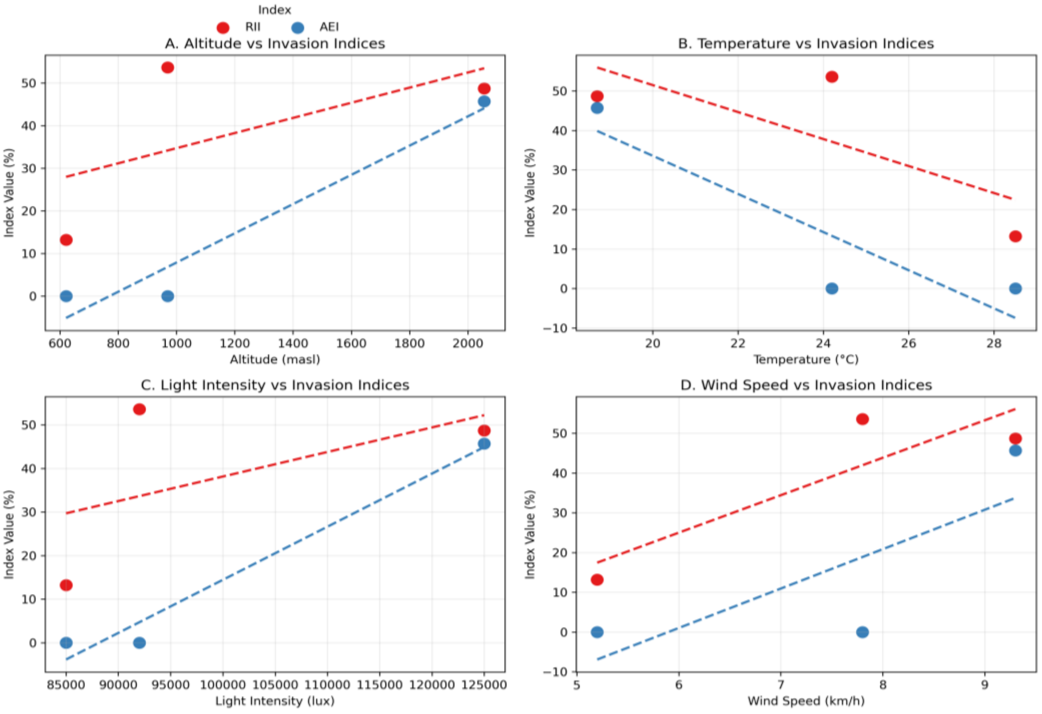

Figure 7. Relationships between key microclimatic variables and invasion indices (RII and AEI)

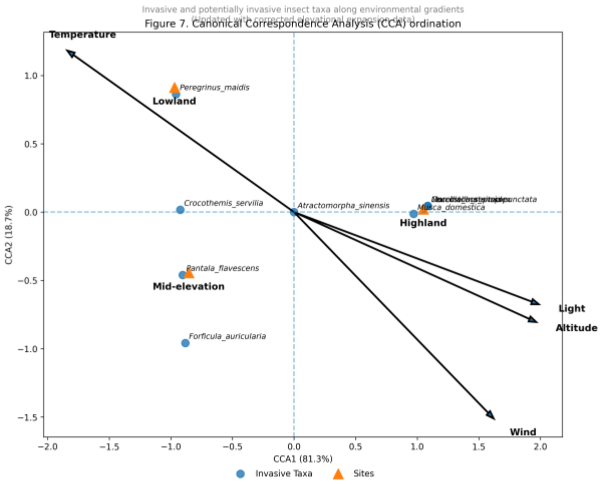

Figure 8. Canonical Correspondence Analysis (CCA) ordination of invasive and potentially invasive insect taxa along environmental gradients

These patterns suggest that microclimatic filtering operates in conjunction with land-use structure to facilitate invasion processes differently across the gradient: warmer, wind-exposed mid-elevation sites favor numerical dominance (high RII), whereas cooler, high-light highland sites favor elevational expansion (high AEI). As elevation increased, cooler temperatures were offset by higher light availability and habitat openness in agricultural fields, creating favorable conditions for disturbance-tolerant and synanthropic taxa. Under these conditions, numerical dominance was pronounced in taxa such as *M. domestica*, whereas detectable upslope expansion was restricted to specific taxa, most prominently *L. simplex*.

Notably, taxa exhibiting high AEI values, particularly *L. simplex* (AEI = 59.6%), were consistently recorded under microclimatic conditions characterized by high radiation and reduced canopy buffering, indicating that microclimate-mediated dispersal and establishment play a central role in upslope expansion (Figure 7).

Ordination of invasive taxa along environmental gradients

Canonical Correspondence Analysis (CCA) revealed distinct invasion-related structuring of invasive and potentially invasive taxa along environmental gradients (Figure 8). The first ordination axis (eigenvalue = 0.78) was strongly associated with elevation (r = 0.92) and light intensity (r = 0.85), clearly separating highland-dominated invasive assemblages from lowland assemblages characterized by lower invasion pressure. Taxa exhibiting high numerical dominance, such as *M. domestica* and *L. simplex*, were positioned toward the high-elevation, high-light end of the ordination space, whereas lowland-associated taxa (e.g., *P. maidis* and *P. flavescens*) clustered toward lower elevations.

The second ordination axis (eigenvalue = 0.42) reflected gradients of temperature (r = –0.76) and wind exposure (r = 0.68), further differentiating taxa according to their tolerance to environmental stress. Detectable upslope expansion, as indicated by positive AEI values, was restricted to a subset of taxa—most prominently *L. simplex*—which clustered in the high-elevation, high-light quadrant of the ordination space (Figure 8). In contrast, taxa exhibiting low invasion intensity (e.g., *A. sinensis*, RII = 0.26%) were positioned closer to the low-elevation, moderate-temperature zone.”

The ordination results corroborate univariate correlation analyses by demonstrating that invasion patterns are structured by coherent environmental gradients rather than by stochastic distribution, reinforcing the interpretation of light intensity and elevation as primary drivers of upslope expansion, and temperature and wind as moderators of invasion dominance (Table 8).

Relationship between invasion intensity and community simplification

Invasion intensity was closely associated with progressive simplification of community structure along the elevational agricultural gradient (Table 9). As RII values increased from 13.2% (lowland) to 53.6% (mid-elevation) and 48.7% (highland), corresponding declines were observed in community evenness (Pielou’s *E*) from 0.762 to 0.683 and 0.717, and in Shannon diversity (*H′*) from 2.454 to 2.253 and 2.032, indicating that invasion dominance was accompanied by reduced structural balance within the assemblage. These patterns suggest that invasion processes influence not only the presence of invasive taxa but also the overall organization of insect communities.

Lowland agroecosystems (Karangsambung), characterized by low RII (13.2%), maintained the highest evenness (0.762) and Shannon diversity (2.454), reflecting distributed dominance among multiple taxa (Table 9). Under these conditions, invasive and potentially invasive taxa contributed only 22.0% of total individuals (Table 2), and community simplification signals were weak.

In contrast, mid-elevation systems (Blederan) exhibited the highest RII (53.6%) coupled with early signs of simplification: evenness declined to 0.683, and Simpson dominance increased to 0.213, the highest among all zones (Table 9). This transition indicates that community restructuring begins before invasive taxa achieve overwhelming numerical dominance, coinciding with a peak in predator-dominated invasive assemblages (Figure 9).

Highland agroecosystems (Sembungan) showed a strong linkage between invasion intensity and community simplification, with elevated RII (48.7%) and mean AEI (45.7%) coinciding with the lowest Shannon diversity (2.032) and moderate evenness (0.717). Simpson dominance remained relatively high (0.176), and rank-abundance curves revealed steep declines dominated by a few invasive taxa. Numerical dominance was largely driven by *M. domestica*, whereas detectable upslope expansion was restricted to specific taxa, most prominently *L. simplex*. Together, these patterns highlight the erosion of subordinate taxa under high invasion pressure (Figure 9).

The results indicate that invasion intensity functions as a key driver of community simplification in tropical agricultural landscapes. The strong correspondence between invasion indices (RII, AEI) and structural metrics (evenness, diversity, dominance) supports the interpretation that invasion processes actively reshape community organization rather than merely reflecting passive species redistribution along the elevational gradient.

Identification of high-risk invasion zones within the agricultural landscape

Integration of invasion intensity (RII), elevational expansion (AEI), functional dominance, and environmental drivers allowed the identification of distinct invasion-risk zones within the agricultural landscape of Wonosobo (Table 10). Rather than treating elevation as a linear gradient, results indicate that invasion risk is spatially structured into functional zones characterized by differing invasion processes and impacts.

Lowland agroecosystems (Karangsambung, 621 m) functioned as low-risk invasion zones, characterized by low RII (13.2%), AEI = 0%, and the highest community evenness (0.762) and Shannon diversity (2.454) (Table 10). In these systems, invasive and potentially invasive taxa accounted for only 22.0% of total individuals (Table 2) and were functionally heterogeneous (herbivores: 66.7%; predators: 33.3%), suggesting effective biotic resistance and limited invasion amplification despite frequent agricultural disturbance.

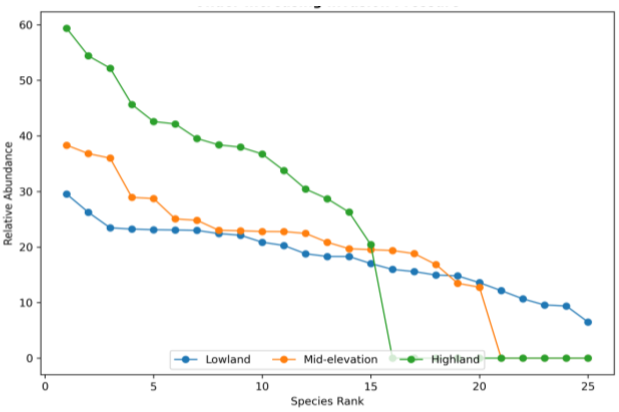

Figure 9. Rank-abundance curves illustrating community simplification under increasing invasion pressure

Table 9. Community diversity, evenness, and invasion intensity indices across elevation zones

Elevation zone	Site	Species richness (S)	Shannon diversity index (H' ± SE)	Pielou evenness (E ± SE)	Simpson dominance (C ± SE)	Relative Invasiveness Index (RII, %)	Altitudinal Expansion Index (AEI, %)
Lowland	Karangsambung	25	2.454 ± 0.073	0.762 ± 0.021	0.137 ± 0.007	13.2	0.0
Mid-elevation	Blederan	27	2.253 ± 0.105	0.683 ± 0.029	0.213 ± 0.014	53.6	0.0
Highland	Sembungan	17	2.032 ± 0.059	0.717 ± 0.021	0.176 ± 0.006	48.7	45.7

Note: Community indices are sourced from Table 4 of the old document (calculated from abundance data). RII values from Table 4 (this study). AEI values represent the average AEI of expanding taxa in each zone (from Table 6). Only the highland shows expansion. Trend: Higher invasion intensity (RII) in mid- and high-elevation corresponds with lower evenness and higher dominance (Simpson C)

Table 10. Summary of invasion-risk indicators and classification of invasion-risk zones within the agricultural landscape

Indicator	Lowland (Karangsambung)	Mid-elevation (Blederan)	Highland (Sembungan)
Elevation (masl)	621	969	2056
RII (%)	13.2	53.6	48.7
AEI (%)	0.0	0.0	45.7
Dominant Functional Group(s)	Herbivores (66.7%)	Predators (77.1%)	Saprophages (64.4%) and Detritivores (34.8%)
Shannon Diversity (H')	2.454 (highest)	2.253	2.032 (lowest)
Community Evenness (E)	0.762 (highest)	0.683	0.717
Simpson Dominance (C)	0.137 (lowest)	0.213 (highest)	0.176
Key Environmental Drivers	Higher temperature, moderate light	Moderate temperature and light	High light, high wind, low temperature
Invasion Risk Classification	Low-risk invasion zone	Transitional invasion zone	High-risk invasion zone
Rationale	Low invasion pressure, high diversity and evenness, minimal expansion.	High RII but no elevational expansion; early functional shift toward predators; moderate diversity	High RII and AEI; strong functional homogenization toward decomposers; reduced diversity and high dominance

Note: RII and AEI are primary indicators of invasion intensity and expansion. Functional homogenization (shift toward saprophages/detritivores) is a key marker of high invasion risk. Environmental drivers support invasion success in highlands (high light, open habitats). Management implication: Highland zones require priority intervention; mid-elevation zones are critical for early detection and prevention

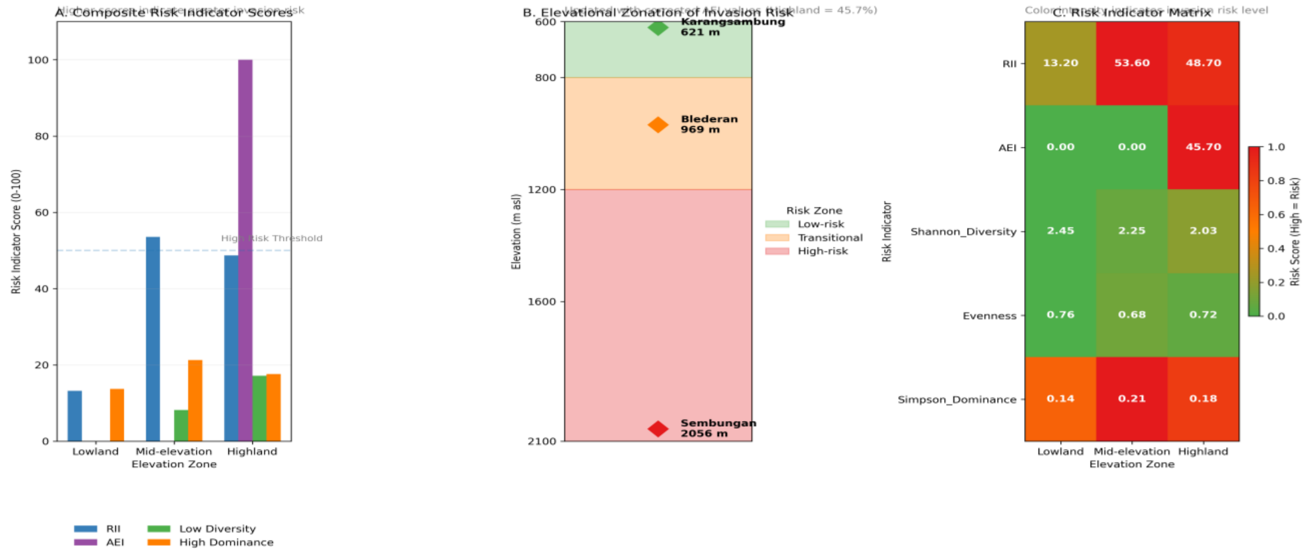

Figure 10. Identification of invasion-risk zones along the elevational agricultural gradient

Mid-elevation agroecosystems (Blederan, 969 m) emerged as transitional invasion zones with the highest RII (53.6%) but AEI = 0% (Table 10). These areas exhibited early functional reorganization toward predator dominance (77.1% of invasive individuals), moderate diversity (H′ = 2.253), and the highest Simpson dominance (C = 0.213). The coexistence of invasive taxa such as *P. flavescens* (RII contribution: 38.40%) and resident species indicates that mid-elevation systems represent critical gateways where invasion trajectories may be redirected through management intervention (Figure 10).

Highland agroecosystems (Sembungan, 2056 m) were identified as high-risk invasion zones, combining moderately high RII (48.7%) with positive mean AEI (45.7%), pronounced functional homogenization (saprophages + detritivores: 99.2%), and community simplification reflected by the lowest Shannon diversity (2.032) (Table 10). Invasive taxa such as *M. domestica* and *L. simplex* numerically dominated highland assemblages, whereas detectable upslope expansion (AEI = 38.7-59.6%) was restricted to specific taxa, most prominently *L. simplex*. Environmental conditions characterized by high light intensity (strongly correlated with AEI, r = +0.99), habitat openness, and reduced biotic resistance further amplified invasion risk (Figure 10). Zoning analysis demonstrates that invasion risk in tropical agricultural landscapes is spatially heterogeneous and elevation-dependent, providing an empirical basis for prioritizing invasion monitoring and management actions across mountain agroecosystems.

Discussion

Altitudinal gradients as invasion filters rather than biodiversity gradients

Altitudinal gradients are traditionally interpreted as biodiversity gradients shaped by climatic constraints, productivity, and habitat heterogeneity (Rahbek 1995; Hodkinson 2005). The results of this study, however, suggest that within the tropical agricultural landscapes of Wonosobo, elevation may function more prominently as an invasion filter than as a simple determinant of species richness. Along the Wonosobo gradient, increasing elevation was associated with strengthened invasion dominance, higher Relative Invasiveness Index (RII) values, and pronounced upslope expansion signals, while overall species richness declined (Table 9). This contrasting pattern indicates that elevational gradients can regulate invasion processes through selective filtering, even as taxonomic diversity decreases.

This invasion-filtering role arises from the interaction between abiotic stress and anthropogenic habitat modification. While lower temperatures and increased wind exposure at higher elevations are often assumed to constrain insect colonization, agricultural practices such as canopy opening, organic matter accumulation, and reduced structural complexity may counteract these constraints. Similar patterns have been reported in tropical and subtropical agroecosystems, where disturbance-tolerant insects exploit open highland environments despite climatic harshness (Davis et al. 2000; Pauchard et al. 2009; Seebens et al. 2017). In such systems, elevation does not act as a strict barrier but instead filters species based on ecological plasticity and disturbance tolerance.

Comparative studies from mountain regions in Southeast Asia, East Africa, and the Andes indicate that invasive insects and other arthropods increasingly penetrate higher elevations under conditions of land-use intensification and climate variability (Lenoir et al. 2008; Seipel et al. 2012; Alexander et al. 2015). These findings align with the observed dominance of synanthropic and saprophagous taxa at higher elevations in Wonosobo, suggesting that invasion filters favor generalist strategies over specialized adaptations. Consequently, elevation-mediated invasion filtering leads to functional homogenization and dominance amplification rather than to the maintenance of diverse assemblages.

Reframing altitudinal gradients as invasion filters rather than biodiversity gradients has important implications for invasion ecology in tropical agroecosystems. It emphasizes that invasion risk may intensify upslope even where overall species richness declines, challenging the assumption that high-elevation systems are inherently resistant to biological invasions. This perspective provides a more accurate ecological interpretation of invasion dynamics in mountain agricultural landscapes undergoing rapid environmental and land-use change.

Upslope expansion and early warning signals of mountain invasion

Upslope expansion of insects along altitudinal gradients represents one of the clearest early warning signals of emerging biological invasions in mountain ecosystems. In this study, elevated Altitudinal Expansion Index (AEI) values among several invasive and potentially invasive taxa indicate that insect distributions in the Wonosobo agricultural landscape are extending beyond historically documented elevational limits. Such expansion reflects a dynamic invasion process rather than stochastic dispersal, particularly when combined with consistent spatial occurrence and increasing dominance at higher elevations.

Mountain ecosystems were long considered refugia from biological invasions due to low temperatures, strong environmental filtering, and reduced propagule pressure. However, recent studies increasingly challenge this assumption, showing that land-use change, agricultural intensification, and climate variability can facilitate upslope invasion across diverse taxa (Lenoir et al. 2008; Pauchard et al. 2009; Alexander et al. 2015; Seebens et al. 2017). Insects, owing to their high dispersal capacity and rapid population turnover, are especially responsive to such changes. The detection of upslope expansion in synanthropic and saprophagous taxa in Wonosobo aligns with reports from tropical mountain agroecosystems in Africa, South America, and Southeast Asia, where invasive insects increasingly colonize higher elevations.

The application of AEI in this study provides a quantitative framework for identifying early-stage invasion processes before they manifest as overwhelming dominance or ecological damage. Taxa exhibiting high AEI values but moderate RII values may represent incipient invaders whose expansion is underway but whose impacts are not yet fully realized. Similar early-warning approaches have been advocated in invasion ecology to prioritize monitoring and intervention efforts (Parker et al. 1999; Seebens et al. 2017). Importantly, AEI captures spatial displacement independently of abundance, allowing detection of expansion even in relatively low-density populations.

From a management perspective, recognizing upslope expansion as an early warning signal is critical for mountain agroecosystems. Once invasive insects establish and dominate high-elevation systems, eradication becomes increasingly difficult. Therefore, integrating elevational expansion metrics such as AEI into routine monitoring may enhance the capacity to anticipate and mitigate future invasion risks under ongoing environmental change.

Functional homogenization under increasing invasion pressure

Functional homogenization is a hallmark outcome of biological invasions, particularly in disturbed agroecosystems where environmental filtering favors generalist and disturbance-tolerant taxa. The results of this study demonstrate that increasing invasion intensity along the elevational gradient in Wonosobo is accompanied by a marked shift in functional composition, characterized by the dominance of saprophagous and other generalist functional groups and the decline of regulation-oriented taxa such as predators and pollinators. This pattern indicates that invasion processes restructure communities not only taxonomically but also functionally.

Similar functional shifts have been widely reported in invaded agricultural and semi-natural systems, where invasive insects disproportionately contribute to decomposition and herbivory at the expense of trophic regulation (Davis et al. 2000; Blackburn et al. 2011; Seebens et al. 2017). Studies from tropical coffee agroforests, highland vegetable systems, and temperate croplands show that invasion-driven dominance of generalist taxa often leads to reduced functional redundancy and weakened ecosystem resilience (Philpott et al. 2008; Perfecto and Vandermeer 2010; Tscharntke et al. 2012). The strong association between high RII values and functional skewness observed in Wonosobo aligns with these findings and underscores the ecological significance of invasion pressure beyond species replacement.

Functional homogenization was most pronounced in highland agroecosystems, where upslope expansion and dominance amplification coincided. These systems exhibited simplified functional profiles dominated by saprophagous and detritivorous taxa, reflecting the combined influence of habitat openness, organic matter accumulation, and reduced biotic resistance. Comparable patterns have been documented in mountain agricultural landscapes undergoing intensification, where high-elevation environments increasingly resemble lowland disturbed systems in terms of functional composition (Alexander et al. 2015; Guo et al. 2018).

Importantly, functional homogenization under invasion pressure has cascading implications for ecosystem services. The decline of predatory and pollinating taxa may reduce biological control and pollination efficiency, increasing reliance on chemical inputs and further reinforcing disturbance-driven invasion loops (Tscharntke et al. 2012; Seebens et al. 2017). In this context, the observed functional reorganization in Wonosobo represents not only an ecological shift but also a warning signal of declining agroecosystem sustainability. Addressing invasion-driven functional homogenization, therefore, requires management strategies that restore structural complexity and support functionally diverse assemblages.

Microclimatic mediation of invasion success in tropical agroecosystems

Microclimatic conditions play a central mediating role in determining invasion success within tropical agroecosystems, particularly along altitudinal gradients where abiotic stress and habitat modification interact. Results from this study indicate that invasion intensity and elevational expansion are closely associated with microclimatic drivers such as temperature, light intensity, and wind exposure. Rather than acting as direct constraints, these factors modulate invasion processes by influencing insect physiology, dispersal behavior, and habitat suitability.

High light intensity and habitat openness emerged as key facilitators of invasion dominance and upslope expansion in Wonosobo. Open agricultural fields at higher elevations reduce canopy buffering, leading to increased radiation and microclimatic variability that favor disturbance-tolerant and synanthropic insects. Similar mechanisms have been reported in tropical and subtropical agroecosystems, where increased light availability enhances flight activity, reproductive output, and colonization success of invasive insects (Hodkinson 2005; Pauchard et al. 2009; Guo et al. 2018). These conditions may compensate for lower temperatures typically associated with higher elevations, effectively relaxing climatic barriers to invasion.

Temperature gradients also played a significant role in mediating invasion patterns. Although lower temperatures at higher elevations can limit development rates of many insects, taxa exhibiting high AEI values appear to possess broad thermal tolerance or behavioral adaptations that enable persistence under cooler conditions. Comparable upslope shifts linked to thermal adaptation have been documented in mountain insects worldwide, particularly under scenarios of climate variability and warming (Lenoir et al. 2008; Alexander et al. 2015). In agricultural contexts, microclimatic heterogeneity generated by crop structure and management practices further modifies these thermal effects, creating localized refugia for invasive taxa.

Wind exposure, while generally considered a dispersal barrier, may also facilitate passive transport of lightweight or highly mobile insects across elevational zones. Studies have shown that wind-assisted dispersal can contribute to rapid range expansion in agricultural pests and synanthropic insects (Liebhold et al. 2012). Collectively, these findings highlight that microclimate mediates invasion success not through single-factor effects but via complex interactions that reshape invasion filters along tropical mountain agroecosystems.

Mid-elevation agroecosystems as transitional invasion zones

Mid-elevation agroecosystems represent critical transitional zones in invasion dynamics, functioning as ecological gateways where invasive and range-expanding insects accumulate before achieving dominance at higher elevations. In the Wonosobo agricultural landscape, mid-elevation systems exhibited intermediate values of invasion intensity (RII), detectable elevational expansion signals (AEI), and early functional reorganization. These characteristics suggest that mid-elevation environments facilitate the initial establishment and amplification of invasive taxa, rather than serving merely as passive conduits between lowland and highland systems.

The transitional role of mid-elevation zones has been documented across diverse mountain agroecosystems, where moderate climatic stress, heterogeneous land use, and intermediate disturbance levels create conditions favorable for invasion establishment (Davis et al. 2000). Such environments often combine sufficient propagule pressure from lowlands with reduced biotic resistance compared to intact highland ecosystems, allowing invasive taxa to expand spatially and adapt to novel conditions. Studies from tropical coffee agroforests and vegetable production systems have similarly identified mid-elevation belts as invasion hotspots and stepping stones for upslope expansion (Philpott et al. 2008; Perfecto and Vandermeer 2010; Alexander et al. 2015).

In Wonosobo, mid-elevation agroecosystems supported a mixture of resident and expanding taxa, reflecting functional and compositional overlap with both lowland and highland assemblages. This overlap likely enhances invasion success by providing ecological continuity and reducing dispersal barriers. Moreover, agricultural management practices at mid-elevation as mixed cropping, moderate canopy cover, and organic input use-may inadvertently promote invasion by increasing habitat heterogeneity while maintaining sufficient disturbance (Tscharntke et al. 2012; Guo et al. 2018).

From a management perspective, recognizing mid-elevation agroecosystems as transitional invasion zones is crucial. Interventions targeting these zones may prevent the progression of invasion fronts toward high-risk highland systems. Monitoring invasion indices and functional shifts at mid-elevation can therefore provide early warning signals and strategic entry points for invasion mitigation before dominance amplification occurs at higher elevations.

Implications for agroecosystem resilience and biological regulation

The observed increase in invasion intensity and functional homogenization along the elevational gradient has important implications for agroecosystem resilience and the maintenance of biological regulation. Resilience in agricultural systems is closely linked to functional diversity, redundancy, and the presence of regulation-oriented taxa such as predators and parasitoids that suppress pest populations. In this study, high invasion pressure-particularly in highland and transitional mid-elevation systems-was associated with reduced functional balance and increased dominance of saprophagous and generalist taxa, suggesting a weakening of intrinsic regulatory mechanisms.

Invasion-driven dominance can undermine biological regulation by displacing or suppressing native predators and parasitoids through competition, habitat alteration, or trophic decoupling. Similar outcomes have been reported in invaded agroecosystems worldwide, where increases in invasive insects correlate with reduced efficacy of natural enemies and higher pest outbreak frequency (Liebhold et al. 2012; Tscharntke et al. 2012). The decline in regulation-oriented functional groups observed in Wonosobo is therefore likely to translate into reduced stability of pest control services, particularly under conditions of continued disturbance and habitat simplification. Similar linkages between agricultural management practices, farmer behavior, and insect community structure have been documented in other Indonesian agroecosystems, such as cocoa plantations in West Sumatra, where management intensity influences both pest and beneficial insect assemblages (Rosalia et al. 2022). Comparable management-driven effects have also been reported from rice agroecosystems in South Sulawesi, where integrated pest management reduced *Scirpophaga innotata* populations while maintaining higher abundances of natural enemies, underscoring the role of management practices in sustaining biological control functions (Rahmawasiah et al. 2022).

Agroecosystem resilience is further compromised when invasion processes interact with environmental stressors such as climatic variability and land-use intensification. In mountain agricultural landscapes, reduced resilience may manifest as increased sensitivity to pest invasions, yield instability, and reliance on chemical inputs. Studies from tropical and subtropical systems demonstrate that invasion-induced functional simplification can trigger feedback loops, where pesticide use further disrupts community structure and facilitates additional invasions (Perfecto and Vandermeer 2010; Tscharntke et al. 2012).

The implications extend beyond pest regulation to other ecosystem services, including pollination and nutrient cycling. Although pollinating taxa were not dominant among invasive groups, their reduced representation under high invasion pressure raises concerns about service co-decline. Maintaining agroecosystem resilience, therefore, requires strategies that counteract invasion-driven homogenization, such as increasing structural complexity, enhancing habitat heterogeneity, and supporting functionally diverse assemblages. These findings underscore that invasion dynamics should be explicitly integrated into agroecological management frameworks aimed at sustaining long-term productivity and ecological stability (Seebens et al. 2017; Altieri 2018).

Methodological contributions and analytical limitations

This study offers a methodological contribution by integrating invasion-oriented indices with environmental ordination to examine invasion dynamics along an elevational agricultural gradient. The combined use of the Relative Invasiveness Index (RII) and the Altitudinal Expansion Index (AEI) enables a process-based assessment that moves beyond traditional diversity metrics. RII captures dominance and spatial occurrence of invasion-relevant taxa, while AEI detects spatial displacement beyond historical elevational limits, allowing early identification of expansion processes before overt ecological impacts occur. Similar index-based approaches have been advocated in invasion ecology to prioritize dominance and spread over species counts (Parker et al. 1999; Blackburn et al. 2011).

The integration of these indices with Canonical Correspondence Analysis (CCA) further strengthens inference by explicitly linking invasion patterns to environmental drivers. This multivariate framework facilitates the identification of invasion filters and amplification zones along complex gradients, an approach increasingly recommended for invasion studies in heterogeneous landscapes (Legendre and Legendre 2012; Alexander et al. 2015). By restricting analyses to invasive and potentially invasive taxa, the methodology avoids redundancy with biodiversity-focused assessments and aligns analytical resolution with the study's invasion-centered objectives.

Several limitations should be acknowledged. First, the analysis is based on a single sampling period, which constrains inference regarding the temporal dynamics of invasion. Seasonal variation may influence the abundance and detectability of invasive taxa, particularly in tropical agroecosystems with pronounced phenological cycles. Second, historical elevational baselines were derived from published literature and global databases, which may vary in spatial resolution and sampling intensity. While a conservative interpretation of AEI was applied to mitigate this uncertainty, some expansion signals may reflect gaps in historical documentation rather than recent shifts.

Finally, invasion indices such as RII and AEI are proxies for ecological impact and should not be interpreted as direct measures of ecosystem damage. Their strength lies in detecting relative patterns and early warning signals rather than quantifying absolute effects. Future studies integrating multi-season sampling, experimental validation, and direct impact assessments would further refine invasion-risk evaluation in tropical mountain agroecosystems (Liebhold et al. 2012; Seebens et al. 2017).

Management relevance and invasion-risk prioritization

The identification of invasion-risk zones along the elevational agricultural gradient of Wonosobo provides a practical foundation for invasion management and prioritization. By integrating invasion intensity (RII), elevational expansion (AEI), functional reorganization, and environmental drivers, this study moves beyond descriptive assessments and offers a risk-based framework that can inform targeted intervention. Such prioritization is essential in tropical agroecosystems, where resources for monitoring and control are often limited and management actions must be strategically allocated.

Highland agroecosystems, characterized by strong invasion dominance, pronounced functional homogenization, and consistent upslope expansion signals, should be prioritized as high-risk invasion zones. In these systems, management efforts should focus on reducing habitat openness, limiting organic waste accumulation, and restoring structural complexity to enhance biotic resistance. Similar strategies have been recommended in invaded mountain agroecosystems worldwide, where increasing habitat heterogeneity has been shown to suppress invasive taxa and stabilize community structure (Perfecto and Vandermeer 2010; Tscharntke et al. 2012; Altieri 2018).

Mid-elevation agroecosystems represent strategic intervention zones, where early invasion signals are detectable but dominance amplification has not yet fully occurred. Targeted monitoring and rapid response in these transitional zones may prevent the progression of invasion fronts toward highland systems. Early detection approaches emphasizing range expansion metrics, such as AEI, have been widely advocated as cost-effective tools for invasion management (Parker et al. 1999). In practical terms, this may include periodic monitoring of invasion-relevant taxa, adjustment of crop management practices, and promotion of landscape features that support native predators and competitors.

Lowland agroecosystems, while exhibiting lower invasion risk, remain important sources of propagule pressure. Management in these areas should aim to reduce the spread of invasive taxa through improved sanitation, regulation of organic inputs, and coordination among farmers to limit dispersal pathways. Coordinated, landscape-scale approaches are increasingly recognized as critical for effective invasion control in agricultural systems (Blackburn et al. 2011; Liebhold et al. 2012).

Overall, prioritizing invasion management based on elevation-specific risk enhances the efficiency and effectiveness of intervention strategies. By explicitly linking ecological indicators with management relevance, this study provides a scalable framework for invasion-risk prioritization in tropical mountain agroecosystems under ongoing environmental and land-use change.

In conclusion, this study demonstrates that invasion dynamics in tropical agricultural landscapes of Wonosobo are strongly structured by elevation and associated microclimatic conditions. Of the 692 insect individuals recorded, 295 individuals (42.6%) belonged to nine invasive or potentially invasive taxa, indicating substantial invasion pressure across the landscape. Invasion intensity, quantified using the Relative Invasiveness Index (RII), peaked at mid-elevation systems (53.6%), followed by highland systems (48.7%), and was lowest in lowland systems (13.2%), confirming that invasion dominance does not increase linearly with altitude. Elevational range expansion, assessed using the Altitudinal Expansion Index (AEI), was detected exclusively in highland agroecosystems, with mean AEI values of 45.7% and a range of 38.7-59.6%. Detectable upslope expansion was restricted to specific saprophagous Diptera, most prominently *Leucostoma simplex*, which was recorded up to 856 m above its historically documented upper elevational limit. Along the elevational gradient, functional composition shifted from herbivore-dominated assemblages in lowland systems to predator-dominated assemblages at mid-elevation, and ultimately to saprophage–detritivore-dominated assemblages at high elevation, indicating functional homogenization under increasing invasion pressure. Environmental analyses identified elevation and light intensity as primary drivers of upslope expansion, whereas temperature and wind exposure were more closely associated with invasion dominance. Overall, elevational gradients in tropical agricultural landscapes function as invasion filters rather than biodiversity gradients, with mid-elevation systems acting as transitional invasion hotspots and highland systems representing high-risk zones for invasion-driven community simplification.

ACKNOWLEDGEMENTS

We would like to thank local farmers in Wonosobo District, Central Java, Indonesia, for their cooperation and support during field sampling.

REFERENCES

Adnan BA, Kurniawati T, Trianto M. 2024. Diversity and abundance of soil arthropods in the terrestrial area of Situ Lengkong Panjalu, West Java, Indonesia. Jurnal Biodjati 9 (1): 66-79. DOI: 10.15575/biodjati.v9i1.33980.

Alexander JM, Diez JM, Levine JM. 2015. Novel competitors shape species' responses to climate change. Nature 525: 515-518. DOI: 10.1038/nature14952.

Altieri MA. 2018. Agroecology: The science of sustainable agriculture. CRC Press, Boca Raton. DOI: 10.1201/9780429495465.

Andriani DM, Setianingsih M, Susilo, Metiani, Darma AP. 2017. Keanekaragaman dan pola penyebaran insekta permukaan tanah di Resort Cisarua Taman Nasional Gunung Gede Pangrango Jawa Barat. Jurnal Pendidikan Biologi dan Biosains 1 (1): 24-30. DOI: 10.29405/bioeduscience/24-30111179. [Indonesian]

Bauer T. 2024. *Coccinella septempunctata* (seven-spotted lady beetle). Animal Diversity Web, University of Michigan Museum of Zoology. https://animaldiversity.org/accounts/Coccinella_septempunctata/

Belioka MP, Achilias DS. 2024. The effect of weathering conditions in combination with natural phenomena/disasters on microplastics' transport from aquatic environments to agricultural soils. Microplastics 3 (3):518-538. DOI: 10.3390/microplastics3030033.

Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JRU, Richardson DM. 2011. A proposed unified framework for biological invasions. Trends Ecol Evol 26 (7): 333-339. DOI: 10.1016/j.tree.2011.03.023.

CABI. 2024. Invasive Species Compendium. Wallingford, UK: CAB International. Available at: https://www.cabidigitallibrary.org.

CBD [Convention on Biological Diversity]. 2002. Guiding principles for the prevention, introduction, and mitigation of impacts of alien species that threaten ecosystems, habitats, and species. Convention on Biological Diversity, COP 6 Decision VI/23.

CBD [Convention on Biological Diversity]. 2023. Indonesia - country profile: biodiversity facts. Convention on Biological Diversity. Accessed 29 Nov 2025. https://www.cbd.int/countries/profile

Corbet PS. 1999. Dragonflies: Behavior and Ecology of Odonata. Cornell University Press, Ithaca.

Crosskey RW. 1976. A taxonomic conspectus of the Tachinidae (Diptera) of the Oriental Region. Bulletin of the British Museum (Natural History), Entomology Series, Supplement 26: 1-357.

Davis MA, Grime JP, Thompson K. 2000. Fluctuating resources in plant communities: A general theory of invasibility. J Ecol 88: 528-534. DOI: 10.1046/j.1365-2745.2000.00473.x.

Fajarfika R. 2020. Keanekaragaman dan dominansi serangga pada agroekosistem tanaman tomat (*Lycopersicum esculentum* Mill.). Jurnal Agro Wiralodra 3 (2): 68-73. DOI: 10.31943/agrowiralodra.v3i2.51. [Indonesian]

Gani RA, Purwanto S, Sukarman S. 2021. Karakteristik tanah vulkanik di Kabupaten Wonosobo dan pengelolaannya untuk pertanian. Jurnal Tanah dan Iklim 45 (1):1-11. DOI: 10.21082/jti.v45n1. [Indonesian]

GBIF. 2024. Global Biodiversity Information Facility. https://www.gbif.org.

Gul S, ur Rehman F, Taj MK, Gul S, Khan MA, Taj I, Khan S. 2024. The house flies, *Musca domestica*, as a mechanical vector and its management to control in Quetta City, Balochistan. Pak-Euro J Med Life Sci 7 (3): 437-448. DOI: 10.31580/87hj0c23.

He Q, Jiang X, Zhang Y. 2024. The gains and losses of cultivated land requisition-compensation balance: Analysis of spatiotemporal trade-offs and synergies in ecosystem services using Hubei Province as a case study. Land 13 (10): 1641. DOI: 10.3390/land13101641.

Heong KL, Aquino GB, Barrion AT. 1991. Arthropod community structures of rice ecosystems in the Philippines. Bull Entomol Res 81 (4): 407-416. DOI: 10.1017/S0007485300031977.

Hodkinson ID. 2005. Terrestrial insects along elevation gradients: Species and community responses to altitude. Biol Rev 80 (3): 489-513. DOI: 10.1017/S1464793105006767.

iNaturalist. 2024. iNaturalist.org species database. https://www.inaturalist.org.

ITIS. 2024. Integrated Taxonomic Information System. https://www.itis.gov.

Kumar P, Thakur TS, Deepika, Sharma N. 2022. Diversity studies on insect pests of high-altitudinal transitional zones of the North-western Himalayas. Nusantara Bioscience 14 (2): 203-210. DOI: 10.13057/nusbiosci/n140211.

Legendre P, Legendre L. 2012. Numerical Ecology. 3rd ed. Elsevier, Amsterdam.

Leksono AS. 2017. Ekologi Arthropoda. Universitas Brawijaya Press, Malang. [Indonesian]

Lenoir J, Gégout JC, Marquet PA, de Ruffray P, Brisse H. 2008. A significant upward shift in plant species optimum elevation during the 20th century. Science 320: 1768-1771. DOI: 10.1126/science.1156831.

Liebhold AM, Brockerhoff EG, Garrett LJ, Parke JL, Britton KO. 2012. Live plant imports: The major pathway for forest insect and pathogen invasions of the US. Front Ecol Environ 10:135-143. DOI: 10.1890/110198.

Lukvitasari L, Triwidodo H, Rizali A, Buchori D. 2021. Pengaruh lokasi terhadap serangan lalat puru *Cecidochares connexa* (Macquart) pada tumbuhan eksotik invasif *Chromolaena odorata* (L.) King and Robinson dan interaksinya dengan komunitas serangga lokal. Jurnal Entomologi Indonesia 18 (2):127-137. DOI: 10.5994/jei.18.2.127. [Indonesian]

Nault LR. 1990. Evolution of an insect pest: Maize and the corn planthopper, *Peregrinus maidis* (Hemiptera: Delphacidae). American Entomologist 36: 165-175.

Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, Von Holle B, Moyle PB, Byers JE, Goldwasser L. 1999. Impact: Toward a framework for understanding the ecological effects of invaders. Biological Invasions 1: 3-19. DOI: 10.1023/A:1010034312781.

Pauchard A, Kueffer C, Dietz H, Daehler CC, Alexander J, Edwards PJ, Arévalo JR, Cavieres LA, Guisan A, Haider S. 2009. Ain't no mountain high enough: Plant invasions reaching new elevations. Frontiers in Ecology and the Environment 7 (9): 479-486. DOI: 10.1890/080072.

Perfecto I, Vandermeer J. 2010. The agroecological matrix as an alternative to the land-sparing/agriculture intensification model. Proc Nat Acad Sci USA 107: 5786-5791. DOI: 10.1073/pnas.0905455107.

Philpott SM, Arendt WJ, Armbrecht I, et al. 2008. Biodiversity loss in Latin American coffee landscapes: Review of the evidence on ants, birds, and trees. Conserv Biol 22 (5): 1093-1105. DOI: 10.1111/j.1523-1739.2008.01029.x.

Pont AC. 1977. Family Muscidae. In: Delfinado MD, Hardy DE (eds). A Catalogue of the Diptera of the Oriental Region. Vol. 3. Suborder Cyclorrhapha (excluding Division Aschiza). University Press of Hawaii, Honolulu.

Quinn GP, Keough MJ. 2002. Experimental Design and Data Analysis for Biologists. Cambridge Univ Press, Cambridge.

Rahbek C. 1995. The elevational gradient of species richness: A uniform pattern? Ecography 18: 200-205. DOI: 10.1111/j.1600-0587.1995.tb00341.x.

Rahmadhani SE, Salsabila S, Andrianto R, Rosyida SH, Ainia Q, Dewangga A, Setyawan AD. 2025. Diversity and potential invasiveness of insects in agricultural landscapes of Wonosobo, Central Java, Indonesia. Asian J Agric 9: 663-677. DOI: 10.13057/asianjagric/g090234.

Rahmawasiah, Abadi AL, Mudjiono G, Rizali A. 2022. The effect of integrated pest management on *Scirpophaga innotata* population and natural enemies on rice fields in South Sulawesi, Indonesia. Biodiversitas 23 (9): 4510-4516. DOI: 10.13057/biodiv/d230917.

Rentz DCF. 1996. Grasshopper Country: The Abundant Orthopteroid Insects of Australia. University of New South Wales Press, Sydney, Australia.

Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta FD, West CJ. 2000. Naturalization and invasion of alien plants: Concepts and definitions. Divers Distrib 6: 93-107. DOI: 10.1046/j.1472-4642.2000.00083.x.

Rosalia S, Yonariza, Syahrawati M. 2022. Effect of farmers' behavior in cocoa management on insect diversity in Salayo Cocoa Plantation, West Sumatra, Indonesia. Biodiversitas 23 (10): 5064-5073. DOI: 10.13057/biodiv/d231013.

Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pyšek P, Winter M, Arianoutsou M, et al. 2017. No saturation in the accumulation of alien species worldwide. Nat Commun 8:14435. DOI: 10.1038/ncomms14435.

Seipel T, Kueffer C, Rew LJ, Daehler CC, Pauchard A, Naylor BJ, Alexander JM, Edwards PJ, Parks CG, Jakobs G, McDougall K, Walsh N. 2012. Processes at multiple scales affect the richness and similarity of non-native plant species in mountains around the world. Global Ecol Biogeography 21: 236-246. DOI: 10.1111/j.1466-8238.2011.00664.x

Shannon CE, Wiener W. 1949. The Mathematical Theory of Communication. Univ Illinois Press, Urbana.

Skidmore P. 1985. The Biology of the Muscidae of the World. Series Entomologica. Springer, Dordrecht.

Sofian M, Haryanto H, Fauzi MT. 2023. Keragaman serangga hama dan musuh alami pada tanaman cabai rawit (*Capsicum frutescens* L.) di Kecamatan Labuhan Haji Kabupaten Lombok Timur. Jurnal Ilmiah Mahasiswa Agrokomplek 2: 349-361. DOI: 10.29303/jima.v2i3.3564. [Indonesian]

Tscharntke T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C. 2005. Landscape perspectives on agricultural intensification and biodiversity-ecosystem service management. Ecol Lett 8 (8): 857-874. DOI: 10.1111/j.1461-0248.2005.00782.x.

Vincent M. 2024. *Forficula auricularia* (European earwig). Animal Diversity Web, University of Michigan Museum of Zoology. https://animaldiversity.org/accounts/Forficula_auricularia/

Zumpt F. 1965. Myiasis in Man and Animals in the Old World. Butterworths, London, UK.