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ORIGINAL RESEARCH

Ecosystem type might mask the effect of ecosystem recovery on parasitoids' biodiversity quality

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Abstract

Ecological restoration is considered a tool for repairing anthropogenic habitat disturbances, but the biodiversity recovering needs to be monitored. Here we evaluate a comprehensive approach for biodiversity: Biodiversity Quality, which comprises a set of 10 indices representing different components of diversity and providing an holistic overview. This approach was tested in a hyper-diverse insect group, the Ichneumonidae family in three different levels of conservation, i.e., a degraded area, a well-conserved area and an area undergoing ecological restoration for 10–15 years. Comparisons were done in three different ecosystems from southern Ecuador, i.e., Andean forest, rainforest and dry forest. We also compared the species assemblages through beta diversity indices. A total of 36 Townes style white Malaise traps were installed at three different conservation levels in 12 natural reserves, and all Ichneumonid insects collected were sorted, mounted and identified to operational taxonomic units (OTUs). A total of 2929 individuals in 708 OTUs were collected, which represented 1264.78 g of biomass. No differences were found between conservation levels, but all indices showed significant differences when comparing ecosystem types. Andean forests had significantly more richness, diversity, population and biomass than the other ecosystems, and less dominance and rarity than dry forests. Species composition of Ichneumonidae assemblages were also different between ecosystems and not so between conservation levels. When comparing in every ecosystem separately, degraded areas in dry forest had significantly more density and biomass than conserved areas. This represents a first attempt of applying this comprehensive approach in such a species-rich family.

Keywords Ichneumonidae · Darwin wasps · Andean forests · Rainforests · Dry forests

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Introduction

Current habitat fragmentation processes may be leading to an extinction debt (i.e., time-delayed extinctions) (Krauss et al. 2010). Its repairing requires not only conservation efforts but also the reversal of this fragmentation. Ecological restoration may help but suitable indicators are needed to monitor its performance. Tropical ecosystems undergoing ecological restoration, especially those in Latin America, have been poorly monitored, and vegetation structure and diversity-related indicators are commonly used (Mazón et al. 2019). When evaluating how human-induced disturbances are impacting on tropical ecosystems and how they are recovering afterwards, it is important to include as many indicator groups as possible (Whitworth et al. 2018). Often there are not enough specialists or time for monitoring all groups, so indicator groups should be tested for suitability in evaluating restoration trajectory (Massi et al. 2021).

Insects may be suitable ecological indicators, with some groups having a fundamental role in ecosystem functions. Hymenoptera are probably the most diverse group of organisms in the world thanks to species-rich (and mostly unknown) parasitoid wasps (Forbes et al. 2018). Pest control functions provided by insects have been estimated to be more than 4 billion dollars per year just for the United States (Losey and Vaughan 2006). These natural enemies of pests are the most affected by the land-use changes in tropical forests (Barnes et al. 2014). Among them, parasitoid wasps have been shown to be highly sensitive to ecosystem disturbances (Marrec et al. 2018) and to climate change (Kankaanpää et al. 2020) making them suitable for monitoring changes. To evaluate how parasitoid assemblages are affected by environmental changes, alpha diversity assessment (i.e., the inherent diversity in every habitat) has been widely used. Other indicators may provide more useful information. Beta diversity (i.e., species turnover between habitats) may be more helpful: even in apparently homogeneous landscapes, beta diversity may vary significantly in parasitoids (Torné-Noguera et al. 2020). A recent approach proposes using a set of biodiversity indices to give a comprehensive understanding of the assemblage's functionality in a changing environment (Feest et al. 2010). This set of indices, known as Biodiversity Quality, includes biomass, which is an essential variable for food webs (Lister and Garcia 2018; Orihuela-Torres et al. 2018). Although this approach has been used once before on tropical insects (Juen and Feest 2019), it has not been tested with such a species-rich group as Darwin wasps (Hymenoptera: Ichneumonidae), one of the largest insect families (Klopfstein et al. 2019).

The aims of this paper are: (1) to evaluate how Ichneumonidae Biodiversity Quality differs in areas with different conservation levels, (2) to determine if those differences are found in different ecosystems, (3) to assess if Ichneumonidae biomass is more impacted by perturbation than taxonomic-based biodiversity indices, and (4) to evaluate if Ichneumonidae assemblages are more related to the conservation level or to the ecosystem type. We hypothesized (H1) that Biodiversity Quality in areas under ecological restoration will be similar (i.e., non-significantly different, with significance levels >0.05) to that from the well-conserved forests, and different from that in degraded areas. We expected (H2) that differences in Biodiversity Quality will be less significant, or not significant at all, in the dry forest ecosystems. This hypothesis is supported by the severe abiotic conditions in this ecosystem, that causes a slower ecosystem recovery (Ceccon et al. 2006). We also hypothesized (H3) that Ichneumonidae assemblages will be more determined by the ecosystem type than by the conservation level, but in all ecosystems, we expected that assemblages from restoration areas will be like the forests rather than the open areas. When conducting ecological restoration, efforts should lead to not only recover biodiversity metrics, but also the species composition in order to assure the functionality of the ecosystem (Ramírez et al. 2015). Therefore, both biodiversity and species composition should be more and more resembling that of the reference ecosystem (i.e., conserved forests). Furthermore, we expected (H4) the biomass will be more sensitive (i.e., more significant differences will be found when comparing biomass) to conservation level than taxonomic-based indices.

Methods

Study area

The research took place in 12 natural reserves (one of them belonging to the Ecuadorian National System of Protected Areas, and the rest of them belonging to NGO's: Naturaleza y Cultura Internacional NCI, Jocotoco Foundation, or private reserves) from three different tropical ecosystems: Andean forest, rainforest and dry forest. In every reserve, three areas in different conservation status were identified: an area clearly degraded (open pasture-like), an area undergoing ecological restoration (either active or passive, with about 10–15 years of recovery) and a well-conserved area (unperturbed forest) (Table 1).

Sampling and identification

Sampling was done in different sampling periods from November 2015 to January 2019. In each conservation area, a Townes style white Malaise trap was installed and kept in the field for six consecutive weeks. Sampling pots were filled with ethanol 70% and replaced every two weeks, having a total of three samples per Malaise trap and a total of 36 traps. The three traps in every reserve were working simultaneously, and traps for the same ecosystem were also simultaneous for most of the reserves (except for Tapichalaca, Buenaventura and Arenillas reserves that were installed in different years).

All insects from the Ichneumonidae family were separated, mounted, and identified to subfamily. Then, individuals were sorted to operational taxonomic units (OTUs), based on external morphological characters. All specimens are preserved in LOUNAZ collection (Universidad Nacional de Loja, Ecuador).

Data analyses

To clarify the nature of biodiversity and improve its measurement, Feest et al. (2010) introduced the concept of biodiversity as a quality defined by a number of functional indices since the Convention on Biological diversity definition does not create this possibility (the term variability in the convention is undefined) (UN 1992). Changes or differences in any of the indices will show how Biodiversity Quality has changed or differs and one reviews the data holistically.

Biodiversity Quality was calculated as described in Feest et al. (2010), which includes the species richness, the population density, the species conservation value index (SCVI), the biomass index, the Shannon-Wiener and Simpson indices for alpha diversity, the Berger-

Table 1 Location of trapping sites in the three conservation levels of the four Andean Forest, Rainforest and Dry Forest reserves

Ecosystem	Reserve	Conservation level	Coordinates X	Coordinates Y	Altitude (masl)
Andean forest	ECSF	High	713,462	9,560,606	1872
		Medium	713,360	9,560,405	1858
		Low	713,276	9,560,692	1839
	Arcoíris	High	711,535	9,558,969	2158
		Medium	711,715	9,559,006	2162
		Low	711,724	9,558,889	2161
	Madrigal	High	703,419	9,551,962	2519
		Medium	702,651	9,552,712	2349
		Low	702,550	9,552,460	2402
	Tapichalaca	High	0707916	9,503,541	2574
		Medium	0707484	9,503,129	2523
		Low	0707931	9,503,435	2622
Rainforest	El Padmi	High	764,725	9,585,924	822
		Medium	764,809	9,586,079	822
		Low	764,912	9,585,813	805
	Jamboé	High	729,037	9,539,043	1196
		Medium	728,897	9,536,109	1411
		Low	728,923	9,536,831	1288
	Copalinga	High	726,017	9,547,690	1082
		Medium	726,483	9,547,573	1041
		Low	726,540	9,547,508	988
	Buenaventura	High	636,737	9,596,069	521
		Medium	636,856	9,596,127	547
		Low	640,134	9,596,098	960
Dry forest	Zapotepamba	High	634,805	9,553,882	1128
		Medium	635,708	9,553,103	940
		Low	635,281	9,553,012	954
	La Ceiba	High	575,808	9,527,506	495
		Medium	574,466	9,527,795	480
		Low	575,787	9,527,257	486
	Laipuna	High	623,192	9,534,572	690
		Medium	624,302	9,534,757	678
		Low	623,499	9,534,142	568
	Arenillas	High	595,472	9,605,315	51
		Medium	596,520	9,608,803	22
		Low	597,044	9,613,035	8

Parker dominance index, and non-parametric species richness estimators (Chao 1, Chao 2 and Jackknife), as explained in Feest et al. (2010) and in Juen and Feest (2019). The SCVI is generally assigned according to the "conservation value" that each species has. However, considering that information on tropical Ichneumonidae species is scarce, and that most species were not identified, we have utilized this index as a rarity/commonness index. We used the reciprocal of the OTUs population multiplied by 100 such that a sample population of 1 had a value of 100 ((1/1) x 100) and 5 a value of 20 ((1/5) x100) and 100 a value of 1 ((1/100) x 100). The SCVI was then the mean (and Standard Deviation) of all OTUs recorded in every site, meaning that we considered the SCVI at a regional scale, i.e., the SCVI of each OTU is calculated based on all individuals collected in this research. All indices were calculated for every conservation level in every ecosystem type and separately for every conservation level in every reserve to make statistical comparisons.

Insect weights were evaluated from the fore wing length based on the allometric equation presented by Mazón et al. (2020), so the forewing length of all OTUs (male and female separately) was measured from the base to the apex using a ZEISS Stemi 2000-C with an ocular micrometer.

Due to the great number of rare OTUs represented by single individuals (nearly 50%) the data were not normal or transformable and non-parametric statistical tests were used (Kruskal-Wallis and post-hoc Dunn tests) to compare all Biodiversity Quality indices according to (a) conservation level, (b) ecosystem type, and (c) conservation level separately in every ecosystem type. Also, to represent the sampling completeness, the proportion of OTUs predicted by the richness estimators from the observed richness is included.

For beta diversity, we conducted a non-metric multidimensional scaling (NMDS), which represents in a 2D plot differences in assemblage composition in every disturbance level and every reserve from the three ecosystem types. Furthermore, statistical differences among Ichneumonidae assemblages were tested with a 9999 permutations PERMANOVA test. Differences were checked among conservation levels and among reserves, but separately for every ecosystem type. Due to the high proportion of singletons and doubletons, both NMDS and PERMANOVA were based on Jaccard similarity index, which only considers presence/absence of species. Beta diversity analyses and Kruskal-Wallis comparisons were done with software Past version 3.0 (Hammer et al. 2001).

Results

We collected a total of 2929 individuals belonging to 708 OTUs, with a total biomass of 1264.78 g (Table S1). The highest species richness, biomass and densities were found in Andean forests. Rarity was high in all samples but specially in the rainforest samples. Regarding sampling completeness, proportions of collected OTUs from the total estimated ranged from 64.38 to 69.53%, according to the Jackknife estimator (Table S2).

None of the variables followed the same patterns in the three ecosystems (Table S2). Areas undergoing restoration showed intermediate values between degraded and well-conserved areas in Andean forests in most indices, except for SCVI. In rainforests, restoration areas showed the lowest values in almost all indices except for biomass, which was intermediate between the other two. In dry forests, indices behaved very differently: while richness and diversity were the lowest in the degraded areas, they had a higher biomass than the other areas.

When running Kruskal-Wallis tests, we observed that there were no statistical differences among conservation levels in any index, but differences were all significant between ecosystem types (Table 2). According to the post-hoc tests, Andean forest had significantly ($p=<0.05$) more species richness (observed and estimated), diversity, population and biomass than the other ecosystems, less dominance than dry forest and less rarity than rainfor-

Table 2 Results from the Kruskal-Wallis test (H) and p-value (p) for every Biodiversity Quality index of Ichneumonidae assemblages when comparing conservation level (conservation), ecosystem types (ecosystem) and separately conservation level in every ecosystem type (Andean forest, rainforest and dry forest) evaluated in southern Ecuador

	conservation		ecosystem		Andean forest		rainforest		dry forest	
	H	**p**	**H**	**p**	**H**	**p**	**H**	**p**	**H**	**p**
S	0.3103	0.856	12.05	0.002	1.52	0.465	0.808	0.664	0.868	0.641
Shannon-W	1.408	0.495	9.679	0.008	5.945	0.051	0.808	0.668	0.111	0.946
Simpson	1.929	0.381	9.613	0.008	3.818	0.148	0.346	0.841	1.444	0.486
Dominance	2.07	0.355	6.108	0.047	1.145	0.564	0.038	0.981	1.444	0.486
Density	0.273	0.872	10.46	0.005	1.964	0.375	0.500	0.778	4.694	0.096
SCVI	0.145	0.930	6.597	0.037	1.364	0.506	1.192	0.551	1.806	0.405
Biomass	0.319	0.853	11.92	0.003	0.873	0.646	0.115	0.944	4.25	0.119
Jackknife	0.502	0.778	12.1	0.002	1.964	0.375	1.385	0.500	0.222	0.895

est (Fig. 1). When testing for differences among conservation levels in each ecosystem type, no significant differences were found (Table 2). However, post-hoc tests showed some: in Andean forests, diversity in conserved areas was significantly higher ($p = < 0.05$) than in degraded areas (Fig. 2 A) and in dry forests both population (Fig. 2B) and biomass (Fig. 2 C) were significantly higher ($p = < 0.05$) in degraded areas than in conserved forests.

In Beta diversity, assemblages were clearly more similar between the same ecosystem type than between conservation types, and even within the same ecosystem type assemblages did not aggregate by conservation level (Fig. 3). Assemblages were significantly different between reserves (Table 3).

Discussion

Here we have shown it is possible to conduct a comprehensive analysis of such a highly speciose data set as of Darwin wasps, including a wide range of biodiversity measures in different habitats and conservation status.

Of the research hypotheses, H1 is partly supported by the data. Sites undergoing ecological restoration had diversity and dominance intermediate between the other two treatments, with values like those from high conserved areas rather than from degraded lands, at least in Andean and dry forest. However, none of these results were statistically significant. A relatively high diversity in open or degraded areas seems to be the consequence of a higher occurrence of vagrant species, especially when using interception traps (Sverdrup-Thygeson and Birkemoe 2009) such as Malaise traps. Open areas may favour biodiversity in closed, forest habitats, and they are promoted as conservation management strategies in temperate ecosystems (Korpela et al. 2015; Plewa et al. 2020), although not fully demonstrated in tropical habitats (Peh et al. 2006). However, non-significant differences might be due to a relatively low proportion of species collected regarding the estimated richness, although the Jackknife estimator, which usually does not tend to overestimate sampling (Mazón and Bordera 2008), gave proportions proximate to 70%. The apparently low efficiency is a common issue when collecting Ichneumonidae, and it seems hard to improve even when increasing the sampling effort because of the high proportion of singletons that are usually found. For instance, Gómez et al. (2018) had a 7710 Malaise trap days effort in Peruvian Amazonia and

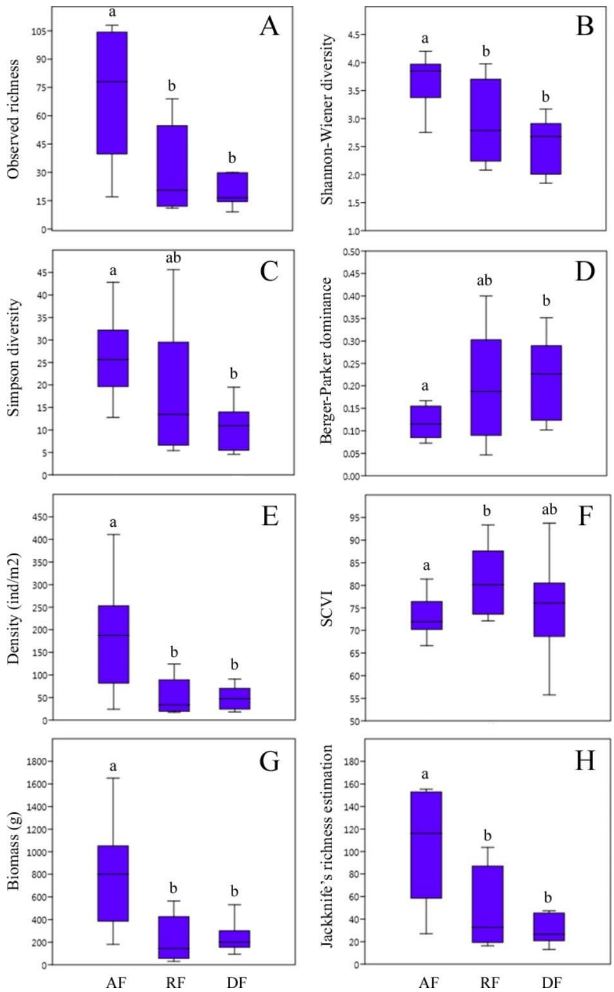

Fig. 1 Box plots comparing differences among ecosystem types (AF = Andean Forest, RF = Rainforest, DF = Dry Forest) in every Biodiversity Quality index of Ichneumonidae assemblages: observed richness (A), Shannon-Wiener index (B), Simpson index (C), Berger-Parker Dominance (D), Density (E), SCVI (F), Biomass (G) and Jackknife's richness estimation (H). Different letters show significant differences ($p < 0.05$)

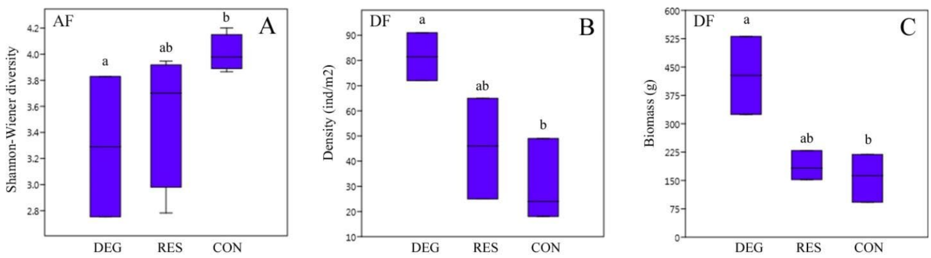

Fig. 2 Box plots comparing differences among conservation levels (DEG = degraded, RES = undergoing restoration, CON = conserved) in Shannon-Wiener index in Andean forests (AF) (A) and Density (B) and Biomass (C) in dry forests (DF) of Ichneumonidae assemblages. Different letters show significant differences ($p < 0.05$)

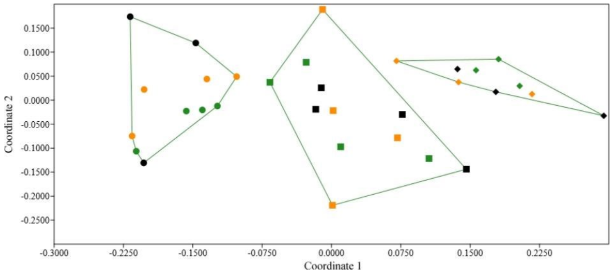

Fig. 3 NMDS obtained for comparing the Ichneumonidae assemblages in the three conservation levels (high in green, medium in orange and low in black) of every reserve in ecosystem type (circle=Andean Forest; diamond=Dry Forest; square=Rainforest). Differences are based on Jaccard similarity index

Table 3 Differences in assemblage composition of Ichneumonidae species according to the PERMANOVA test, based on Jaccard similarity index. Statistical differences are shown among the three levels of conservation (cons level) and among the four reserves in each ecosystem type

	Andean forest		Dry forest		Rainforest	
	cons level	reserves	cons level	reserves	cons level	reserves
F	1.028	1.505	0.9137	1.58	1.018	1.333
p	0.3877	0.0054	0.6439	0.0002	0.3745	0.0008

collected about 60% of potential Ichneumonidae richness, and Saunders and Ward (2018) in Australia, with a sampling effort of 840 Malaise trap days, reached about 66% of estimated richness. Considering that we had a sampling effort of c. 1620 Malaise trap days, a 65–70% of completeness might be assumed as respectable.

Furthermore, the use of OTUs based on morphological characters may be underestimating species richness. Some Ichneumonidae subfamilies have cryptic species (Veijalainen et al. 2012), and DNA analyses or genitalia treatment are needed to disclose them (e.g., for Ophioninae species, Gauld 1985, Fernández-Triana 2005). However, this kind of analyses requires time and money, which is not always available, and OTUs also called morphospecies, are commonly used in Ichneumonidae diversity assessments (Mazón 2016, Saunders and Ward 2018).

Therefore, the absence of differences between conservation levels seems to be mainly masked by the ecosystem type, which gave significant results in all Biodiversity Quality Indices. Andean forests showed significantly higher species richness, diversity, density and biomass, and less dominance and rarity than the other ecosystems. Rainforests have been associated with a large richness of Darwin wasps (Veijalainen et al. 2012, Gómez et al. 2018), but in this research we found that Andean forests are even more diverse and richer. Parasitoid distribution and richness are highly related to that of their hosts (Barbosa & Caldas 2004; Nascimento et al. 2015), most of them herbivores. The high diversity of herbivorous insects in rainforest seems to be also related to a high diversity of plants (Novotny et al. 2006), however, plant species richness in tropical Andes seems to increase with altitude up to about 1500 masl (Malizia et al. 2020), so a higher plant diversity in Andean forests might harbour a higher diversity of potential hosts and therefore a higher richness of parasitoids. Plant diversity was one of the main features explaining Ichneumonidae diversity in a Peruvian rainforest (Sääksjärvi et al. 2006).

On the other hand, rainforests from southern Ecuador have experienced an intense deforestation in the last decades, more than the other ecosystem types (Tapia-Armijos et al. 2015), so they may be having a lower arthropod diversity than expected in this type of ecosystem. Andean forests in southern Ecuador also harboured a higher richness of leaf beetles compared to rainforests in this region (Thormann et al. 2018). Further, to evaluate how human-induced disturbances are impacting on rainforests, it would be important to sample in the different vertical strata, since invertebrates in the canopy seem to be more sensitive to these perturbances than those from the understory (Whitworth et al. 2018). In parasitoid Hymenoptera, the height from the ground where the trap was installed may significantly influence the species composition (Chan-Canché et al. 2020).

When evaluating the conservation level effect in every ecosystem type separately, significant differences were only found at higher diversity in well conserved areas of Andean forests, and at higher density and biomass in degraded areas of dry forests. These results do not support H2, and even showed dynamics opposite to that expected in dry forests. Dry forests in southern Ecuador are subjected to a high human impact (Graefe et al. 2020). Also, the strong seasonality might be biasing results, depending on the synchrony or asynchrony of sampling and the rainy season, which is not always easy to establish. Ultimately, Ichneumonidae abundance or richness are not easy to predict. For instance, Gómez et al. (2018) found more individuals in secondary and in altered areas than in primary forests, and Saunders and Ward (2018) found that neither habitat nor season or surrounding vegetation explained catches made by each trap.

Ecosystems rather than conservation level determined differences, not only in Biodiversity Quality but also in the species composition, supporting H3, although the statistical tests were somewhat compromised by the very high number of very rare species (those occurring only once). These ecosystems, despite being relatively close to each other, seem to be very particular in their insect composition. For instance, in this region the biodiversity of ants and a predation function associated with them was better explained by habitat conditions than by abiotic variables in an altitudinal gradient (Wallis et al. 2021), and Thormann et al. (2018) showed that species composition of leaf beetles clearly changed between Andean forests and rainforests even when they were connected and part of the same mountain range. SCVI reached nearly 100 at some of the reserves in dry forests and rainforests, meaning that nearly 100% of individuals in those samples were represented by only one species.

Finally, H4 was not supported since biomass did not show different results than the taxonomic-base diversity indices. However, the dry forest showed a differing pattern than the other two ecosystem types, where biomass increased when conservation level decreased, opposite to the rising biomass observed in the other ecosystems when conservation level increased. A high plant diversity helps to reduce the herbivore pressure by enhancing the biomass of their natural enemies (Barnes et al. 2020), but in some cases plant traits instead of plant diversity affects the plant-herbivore interactions more in tropical and subtropical high diverse ecosystems (Wang et al. 2020), and biomass might be altered. Also, in degraded areas, the dominance of a relatively few generalist species will be translated into a low diversity but a high abundance and consequently a high biomass (Ruan et al. 2021) For instance, dung beetles showed a higher biomass in areas with high level of deforestation (Cultid-Medina and Escobar 2016) as seen here in dry forests. Therefore, although biomass gives much information useful for food webs and the conservation status of ecosystems, it may not be reflecting all diversity changes occurring in insect assemblages (Vereecken et al. 2021), and will not represent the loss of small, rare species (Seibold et al. 2019). Furthermore, dry forest functions recover more slowly than wet forests after a perturbation

(Poorter et al. 2021), so the 10–15 years of restoration might not be enough for representing significant changes in this ecosystem.

Conclusion

Here we found limited support to demonstrate habitat recovering effects on Ichneumonidae Biodiversity Quality in the three ecosystems along the Southern Ecuador. However, this was a first attempt of representing an extensive sampling of Darwin wasps in this region, with an impressive 700 OTUs set in a 54 trap months sampling effort, and it is approximately a 60–70% of the estimated richness for this region. Also, we found a high proportion of rarity in many of the studied reserves, which is critical for species conservation and the ecosystem services they provide. Habitat fragmentation in tropical forests seems to alter Ichneumonidae richness and abundance but also the species turnover (Ruiz-Guerra et al. 2013) and impacts of land use changes on arthropod diversity are expected to increase with climate change (Sohlström et al. 2022), so there is an urgent need to recover unused degraded lands.

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Author contributions Conceptualization and identification of the OTUs were performed by Marina Mazón. Methodology and field work were carried out by Marina Mazón and Oscar Romero. The analyses were conducted by Marina Mazón and Alan Feest. The first draft of the manuscript was written by Marina Mazón, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The datasets analyzed during the current study are available from the corresponding author on request.

Statements and declarations

Competing interests The authors declare that they have no competing interests.

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