BIODIVERSITAS
Volume 27, Number 4, April 2026
Pages: 18

ISSN: 1412-033X
E-ISSN: 2085-4722
https://doi.org/10.13057/biodiv/d270402

Habitat heterogeneity influences Odonata (Arthropoda: Insecta) diversity and reveals a new record from Mindanao, Philippines

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Manuscript received: 6 January 2026. Revision accepted: 3 April 2026.

Abstract. *Manangan JLV, Omandam JE, Nuñeza OM, Villanueva RJT. 2026. Habitat heterogeneity influences Odonata (Arthropoda: Insecta) diversity and reveals a new record from Mindanao, Philippines. Biodiversitas 27 (4): d270402. https://doi.org/10.13057/biodiv/d270402.* Sitio Talangisog, an ancestral domain in Misamis Oriental, is one of the remaining dipterocarp forest frontiers in the province and contains a mosaic of interconnected freshwater habitats. This study assessed Odonata assemblages across three sampling sites in each of four habitat types using standardized time-constrained sampling with sweep-netting and handpicking during the dry (January-February 2025) and wet (June 2025) seasons. Systematic sampling recorded 52 species belonging to 12 families and 39 genera. Twenty-four species are endemic, including five of conservation concern: one Near Threatened, two Vulnerable, and two Endangered, notably *Drepanosticta clados* and *Sangabasis bukid*. The Asian bronze flutterer, *Rhyothemis obsolescens*, represents the first confirmed record from Mindanao Island and only the second national record in more than three decades. The most frequently encountered species was *Risiocnemis appendiculata* (7.12%), while *Prodasineura integra* occurred in all habitat types. One additional species, the endemic and Vulnerable *Indaeschna baluga*, was recorded incidentally and excluded from quantitative analyses but reported as a species record. Habitat-averaged diversity indices (n: 3 sites per habitat) were highest in lentic habitats. Bray-Curtis similarity revealed compositional affinity between open and shaded lotic habitats and between lentic and agroecosystems. Distance-based redundancy analysis (db-RDA), supported by non-metric multidimensional scaling (NMDS), showed that environmental variables significantly structured species composition (p: 0.005, adjusted R^2: 0.742), with dissolved oxygen, pH, relative humidity, and water temperature identified as significant drivers. Species turnover followed a gradient from warmer, slightly acidic, lower-oxygen waters dominated by generalists in lentic and agroecosystems to cooler, slightly alkaline, well-oxygenated lotic habitats preferred by many endemics. These findings highlight the role of habitat heterogeneity in structuring Odonata communities and emphasize the conservation value of Sitio Talangisog as a refuge for endemic and threatened species.

Keywords: Community structure, conservation, endemic species, environmental variables, freshwater habitats

INTRODUCTION

Dragonflies (Anisoptera) and damselflies (Zygoptera) belong to the insect order Odonata (Subramanian and Babu 2019), a diverse group of freshwater-associated insects comprising over 6,442 species worldwide (Paulson et al. 2025), with the majority occurring in tropical regions (Kalkman et al. 2018; Kuznetsova and Golub 2020). The significance of Odonata extends far beyond their ancient lineage, which stretches back to the late Triassic (Kohli et al. 2021). As amphibiotic macroinvertebrates, they require both aquatic environments for their larval stage and terrestrial landscapes for their adult stage (Dolný et al. 2021). Notable for their striking colors (Okude and Futahasi 2021), Odonata are widely recognized as flagship taxa, serving as indicators of ecosystem health (Janssen et al. 2018). Their life history is strongly tied to environmental conditions, making them valuable ecological models (Pimenta and Pelli 2019).

Habitat specificity among Odonata is well documented and serves as a reflection of evolutionary adaptation (Hykel et al. 2016; Khelifa 2019; Pereira-Moura et al. 2023). Species are generally categorized into ecological generalists, which exhibit broad distribution and high tolerance for degraded environments, and specialists, which are restricted to specific, stable niches and are less adaptable to change (Vilenica et al. 2021). Habitat use is influenced by a wide range of environmental variables (Mendes et al. 2021), along with structural elements including microhabitat features, vegetation, and whether habitats are lotic (flowing) or lentic (standing) waters (Vilenica et al. 2024). In addition, ecological processes such as predation, competition, and habitat selection are crucial in shaping species assemblages (Susanto et al. 2024).

The Philippines, among Southeast Asia's most biodiverse nations, hosts over 300 Odonata species, about 60% of which are endemic (Hämäläinen 2004; Gapud 2006). Their abundance and diversity are influenced by archipelagic tropical climatic patterns (Leksono et al. 2017). Mindanao, the second-largest island, supports over 130 species, making it the second most diverse island for Odonata (Hämäläinen and Müller 1997). However, despite this diversity, the country faces habitat degradation and biodiversity loss (Botterill-James et al. 2024), and many areas remain understudied, including ancestral or community-managed landscapes such as Sitio Talangisog. Its remote location, 37 km from the city proper of Gingoog, combined with rugged, rolling terrain and poor road access, has limited previous surveys, leaving its heterogeneous habitats largely unexplored for a wide range of taxa, including Odonata.

In this study, habitat heterogeneity is defined as variation in aquatic flow regime (lotic or lentic), canopy cover (open or shaded), and degree of anthropogenic disturbance, which together structure distinct habitat types across the landscape. We addressed the ecological gap by examining how Odonata diversity and community composition respond to habitat heterogeneity within an ancestral-domain landscape. We hypothesized that species composition and diversity would differ across habitat types due to environmental filtering and varying levels of anthropogenic disturbance in the area. Furthermore, because Sitio Talangisog remains a scientifically undocumented area, we hypothesized that the survey would yield new species records for the region or taxa previously unknown from the locality. Specifically, we expected community composition to vary between open lotic habitats (OLH) and shaded lotic habitats (SLH), lentic habitats (LEH), and agroecosystems (AGR). Accordingly, we predicted that (i) diversity indices would vary among habitat types, (ii) community similarity analysis (Bray-Curtis clustering) would reveal distinct assemblage groupings among habitat categories, (iii) multivariate analyses (db-RDA and NMDS) would identify environmental variables as significant drivers of species composition.

This study is significant as it provides the first empirical ecological baseline for Sitio Talangisog and contributes to the broader understanding of Mindanao Odonata fauna. By documenting species composition and diversity across distinct habitat types, the study aids in identifying "priority areas" for conservation within ancestral lands, ensuring that endemic populations are recognized and protected before they face local extinction from habitat loss. Specifically, this research assessed Odonata in Sitio Talangisog by (i) documenting species composition and diversity across habitat types, (ii) establishing baseline conservation data and identifying potential new geographic records, (iii) identifying habitat associations relevant to localized land-management strategies. By integrating biodiversity inventory with quantitative community analyses, this study provides an ecological framework linking habitat heterogeneity to Odonata assemblage structure in a previously undocumented landscape.

MATERIALS AND METHODS

Study area

The study was conducted in the Baliguihan-Higaonon Ancestral Domain (CADT 248), Sitio Talangisog, Eureka, Misamis Oriental, Philippines (08°42′23.04″N, 125°11′45.60″E), near the Northern Mindanao-Caraga regional boundary (Figure 1, Figure 2, Table 1). The area is lower montane to mid-elevation and experiences a Type II climate (PAGASA 2020), with no pronounced dry season and peak rainfall from October to March; observed 2025 conditions are discussed relative to the 1991-2020 climatological baseline (DOST-PAGASA 2024). In this study, "dry" and "wet" sampling periods refer to relatively drier (January-February) and wetter (June) field conditions associated with seasonal rainfall variation rather than strict climatic seasons. The landscape comprises a mosaic of freshwater bodies interspersed with forested and agricultural areas.

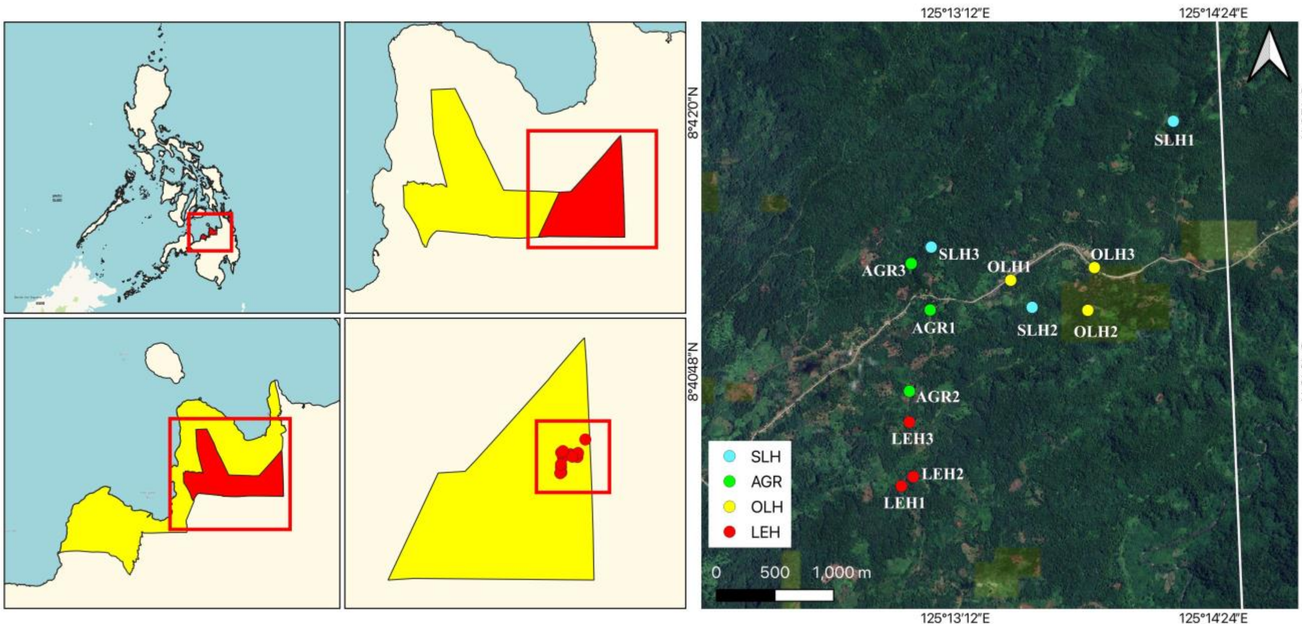

Figure 1. Map of the study area showing sampling sites by habitat types (● OLH, ● SLH, ● LEH, and ● AGR) in Sitio Talangisog Ancestral Domain, Eureka, Misamis Oriental, Northern Mindanao, Philippines (ArcGIS v. 10.8)

Figure 2. Representative photos of habitat types. A. Open lotic habitats (OLH), B. Shaded lotic habitats (SLH), C. Lentic habitats (LEH), D. Agroecosystems (AGR)

Table 1. Location of sampling sites per habitat type

Habitat type	Site	Coordinates
OLH	OLH1	08°40′34.0″N 125°12′59.2″E
	OLH2	08°40′18.8″N 125°13′00.3″E
	OLH3	08°40′16.2″N 125°12′57.0″E
SLH	SLH1	08°41′57.7″N 125°14′12.8″E
	SLH2	08°41′05.9″N 125°13′33.4″E
	SLH3	08°41′22.7″N 125°13′05.3″E
LEH	LEH1	08°41′05.2″N 125°13′05.0″E
	LEH2	08°40′42.6″N 125°12′59.2″E
	LEH3	08°41′18.1″N 125°12′59.7″E
AGR	AGR1	08°41′13.4″N 125°13′27.5″E
	AGR2	08°41′05.1″N 125°13′48.9″E
	AGR3	08°41′17.0″N 125°13′50.8″E

Site selection followed a purposive approach due to access constraints and the need to confirm active Odonata use. As a limitation, replicate sites within each habitat type were selected using structured, non-random criteria to maximize environmental contrast and spatial separation under comparable accessibility conditions.

Habitats were classified using predefined field thresholds and rapid visual assessment. Sites were first categorized as lotic or lentic based on water flow measured using the float method, with lotic habitats exhibiting measurable downstream flow (>0.1 m/s) and LEH lacking observable current. Lotic habitats were further distinguished by canopy cover: OLH had <50% canopy cover and SLH had >70%, estimated through visual assessment of overhead canopy closure within the sampling reach using predefined cover classes, following visual canopy assessment approach (Allan and Castillo 2007), while sites with intermediate cover (50-70%) were excluded to maintain clear separation. LEH comprised standing freshwater bodies dominated by emergent or marsh vegetation, while AGR were freshwater-associated sites embedded within actively cultivated landscapes and characterized by anthropogenic vegetation structure. Habitat classification was supplemented by qualitative observations of channel morphology, riparian vegetation, and disturbance intensity, consistent with rapid habitat assessment approaches in stream ecology and Odonata studies (Hankin and Reeves 1988; Bried and Samways 2015).

Three independent replicate sites were established per habitat type (n: 3). To reduce potential spatial autocorrelation, SLH sites were separated by >100 m to account for continuous forested riparian corridors that may facilitate adult movement, whereas OLH, LEH, and AGR sites were separated by >50 m due to clearer habitat boundaries and reduced functional connectivity among patches. These separation distances follow habitat-based sampling approaches used in previous Odonata ecological studies (Dolný et al. 2014; Cezário et al. 2021). Map-based measurements confirmed that inter-site distances exceeded the minimum separation thresholds across all sampling locations (Figure 1, Figure 2, Table 1).

Description of habitat types

Open lotic habitats (OLH)

These sites, located between 648 and 663 meters above sea level (m asl) along the Minsalawagan River, featured fast-flowing (0.3-0.6 m/s) streams and rivers (1-10 m wide) with boulders, sandy substrates, deep pools, and common leaf litter and woody debris. Open to semi-open canopies

(30-50% cover) promoted algal growth. Vegetation structure reflected a clear disturbance gradient: pioneer species (*Cecropia peltata*, *Piper aduncum*) dominated disturbed sites with simple associations, while less disturbed montane dipterocarp forest supported complex, multi-layered native forest with canopy trees (*Lithocarpus* sp., *Syzygium* spp., *Shorea* spp., *Dipterocarpus* sp.), epiphytes, and diverse ferns and herbs.

Shaded lotic habitats (SLH)

These sites, situated between 589 and 664 m asl within montane dipterocarp forest, consisted of slow- to moderate-flowing (0.1-0.3 m/s) streams (1-2 m wide) with sandy substrates, exposed rocks, fallen logs, and moss-covered leaf litter. They were characterized by dense canopies (70-90% cover) that limited light penetration. The riparian vegetation was structurally complex, comprising distinct layers of aroids (*Schismatoglottis plurivenia*, *Alocasia* spp., *Aglaonema* sp.), ferns, gingers, and palms in the understory, while tree layers hosted epiphytic ferns (*Cephalomanes* sp., *Hymenasplenium* sp., *Selaginella* spp.), orchids, mosses, vines, and climbers (*Calamus* spp., *Dinochloa* sp.). The presence of pioneer species (*P. aduncum*, *C. peltata*) near agricultural edges indicated minor disturbance.

Lentic habitats (LEH)

These sites, located between 651 and 681 m asl, consisted of shallow marshes or pools with mostly muddy substrates and standing water. Canopies were open, with partial shade from nearby forest patches or scattered trees. Vegetation was simple and dominated by a continuous mat of grasses (*Paspalum conjugatum*, *Urochloa* spp.), sedges (*Rhynchospora corymbosa*, *Cyperus albescens*), and interspersed with ferns (*Stenochlaena palustris*, *Christella* spp., *Nephrolepis* spp.). Margins supported disturbance-associated herbs (*Chromolaena odorata*, *Stachytarpheta jamaicensis*, *Acmella grandiflora*). The surroundings featured pioneer species (*P. aduncum*, *C. peltata*) and bracken ferns (*Dicranopteris* spp.), indicating varied anthropogenic influence.

Agroecosystem (AGR)

These sites, situated between 548 and 622 m asl, were located within or near secondary forest patches and were actively cultivated, primarily with tiger grass (*Thysanolaena latifolia*) and crops like banana (*Musa* sp.) and sweet potato (*Ipomoea batatas*). The vegetation was a distinct two-layered structure, characterized by a cultivated layer over a mixed native understory of vegetation such as *Begonia rieckei* and ferns. Water sources with variable flow included spring-fed pools, seep zones, and the Muya River, with leaf-littered, rocky beds. Riparian vegetation comprised a mix of grasses, sedges, herbs, ferns, and pioneer trees (*P. aduncum*, *C. peltata*).

Field sampling design

With the Wildlife Gratuitous Permit (WGP No. R10-2025-56) issued by the Department of Environment and Natural Resources-Region 10 (DENR-X), adult Odonata were sampled using a standardized time-constrained design with active methods (sweep-netting and handpicking). Surveys were conducted during the dry (January 30-February 2, 2025) and wet (June 16-19, 2025) seasons between 0900 and 1700 hours to coincide with peak adult activity.

A team of four collectors (three researchers and one local guide) sampled each habitat type collectively to ensure consistent observer effort. Each habitat type was surveyed for one full day per season, yielding 32 collector-hours per habitat per season (64 collector-hours per habitat overall) and a cumulative effort of 256 collector-hours. Within each habitat, the three replicate sites were sampled sequentially within the same day, with effort evenly allocated, approximately 10-11 collector-hours per site per season, and collectors rotated among sites to minimize observer bias. Site order followed logistical accessibility rather than randomization; however, surveys were conducted during peak Odonata activity periods, and standardized effort together with coverage-based richness metrics helps reduce potential time-of-day detectability bias.

Sampling was limited to up to three individuals per species for identification, with additional individuals released after recording. Recorded individuals included all observed or captured during sampling and were counted at first encounter. Observers maintained continuous forward movement and avoided revisiting previously surveyed microhabitats to minimize recounting of mobile individuals. Sampling completeness was assessed using coverage-based rarefaction and extrapolation (Hill numbers) in the *iNEXT* R package (Hsieh et al. 2016). Because individuals were not marked, abundance values are interpreted as encounter-based counts rather than exact population size estimates.

Specimen processing and identification

Voucher specimens were placed individually in labeled 9 cm × 13 cm plastic zip bags with wings folded over the back; mating pairs were kept together. Specimens were euthanized using ethyl acetate (5-10 minutes) and preserved in Scharlau acetone (ExpertQ®, ACS, ISO, Reag. Ph. Eur.) for 12 hours (damselflies and dragonflies with <4 cm body length) or 24 hours (larger dragonflies with >4 cm body length), then air-dried, transferred to triangular glassine envelopes, and stored in sealed containers with naphthalene to prevent infestation.

Specimens were photographed laterally and measured using ImageJ v. 1.54g (Schneider et al. 2012) with a 10 mm scale bar. Morphometric measurements included body length (BL), forewing length (FL), and hindwing length (HL). Microscopic examination of diagnostic structures was conducted using an Olympus SZ61 stereomicroscope with a ToupCAM (Xcam Full HD) camera, calibrated via Toupview (OMAX) software. Initial identification was performed by the first author and verified by the last author, a specialist in Philippine Odonata taxonomy, using authoritative regional keys and diagnostic literature (Hämäläinen and Müller 1997; Villanueva 2011). Verified specimens were identified to species or subspecies following the World Odonata List (Paulson et al. 2025) and Catalogue of Life (Bánki et al. 2025).

Geographic distributions were categorized as Philippine endemic (PE: species restricted to the Philippine archipelago), Greater Mindanao endemic (GME: species occurring within the Greater Mindanao biogeographic region, including Mindanao and associated satellite islands), Mindanao endemic (ME: species restricted to Mindanao Island), Oriental (O: species distributed within the Oriental biogeographic region), and Circumtropical (C: species occurring widely across tropical regions worldwide). Conservation status (EN: Endangered, VU: Vulnerable, NT: Near Threatened, LC: Least Concern), and population trends were assessed using various databases (DENR 2019; IUCN 2025).

Vouched specimens were deposited in the Natural Science Museum, Mindanao State University-Iligan Institute of Technology (NSM MSU-IIT), under sample codes 25-0001-25-0106 (accession nos. NSM-4995-NSM-5049D); specimens from the same collection event were curated as series using alphabetical suffixes (e.g., NSM-5010A, NSM-5010B).

Environmental variables

Environmental variables were measured in triplicate at three sampling sites per habitat type during each sampling event (dry and wet seasons). Triplicate readings were averaged to obtain site-level means, which were then summarized as mean±standard deviation (SD) by habitat type and season. Measurements were standardized between 0900 and 1100. Although Odonata sampling continued until 1700 hours, environmental measurements were restricted to the morning to standardize comparisons; therefore, values represent baseline stable stream conditions rather than full diurnal variability. Water flow and canopy cover were used as categorical criteria for habitat classification and excluded as quantitative environmental predictors. Recorded variables included air temperature (AT; °C) and relative humidity (RH; %) measured using a hygrometer; water temperature (WT; °C) and pH measured using a Yinmik water quality tester; and dissolved oxygen (DO; mg/L) measured using an Extech DO600 meter. All instruments were calibrated following manufacturer guidelines, and water quality probes were rinsed with distilled water prior to each recording.

Data analysis

Encounter-based abundance (EBA) was defined as the total number of individuals recorded per species during sampling, including individuals released after identification. Relative abundance (RA) was calculated as the proportion of individuals recorded per species relative to the total EBA in the study area. Endemism was computed as the number of endemic species relative to the total species richness (S). Derived RA and endemism were expressed as percentages. Incidental records were excluded from community computations and from all subsequent analyses.

Species diversity, evenness, and richness were assessed for each sampling site using the Shannon-Wiener diversity index (H′) (Shannon and Wiener 1963), Pielou's evenness index (J′) (Pielou 1975), and Margalef's richness index (d) (Margalef 1958), respectively. Calculated indices per site were averaged and comparatively interpreted by habitat type (n: 3) per season and expressed as mean±SD. Differences in diversity indices among habitat types and seasons were evaluated using permutation-based two-way analysis of variance (ANOVA) with habitat type and season as factors (999 permutations).

A combined Bray-Curtis similarity heat map and hierarchical dendrogram was used to examine species distribution and clustering patterns among habitat types based on EBA. To examine differences in community composition among habitats and seasons, permutational multivariate analysis of variance (PERMANOVA) based on Bray-Curtis dissimilarity was performed (999 permutations). Bray-Curtis dissimilarity was calculated from the abundance matrix, and hierarchical agglomerative clustering was performed using the group-average (UPGMA) linkage method. Clustering robustness was evaluated using the cophenetic correlation coefficient (*r*).

RA data were Hellinger-transformed prior to ordination to reduce the influence of dominant species. The community matrix consisted of 24 sampling units (rows) representing site-season combinations from 12 sampling sites surveyed during dry and wet seasons (4 habitat types × 3 sites × 2 seasons), and 52 species columns corresponding to the recorded Odonata taxa. Species individual counts represent EBA recorded during each sampling event, with each row corresponding to a single site-season sampling unit.

Distance-based redundancy analysis (db-RDA) was used to examine relationships between species composition and environmental variables based on Bray-Curtis dissimilarities. Environmental predictors were screened for multicollinearity using variance inflation factors (VIF), and variables with high redundancy (VIF>10) were excluded. The final model retained predictors with acceptable collinearity (VIF<5). Significance of the overall model, canonical axes, and environmental variables was assessed using permutation tests (999 permutations), with permutations restricted by site to account for repeated dry and wet season sampling (model df: 4, residual df: 19). Adjusted R^2 values were calculated to estimate explained variation. To assess the robustness of db-RDA results, non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarities was also performed. Relationships between community composition and environmental variables were evaluated using the envfit procedure (999 permutations). All statistical analyses and figures were obtained in RStudio v. 4.5.1 (R Core Team 2025) using the packages *vegan* (Oksanen et al. 2024) and *ggplot2* (Wickham 2016).

RESULTS AND DISCUSSION

Species composition and abundance of Odonata

Coverage-based rarefaction and extrapolation curves were used to compare species richness among habitat types because coverage-based standardization allows assemblages to be compared at equivalent levels of sampling completeness rather than equal sample size, which is more appropriate when sample sizes or detection probabilities differ among habitats. Richness comparisons were standardized to a common endpoint coverage approaching complete sampling (coverage: 1.0). Sample coverage was uniformly high across habitats (OLH: 0.995; SLH: 0.992; LEH: 0.997; AGR: 1.000) and seasons (Dry: 0.998; Wet: 0.996), indicating near-complete sampling.

AGR exhibited the highest estimated richness, followed by LEH, while SLH and OLH showed comparatively lower richness. The AGR curve remained relatively steep at high coverage values, indicating the presence of many rare species, whereas OLH approached an asymptote earlier, suggesting that most species present were already detected. Shaded bands around the curves represent 95% confidence intervals, which provide an estimate of uncertainty in richness estimates. Although some overlap occurs among confidence intervals at intermediate coverage levels, the overall separation of the curves at high coverage indicates consistent differences in species richness among habitats. Overall, curves converged at very high coverage values, indicating that observed richness differences reflect ecological variation among habitats rather than differences in sampling effort (Figure 3).

Following this standardized comparison, a total of 52 species comprising 1,166 individuals were recorded, belonging to 12 families and 39 genera (Table 2). Because individuals were not marked, counts represent EBA rather than exact population sizes. The assemblage included 27 dragonfly species, dominated by the family Libellulidae with 24 taxa, while Corduliidae, Idionychidae, and Macromidiidae were each represented by a single species. Within Libellulidae, the genus *Orthetrum* was the most species-rich, with four species (*O. chrysis*, *O. pruinosum clelia*, *O. sabina sabina*, and *O. testaceum*). In contrast, 25 damselfly species were recorded, dominated by the family Coenagrionidae with nine taxa, followed by Platycnemididae (6 species), Chlorocyphidae (3 species), Calopterygidae and Platystictidae (2 each), and Euphaeidae, Devadattidae, and Lestidae with 1 species each. The genus *Teinobasis* comprises three species: *T. annamaijae*, *T. filamentum*, and *T. samaritis*.

From the composition, 24 species are endemic to the Philippines. These include 15 Philippine endemics; three Greater Mindanao endemics, namely *Cyrano angustior*, *Euphaea amphicyana*, and *Risiocnemis appendiculata*; and six Mindanao endemics, specifically *Sangabasis bukid*, *Devadatta basilanensis*, *Coeliccia exoleta*, *Igneocnemis tendipes*, *Drepanosticta flavomaculata*, and *Drepanosticta clados*. In contrast, 26 species are Oriental, while *Pantala flavescens* and *Tholymis tillarga* are circumtropical.

Most endemic species occurred in OLH and SLH, which exhibited high endemism rates of 70% (14 species) and 90% (18 species), respectively. Philippine endemics *Heteronaias heterodoxa*, *Macromidia samal*, and *Neurobasis anumariae* were exclusively recorded in OLH. In SLH, endemic species *T. filamentum*, *I. tendipes*, *D. clados*, and *D. flavomaculata*, as well as the Oriental species *Cratilla lineata assidua* and *Tetrathemis irregularis irregularis*, were recorded. The most frequently encountered species in both OLH and SLH was the endemic *R. appendiculata*, which was also the most frequently encountered species in the study area (7.12%), followed by *Rhinocypha turconii* and *Rhinocypha colorata*. In contrast, *T. irregularis irregularis*, *M. samal*, and *T. filamentum* were rarely recorded, each represented by a single individual.

In contrast, LEH collectively harbored lower endemism (19%; five species), as these habitats were dominated by widespread Oriental and circumtropical taxa. Frequently encountered species in LEH included the Oriental *Argiocnemis rubescens intermedia*, followed by *Trithemis festiva* and *Lestes praemorsus praemorsus*. Notably, the endemic *S. bukid* was recorded exclusively in LEH, co-occurring with other LEH odonates such as *Nannophya pygmaea*, *Rhyothemis obsolescens*, *Rhyothemis resplendens*, and *Tramea transmarina euryale*.

AGR was likewise dominated by widespread species, including *Acisoma panorpoides panorpoides*, *Diplacodes trivialis*, *Pantala flavescens*, *Ceriagrion lieftincki*, and *Tholymis tillarga*, the latter also occurring in LEH. Because these AGR sites were located within or adjacent to forested areas, several forest-associated species were sparsely recorded, including the Philippine endemic *Prodasineura integra*, which occurred across all habitat types.

Species richness and EBA increased from the dry to the wet season. Several species were recorded exclusively during the wet season, while all species observed in the dry season were also present in the wet season. Among habitats, OLH and SLH supported fewer individuals and species overall, harboring 20 species represented by 206 and 262 individuals, respectively. In contrast, LEH supported 27 species from 312 individuals, while AGR exhibited the highest values, with 33 species represented by 386 individuals.

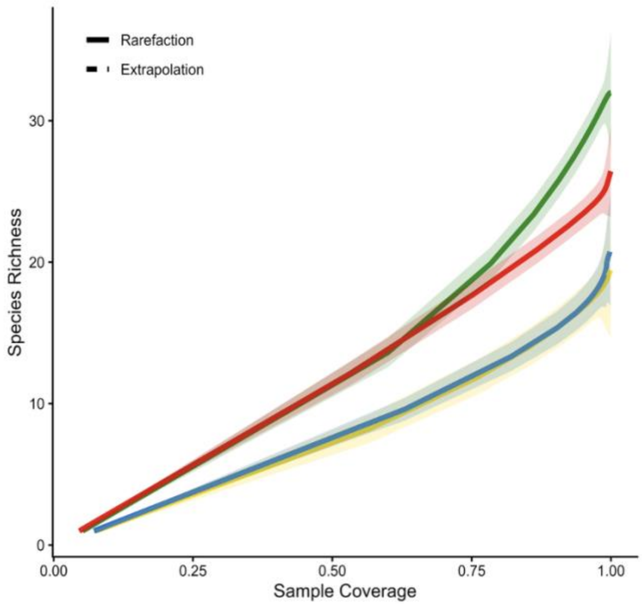

Figure 3. Habitat-pooled coverage-based rarefaction and extrapolation curves of Odonata species richness across habitat types (shaded bands indicate 95% confidence intervals): ● OLH, ● SLH, ● LEH, and ● AGR

Table 2. Species composition, geographic distribution, conservation status, endemism, and seasonal EBA of Odonata across habitat types based on systematic sampling

Taxa	**Habitat types**												**Total**	**RA (%)**
	OLH			**SLH**			**LEH**			**AGR**				
	Seasons			**Seasons**			**Seasons**			**Seasons**				
	Dry	**Wet**	**n**	**Dry**	**Wet**	**n**	**Dry**	**Wet**	**n**	**Dry**	**Wet**	**n**		
Suborder Anisoptera (Dragonflies)														
Family Corduliidae														
Heteronaias heterodoxa (Selys, 1878) [PE] [LC]	0	6	6	0	0	0	0	0	0	0	0	0	6	0.51
Family Idionychidae														
Idionyx philippa Ris, 1912 [PE] [LC]	2	6	8	1	4	5	0	0	0	0	0	0	13	1.11
Family Libellulidae														
Acisoma panorpoides panorpoides Rambur, 1842 [O] [LC]	0	0	0	0	0	0	0	0	0	3	2	5	5	0.43
Agrionoptera insignis (Rambur, 1842) [O] [LC]	1	3	4	0	0	0	4	5	9	3	3	6	19	1.63
Cratilla lineata assidua Lieftinck, 1953 [O] [LC]	0	0	0	1	3	4	0	0	0	0	0	0	4	0.34
Diplacina bolivari Selys, 1882 [PE] [LC]*	4	7	11	1	3	4	0	0	0	1	2	3	18	1.54
Diplacodes trivialis (Rambur, 1842) [O] [LC]	0	0	0	0	0	0	0	0	0	5	9	14	14	1.20
Nannophya pygmaea Rambur, 1842 [O] [LC]	0	0	0	0	0	0	4	6	10	0	0	0	10	0.86
Neurothemis ramburii ramburii (Brauer, 1866) [O] [LC]	0	0	0	0	0	0	4	5	9	9	12	21	30	2.57
Neurothemis terminata Ris, 1911 [O] [LC]	0	0	0	0	0	0	3	3	6	7	8	15	21	1.80
Orthetrum chrysis (Selys, 1891) [O] [LC]	0	2	2	0	0	0	6	8	14	1	2	3	19	1.63
Orthetrum pruinosum clelia (Selys, 1878) [O] [LC]	4	7	11	0	0	0	6	5	11	14	14	28	50	4.29
Orthetrum sabina sabina (Drury, 1773) [O] [LC]	0	0	0	0	0	0	4	5	9	9	9	18	27	2.32
Orthetrum testaceum (Burmeister, 1839) [O] [LC]	1	1	2	0	0	0	7	8	15	6	8	14	31	2.66
Pantala flavescens (Fabricius, 1798) [C] [LC]	0	0	0	0	0	0	0	0	0	2	3	5	5	0.43
Potamarcha congener (Rambur, 1842) [O] [LC]	0	0	0	0	0	0	5	6	11	5	6	11	22	1.89
Rhodothemis rufa (Rambur, 1842) [O] [LC]	0	0	0	0	0	0	1	1	2	2	2	4	6	0.51
Rhyothemis obsolescens Kirby, 1889 [O] [LC]♥	0	0	0	0	0	0	0	8	8	0	0	0	8	0.69
Rhyothemis regia regia (Brauer, 1867) [O] [LC]	0	0	0	0	0	0	0	8	8	0	2	2	10	0.86
Rhyothemis resplendens Selys, 1878 [O] [LC]	0	0	0	0	0	0	0	11	11	0	0	0	11	0.94
Tetrathemis irregularis irregularis Brauer, 1868 [O] [LC]	0	0	0	0	1	1	0	0	0	0	0	0	1	0.09
Tholymis tillarga (Fabricius, 1798) [C] [LC]	0	0	0	0	0	0	0	0	0	3	4	7	7	0.60
Tramea transmarina euryale (Selys, 1878) [O] [LC]	0	0	0	0	0	0	3	8	11	0	0	0	11	0.94
Trithemis aurora (Burmeister, 1839) [O] [LC]	0	0	0	0	0	0	7	12	19	12	16	28	47	4.03
Trithemis festiva (Rambur, 1842) [O] [LC]	2	5	7	0	0	0	9	14	23	22	21	43	73	6.26
Zyxomma obtusum Albarda, 1881 [O] [LC]	0	0	0	0	0	0	1	2	3	4	4	8	11	0.94
Family Macromidiidae														
Macromidia samal Needham & Gyger, 1937 [PE] [LC]*	0	1	1	0	0	0	0	0	0	0	0	0	1	0.09
Suborder Zygoptera (Damselflies)														
Family Calopterygidae														
Neurobasis anumariae Hämäläinen, 1989 [PE] [LC]*	4	8	12	0	0	0	0	0	0	0	0	0	12	1.03
Vestalis melania Selys, 1873 [PE] [LC]	5	10	15	8	15	23	0	0	0	4	3	7	45	3.86
Family Chlorocyphidae														
Cyrano angustior Hämäläinen, 1989 [GME] [NT]*	2	3	5	10	14	24	0	0	0	2	1	3	32	2.74
Rhinocypha colorata Hagen in Selys, 1869 [PE] [LC]*	8	14	22	6	11	17	0	0	0	3	5	8	47	4.03

Rhinocypha turconii Selys, 1891 [PE] [LC]*	8	16	24	7	16	23	0	0	0	5	5	10	57	4.89
Family Coenagrionidae														
Agriocnemis pygmaea (Rambur, 1842) [O] [LC]	0	0	0	0	0	0	5	6	11	3	4	7	18	1.54
Argiocnemis rubescens intermedia Selys, 1877 [O] [LC]	0	0	0	0	0	0	9	18	27	13	10	23	50	4.29
Ceriagrion lieftincki Asahina, 1967 [PE] [LC]	0	0	0	0	0	0	0	11	11	0	7	7	18	1.54
Pseudagrion pilidorsum pilidorsum (Brauer, 1868) [O] [LC]	2	4	6	0	0	0	6	6	12	16	18	34	52	4.46
Sangabasis bukid Villanueva & Dow, 2014 [ME] [EN]*	0	0	0	0	0	0	8	10	18	0	0	0	18	1.54
Teinobasis annamaijae Hämäläinen & Müller, 1989 [PE] [LC]*	3	7	10	6	8	14	0	0	0	0	0	0	24	2.06
Teinobasis filamentum Needham & Gyger, 1939 [PE] [LC]	0	0	0	0	1	1	0	0	0	0	0	0	1	0.09
Teinobasis samaritis Ris, 1915 [PE] [LC]	0	0	0	0	0	0	5	7	12	2	2	4	16	1.37
Xiphiagrion cyanomelas Selys, 1876 [O] [LC]	0	0	0	0	0	0	8	7	15	8	8	16	31	2.66
Family Devadattidae														
Devadatta basilanensis Laidlaw, 1934 [ME] [VU]*	0	0	0	5	11	16	1	0	1	1	1	2	19	1.63
Family Euphaeidae														
Euphaea amphicyana Ris, 1930 [GME] [LC]	6	12	18	12	9	21	0	0	0	3	4	7	46	3.95
Family Lestidae														
Lestes praemorsus praemorsus Hagen in Selys, 1862 [O] [LC]	0	0	0	0	0	0	10	10	20	0	0	0	20	1.72
Family Platycnemididae														
Coeliccia dinocerus Laidlaw, 1925 [PE] [LC]*	0	0	0	4	5	9	0	0	0	1	1	2	11	0.94
Coeliccia exoleta Lieftinck, 1961 [ME] [VU]*	0	0	0	0	3	3	0	0	0	0	0	0	3	0.26
Igneocnemis flammea (Selys, 1882) [PE] [LC]*	0	3	3	0	9	9	0	0	0	0	0	0	12	1.03
Igneocnemis tendipes (Needham & Gyger, 1941) [ME] [LC]*	0	0	0	4	8	12	0	0	0	0	0	0	12	1.03
Prodasineura integra (Selys, 1882) [PE] [LC]	3	5	8	7	10	17	3	3	6	5	3	8	39	3.34
Risiocnemis appendiculata (Brauer, 1868) [GME] [LC]*	11	20	31	20	19	39	0	0	0	6	7	13	83	7.12
Family Platystictidae														
Drepanosticta clados van Tol, 2005 [ME] [EN]*	0	0	0	5	7	12	0	0	0	0	0	0	12	1.03
Drepanosticta flavomaculata van Tol, 2005 [ME] [LC]*	0	0	0	4	4	8	0	0	0	0	0	0	8	0.69
Total individuals (systematic sampling)	66	140	206	101	161	262	119	193	312	180	206	386	1,166	
Total species recorded (S)	16	20	20	16	20	20	23	26	27	31	33	33	52	
Total endemic species	11	14	14	15	18	18	4	4	5	11	12	12	24	
Endemism (%)	69	70	70	94	90	90	17	15	19	35	36	36	46	

Note: Geographic distribution: PE: Philippine endemic, GME: Greater Mindanao endemic, ME: Mindanao endemic, O: Oriental, C: Circumtropical. Conservation status: EN: Endangered, VU: Vulnerable; NT: Near threatened; LC: Least concern. *Decreasing population trend according to IUCN. ♥New Mindanao Island record. n: Total individuals recorded per species within each habitat (dry and wet seasons combined). RA: Relative abundance (see Data Analysis section); values expressed as percentages

New Mindanao record

Materials examined

Philippines: Mindanao Island, Misamis Oriental, Eureka, Sitio Talangisog (08°41′05.2″N 125°13′05.0″E), site LEH1, pond margin. *R. obsolescens* Kirby, 1889, 2 ♂♂, 16.vi.2025, vouchers NSM-5010, NSM-5010A, leg. J.L. Manangan. *R. regia regia* (Brauer, 1867), 1 ♂, 16.vi.2025, voucher NSM-5011, leg. J.L. Manangan. *R. resplendens* Selys, 1878, 2 ♂♂, 16.vi.2025, vouchers NSM-5012, NSM-5012A, leg. J.L. Manangan.

Measurements (mm)

R. obsolescens — BL: 23.63-23.73, FL: 21.46-21.57, HL: 21.62-21.85; *R. regia regia* — BL: 36.87-37.02, FL: 34.27-34.34, HL: 34.44-34.77; *R. resplendens* — BL: 27.09-27.45, FL: 25.21-25.43, HL: 24.67-24.97.

Taxonomic notes

Members of the genus *Rhyothemis* (flutterers) are characterized by a distinctive fluttering flight and often striking wing coloration and patterning (Sarsavan et al. 2025). Identification of *R. obsolescens* was based on adult male wing morphology, specifically: (i) bronze-tinted wings with scattered dark punctations; (ii) faint metallic iridescence near the wing base; (iii) absence of the broad metallic basal suffusion typical of *R. regia regia*; and (iv) absence of the nearly straight half-width metallic blue basal band with hyaline apices diagnostic of *R. resplendens* (Figure 4). Because *Rhyothemis* species are readily separable based on stable wing pattern characters in adult males, these traits provide reliable species-level diagnosis. Direct comparison with sympatric specimens of *R. regia regia* and *R. resplendens* collected from the same locality further confirmed the identification. The observed characters are consistent with the original species description of *R. obsolescens* from Borneo (Kirby 1889), which notes bronze-tinted wings with dark punctation, a dark metallic thorax and abdomen, and relatively narrow wings with inconspicuous anal appendages. The measurements of the examined specimens also fall within the size range reported in the original description, and the identification agrees with subsequent diagnostic treatments of the genus (Ramos and Gapud 2007; Kosterin 2012).

Distribution notes

Published literature indicates that *R. obsolescens* has historically been recorded in the Philippines only from Mindoro Island in Luzon (Hämäläinen and Müller 1997). Subsequent regional surveys and locality-based inventories across the archipelago have not reported additional occurrences of this species. A search of global biodiversity databases likewise revealed no verified records from Mindanao Island (GBIF 2025). Based on available literature and accessible occurrence data, the present materials therefore represent the first confirmed record of *R. obsolescens* from Mindanao, extending the known distribution of the species southward and suggesting that its Philippine range may be broader than previously recognized.

Conservation status

Conservation-priority species

Five endemic Odonata species recorded from the sampling are of conservation concern (Figure 5), comprising one Near Threatened species, *C. angustior* (Dow 2020a), and four threatened species: the Vulnerable *C. exoleta* (Villanueva 2009; DENR 2019) and *D. basilanensis* (DENR 2019; Dow 2020b), and the Endangered *D. clados* (Dow 2020c) and *S. bukid* (Dow 2020e). Most of these species were associated with OLH and SLH (except *S. bukid*), although they were sparsely recorded in AGR located near or within forest patches. According to IUCN (2025) and DENR (2019), these species are generally threatened by habitat loss, degradation of forested streams, and disturbance of riparian vegetation across their known ranges. Such pressures are widely recognized as key drivers of population decline in habitat-specialist Odonata. Additionally, 11 endemic species currently classified as Least Concern also exhibit declining population trends. These include *Diplacina bolivari*, *M. samal*, *N. anumariae*, *R. colorata*, *R. turconii*, *T. annamaijae*, *Coeliccia dinocerus*, *Igneocnemis flammea*, *I. tendipes*, *R. appendiculata*, and *D. flavomaculata* (Table 2), suggesting that even taxa not presently categorized as threatened may become vulnerable under continued habitat disturbance.

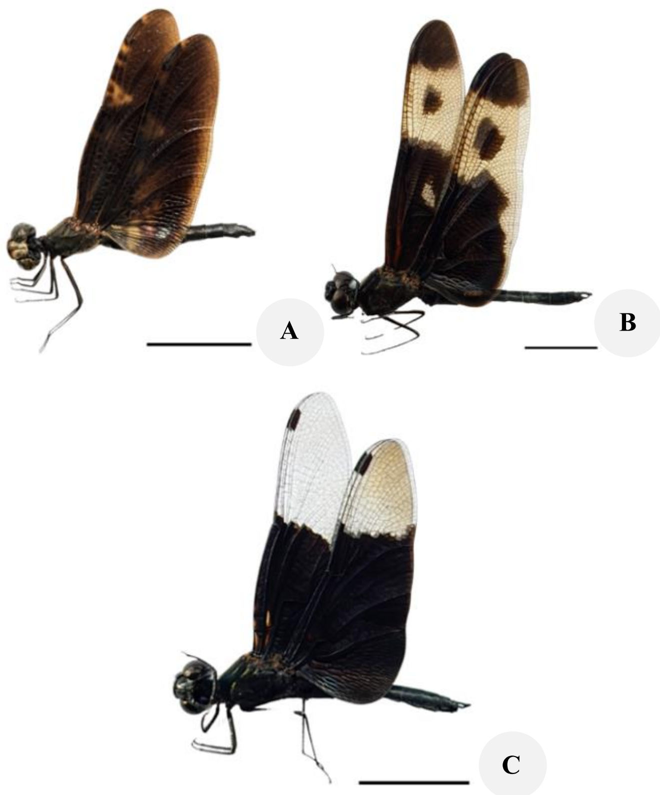

Figure 4. Lateral habitus of *Rhyothemis* species in Sitio Talangisog. A. New Mindanao record *R. obsolescens*, male, B. *R. regia regia*, male, C. *R. resplendens*, male. Scale bar: 10 mm

Site-level threat assessment

Field observations documented ongoing small-scale logging and forest clearing within parts of Sitio Talangisog (Figure 6). These locally observed disturbances primarily affect OLH and SLH through canopy removal, habitat fragmentation, and increased sedimentation in adjacent streams. Such activities may reduce habitat quality for forest-associated Odonata species that depend on intact riparian vegetation and stable microclimatic conditions. Although these threats were recorded directly during field surveys, their intensity and spatial extent were not quantitatively measured in the present study. Nevertheless, continued forest clearing and expansion of agricultural areas may exacerbate habitat degradation in the landscape, potentially increasing the risk of local population declines or extirpations (Table 3).

Incidental record

One additional species: *Indaeschna baluga*, was recorded incidentally inside a house near residential areas based on photographic and video records provided by a local resident (Figure 7). This species is a Philippine endemic dragonfly belonging to the Aeshnidae family, and is classified as Vulnerable with decreasing population trend influenced by deforestation and land-use modification, specifically logging, mining and quarrying (Dow 2020d; Table 4). As this record was not obtained through standardized sampling, it was excluded from quantitative analyses.

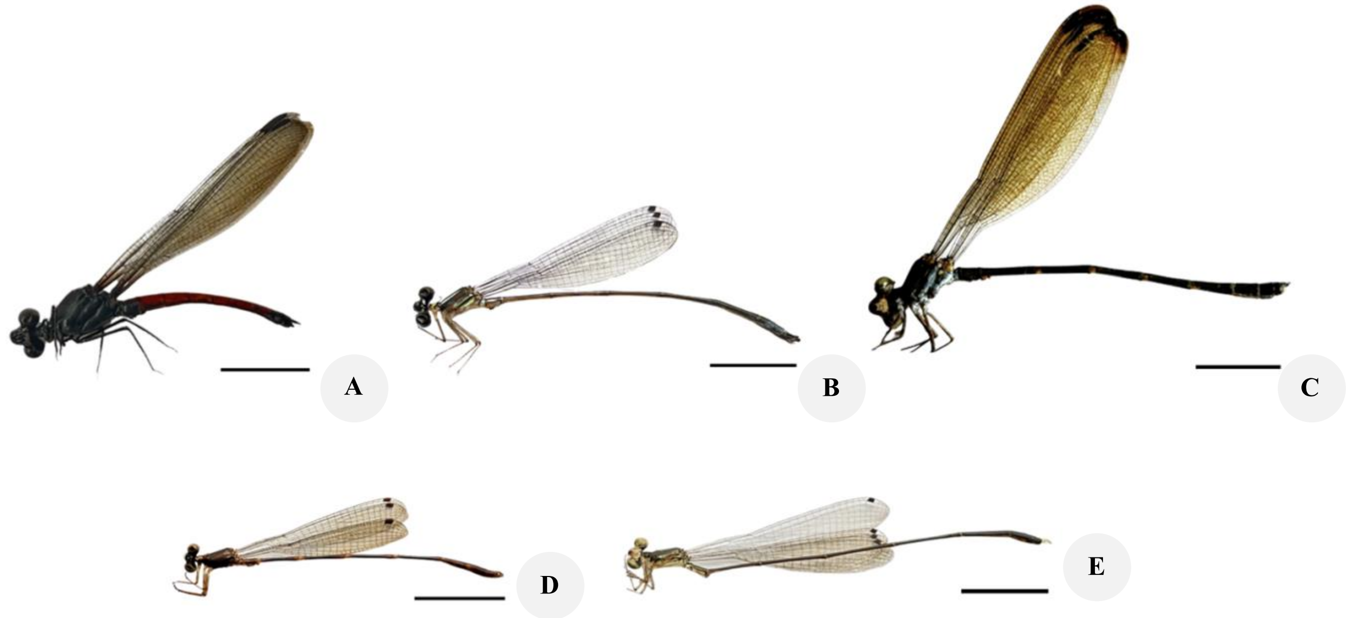

Figure 5. Lateral habitus of A. *Cyrano angustior* (male), B. *Coeliccia exoleta* (male), C. *Devadatta basilanensis* (male), D. *Drepanosticta clados* (male), and E. *Sangabasis bukid* (male). Scale bar: 10 mm

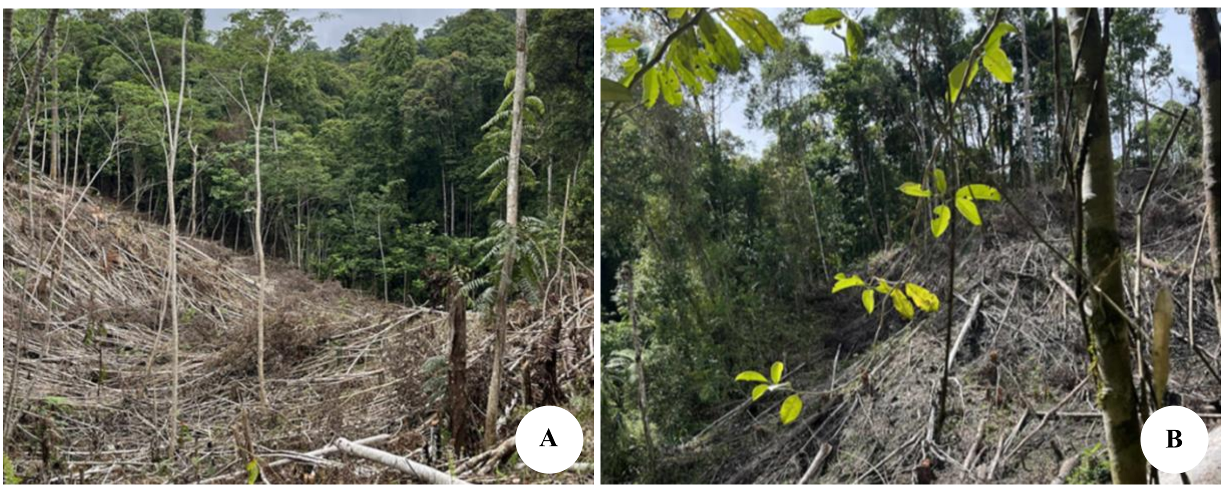

Figure 6. Logging-related anthropogenic activities recorded in the area. A. tree cutting along forest edges indicating edge disturbance, and B. Forest-agriculture transition zone showing post-logging land conversion

Table 3. List of recorded species classified as Near Threatened and Threatened, and their main anthropogenic threats

Taxa	Conservation status	Main threats	Habitat associations	Accession Nos.
Cyrano angustior	Near Threatened	Logging, mining, and quarrying (Dow 2020a)	OLH, SLH	NSM-5043, NSM-5043A
Coeliccia exoleta	Vulnerable	Urbanization, freshwater aquaculture, and pollution (Villanueva 2009; DENR 2019).	SLH	NSM-5034
Devadatta basilanensis	Vulnerable	Logging, mining, and quarrying (DENR 2019; Dow 2020b).	SLH	NSM-5047
Drepanosticta clados	Endangered	Logging (Dow 2020c).	SLH	NSM-5040, NSM-5040A, NSM-5040B
Sangabasis bukid	Endangered	Logging, mining, and quarrying (Dow 2020e)	LEH	NSM-5028, NSM-5028A, NSM-5028B

Biodiversity indices

Diversity indices are presented as mean±SD across three sites per habitat type (n: 3). Permutation-based two-way analysis of variance (ANOVA) indicated that Shannon-Wiener diversity (H′) differed significantly among habitats and seasons (R^2: 0.686, F: 4.988, *p*: 0.006), whereas Pielou's evenness (J′) showed no significant differences (R^2: 0.124, F: 0.325, *p*: 0.93). Margalef richness (d) showed a marginal response to habitat and season (R^2: 0.507, F: 2.352, *p*: 0.061). Seasonal comparisons further highlight distinct patterns of biodiversity among habitat types in Sitio Talangisog (Figure 8).

Based on the H′ index, LEH consistently exhibited the highest diversity and a seasonal increase (Dry: 2.751±0.183, Wet: 2.880±0.249), followed by AGR (Dry: 2.668±0.038, Wet: 2.772±0.030). Among lotic habitats, SLH increased markedly from dry to wet season (2.441±0.032 to 2.726±0.023), whereas OLH recorded the lowest H′ values overall, although it also showed seasonal improvement (2.410±0.125 to 2.626±0.111).

The J′ index remained consistently high across habitats and seasons (>0.93), indicating relatively balanced distributions. Slight seasonal declines were observed in LEH (0.948±0.009 to 0.935±0.017) and OLH (0.950±0.016 to 0.935±0.007), whereas AGR showed a small increase (0.936±0.017 to 0.942±0.011). SLH maintained stable evenness between seasons.

The d index further highlighted LEH as the richest habitat (Dry: 4.711±0.793, Wet: 5.038±0.869), followed by AGR (4.015±0.305 to 4.275±0.192) and SLH (3.662±0.357 to 4.476±0.400), both showing wet-season increases. OLH remained comparatively lower but also increased during the wet season (3.804±0.504 to 4.101±0.211).

Overall, diversity and richness were higher during the wet season across all habitat types, with LEH contributing most strongly to species richness, while evenness remained uniformly high.

Distribution and habitat similarity

Permutational multivariate analysis of variance (PERMANOVA) based on Bray-Curtis dissimilarity indicated significant differences in Odonata species composition among habitat types and seasons (R^2: 0.712, F: 5.646, *p*: 0.001). The abundance and distribution patterns of Odonata showed consistent habitat-associated similarity patterns across both widespread and endemic species. Based on the Bray-Curtis similarity heat map and hierarchical clustering, widespread species, particularly dragonflies, were more frequently associated with LEH and AGR habitats, whereas endemic and threatened species, largely damselflies, were primarily associated with OLH and SLH.

These patterns were reflected in the formation of two major habitat groupings: OLH and SLH clustered together at approximately 41% similarity, while LEH and AGR formed a second cluster at approximately 45% similarity. The dendrogram showed a high cophenetic correlation coefficient (*r*: 0.946), indicating excellent agreement between the clustering structure and the original Bray-Curtis dissimilarity matrix. The heat map further highlighted shared species composition within each grouping, emphasizing the separation between assemblages associated with lotic versus lentic and agricultural environments, as well as species occurring across multiple habitat types (Figure 9).

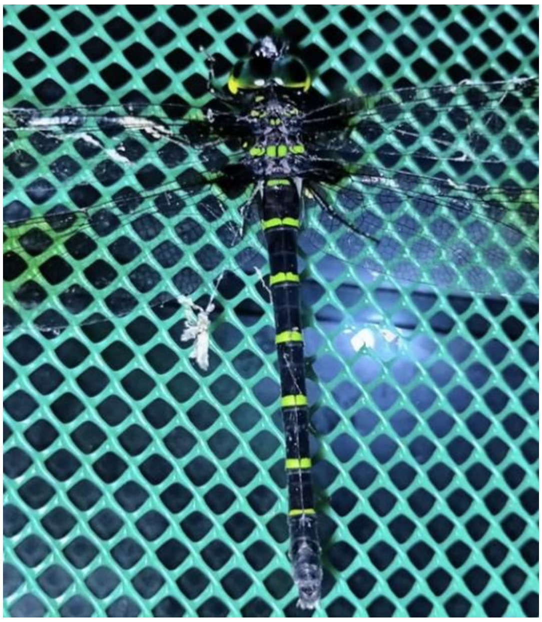

Figure 7. Incidental record of *Indaeschna baluga*

Table 4. Incidental record of Odonata in the area

Taxon	Main threats
Suborder Anisoptera (Dragonflies)	
Family Aeshnidae	
Indaeschna baluga Needham & Gyger, 1937 [PE] [VU]*	Logging, mining, and quarrying (Dow 2020d).

Note: Geographic distribution: PE-Philippine endemic. Conservation status: VU-Vulnerable. *Decreasing population trend according to IUCN

Environmental conditions

Across seasons, AT was generally higher during the dry season, particularly in LEH and AGR. LEH recorded the highest temperatures in both seasons (Dry: 33.8±1.5°C, Wet: 32.3±1.5°C), followed by AGR (Dry: 33.6±2.9°C, Wet: 32.1±3.1°C). In contrast, SLH remained the coolest habitat (Dry: 27.7±1.0°C, Wet: 26.0±0.8°C), while OLH showed intermediate values (Dry: 31.0±3.6°C, Wet: 29.7±3.4°C). RH showed the opposite pattern, with higher values during the wet season across all habitats, particularly in SLH (Wet: 84.8±2.9%, Dry: 78.6±3.9%).

WT followed a similar seasonal trend, with higher values during the dry season, especially in AGR and LEH. AGR recorded the highest temperatures (Dry: 27.7±3.1°C, Wet: 26.8±3.1°C), followed by LEH (Dry: 26.5±0.6°C, Wet: 24.9±0.6°C). OLH (Dry: 24.5±0.5°C, Wet: 23.7±0.7°C) and SLH (Dry: 24.1±0.1°C, Wet: 23.6±0.5°C) remained comparatively cooler.

Water pH varied only slightly among habitats. LEH waters were slightly acidic in both seasons (Dry: 6.9±0.2, Wet: 6.9±0.6), OLH (Dry: 7.5±0.1, Wet: 7.3±0.6) and AGR (Dry: 6.7±0.3, Wet: 7.4±0.7) were near neutral, whereas SLH remained slightly alkaline (Dry: 7.8±0.1, Wet: 8.2±0.5).

DO concentrations were consistently highest in SLH (Dry: 7.6±0.1 mg/L, Wet: 7.8±0.1 mg/L), followed by OLH (Dry: 6.6±0.8 mg/L, Wet: 6.8±0.7 mg/L). In contrast, DO levels were markedly lower in AGR (Dry: 1.9±1.0 mg/L, Wet: 2.2±1.3 mg/L) and LEH (Dry: 1.3±0.3 mg/L, Wet: 1.5±0.6 mg/L) (Figure 10).

Environmental correlations

Variance inflation factors (VIF) for the final predictor set were low for RH (2.086), WT (1.946), pH (2.990), and DO (3.519), indicating acceptable collinearity. AT was excluded due to high collinearity (12.029) and strong correlation with WT.

Distance-based redundancy analysis (db-RDA), performed on Hellinger-transformed species abundance data using Bray-Curtis dissimilarities and site-restricted permutations for repeated dry and wet season sampling (999 permutations), revealed that environmental variables significantly structured Odonata assemblages. The model was significant (F: 14.22, *p*: 0.005, df: 4, 19, constrained inertia: 4.377) and explained 74.2% of the variation in species composition (adjusted R^2: 0.742). The first two dbRDA axes accounted for 89.3% and 5% of the constrained variation, respectively, while subsequent axes were not significant.

Sequential permutation tests indicated significant contributions of RH (*p*: 0.001), DO (*p*: 0.001), WT (*p*: 0.001), and pH (*p*: 0.043). Biplot interpretation showed that DO, pH, and RH were positively associated with dbRDA1, whereas WT was negatively associated, indicating a dominant environmental gradient from warmer, lower-oxygen, slightly acidic LEH and AGR to cooler, well-oxygenated, higher-pH OLH and SLH. Including season as an additional constraint did not significantly improve model fit (F: 2.02, *p*: 0.124), indicating that seasonal differences were largely captured by measured environmental variation.

The parameter RH was retained because it reflects riparian microclimatic conditions at the aquatic-terrestrial interface, particularly canopy cover and shading, which strongly influence adult Odonata activity, thermoregulation, and desiccation risk. Although terrestrial in origin, RH serves as an integrative proxy for habitat structure and microhabitat conditions, especially in SLH.

Non-metric multidimensional scaling (NMDS) provided stable two-dimensional solution (stress: 0.064). Environmental fitting identified DO (r^2: 0.93, *p*: 0.001), pH (r^2: 0.59, *p*: 0.001), RH (r^2: 0.49, *p*: 0.003), and WT (r^2: 0.49, *p*: 0.001) as significant correlates, with gradient directions consistent with db-RDA results, supporting the robustness of the observed species-environment relationships (Figure 12).

Integrative synthesis across habitats

Across habitat types, a clear integrative pattern emerged linking habitat heterogeneity, environmental conditions, species composition, and diversity outcomes (Table 5). Species richness and diversity were highest in LEH and AGR, but these habitats exhibited relatively low endemism. In contrast, OLH and SLH supported fewer species and slightly lower diversity, yet harbored substantially higher endemism. These patterns reflect strong environmental filtering, where cooler, well-oxygenated, slightly alkaline, and more humid conditions in OLH and SLH favor endemic specialist taxa, whereas warmer, slightly acidic, lower-oxygen environments in LEH and AGR support widespread generalist species. This establishes a consistent ecological pathway in which habitat type determines key environmental drivers (DO, WT, RH, pH), which in turn structure species composition and ultimately shape observed diversity and endemism patterns. Collectively, this synthesis suggests that habitat heterogeneity not only increases overall species richness but also partitions biodiversity between endemic specialists in intact lotic systems and generalists in more disturbed or lentic environments.

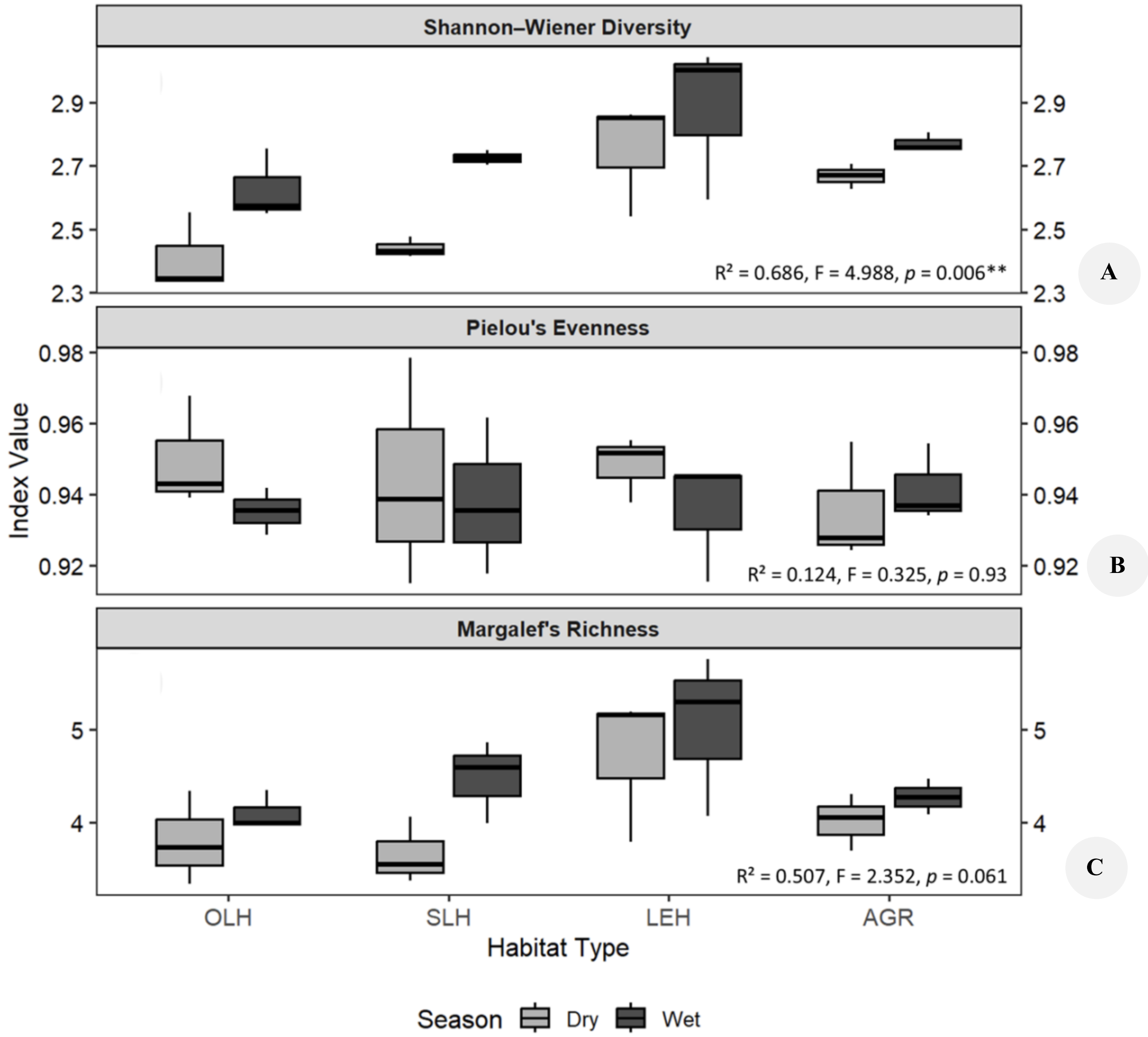

Figure 8. Box plots of habitat-averaged biodiversity indices during the dry and wet seasons: A. Shannon-Wiener diversity (H′), B. Pielou's evenness (J′), and C. Margalef's richness (d)

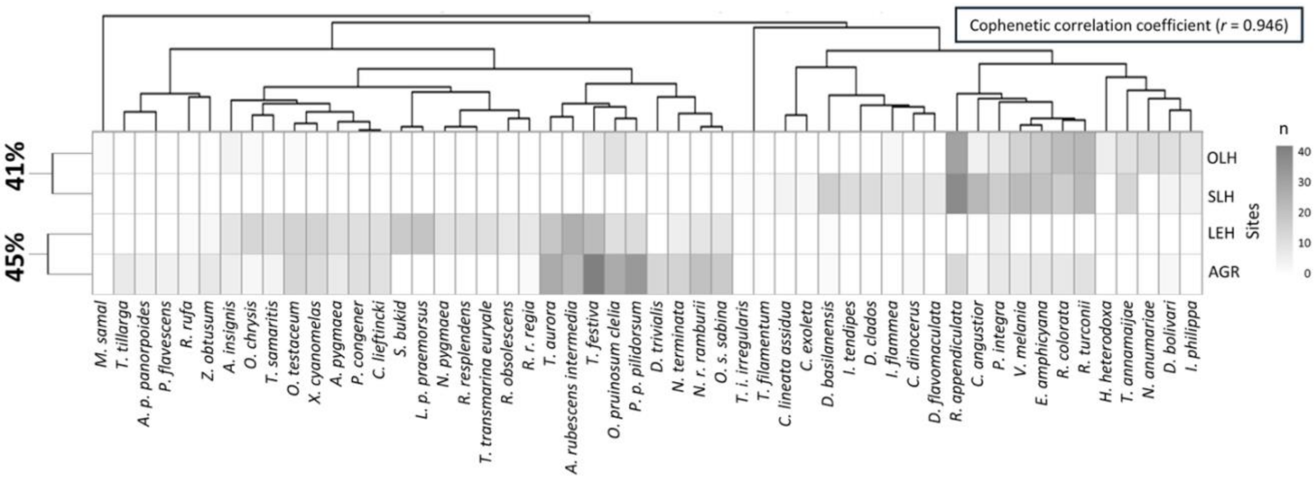

Figure 9. Bray-Curtis similarity heat map and hierarchical clustering dendrogram of Odonata assemblages across habitat types based on EBA (UPGMA linkage, cophenetic *r*: 0.946)

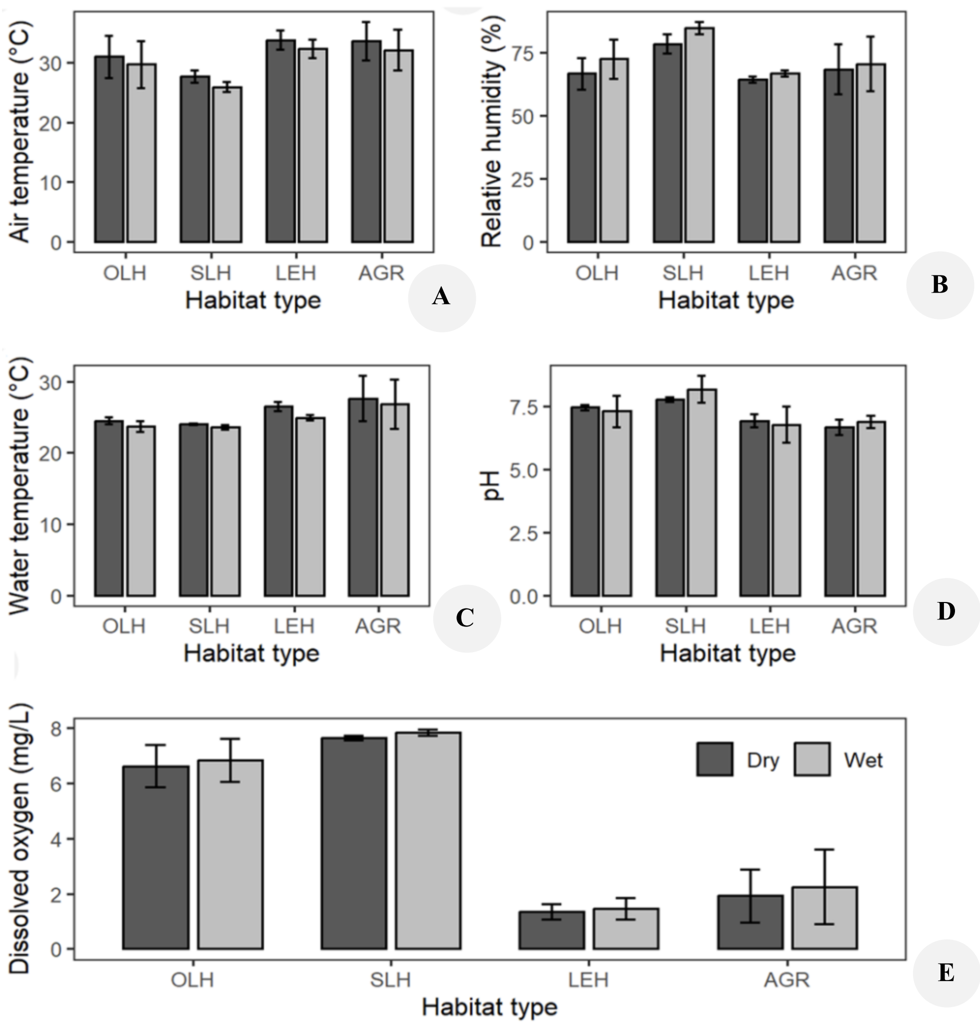

Figure 10. Mean±standard deviation values of A. AT (°C), B. RH (%), C. WT (°C), D. pH, and E. DO (mg/L) across habitat types during the dry and wet seasons

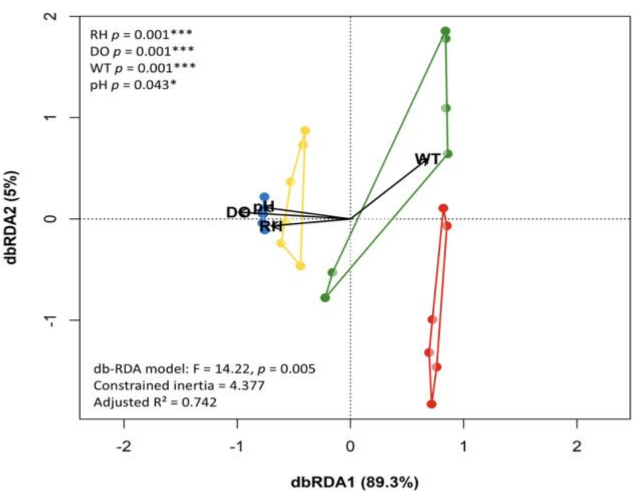

Figure 11. Distance-based redundancy analysis (db-RDA) ordination of Odonata assemblages in relation to environmental variables across habitat types: ● OLH, ● SLH, ● LEH, and ● AGR (F: 14.22, *p:* 0.005, df: 4, 19, constrained inertia: 4.377, adjusted R²: 0.742)

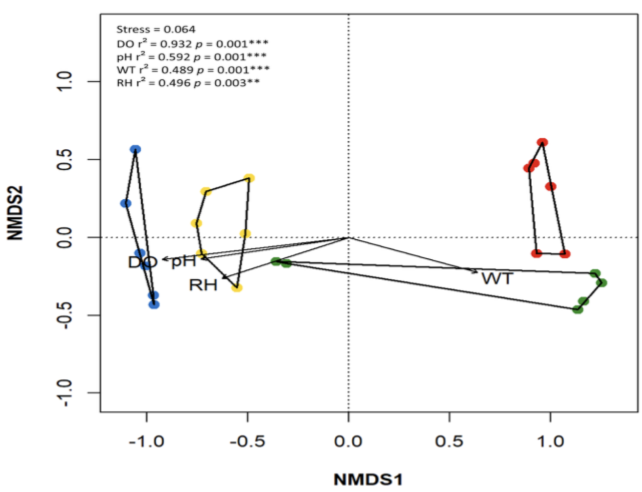

Figure 12. Non-metric multidimensional scaling (NMDS) ordination of Odonata assemblages in relation to environmental variables across habitat types: ● OLH, ● SLH, ● LEH, and ● AGR (stress: 0.064)

Table 5. Integrative summary table of observed richness, diversity, endemism, and key environmental drivers across habitat types

Habitats	S	H′ dry	H′ wet	PE	Key environmental drivers
OLH	20	2.410±0.125	2.626±0.111	70%	Higher DO, RH, and pH; lower temperature
SLH	20	2.441±0.032	2.726±0.023	90%	Higher DO, RH, and pH; lower temperature
LEH	27	2.751±0.183	2.880±0.249	19%	Lower DO, RH, and pH; higher temperature
AGR	33	2.668±0.038	2.772±0.030	36%	Lower DO, RH, and pH; higher temperature

Note: S: number of species, H′: Shannon-Wiener diversity Index, PE: percent endemism

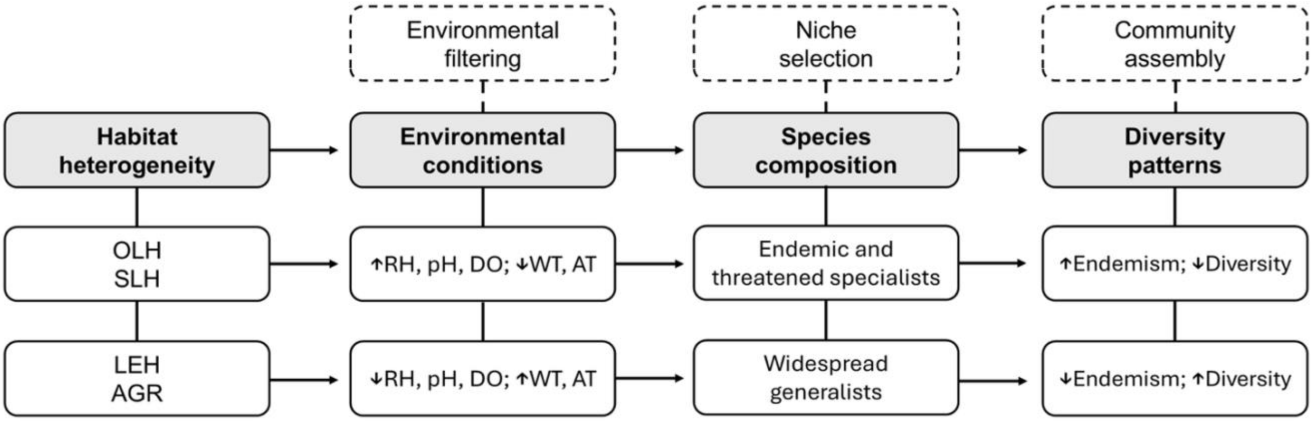

Figure 13. Conceptual model illustrating the ecological pathway linking habitat heterogeneity, environmental conditions, species composition, and diversity patterns in the study

Discussion

The Odonata assemblage recorded in Sitio Talangisog highlights the substantial diversity of the area and supports the hypothesis that habitat heterogeneity influences species composition and diversity. The 52 species documented add to several previous locality-based surveys in Misamis Oriental, including nine species in Bolyok Falls, Naawan (Daso et al. 2021) and 27 species in Mimbilisan Protected Landscape, Balingoan (Ramos et al. 2020), and are comparable to provincial surveys in Northern Mindanao (Aspacio et al. 2013; Mapi-ot et al. 2013; Malawani et al. 2014). This record represents a considerable proportion of the Odonata fauna historically reported from Mindanao (Hämäläinen and Müller 1997) and adds new locality-based information to the region. Notably, the survey also documented a new record for Mindanao Island, supporting the expectation that previously undocumented habitats may reveal additional distribution records.

Clear habitat-related differences were observed in both diversity and species composition. LEH and AGR exhibited higher species diversity but lower endemism, reflecting their capacity to support widespread generalist taxa adapted to open or standing-water environments (Seidu et al. 2019). In contrast, OLH and SLH contained fewer species overall but harbored most endemic taxa, indicating the importance of structurally complex riparian habitats for Philippine Odonata, particularly damselflies associated with shaded streams (Sakai et al. 2019; Wijesooriya et al. 2022; Manangan et al. 2026). These habitats also supported most threatened species recorded in the study, whose populations are increasingly affected by deforestation and land-use change (DENR 2019; IUCN 2025). An exception was the Endangered *S. bukid*, observed in LEH, consistent with reports that the species may occur in swampy or lentic environments within forest landscapes (Villanueva and Dow 2014).

Environmental variables further explained patterns of species turnover. The db-RDA and NMDS analyses indicated that DO, pH, WT, and RH significantly structured community composition. DO influences larval respiration and survival (Brito et al. 2021), while pH and temperature affect physiological tolerance and habitat suitability of aquatic macroinvertebrates (Mendes et al. 2018). These factors likely contributed to the observed pattern in which endemic damselflies were primarily associated with cooler, well-oxygenated OLH and SLH, whereas many widespread or Oriental species occurred more frequently in warmer LEH and AGR environments. To further synthesize these relationships, a conceptual model (Figure 13) is proposed to illustrate the ecological pathway linking habitat heterogeneity, environmental conditions, species composition, and resulting diversity patterns observed in this study.

The model depicts a directional gradient wherein OLH and SLH are characterized by cooler, slightly alkaline, oxygen-rich, and more humid conditions that favor endemic specialist taxa. In contrast, LEH and AGR are associated with warmer, slightly acidic, and lower-oxygen environments dominated by widespread generalist species. These patterns indicate that community assembly is primarily driven by niche selection mediated through environmental filtering across habitat types.

Seasonal patterns were also evident, with abundance, richness, and diversity increasing during the wet season. Similar trends have been reported in other tropical systems where increased water availability expands aquatic habitats and enhances opportunities for reproduction and emergence (Vilela et al. 2016; Manu et al. 2023). However, ordination results suggested that local habitat conditions exerted a stronger influence on community composition than season alone.

Several methodological considerations should be acknowledged. Sampling sites were selected purposively, and although spatial separation among replicate sites was maintained based on distances used in previous Odonata ecological studies (Dolný et al. 2014; Cezário et al. 2021), adult Odonata are capable of dispersing between nearby habitats. Nevertheless, many species exhibit territorial behavior and strong site fidelity around breeding sites, particularly along streams and pond margins, which can limit routine movement and allow assemblages to reflect local habitat conditions (Minot et al. 2021). In addition, abundance values represent EBA rather than exact population sizes because individuals were not marked during surveys. Despite these limitations, the consistent habitat-associated patterns observed across sites suggest that assemblage structure largely reflects local habitat conditions.

The findings emphasize the conservation importance of Sitio Talangisog. Lotic habitats supported most endemic and threatened species, highlighting the ecological value of intact riparian systems. Continued forest clearing and land-use change may therefore pose significant risks to these habitat specialists. Protecting heterogeneous freshwater landscapes within ancestral domains may be essential for maintaining both endemic and widespread Odonata assemblages and for safeguarding regional biodiversity.

In conclusion, Sitio Talangisog supported a diverse Odonata assemblage comprising 52 species, including 24 endemic taxa and five species of conservation concern. Diversity and richness were highest in LEH (H′: 2.751-2.880, S: 27) and AGR (H′: 2.668-2.772, S: 33), whereas OLH and SLH harbored fewer species (S: 20 each) but much higher endemism (70-90%). Species turnover followed an environmental gradient from warmer, lower-oxygen habitats dominated by generalists to cooler, well-oxygenated habitats supporting endemic specialists. A new Mindanao record of *R. obsolescens* further highlights the area's biogeographic importance. These findings emphasize the role of habitat heterogeneity in structuring Odonata communities. However, the study is limited by short sampling duration, purposive site selection, and encounter-based counts. Future research should incorporate long-term monitoring and broader spatial coverage. Conservation efforts should prioritize intact lotic habitats while managing increasing pressures in lentic and agroecosystem areas to sustain endemic biodiversity.

ACKNOWLEDGEMENTS

The authors acknowledge support from DOST-SEI ASTHRDP, DENR-X for granting permits, and the local government of Gingoog City, with the barangay officials of Eureka, for their assistance. Special thanks are extended to Datu Ramil P. Ansihagan and the Baliguihan-Higaonon ancestral community in Sitio Talangisog for their hospitality. The authors also thank the MEP Laboratory, Justin Maceda, Christine Hope Dela Cruz, Joriemar Magallanes, Donn Jericho Jake Densing, Elbert Caballero, Kimberly Jane Adrias, Eissa Matiyn Pandangan, Keana Aubrey Valdehueza, and Claudine Ann Nakila for their help and support.

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