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ORIGINAL ARTICLE

Complementary roles of agricultural and natural habitats in supporting moth diversity in semi-arid landscapes of Morocco

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Key words. Lepidoptera, Noctuidae, Erebidae, species composition, abundance, sugar bait, agriculture, conservation, High Atlas Mountains, North Africa

Abstract. Human activities, particularly those exacerbated by climate change, are major drivers of biodiversity change. While many human actions degrade biodiversity, some anthropogenic habitats can provide refuges for certain species, insects in particular. Research on the human impact on biodiversity remains uneven both geographically and taxonomically. In this study, nocturnal moth assemblages were compared across three habitat types (forest, riverbanks and olive groves) representing a gradient from natural to heavily human-altered environments in a semi-arid landscape of Morocco. Moths were systematically sampled across an altitudinal gradient ranging from 900 to 1600 m using automatic sugar-bait traps. We recorded 105 macroheteroceran species, most of which belonged to the families Noctuidae and Erebidae. The differences in moth assemblages among the studied habitats were statistically significant, with magnitudes comparable to those observed among the study sites. Altitude had a relatively weak influence on abundance and species richness. Olive groves exhibited the highest moth abundance and species richness, though they were dominated by common and widespread species. Forests supported a greater number of rare species, while riverbanks had lower abundance and species richness. In conclusion, while traditional agriculture can support species-rich insect communities in semi-arid landscapes, maintaining natural vegetation remains crucial, as forests, though less species-rich, still enhance overall moth diversity.

INTRODUCTION

Human activities, intensified by climate change, are major drivers of biodiversity loss. Key stressors, such as habitat destruction, pollution, overexploitation, and invasive species, continue to alter ecosystems (Bellard et al., 2012; Hald-Mortensen, 2023). Converting habitats for agriculture or urbanization is a widespread cause of degradation (Dudley & Alexander, 2017; Ma et al., 2023), and the unsustainable use of resources further reduces the ecosystems' ability to sustain biodiversity (Arora, 2018).

Numerous studies have documented the impact of human activities on both natural and semi-natural habitats, usually revealing significant biodiversity loss when these environments are disrupted. Natural habitats, rich in specialist species, are especially sensitive to disturbance (Newbold et al., 2013; Carrara et al., 2015), while semi-natural habitats, which offer refuge during environmental changes, are increasingly degraded by land-use conversion (Aune et al., 2018; Mohamed et al., 2024). However, some human-modified landscapes, such as clear-cuts, road verges, and power-line corridors, can support diverse insect communities, particularly grassland-associated species, an ecosystem facing rapid decline in Europe (e.g. Berg et al., 2011; Viljur & Teder, 2016). Sustainable farming practices, including organic and conservation agriculture, may also enhance biodiversity and offset negative impacts (Jankielsohn, 2023 and references therein).

Research efforts on the impact of human activities on biodiversity are unevenly distributed across the globe, with some regions and taxonomic groups receiving far less attention than others. Northern Africa, for instance, is underrepresented in many studies. In Morocco in particular, attention has been given to the effects of human activities on specific taxa, including mammals, birds, reptiles and plants, as well as certain insect groups, such as Hymenoptera, Coleoptera, Diptera, and diurnal Lepidoptera (Alaoui

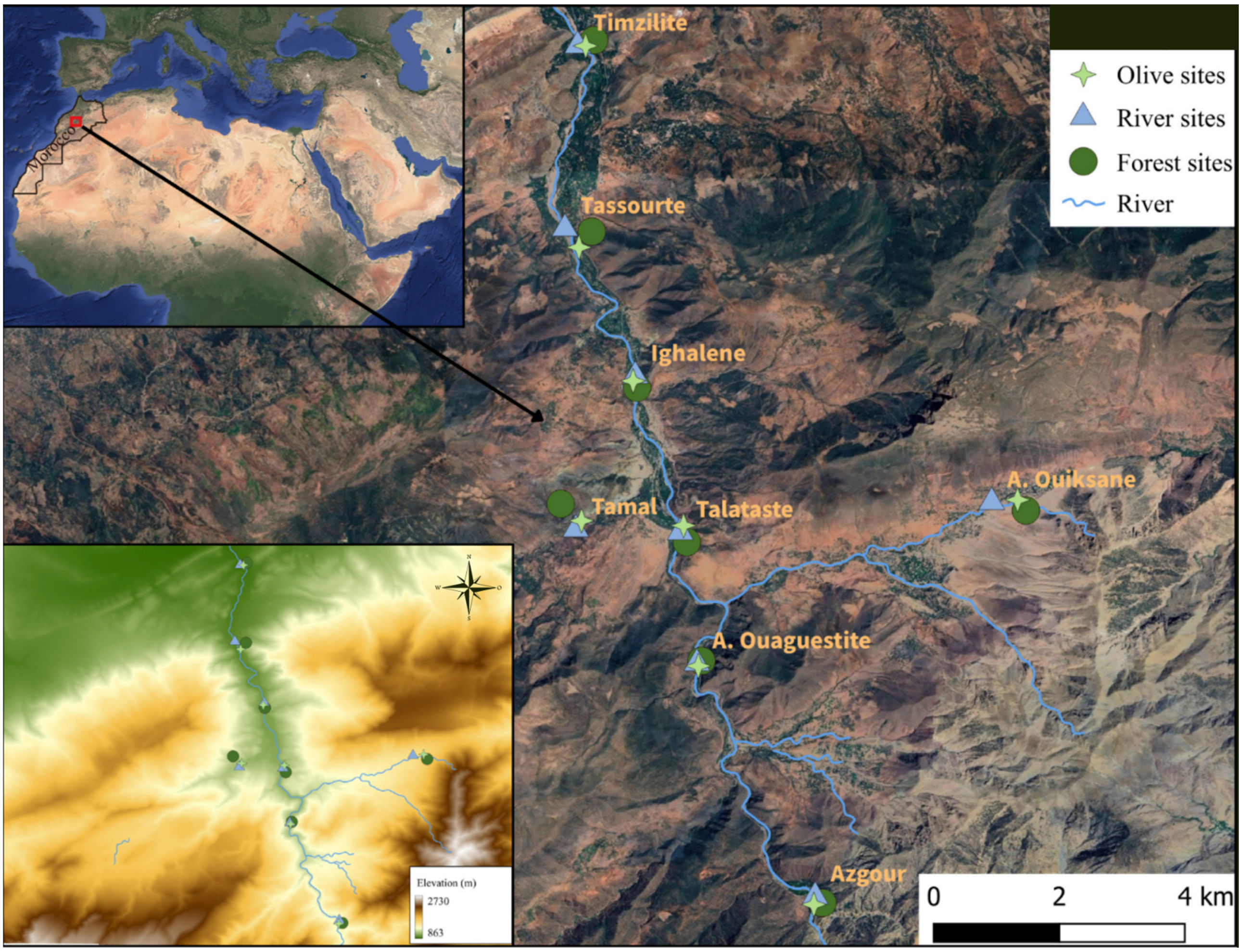

Fig. 1. Map of the study sites in the central High Atlas Mountains showing the three habitat types within each of the villages. The inset in the bottom left illustrates elevation (in m).

Haroni et al., 2009; Martínez-Freiría et al., 2013; El Alami, 2019; El Alami et al., 2021; Mounir et al., 2022, 2024; El Harche et al., 2023). However, ecological studies on nocturnal Lepidoptera, a species-rich group of pollinators, are still entirely lacking in this region.

Macro-moths are widely used as bioindicators due to their abundance, ease of sampling, and often also unambiguous identification (Fiedler et al., 2008; MacGregor et al., 2015). They are highly sensitive to environmental changes, which can influence their population dynamics, causing both outbreaks and declines (Braga & Diniz, 2018; Hill et al., 2021). Climate change has driven many species to shift their ranges toward cooler areas, altering community composition and favoring generalists over specialists (Fox et al., 2014; Mangels et al., 2017; Uhl et al., 2022). Other stressors, such as increased predation and light pollution, may further contribute to population changes (Boyes & Holland, 2021).

The High Atlas Mountains are a key biodiversity hotspot (Medail & Quezel, 1999; Myers et al., 2000), yet they face growing threats from climate change and habitat fragmentation (El Alami, 2022). Despite this, research on Lepidoptera in Morocco remains limited. Since the butterfly study by Thomas & Mallorie (1985), few ecological investigations have been conducted, and the moth fauna remains poorly documented (Fetnassi et al., 2025). This knowledge gap hinders our understanding of the ecology of moths in the region and impedes efforts to develop effective strategies for preserving biodiversity in the region.

In this study, we aimed to assess the structure of nocturnal moth communities in the semi-arid central High Atlas Mountains by comparing three distinct habitat types: forests, riverbanks, and olive groves. Specifically, we examined differences in moth abundance, species richness, and species composition among these habitats. To achieve this, we sampled moths using bait-trapping technique during the autumn of 2022. In our analysis, we address the ecological determinants of moth community composition and discuss the results in conservation-biological context.

MATERIAL AND METHODS

Study area

Our study was conducted in the High Atlas Mountains, the largest segment of the Atlas mountain range extending across northwest Africa, specifically in Morocco and Algeria (Ellero et al., 2012). The terrain is notably rugged, featuring steep slopes, deep valleys, and high plateaus (Bell et al., 2022). Specifically, the study area falls within two distinct bioclimatic zones, determined by altitude: a semi-arid zone with colder winters at

Table 1. Location of the studied villages in the Central High Atlas Mountains and respective sampling periods.

Village	Coordinates[1]		Altitude (m a.s.l.)	Sampling periods in 2022
	Latitude	Longitude		
Timzilite[2]	31°29′33.70″N	7°32′8.90″W	904	September to November
Tassourte[2]	31°27′38.30″N	7°32′10.30″W	980	September to November
Ighalene[2]	31°26′4.10″N	7°31′43.00″W	1020	September to November
Talataste[3]*	31°24′42.62″N	7°31′14.80″W	1080	late October to November
Tamal[2]	31°24′54.10″N	7°32′29.00″W	1143	September to November
Ait Wagestite[4]*	31°23′19.40″N	7°31′4.20″W	1170	September to late October
Azgour[2]	31°20′57.40″N	7°29′55.70″W	1300	September to November
Ait Ouiksane[5]*	31°24′55.10″N	7°28′9.30″W	1600	September

[1] Coordinates of the approximate center of the village; [2] Villages with complete time series; [3] A replacement village for Ait Wagesite, added later during the sampling; [4] A replacement village for Ait Ouiksane, added later during the sampling; [5] Village later excluded from the sampling; * Villages with incomplete time series.

higher altitudes (above 1,500 m) and a more humid zone with milder winters at lower altitudes (800–1,500 m) (AHT Groupe Ag-Resing, 2016). The region is characterized by a semi-arid to arid climate, with two distinct seasons: a wet period lasting from October to May and a dry period from June to September (Bouamri et al., 2018). Precipitation in the High Atlas of Morocco varies widely, from approximately 150 mm annually in the plains to around 800 mm in the mountains (Boudhar et al., 2009; Bouamri et al., 2018). The region features diverse habitats, including forests, shrublands, and grasslands, within a mosaic of natural and semi-natural landscapes (Barrow & Hicham, 2000; Nguyen et al., 2023).

Study sites

Our study was conducted in eight small villages (*villages*, hereafter) situated within the valley of Zat river in the central part of the High Atlas Mountains. The villages were located at least three kilometers apart (Table 1 and Fig. 1). All the villages supported small-scale agriculture. In each village, we selected three patches representing different habitats (*habitat types*, hereafter), with each habitat patch within a village called a *study site*. These habitat types included (1) natural areas consisting of heterogeneous forests (labeled *forest*), (2) semi-natural areas represented by riverbanks (labeled *river*), and (3) agricultural lands featuring various crop plantations (labeled *olive*). These three habitat types were selected to represent a gradient from natural to heavily human-altered environments.

The *forest* habitats represent the natural vegetation of the mountain slopes characteristic of the Mediterranean High Atlas Juniper Steppe ecoregion (One Earth, 2025). The woody plants that characterize this habitat are primarily shrubs of *Juniperus phoenicea* (Linnaeus, 1753) and *J. oxycedrus* (Linnaeus, 1753) but also include *Pistacia lentiscus* (Linnaeus, 1753), *Retama* spp., *Tetraclinis articulata* (Vahl.) Masters 1893, *Ceratonia siliqua* (Linnaeus, 1753), and *Quercus ilex* (Linnaeus, 1753). Study sites representing the forest habitat were situated on slopes about 10 m above the level of the river. The *river* sites were characterized by riparian vegetation, with *Populus alba* (Linnaeus, 1753), *Salix pedicellata* (Desfontaines, 1799), *Nerium oleander* (Linnaeus, 1753), *Arundo donax* (Linnaeus, 1753), *Phragmites australis* (Cavanilles) Trinius. ex. Steudel, 1841 and *Tamarix africana* (Poiret, 1789) as dominant plant species (Mostakim et al., 2022b). The riverbanks have undergone some alterations due to dam construction, rock extraction for building purposes (Mostakim et al., 2022a), and traditional irrigation practice known as seguia (Peyron, 1976; Mostakim et al., 2022a). Lastly, *olive* habitats consisted of patches of dense olive groves (*Olea europaea* Linnaeus, 1753) covering a minimum area of three hectares. These groves were interspersed with various annual herbs, including alfalfa (*Medicago sativa* Linnaeus, 1753), lemon verbena (*Aloysia citrodora* Paláu, 1784), and corn (*Zea mays* Linnaeus, 1753). Prickly pear [*Opuntia ficus-indica* (Linnaeus) Miller, 1768] plants were occasionally found growing along the field edges in villages located at lower altitudes. These crops are irrigated using the seguia system, a traditional technique that channels water to agricultural fields. Depending on the source, irrigation water is either diverted from rivers through seguia or drawn from mountain springs and directed through the same method, ensuring a reliable supply during the dry season.

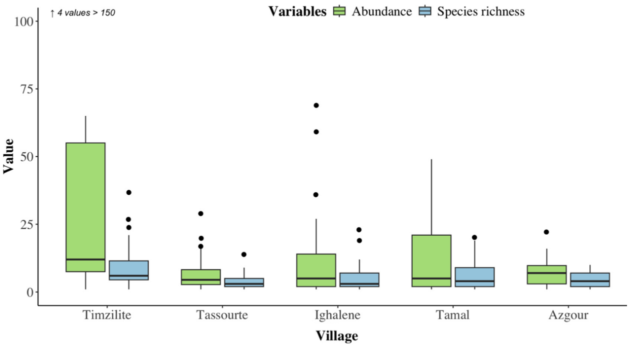

Fig. 2. Abundance and species richness estimated using Chao method based on individual trap samples collected in five villages. Villages are arranged based on altitude from the lowest to the highest (left to right). Median and quartiles are shown. Black dots indicate outliers.

Moth sampling

To sample nocturnal moths from the study sites, we used the automatic sugar bait trapping technique as described by Fetnassi et al. (2022). The bait consisted of a mixture of 1 kg of sugar dissolved in 5 l of a mixture of red wines, "Vin du Sahari" and "Vin Touareg," both of which have an alcohol content of 13%. The sponges were placed in 500 ml cups. The traps were suspended from tree branches at a standard height of 1.5 m using ropes.

On 13 days between 22 September and 15 November 2022, a total of 24 traps were set up at the study sites (reduced to 18 traps following the exclusion of some villages, below). The choice of the autumn season was informed by a pilot study (see Discussion for more details). In all villages, the traps were distributed across the three habitat types, with one trap per river and olive habitat type. In the forest habitat, where public access and sparse vegetation made the traps more visible and vulnerable, two traps were occasionally deployed to ensure that at least one remained functional. Traps within the same village were placed at least 100 m apart which is a sufficient distance to achieve independence of the samples (Ude et al., 2025). Additionally, within each site, the traps were relocated a minimum of 30 m at each sampling round with the aim to focus on the habitat patch as a whole and to minimize the effect of microsite-specific conditions. The duration of each of the thirteen sampling rounds – defined as the time from setting up the traps to emptying them – varied slightly depending

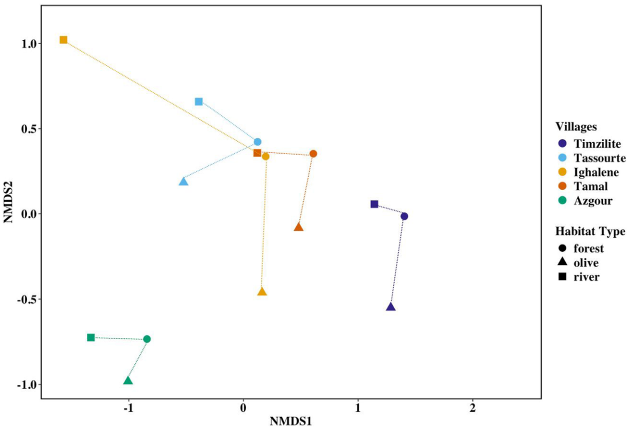

Fig. 3. Nonmetric multidimensional scaling (NMDS) plots showing moth species composition in different habitat types and villages. Note qualitatively consistent differences among the habitat types across the villages.

on weather conditions. When it was hot, the traps were checked and replenished after three days. During cooler periods, when the bait mixture remained effective longer, we replenished the traps every five to seven days.

Not all eight villages could be sampled throughout the entire study period. Specifically, Ait Ouiksane and Ait Ouagestite were replaced by Azgour and Talataste due to technical issues, conflicts with the local population, or instances of traps being stolen (Table 1). However, in five villages, sampling was successfully conducted throughout the entire sampling period.

Moths were identified based on morphological and anatomical characteristics, with DNA barcoding used when necessary. Nearly all individuals were identified at the species level, with only a few remaining at the genus level. Details on the identification procedures and faunistic analysis of the collected material have been published elsewhere (Fetnassi et al., 2025).

Data analysis

To evaluate the differences in moth community composition across the three habitat types – forest, river and olive – we conducted a PERMANOVA analysis using a dissimilarity matrix based on the Jaccard index. This index was chosen to satisfy the assumption of homogeneity of group dispersion required by PERMANOVA (Anderson & Walsh, 2013). We verified this assumption using the multivariate homogeneity of group variances test (Anderson, 2006), which was implemented through the vegan R package (Oksanen et al., 2022). Jaccard distance was calculated using a community matrix that organized species abundances by village, habitat, and sampling date. Rare species (those with ≤ 2 individuals in the total sample) and zero samples were excluded from the data matrix. Rare species contribute minimally to the recorded community structure, yet they disproportionately influence dissimilarity measures. This may result in sparsity or undefined distances, thereby compromising the validity and interpretability of multivariate analyses (Legendre & Legendre, 2012).

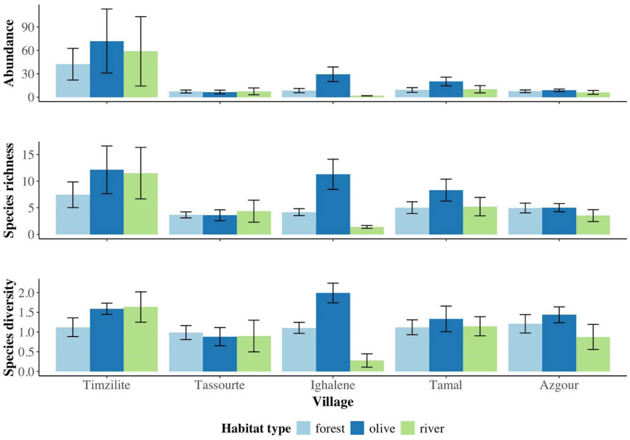

Fig. 4. Abundance, observed species richness and diversity (Shannon index) for each habitat type within each village. Villages are arranged based on altitude from the lowest to the highest (left to right). Error bars represent the standard errors of each of the three variables.

To account for the repeated measurements in our data (each site sampled several times), the PERMANOVA was performed with appropriately restricted permutations. Due to a slight imbalance in the dataset (e.g., missing traps), custom coding was required for the restriction process. This approach followed the principles outlined by Bakker (2024). Specifically, the degrees of freedom for habitat were calculated by first controlling for village and phenology, treating each trap as a blocking variable. Habitat permutations were then restricted within each village. When testing for the effect of village, the process was reversed, with village and habitat switching roles. Pseudo-F statistics and p-values were not generated for other predictors due to their limited relevance for the study questions. Additionally, we conducted a non-metric multidimensional scaling (NMDS) analysis on the Jaccard distances to visually represent the differences in species composition by displaying the data in a two-dimensional space.

Generalized linear mixed models (GLMMs) were fitted to assess the effect of habitat type on moth abundance, species richness and diversity, with villages as a fixed and study sites (habitat patches within villages) as a random factor. The site-specific samples from each sampling round were treated as individual data points. We applied the Chao1 estimator to adjust species richness to sample sizes (Chao, 1984, 1987; Chao & Chiu, 2016). Furthermore, the adjusted Shannon index was estimated using a similar approach (Chao et al., 2013). The computation of both diversity metrics was performed using the iNEXT 3.0.1 R package, em-

Table 2. Permutational analysis of variance (PERMANOVA) for moth community composition across villages (villages nested within habitat types), based on Jaccard dissimilarities. Statistical significance of 'Village' was assessed using restricted permutation, see methods for details. Df – degrees of freedom, SS – sum of squares, R^2 – coefficient of determination.

	Df	SS	R^2	F	P
Habitat type	2	1.186	0.028	1.462	
Phenology	1	1.923	0.037	4.768	
Village	7	3.494	0.067	1.231	< 0.001
Study site	13	7.126	0.136	1.353	
Residual	95	38.501	0.738		
Total	118	52.238	1.0		

Table 3. Permutational analysis of variance (PERMANOVA) for moth community composition across three habitat types (habitat types nested within villages), based on Jaccard dissimilarities. Statistical significance of habitat type was assessed using restricted permutation, see methods for details. Df – degrees of freedom, SS – sum of squares, R^2 – coefficient of determination.

	Df	SS	R^2	F	P
Village	7	5.124	0.099	1.806	
Phenology	1	1.825	0.035	4.504	
Habitat type	2	1.054	0.020	1.301	0.021
Study site	13	5.734	0.110	1.090	
Residual	95	38.501	0.738		
Total	118	52.238	1.0		

Table 4. Generalized Linear Mixed Models (GLMMs) were used to assess the effects of habitat type, phenology, and village (all as fixed factors) on moth abundance, species richness, and diversity. Negative binomial distributions were applied for modeling abundance and species richness, while Tweedie distribution was used for Shannon diversity. Study sites (habitats within villages) were included as a random factor to account for repeated measurements (13 sampling rounds) for each site. Species richness and species diversity were estimated using the Chao method. Villages are arranged altitudinally from the lowest to the highest. "Forest" is the reference level for habitat type and "Timzilite" (the lowest one) for "villages".

	Abundance			Species richness			Species diversity		
	Estimates	Z	p	Estimates	Z	p	Estimates	Z	p
olive	0.641	3.397	< 0.001	0.474	2.639	0.008	0.14	0.864	0.39
river	–0.141	–0.689	0.49	–0.305	–1.522	0.12	–0.148	–0.793	0.43
Phenology	–0.613	–6.160	< 0.001	–0.493	–5.467	< 0.001	–0.136	–1.799	0.07
Phenology^2	0.283	2.524	0.017	0.241	2.282	0.02	–	–	–
Tassourte	–1.778	–6.204	< 0.001	–0.796	–2.879	0.003	–0.231	–0.896	0.37
Ighalene	–1.301	–4.566	< 0.001	–0.545	–1.984	0.047	–0.027	–0.111	0.91
Talataste	–2.940	–4.308	< 0.001	–1.976	–3.073	0.002	–1.605	–1.724	0.08
Tamal	–1.311	–5.110	< 0.001	–0.129	–0.523	0.6	–0.037	–0.166	0.86
Ait Wagestite	–3.231	–6.331	< 0.001	–2.212	–4.529	< 0.001	–1.246	–2.214	0.03
Azgour	–1.246	–4.179	< 0.001	–0.168	–0.603	0.54	0.041	0.169	0.86
Ait Ouiksane	–2.470	–4.586	< 0.001	–1.165	–2.276	0.02	–0.138	–0.312	0.75

ploying Hill numbers with q = 0 for species richness and q =1 for the exponential of Shannon's entropy index (Chao et al., 2014; Hsieh et al., 2016).

All GLMM analyses were conducted using the Chao-estimated values of species richness and diversity as the response variables, applying lme4 package in R. Given the presence of overdispersion in all response variables, the analyses were performed under the assumptions of (1) negative binomial distribution for abundance and species richness, and (2) Tweedie distribution for the Shannon diversity index. To account for phenological effects, we included sampling date as a continuous variable and added its squared term to capture potential nonlinear relationships.

The Indicator Species Analysis was applied to identify species that are associated with particular habitat types and villages using the IndVal method (Dufrêne & Legendre, 1997). This method, implemented via the indicspecies 1.7.15 R package (De Cáceres & Legendre, 2009), integrates two core metrics – specificity and fidelity – to assess species habitat association (Dufrêne & Legendre, 1997). While specificity measures the degree to which a species is restricted to a given group of sites, fidelity, however, measures the degree to which a species is occurring at all sites of a group (Dufrêne & Legendre, 1997; Legendre, 2013).

The primary objective of this study is to compare the habitats. To this end, all PERMANOVA and GLMM analyses were performed on the total data set, including the data from the villages which could not be sampled throughout the entire study period (Table 1, and above). However, a comparison of villages with varying levels of phenological coverage would be problematic. Therefore, such analyses were performed on the data from the five villages that had complete time series (see Tables 5, S2, and S3, and Figs 2, 3, and 4).

RESULTS

A total of 2,308 macroheteroceran moths representing 105 species were collected across 8 villages (24 sites). The majority of the sample belonged to the families Noctuidae and Erebidae, with a few additions from Drepanidae, Geometridae, and Euteliidae (see Table S1 for the list of species, and Fetnassi et al., 2025, for further discussion). The median sample contained five moth individuals (Q1 = 2, Q3 = 13) and four species (Q1 = 2, Q3 = 7).

Table 5. The number of rare species (with ≤ 2 individuals recorded during the study) across villages and habitat type.

	forest	olive	river
Timzilite	3	7	6
Tassourte	2	0	1
Ighalene	4	2	0
Tamal	6	4	4
Azgour	8	2	1

Abundance and estimated species richness varied across the villages, with the lowest altitude village (Timzilite) showing notably higher values for both metrics (Fig. 2). Notable variations in species composition were also observed among villages, as illustrated by the NMDS plots (Fig. 3). These differences were confirmed by PERMANOVA results, which indicated significant differences in community structure across villages (Table 2). The species composition also varied systematically across habitat types (Table 3). The NMDS plots further emphasize this trend, revealing consistent patterns across all villages. The repeating pattern is evident in the symbols for the river habitat, which are positioned in the upper part of the plot for each village, while the symbols for olive habitats are predominantly located in the lower part (Fig. 3). Overall, the variation in species composition among villages was of the same magnitude but still somewhat larger than the variation observed between habitat types within villages (Fig. 3).

Table 6. Indicator species analysis of moth species associated with each habitat type. Only statistically significant results with non-zero IndVal values are presented. The terms "A" and "B" represent the components of the IndVal metric, with "A" indicating specificity and "B" representing fidelity.

	A	B	IndVal	P-value
forest				
Callopistria latreillei	0.862	0.125	0.328	0.013
olive				
Mniotype occidentalis	0.822	0.325	0.517	< 0.001
Xestia c-nigrum	0.961	0.140	0.366	0.005
Trigonophora flammea	0.800	0.162	0.360	0.015
Xestia xanthographa	0.913	0.140	0.357	0.006
forest + olive group				
Agrotis trux	0.950	0.241	0.480	0.011
olive + river group				
Mormo maura	0.930	0.222	0.454	0.014

Table 7. Indicator species analysis of moth species associated with each village. Only statistically significant results with non-zero IndVal values are presented. The terms "A" and "B" represent the components of the IndVal metric, with "A" indicating specificity and "B" representing fidelity.

	A	B	IndVal	P-value
Timzilite				
Spodoptera littoralis	0.762	0.666	0.713	0.002
Xestia xanthographa	0.930	0.333	0.557	0.012
Grammodes stolida	1	0.222	0.471	0.033
Ait Ouiksane				
Eupithecia cooptata	1	0.333	0.577	0.021
Metachrostis velox	0.770	0.333	0.506	0.026
Dichagyris constanti	0.722	0.333	0.491	0.03
Timzilite + Ait Ouiksane group				
Pandesma robusta	0.790	0.809	0.8	0.004
Ighalene + Azgour + Ait Ouiksane group				
Catocala oberthuri	0.775	0.468	0.603	0.023
Timzilite + Ighalene + Tamal + Ait Ouiksane group				
Leucania putrescens	0.937	0.352	0.574	0.033

Species richness and abundance exhibited higher values in the olive habitat; however, these metrics did not demonstrate significant differences between river and forest habitats. Similarly, species diversity also showed no significant differences between river and forest (Tables 4, S2 and Fig. 4). Expectedly, there was a phenological trend in species richness and abundance, with both metrics declining as the season advanced (Tables 4, S2). A total of 46 rare species (one or two in the total sample) were recorded throughout the study. Most villages exhibited a higher number of rare species in the forest habitat, with river habitats generally having the lowest number of rare species (Table 5).

The indicator species analysis identified a total of seven species linked to specific habitats: one species was associated with forest habitat, four species with olive habitat, and two species with multiple habitats. One of these species was characteristic of both olive and forest habitats, and the other was indicative of both olive and river habitats. No species were found to be exclusively associated with the river habitat (Table 6). Furthermore, the analysis indicated that seven species were characteristic of two villages located at different altitudes, while three species were associated with multiple villages (Table 7).

DISCUSSION

This study provides a quantitative assessment of macroheteroceran moth communities sampled in the High Atlas Mountains of Morocco – a global biodiversity hotspot (Medail & Quezel, 1999). Our results suggest that there is a fairly high diversity of macro-moths at mid-altitudes in this semi-arid mountain area, especially if to consider that our study covered only a fraction of the phenological spectrum. Opportunities for an evaluation of these results in terms of species richness and diversity are however limited due to the scarcity of faunistic surveys in the Atlas Mountains or in Morocco as a whole – an issue our study helps to address and minimize. Moreover, our study used bait trapping, making comparisons with analogous studies difficult, as research relying on this method are relatively rare (see, however, Maicher et al., 2018, 2020; Merckx et al., 2018; Mertens et al., 2021). In any case, we can safely conclude that the diversity of moths is sufficiently high in the studied habitats for the taxon to serve as a bioindicator in ecological studies, and for the moth fauna itself being a target of conservation efforts.

Although our sampling covered an altitudinal gradient of 500 m, we did not observe consistent altitudinal trends in any community parameter (e.g. species abundance, richness, and diversity) across the study sites (Fig. 2). However, our results revealed that the village at the lowest altitude (900 m a.s.l.), Timzilite, exhibited notably high moth abundance and, to a lesser extent, higher species richness. This finding was primarily driven by the exceptional abundance of *Pandesma robusta* (Walker, 1858) (n = 630), which was present across all habitat types in Timzilite, with the highest number of individuals recorded in olive habitat. Additionally, indicator species analysis identified *Spodoptera littoralis* (Boisduval, 1833), *Xestia xanthographa* (Denis & Schiffermüller, 1775), and *Grammodes stolida* (Fabricius, 1775) as species strongly associated with the Timzilite village (Table 7). These three species have wide geographic distributions and are considered pests (Sanjayan & Chand, 1997; Boyes & Holland, 2022; Goater et al., 2003; Mokbel & Huesien, 2020). The abundance of these four species in Timzilite is thus likely due to more extensive agriculture surrounding that village compared to the study sites at higher altitudes.

Previous studies in the mountains of the Mediterranean basin have reported species diversity of Lepidoptera to peak in mid-altitude habitats (Piñero et al., 2011; Bernabé-Ruiz et al., 2024). This contrasts to the slightly higher species richness found at the lowest altitude site (Timzilite) which could be attributed to a moderately higher number of olive groves and a distinct composition of natural vegetation compared to the other villages (dominance of *Tamarix africana* and *Retama* spp). Otherwise, the vegetation is relatively uniform in the High Atlas Mountains at altitudes between 800 and 2000 m a.s.l. (Benabid, 1982; Mostakim et al., 2022b), the absence of a strong altitudinal trend in plant species composition likely explains the similar pattern observed in moth communities.

The comparison of moth assemblages across the three habitat types revealed modest yet statistically significant differences in community parameters. Specifically, the differences in moth assemblages among habitat types were similar in magnitude, though slightly smaller than the differences observed among villages (Fig. 3). Olive habitats had higher species richness and diversity compared with other habitats (Table 4). This may be attributed to the good maintenance of olive groves in this semi-arid landscape, where irrigation practices sustain their vitality even during dry periods.

In our study area, olive groves are interspersed with herbaceous plantations, which allows a variety of plant species to grow beneath the trees. Irrigation further enhances this vegetation diversity, creating favorable microclimatic conditions for plant growth, which should, in turn, attract and support a rich insect community. These predictions are consistent with Zucco et al. (2024), who reported that maintaining natural tree-covered areas within olive farms enhances both plant and insect diversity. Some previous studies have also shown that olive groves contribute to increased insect diversity in the Mediterranean region (Calabrese et al., 2012; Chafaa et al., 2019). Other studies have found that Mediterranean agro-ecosystems can serve as important habitats for various insect species adapted to arid environments (González-Estébanez et al., 2011; Khelifa et al., 2021; Santoro et al., 2023). Nevertheless, the overall role of agriculture in sustaining biodiversity in the region remains understudied.

While olive groves provided important habitats and supported a relatively high diversity of moths, the indicator species of these habitats were mainly common and widespread (i.e. *Mniotype occidentalis* Yela, Fibiger, Ronkay & Zilli, 2010*, Trigonophora flammea* (Esper, 1785), *Xestia c-nigrum* (Linnaeus, 1758) and *X. xanthographa*) (Table 6). In contrast, forests exhibited lower overall diversity, but they were more likely to harbor rare species (as defined in this study), implying a high conservation value (Table 5). Despite their ecological importance, forests in the High Atlas Mountains face growing threats from human activities such as wood collection for firewood, overgrazing, and clearing land for cultivation (El Alami et al., 2013; El Alami, 2022). Meanwhile, river habitats exhibited lower species abundance and richness, likely due to their high level of fragmentation caused by both abiotic and biotic factors. Among the abiotic factors, rubble collection for construction contributes significantly to habitat degradation (Mostakim et al., 2022a). Additionally, frequent flooding events (Zkhiri et al., 2017) further intensify habitat disruption, causing severe damage to riparian vegetation (Assahira et al., 2017). This degradation likely affects populations of herbivorous insects that rely on these plants for survival.

The significant variation in moth communities between villages indicates that moth diversity is not evenly distributed across the landscape. This spatial heterogeneity implies that different areas contribute uniquely to regional diversity, which reinforces the need for site-specific conservation approaches. Therefore, protecting a network of habitats rather than focusing on a single type may therefore be essential to preserving overall biodiversity. Given the region's ecological significance and the presence of a variety of natural and semi-natural habitats, it is crucial to strengthen conservation efforts across the High Atlas landscape. For instance, conservation efforts could engage local communities in protection programs and support eco-friendly livelihood alternatives. Such programs could promote agroforestry, sustainable grazing practices, and pesticide-free farming (Wezel et al., 2014; Zhan et al., 2021).

From a technical point of view, our study proved sugar bait trapping to be a feasible method for studying nocturnal Lepidoptera in the region. Despite being an underutilized technique in moth studies, bait trapping offers a practical approach for targeted research, especially in smaller-scale investigations (Ude et al., 2025). However, certain challenges must be considered. Environmental factors, such as temperature, humidity and wind may influence trapping efficiency, leading to variability in captures (Fetnassi et al., 2022). This may introduce a systematic error in comparing different habitats which may also well differ in weather conditions. For these reasons, differences in moth abundance should be treated with appropriate caution, while any parameters of assemblage composition should be less prone to such methodological errors. Additionally, in a semi-arid climate, frequent visits are required to replenish the bait due to high evapotranspiration rates and to monitor the traps in case of any other insect predator attacks (pers. observ.). During a pilot study in late spring and early summer, predatory wasps and honeybees were found to inflict extensive damage to the moth samples. In autumn, such "pests" were limited to mantises (*Sphodromantis viridis* Forsskål, 1775) which was one of the reasons for choosing the timing of the current study. Moreover, it is evident that bait trapping introduces a taxonomic bias, favoring groups where extensive adult feeding occurs and further research is needed to compare our results with studies relying on other methods.

In summary, our study on the autumn aspect of moth fauna highlights that well-managed agricultural landscapes, such as olive groves supported by traditional irrigation methods, can play a vital role in sustaining insect diversity in semi-arid regions. These findings challenge the common view that agriculture negatively impacts insect populations and suggest that certain human practices can benefit biodiversity. However, since different moth species have different habitat requirements, it is essential to maintain a mosaic of habitats – both agricultural and natural – across the landscape to preserve the full range of moth species. A heterogeneous approach to conservation, incorporating diverse habitats like olive groves and forests, appears vital for maintaining overall biodiversity in the High Atlas region.

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Table S1. List of macro-moth species sampled in 2022 in the eight villages of the High Atlas Mountains, as part of this study (Fetnassi et al., 2025).

Species	Total abundance
DREPANIDAE	
Watsonolla uncinula (Borkhausen, 1790)	1
GEOMETRIDAE	
Rhodometra sacraria (Linnaeus, 1767)	1
Eupithecia cooptata Dietze, 1904	2
Stegania trimaculata (de Villers, 1789)	2
Peribatodes powelli (Oberthür, 1913)	1
EREBIDAE	
Indalia uniola (Rambur, 1866)	1
Nodaria nodosalis (Herrich-Schäffer, 1851)	4
Polypogon simplicicornis (Zerny, 1935)	1
Hypena obsitalis (Hübner, 1813)	1
Schrankia costaestrigalis (Stephens, 1834)	1
Antarchaea sp. (near erubescens)	2
Eublemma ostrina (Hübner, 1808)	1
Metachrostis velox (Hübner, 1813)	4
Autophila cataphanes (Hübner, 1813)	1
Apopestes spectrum (Esper, 1787)	1
Catephia alchymista (Denis & Schiffermüller, 1775)	1
Pandesma robusta (Walker, 1858)	896
Zethes insularis Rambur, 1833	6
Heteropalpia acrosticta (Püngler, 1904)	1
Catocala oberthuri Austaut, 1879	85
Catocala puerpera (Giorna, 1791)	6
Catocala dilecta (Hübner, 1808)	8
Catocala optata (Godart, 1824)	11
Tytroca dispar (Püngler, 1904)	70
Ophiusa tirhaca (Cramer, 1777)	104
Clytie illunaris (Hübner, 1813)	95
Clytie infrequens (Swinhoe, 1884)	1
Dysgonia algira (Linnaeus, 1767)	14
Grammodes stolida (Fabricius, 1775)	6
EUTELIDAE	
Eutelia adulatrix (Hübner, 1813)	5
NOCTUIDAE	
Thysanoplusia daubei (Boisduval, 1840)	1
Ctenoplusia accentifera (Lefèbvre, 1827)	1
Chrysodeixis chalcites (Esper, 1789)	2
Autographa gamma (Linnaeus, 1758)	1
Acronicta psi (Linnaeus, 1758)	2
Acronicta rumicis (Linnaeus, 1758)	85
Craniophora pontica (Staudinger, 1879)	8
Tyta luctuosa (Denis & Schiffermüller, 1775)	1
Amphipyra tetra (Fabricius, 1787)	2
Allophyes powelli Rungs, 1952	2
Xylocampa mustapha (Oberthür, 1910)	1
Heliothis peltigera (Denis & Schiffermüller, 1775)	18
Helicoverpa armigera (Hübner, 1808)	19
Condica viscosa (Freyer, 1831)	3
Callopistria latreillei (Duponchel, 1828)	8
Cryphia lusitanica (Draudt, 1931)	2
Cryphia (Euthales) sp. (near pallida)	4
Spodoptera exigua (Hübner, 1808)	37
Spodoptera cilium Guenée, 1852	10
Spodoptera littoralis (Boisduval, 1833)	80
Caradrina proxima Rambur, 1837	2
Caradrina aspersa Rambur, 1834	2
Caradrina germainii (Duponchel, 1835)	1
Caradrina ingrata Staudinger, 1897	1
Caradrina flava Oberthür, 1876	2
Caradrina sp. (near selini)	2
Caradrina flavirena Guenée, 1852	39
Caradrina noctivaga Bellier, 1863	4
Caradrina clavipalpis (Scopoli, 1763)	13
Hoplodrina ambigua (Denis & Schiffermüller, 1775)	6
Anthracia ephialtes (Hübner, 1822)	8
Mormo maura (Linnaeus, 1758)	37
Pseudenargia ulicis (Staudinger, 1859)	4
Agrochola lychnidis (Denis & Schiffermüller, 1775)	4
Anchoscelis meridionalis (Staudinger, 1871)	2
Dryobota labecula (Esper, 1788)	7
Dryobotodes eremita (Fabricius, 1775)	2
Dryobotodes monochroma (Esper, 1790)	29
Dryobotodes roboris (Geyer, 1835)	1
Dryobotodes tenebrosa (Esper, 1789)	2
Ammopolia witzenmanni (Standfuss, 1890)	6
Trigonophora flammea (Esper, 1785)	19
Trigonophora crassicornis (Oberthür, 1918)	2
Aporophyla nigra (Haworth, 1809)	1
Polymixis xanthomista (Hübner, 1819)	3
Polymixis flavicincta (Denis & Schiffermüller, 1775)	12
Polymixis germana (Rothschild, 1914)	7
Polymixis subvenusta (Püngeler, 1906)	4
Mniotype occidentalis Yela, Fibiger, Ronkay & Zilli, 2010	32
Anarta trifolii (Hufnagel, 1766)	9
Hecatera dysodea (Denis & Schiffermüller, 1775)	1
Mythimna vitellina (Hübner, 1808)	1
Mythimna unipuncta (Haworth, 1809)	14
Mythimna languida (Walker, 1858)	10
Mythimna albipuncta (Denis & Schiffermüller, 1775)	2
Mythimna algirica (Oberthür, 1918)	5
Mythimna l-album (Linnaeus, 1767)	9
Leucania zeae (Duponchel, 1828)	1
Leucania putrescens (Hübner, 1824)	80
Leucania punctosa (Treitschke, 1825)	1
Leucania loreyi (Duponchel, 1827)	2
Peridroma saucia (Hübner, 1808)	2
Dichagyris flammatra (Denis & Schiffermüller, 1775)	4
Dichagyris constanti (Millière, 1860)	6
Euxoa temera (Hübner, 1808)	7
Euxoa hastifera (Donzel, 1847)	2
Agrotis segetum (Denis & Schiffermüller, 1775)	73
Agrotis trux (Hübner, 1824)	47
Agrotis ipsilon (Hufnagel, 1766)	22
Agrotis spinifera (Hübner, 1808)	6
Ochropleura leucogaster (Freyer, 1831)	1
Noctua comes Hübner, 1813	23
Xestia kermesina (Mabille, 1869)	64
Xestia xanthographa (Denis & Schiffermüller, 1775)	13
Xestia c-nigrum (Linnaeus, 1758)	29

Table S2. Generalized Linear Mixed Models (GLMMs) were used to assess the effects of habitat type, phenology, and the five villages (all as fixed factors) on moth abundance, species richness, and diversity. Unlike Table 4 in the main text, which includes all eight villages, this analysis is based only on the five villages with complete time series data. Negative binomial distributions were applied for modeling abundance and species richness, while Tweedie distribution was used for Shannon diversity. Study sites (habitats within villages) were included as a random factor to account for site-specific variation. Species richness and species diversity were estimated using the Chao framework. Villages are arranged altitudinally from the lowest to the highest. "Forest" is the reference level for habitat type and "Timzilite" the lowest for "villages".

	Abundance			Species richness			Species diversity		
	Estimates	Z	p	Estimates	Z	p	Estimates	Z	p
olive	0.736	3.682	<0.001	0.557	2.942	0.003	0.188	1.149	0.25
river	–0.092	–0.129	0.66	–0.290	–1.384	0.16	–0.169	–0.882	0.37
Phenology	0.609	–6.108	<0.001	–0.484	–5.396	<0.001	–0.131	–1.764	0.07
Phenology^2	0.309	2.670	0.007	0.255	2.363	0.02	–	–	–
Tassourte	–1.755	–5.966	<0.001	–0.780	–2.762	0.005	–0.223	–0.875	0.38
Ighalene	–1.290	–4.399	<0.001	–0.540	–1.909	0.05	–0.022	–0.089	0.92
Tamal	–1.296	–4.913	<0.001	–0.121	–0.477	0.63	–0.029	–0.128	0.89
Azgour	–1.197	–3.897	<0.001	–0.139	–0.484	0.62	0.05	0.206	0.83

Table S3. Generalized Linear Model (GLM) assuming Poisson distribution to assess the effects of habitat types and villages that had complete time series (all as fixed factors) on the number of rare species (species with ≤ 2 individuals). Villages are arranged altitudinally from the lowest to the highest.

	Estimates	Z	p
olive	–0.174	–0.589	0.55
river	–0.734	–2.090	0.036
Tassourte	–1.674	–2.661	0.008
Ighalene	–0.980	–2.049	0.04
Tamal	0.171	0.506	0.61