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Moth assemblages in Costa Rica rain forest mirror small-scale topographic heterogeneity

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Abstract

In many tropical lowland rain forests, topographic variation increases environmental heterogeneity, thus contributing to the extraordinary biodiversity of tropical lowland forests. While a growing number of studies have addressed effects of topographic differences on tropical insect communities at regional scales (e.g., along extensive elevational gradients), surprisingly little is known about topographic effects at smaller spatial scales. The present study investigates moth assemblages in a topographically heterogeneous lowland rain forest landscape, at distances of less than a few hundred meters, in the Golfo Dulce region (SW Costa Rica). Three moth lineages—Erebidae–Arctiinae (tiger and lichen moths), the bombycoid complex, and Geometridae (inchworm moths)—were examined by means of automatic light traps in three different forest types: creek forest, slope forest, and ridge forest. Altogether, 6,543 individuals of 419 species were observed. Moth assemblages differed significantly between the three forest types regarding species richness, total abundance, and species composition. Moth richness and abundance increased more than fourfold and eightfold from creek over slope to ridge forest sites. All three taxonomic units showed identical biodiversity patterns, notwithstanding their strong differences in multiple eco-morphological traits. An indicator species analysis revealed that most species identified as characteristic were associated either with the ridge forest alone or with ridge plus slope forests, but very few with the creek forest. Despite their mobility, local moth assemblages are highly differentially filtered from the same regional species pool. Hence, variation in environmental factors significantly affects assemblages of tropical moth species at small spatial scales.

Abstract in Spanish is available with online material.

KEYWORDS
abundance, Central America, forest types, herbivore insect assemblages, orographic heterogeneity, species diversity, species richness

1 | INTRODUCTION

For a wide range of organisms on earth, species diversity is heterogeneously distributed along elevational gradients (Nogués-Bravo, Araújo, Romdal & Rahbek, 2008). Elevational gradients massively contribute to biodiversity in tropical hot spot regions (Mittermeier, Turner, Larsen, Brooks & Gascon, 2011). In addition to the strong environmental contrasts that govern communities along extended elevational gradients, topographically heterogeneous landscapes are characterized by environmental variation at small spatial scales that contribute to regional-scale biodiversity of plants and animals (Coblentz & Ritters, 2004; Homeier, Breckle, Günter, Rollenbeck & Leuschner, 2010; Werner & Homeier, 2015; Werner, Homeier, Oesker & Boy, 2012). Topographic variability provides very different microclimatic (e.g., exposure to sun) and edaphic (e.g., soil texture, nutrient availability) conditions and therefore may affect associated ecosystem functions (e.g., mineralization rates, carbon sequestration), at close distances (Hofhansl et al., 2011, 2014; Werner & Homeier, 2015). These ecological determinants alter habitat conditions to a great extent, creating a mosaic of forest types with characteristic vegetation structure and species composition (Costa, Magnusson & Luizao, 2005; Fu, Liu, Ma & Zhu, 2004; Valencia et al., 2004; Weissenhofer, Huber, Koukal, et al., 2008). Many lowland tropical rain forests are not flat, and the resulting mosaic of hilly terrain from creeks through slopes to ridge sites represents important environmental niches for plant species, further enhancing biodiversity of rain forests in regions with substantial relief (Gibbons & Newbery, 2003; Rodríguez-Castañeda et al., 2010; Valencia et al., 2004; Weissenhofer, Huber, Koukal, et al., 2008). Several studies from different tropical regions have indicated the strong influence of such small-scale spatial variability on the assemblages of sessile plants (e.g., Costa et al., 2005; Lippok et al., 2013; Liu, Yunhong & Slik, 2014) as well as mobile animals (e.g., Binz, Schulze & Linsenmair, 2015; Gering, Crist & Veech, 2003; Thormann et al., 2018).

Trophic interactions between plants and insects play a key role in explaining distribution and diversity patterns of herbivorous insects. Across geographic regions and taxonomic groups, insect herbivore communities are characterized by the predominance of food specialists. The frequency of specialists seems to increase toward tropical regions (Forister et al., 2015), but these correlations are not always very tight (Fiedler, 1998; Novotný et al., 2002, 2006). However, several recent studies have shown that plant diversity correlates with species richness or community structures of herbivorous insects (e.g., Axmacher et al., 2009; Lin, Cook, Gullan & Cook, 2015; Novotný et al., 2006). These relationships are often indirect, because specific environmental parameters concomitantly influence the distribution of vegetation and plant-feeding insects along topographic gradients (Axmacher et al., 2009).

During the past two decades, moths have emerged as focal group in a range of biodiversity studies in tropical forest ecosystems throughout the world (e.g., Ashton et al., 2015; Chen et al., 2009; Fiedler, Hilt, Brehm & Schulze, 2007). Moths are species-rich and abundant in most ecosystems and easy to record systematically with light traps. They occupy a broad range of ecological niches and are important for ecosystem functioning as pollinators, herbivores, and food for predators and parasitoids. While a couple of studies have addressed how elevation (Axmacher et al., 2004; Beck et al., 2017; Brehm et al., 2016; Fiedler, Brehm, Hilt, Süssenbach & Häuser, 2008) or disturbance gradients (Alonso-Rodríguez, Finegan & Fiedler, 2017; Beck, Schulze, Linsenmair & Fiedler, 2002; Hilt & Fiedler, 2005; Ricketts, Daily, Ehrlich & Fay, 2001) may drive tropical moth diversity, much less is known about small-scale patterns in moth assemblages along orographic gradients. The hilly topography of the Piedras Blancas National Park in SW Costa Rica is characterized by pronounced environmental heterogeneity with different forest habitat types growing under specific environmental conditions (Morera-Beita et al., 2019; Weissenhofer, Huber, Koukal, et al. 2008). The aim of the present study was to analyze moth assemblages of three major phylogenetic lineages of Lepidoptera between creek forests (hereafter creek), slope forests (slope), and ridge forests (ridge) in the area. In particular, we address the following hypotheses: (1) The investigated forest habitat types harbor moth assemblages of similarly high abundance and local species richness; (2) ecosystem differences between creeks, slopes, and ridges shape the composition of species-rich communities of herbivorous insects; and (3) diversity patterns along the environmental gradient vary between three focal moth groups in association with taxon-specific differences in their eco-morphological traits (see below).

2 | METHODS

2.1 | Study sites

Moth assemblages of old growth creek forest, slope forest, and ridge forest were sampled in the Pacific lowlands of the Golfo Dulce region in southwestern Costa Rica. Study sites were located near the Tropical Field Station La Gamba (8°43′ N, 83°13′ W, 5892 mm annual rainfall), adjacent to the Piedras Blancas National Park, which represents one of the last remaining large tracts of Pacific lowland wet rain forest of Central America (Gilbert et al., 2016). Regional climate is characterized by a dry period from January to March and a precipitation peak from August to November (Weissenhofer & Huber, 2008). More detailed information about geography, geology, and climate of the lowland rain forest of the Golfo Dulce region is provided by Weissenhofer, Huber, Mayer, Pamperl and Weber (2008).

Moths were sampled from July to October 2014 during the rainy season using portable automated light traps (100 cm high; funnel opening: 6 cm diam.; killing agent: chloroform). Each light trap was equipped with an 8W blacklight tube and operated during the entire night with a 12V lithium-ion battery as power supply and a twilight switch. A detailed description of the traps is provided in Brehm and Axmacher (2006). We installed light traps at 18 sites, that is,

six replicates within each forest type. Creek sites were located at the low-lying areas alongside small creeks at elevations between 105 and 151 m asl. Ridge sites were located at the top of the hills at elevations between 161 and 279 m asl. Slope sites were located between the other two forest types at elevations between 137 and 203 m asl (Figure S1; Table S1). The topographic situation causes specific microclimatic and edaphic conditions shaping the vegetation in a characteristic manner (Figure S2; see Weissenhofer, Huber, Koukal, et al., 2008). All sites were connected by surrounding pristine old growth forest, such that there were no evident dispersal barriers for forest animals. Linear distances between sampling sites varied between 100 m and 1.3 km, and sites were distributed over approximately 1.5 km² (Figure S1). The study sites were identical to those sampled for diurnal butterflies in a foregoing study conducted by Binz et al. (2015).

2.2 | Moth sampling and processing

Light traps were installed in the understory at 1–1.5 m aboveground, and we performed seven collecting runs at each site (i.e., 126 nightly samples, assembled during 46 nights) to ensure equal sampling effort. Weak light sources as used in this study minimize cross-attraction of moths from habitats distant to the light trap (Truxa & Fiedler, 2012). To reduce negative effects of moonlight on moth catches, sampling was restricted to four days prior to and after the full moon nights (e.g., McGeachie, 1989). Traps were emptied before sunrise, to prevent ants and other insects from clearing out the bucket. Samples from light traps capture only a subset of moth diversity, because they are biased toward larger species or those that do not settle down immediately upon arrival at the trap (Axmacher & Fiedler, 2004; Brehm & Axmacher, 2006; Wölfling, Becker, Uhl, Traub & Fiedler, 2016). Nevertheless, automated light trapping is the most effective method for long-term and all-night sampling of moths.

After capture, all moth specimens were immediately frozen and later counted and identified to species level. Only a small fraction of moth individuals had substantial wing damage, but it was still possible to relate them to other collected species or to identify them to genus level as additional morpho-species. Thus, it was not necessary to discard any individuals of our three target taxa: A complete coverage of all moth groups was beyond reach given the lack of suitable identification literature and the still very incomplete taxonomic understanding of the Costa Rican moth fauna. We therefore concentrated on three focal groups (Erebidae-Arctiinae, the bombycoid complex, and Geometridae), all nested within the monophyletic Macrolepidoptera (Mitter, Davis & Cummings, 2017). The selection aimed at covering a broad range of moths with regard to phylogeny, morphology, and ecological traits, for which species identifications could be achieved. "Bombycoid-complex" (sensu Lemaire & Minet, 1999) moths are represented by the comparatively species-poor families Bombycidae, Lasiocampidae, Mimallonidae, Saturniidae, and Sphingidae. These are robust, medium- to large-sized moths, without tympanal organs and (with the exception of Sphingidae) often lacking a functional proboscis (Lemaire & Minet, 1999). The

species-rich subfamily Arctiinae (family: Erebidae) comprises tiger and lichen moths. They possess tympanal organs that allow them to escape predacious bats, and their larvae are typically very hairy (Conner, 2009). Many Arctiinae species are chemically well defended and embedded in complex mimicry rings (Conner, 2009). Finally, the Geometridae represent another highly speciose clade of moths, but they are mostly more slender and small- to medium-sized insects (Brehm, Zeuss & Colwell, 2018), whose larvae never have a dense hair cover (Minet & Scoble, 1999). In contrast to Arctiinae, chemical defense, aposematism, and mimicry are rare among geometrids. Arctiinae and Geometridae adults usually have a functional proboscis and visit flower nectar as food. As a consequence of this pronounced eco-morphological variation, we expected the three focal clades to respond differently to the small-scale topographic heterogeneity of their habitats.

Species identification was primarily achieved in comparison with voucher specimens and photographs of type material held in various scientific collections, including the National Biodiversity Institute (INBio) in San José (Costa Rica) that had been visited in the course of an earlier moth survey around La Gamba (Alonso-Rodríguez et al., 2017). Further identifications were achieved using various online resources (e.g., http://www.discoverlife.org/mp/20q?guide =Moth_Costa_Rica, http://janzen.sas.upenn.edu/Wadults/search. lasso) and subsequently reviewed by expert taxonomists (see Acknowledgments2.4). Additionally, the barcode region of the mitochondrial cytochrome oxidase I (COI) gene was sequenced for all Saturniidae species and selected Arctiinae species to improve identifications, using standard laboratory protocols (Janzen et al., 2009). See Table S8 for detailed description of the laboratory method. Voucher specimens are currently deposited at the Division of Tropical Ecology and Animal Biodiversity of the University of Vienna, the Natural History Museum of Vienna, and the Phyletisches Museum (Jena University).

2.3 | Site descriptors

To characterize the vegetation structure at the sampling sites, canopy density, understory density, and herb layer cover at each trap location were scored. Canopy cover and herb layer cover were estimated by taking six photographs per site along a 100-m linear transect with the light trap in the center (camera model: Olympus SP590UZ; image resolution: 2,976 × 3,968 pixels, focal distance: 5 mm, exposure time: 1/1,000 s). Digital images were taken in vertical direction for canopy cover and from precisely gauged squares of one m² on the ground for herb layer cover. Photographs were converted to binary images with the ImageJ 1.48 software (http:// imagej.nih.gov/ij) to compute the percentage of black pixels (e.g., Ishida, 2004). Data of the six images were averaged to obtain a mean percentage as a proxy of canopy cover and herb layer cover at each study site. Understory vegetation density was estimated at each site by measuring the distance to the nearest understory plant with a laser rangefinder (Nikon Laser 800S). Fifty measurements were conducted in a circle around a fixed point at three

spots near the light traps. We removed the ten highest measurements per spot to delete extreme outliers, to reduce measurement errors caused by greater distances. The 120 measurements per site were averaged to get the mean understory density of each site. A lower mean distance of the nearest stems to the trap location indicates a higher understory density.

2.4 | Data analysis

For statistical analysis, the seven nightly samples available per site were aggregated into one quantitative species list per trap location. General linear models (GLMs) were used to test for effects of forest type and habitat descriptors on species abundance, richness, and diversity of the observed moths. One-way analysis of variance (ANOVA) was used to test whether habitat descriptors (canopy closure, understory density, and herb layer cover) differed between the three forest types. Tukey's HSD test was used post hoc to localize significant differences in moth species abundance, richness, and diversity between each forest type. These calculations were performed using the package Statistica 10.0 (StatSoft, Inc., 2011). Prior to analysis, all datasets were graphically checked for near-normal distribution using quantile–quantile plots. All values scored as proportions were logit-transformed (Warton & Hui, 2011), and habitat descriptors were additionally normalized before analysis. Moth species composition (based on Bray–Curtis similarity matrix from square-root-transformed abundances) was tested for effects of forest type and habitat descriptors through a PERMANOVA (999 permutations) using the package PERMANOVA+ for Primer7 (Anderson, Gorley & Clarke, 2008; Clarke & Gorley, 2015). Similarities between sites were visualized using non-metric multidimensional scaling (NMDS) plots (Clarke, 1993). Moreover, pairwise PERMANOVA comparisons and an index of multivariate dispersion (MVDISP) were calculated. Venn diagrams were drawn to visualize species overlap using VENNY 2.1 (2007–2015). The R package "*Indicspecies*" (De Cáceres & Legendre, 2009; De Cáceres, Legendre & Moretti, 2010) was used to statistically determine associations of moth species with one or several forest types, based on the calculated indicator values (IndVal) (Dufrene & Legendre, 1997). Statistical analyses of species diversity were conducted using the R package "*Vegan*" (Oksanen et al., 2013).

3 | RESULTS

3.1 | Abundance, species richness, and species diversity

A total of 6543 moth individuals of the three focal taxa were collected representing 145 Arctiinae, 72 bombycoids, and 202 Geometridae species (see Table S6 for a full species × site matrix). Arctiinae represented the largest fraction and accounted for 50.7% of total moth individuals considered for analysis, but they accounted for only 34.6% of total observed moth species. Geometrids and

bombycoids contributed 38.3% and 11%, respectively, to total observed moth individuals and 48.3% and 17.2%, respectively, to total observed moth species.

Total observed moth species richness, abundance, and species diversity differed prominently among the investigated forest types. However, assemblage metrics showed strikingly uniform patterns across the forest types (Figure 1a–l; Table S2). Mean numbers of moth species or individuals per site were highest at the ridges, followed by slopes, and were lowest at creeks. Observed species richness at ridges was approximately 4.9 and 1.4 times higher than at creeks and slopes, respectively. For moth numbers, these factors amounted even to 8.0 and 1.6, respectively (Table 1). Since observed species richness may strongly depend on sampling success, Shannon's bias-corrected exponential diversity was calculated which is largely independent of sample size. Yet, with this diversity measure exactly the same patterns between the three different forest types were detected as with raw species richness and moth abundance (Figure 1; Table S2). Overall, Tukey's HSD tests ($p < 0.05$) indicated significant differences between all forest types with greatest dissimilarity between ridges and creeks (Figure 1).

Remarkably, these spatial patterns were largely consistent over the three focal moth groups (Figure 1a–l). All forest types differed significantly from each other regarding species richness and species abundance of the three focal groups (Tukey's HSD tests; $p < 0.05$), except for bombycoid abundance, which did not significantly differ between ridges and slopes ($p < 0.713$). Species diversity of all three focal groups differed significantly between ridges and creeks ($p < 0.05$), but there was no significant difference in species diversity between ridges and slopes in Arctiinae ($p < 0.094$) and Geometridae ($p < 0.169$). Independently of the taxonomic moth unit, Euclidean distances of Shannon's bias-corrected exponential diversity values were not correlated with the topographic distances between the sampling sites, although the distance between some sites was less than 150 m (Spearman's matrix rank correlation coefficients, 9,999 permutations; total observed moths: $r_S = −0.009$, $p > 0.502$; Arctiinae: $r_S = −0.021$, $p > 0.554$; bombycoid complex: $r_S = 0.064$, $p > 0.225$; Geometridae: $r_S = −0.003$, $p > 0.483$). This indicates that there was no indication of significant spatial autocorrelation between light trapping sites with regard to their moth species diversity.

Herb layer cover (one-way ANOVA: $F_{2,15} = 8.01$, $p = 0.0043$) and understory density ($F_{2,15} = 10.02$; $p = 0.0017$) varied significantly between the three forest types, and differences in canopy closure were very close to statistical significance ($F_{2,15} = 3.64$; $p = 0.0515$). Understory density and canopy closure were lowest at ridges and equally higher at creeks and slopes. Herb layer cover was highest at ridges and creeks, but much lower at slopes. When these three structural habitat descriptors were included together with forest type as predictors in GLMs, they never contributed significantly to explain additional variance in moth assemblage metrics (Table 2). Nevertheless, all GLMs explained a very sizeable fraction of variance (>76%).
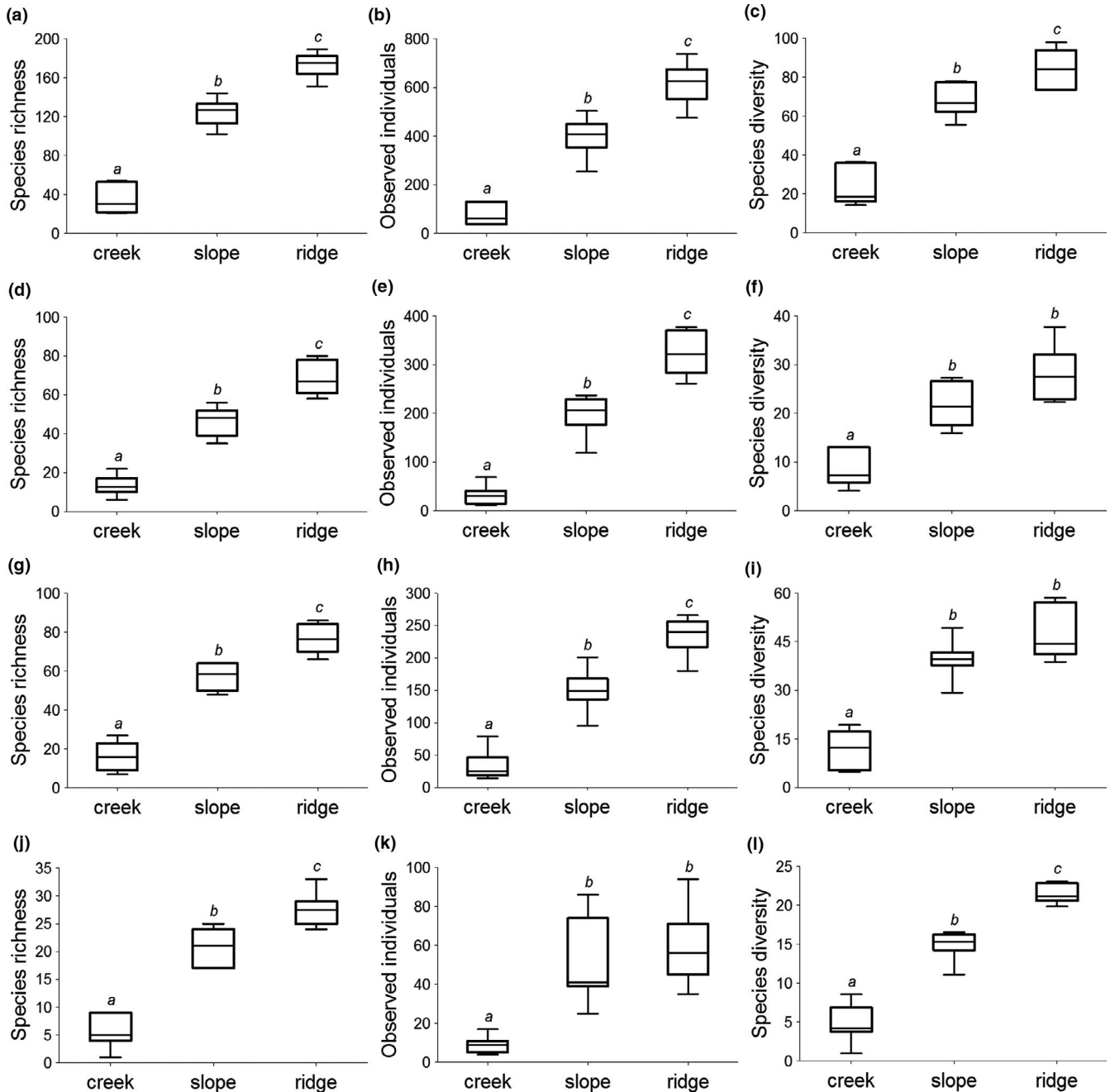
FIGURE 1 Species richness, number of observed individuals, and species diversity (expressed as bias-corrected exponential Shannon's index H') per site (aggregated from 7 nightly samples each) in relation to forest type of (a–c) total moth species (d–f), Arctiinae (g–i), Geometridae, and (j–l) bombycoids at three forest types: creek forest = creek, slope forest = slope, and ridge forest = ridge. Given are medians (horizontal bars), percentiles (boxes), and total range of values (whiskers). Post hoc Tukey's HSD was performed; letters show significant differences between forest types

3.2 | Species composition

Non-metric multidimensional scaling (NMDS) plots based on Bray–Curtis similarities show a clear segregation of the ridge, slope, and creek sites into three point clouds. This indicates the existence of distinct moth assemblages in respective forest types. Remarkably, this pattern was totally concordant across the three focal moth groups (Figure 2a–d). Arctiinae and Geometridae, with large sample sizes, formed well-segregated clusters of moth assemblages in association with respective forest types. Even among bombycoids with much lower sample size, well-defined moth assemblages emerged. The low stress values of all ordinations (<0.11) indicate a reliable visualization of the faunal similarity relationships in reduced ordination space.

	Creek forest	Slope forest	Ridge forest	Total
Arctiinae				
Recorded species (% of total)	39 (26.9)	96 (67.6)	133 (91.7)	145
Observed individuals (% of total)	198 (6)	1,176 (35.4)	1,948 (58.6)	3,322
Bombycoidea				
Recorded species (% of total)	19 (26.4)	48 (66.4)	62 (86.1)	72
Observed individuals (% of total)	55 (7.7)	306 (42.6)	357 (49.7)	718
Geometridae				
Recorded species (% of total)	57 (28.2)	140 (69.3)	159 (78.7)	202
Observed individuals (% of total)	208 (8.3)	897 (35.8)	1,398 (55.9)	2,503

TABLE 1 Summary of moth catches in creek forest, slope forest, and ridge forest

PERMANOVAs performed on the Bray–Curtis similarity matrices tested for effects of forest type on moth species composition and showed significant differences in the assemblages of total observed moths (F = 5.912, p < 0.001) as well as in the assemblages of the Arctiinae (F = 6.881, p < 0.001), bombycoids (F = 4.113, p < 0.001), and Geometridae (F = 5.586, p < 0.001). Only the forest type affected moth species composition, while none of the three tested habitat descriptors contributed significantly to explain additional variance in assemblage composition (Table S3). Results of pairwise PERMANOVA comparisons of the Bray–Curtis similarities indicated significant differences in almost all contrasts between forest types (Table 3).

For all analyzed moth groups, multivariate dispersion (expressed as MVDISP index as implemented in the PRIMER software package) was larger among the creek sites than within the two other forest types, indicating a greater site-to-site variance in species composition in creeks. In contrast, moths at ridge sites formed very strongly clumped assemblages, independently of the taxonomic unit under consideration, while moth assemblages at slope sites were slightly more dispersed (Figure 2a–d; Table S4). Furthermore, Bray–Curtis similarity values were not correlated with the topographic distances between the sampling sites (Spearman's matrix rank correlation coefficients, 9,999 permutations; total observed moths: r_S = 0.020, p > 0.415; Arctiinae: r_S = −0.013, p > 0.436; bombycoid complex:

TABLE 2 Results of GLMs testing the combined influence of forest type (creek forest, slope forest, and ridge forest) and three structural habitat descriptors (canopy closure, herb layer cover, and understory density) on recorded moth species, observed moth individuals, and Shannon's diversity (bias-corrected exponential H'). Given are results for all observed moths and separately for the three focal groups Arctiinae, Bombycoidea, and Geometridae. Habitat variables were logit-transformed and normalized prior to analysis

	Overall moths			Arctiinae			Bombycoidea			Geometridae		
Recorded species	*df*	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*
Forest type	2	66.184	<0.001	2	43.138	<0.001	2	31.443	<0.001	2	54.411	<0.001
Canopy closure	1	0.108	0.748	1	<0.001	0.983	1	0.020	0.891	1	0.545	0.474
Herb layer	1	<0.001	0.995	1	0.014	0.907	1	0.005	0.946	1	0.018	0.895
Understory density	1	0.610	0.450	1	1.848	0.199	1	2.334	0.152	1	0.673	0.428
	R^2_{adj} = 0.9306			R^2_{adj} = 0.8921			R^2_{adj} = 0.8925			R^2_{adj} = 0.9126		
Observed individuals	*df*	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*
Forest type	2	32.107	<0.001		34.707	<0.001		13.225	<0.001	2	27.071	<0.001
Canopy closure	1	0.027	0.872	2	0.087	0.773	2	1.082	0.319	1	0.123	0.732
Herb layer	1	0.532	0.480	1	0.299	0.594	1	0.307	0.590	1	0.745	0.405
Understory density	1	0.371	0.554	1	0.217	0.650	1	20.200	<0.001	1	0.283	0.604
	R^2_{adj} = 0.8871			R^2_{adj} = 0.8845			R^2_{adj} = 0.8388			R^2_{adj} = 0.8618		
Exponential H'	*df*	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*
Forest type	2	40.419	<0.001	2	20.361	<0.001	2	46.899	<0.001	2	46.109	<0.001
Canopy closure	1	0.151	0.704	1	0.021	0.887	1	0.042	0.811	1	0.955	0.348
Herb layer	1	0.176	0.682	1	0.068	0.798	1	0.036	0.854	1	0.865	0.371
Understory density	1	2.601	0.132	1	4.529	0.054	1	0.271	0.612	1	3.827	0.074
	R^2_{adj} = 0.8773			R^2_{adj} = 0.7611			R^2_{adj} = 0.9067			R^2_{adj} = 0.8870		

FIGURE 2 Non-metric multidimensional scaling (NMDS) ordination plots (based on Bray–Curtis similarities) for (a) total observed moths, (b) Arctiinae, (c) bombycoids, and (d) Geometridae assemblages at creek forest = creek, slope forest = slope, and ridge forest = ridge sites. Habitat descriptors canopy closure (CC), herb layer cover (HL), and understory density (UD) were logit-transformed and normalized, and then overlaid post hoc on the ordination diagrams. Arrows indicate direction and strength of the correlations between habitat descriptors and species composition
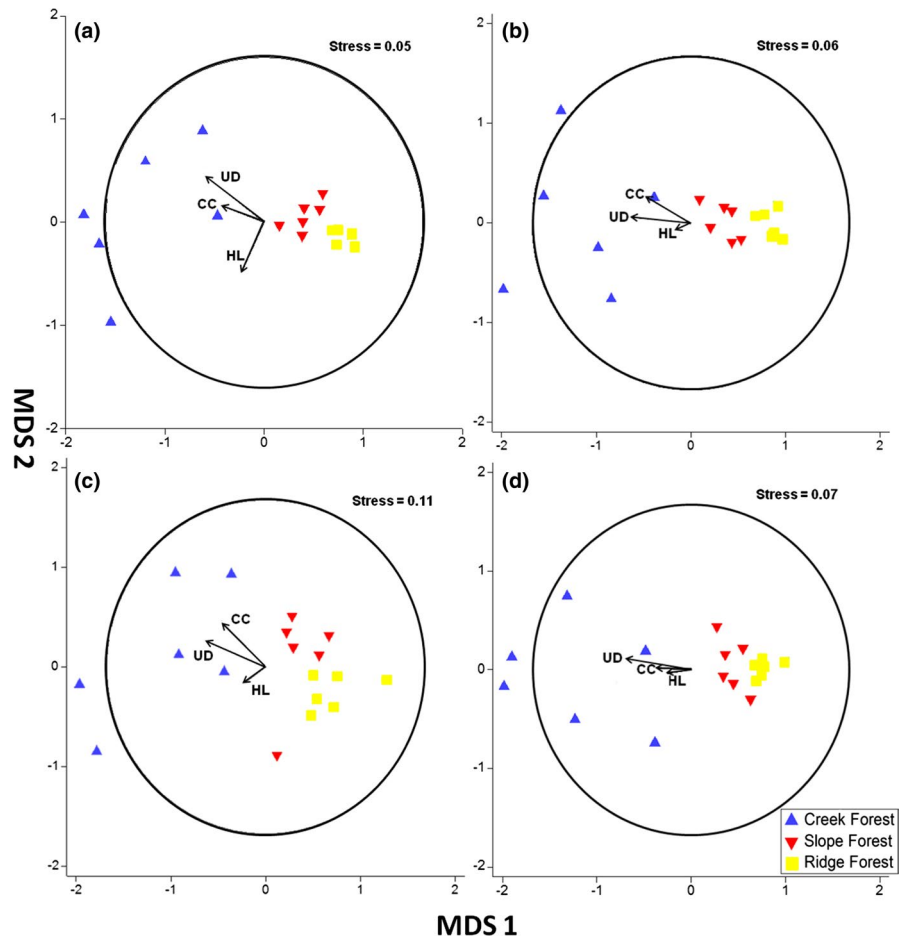
TABLE 3 Results of pairwise post hoc comparisons by PERMANOVA based on Bray–Curtis similarities (square-root-transformed abundances, 999 permutations) testing for the influence of forest type (creek forest, slope forest, and ridge forest) on species composition of overall moths, Arctiinae, bombycoids, and Geometridae

Type of comparison	Overall moths		Arctiinae		Bombycoidea		Geometridae	
	F	p	F	p	F	p	F	p
Creek vs. slope	2.303	0.002	2.449	0.002	1.939	0.002	2.259	0.003
Creek vs. ridge	2.884	0.004	3.068	0.002	2.402	0.002	2.845	0.002
Slope vs. ridge	1.748	0.002	1.938	0.002	1.533	0.013	1.633	0.003

r_S = −0.045, p > 0.597; Geometridae: r_S = −0.030, p > 0.340). This indicates that faunal similarities were not contingent upon spatial proximity of sample sites.

Overall, there was a high overlap in species among the three forest types (Figure 3a–d). Ridges contained the highest, creeks the lowest, and slopes an intermediate number of unique species, and this pattern was very similar between the three focal groups. Ridges and slopes shared the highest percentage of moth species (29.2–33.8%), an even higher proportion than species that were common among the three forest types (21.8–24.8%). It is remarkable that most of the species observed near creeks were also found at ridges and slopes. Only a very small fraction of species at the creeks were unique to these forest sites or were shared with only one of the two other forest types (Figure 3a–d).

3.3 | Indicator value analysis

Altogether, 92 of the 419 evaluated species (21.9%) emerged with statistically significant indicator values. A wide range of moth species was characteristically associated with ridges or shared among ridges and slopes (Table S5), corroborating the higher faunal similarity between these two habitat types that was also apparent from the ordination analyses (see above). 8.4% of all observed moth species were significantly associated with the ridges and another 12.4% with both ridges and slopes. Arctiines and bombycoids comprised a higher proportion of indicator species for ridge sites (12.4% and 13.8%, respectively) and for ridges and slopes combined (15.2% and 33.3%) than Geometridae with
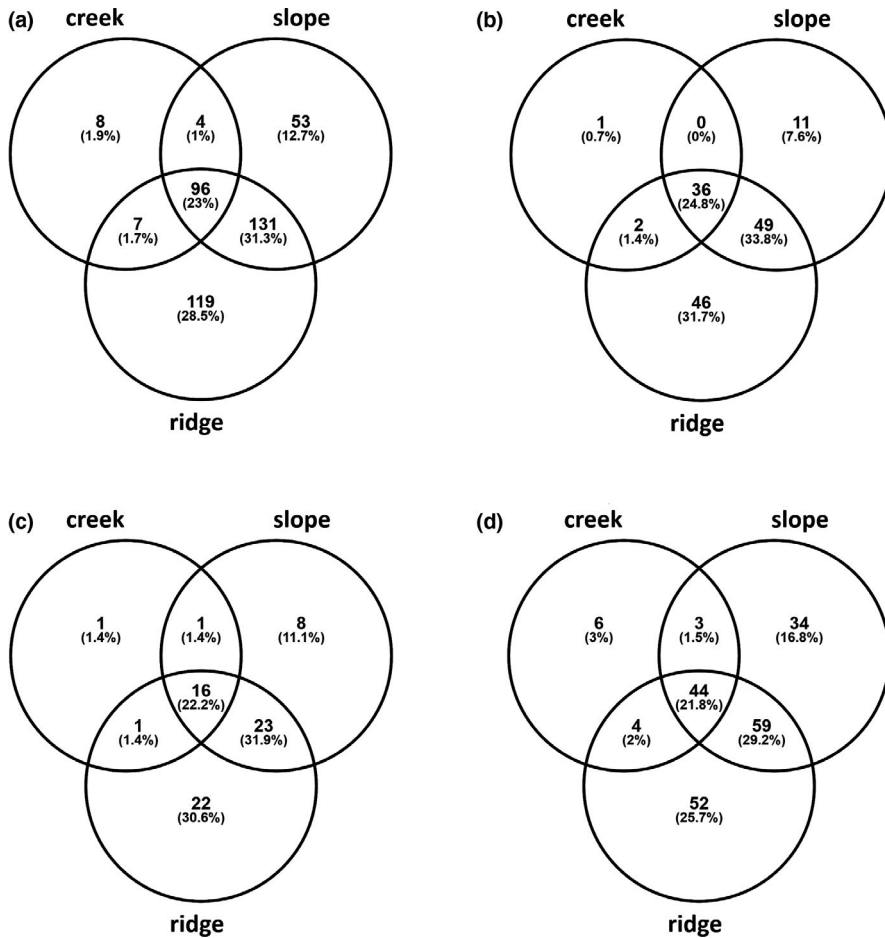
FIGURE 3 Venn diagrams indicating the species overlaps of moth assemblages of (a) total observed moths (b) Arctiinae, (c) Bombycoidea, and (d) Geometridae in relation to forest type: creek forest =creek, slope forest = slope, and ridge forest = ridge sites

a lower proportion of indicator species for ridge sites (3%) and ridge and slope sites (3.5%). Only three species (*Eois* nr. *undulosata* [Geometridae], *Quentalia chromana* [Bombycidae], and *Ochrodota pronapides* [Arctiinae]) were significantly associated with slopes alone. Two further species, *Isochromodes* sp03 (Geometridae) and *Virbia* nr. *mentiens* (Arctiinae), emerged as indicator species of creek and slope sites. On the other hand, no single moth species was significantly associated with the creek sites alone. For detailed information, see Table S5.

4 | DISCUSSION

4.1 | Moth species richness, abundance and diversity

This is the first study to quantitatively evaluate the importance of orographic variation, at very small spatial scales of just a few hundred meters, on biodiversity and community structure of nocturnal insects within an old growth lowland rain forest landscape in Central America. Contrary to our expectations, we observed a steep decline in moth abundance, richness, and species diversity from ridge to creek forest sites. This pattern was concordant across the three studied moth groups, even though there is substantial variation between these organisms with regard to manifold

eco-morphological traits. This observation raises the questions (a) why there were so many moths at ridges or (b) why there were so few in creek forest.

Thus far, only few studies have addressed the influence of topographic heterogeneity on species composition of tropical insects (e.g., Binz et al., 2015; Spitzer, Jaros, Havelka & Leps, 1997; Thormann et al., 2018; Vasconcelos, Macedo & Vilhena, 2003). Nonetheless, these studies revealed that local insect assemblages usually mirror environmental gradients even at small scales of a few dozens to hundreds of meters, despite the fact that most winged insects have substantial dispersal capacity.

A previous investigation on diurnal butterflies conducted in the same study region in SW Costa Rica showed strikingly similar patterns to our observations of topographic habitat associations for nocturnal moths (Binz et al., 2015). While thermal constraints might well differentially govern activity patterns and habitat use of butterflies at sunny versus shaded sites (Pardonnet, Beck, Milberg & Bergman, 2013; Pryke, Vrdoljak, Grant & Samways, 2012), it is much less likely that this pertains to nocturnal insects to the same extent. A recent study based on color patterns of Geometridae moths in China indicated parallels to thermal environments along spatial gradients (Xing et al., 2018), yet another macro-ecological survey of Geometridae moths all across Europe indicated that non-thermal mechanisms could underlie these spatial patterns in

color lightness (Heidrich et al., 2018). However, the rather limited thermal gradients between the three forest habitat types can hardly explain the strong abundance and richness patterns that we found in strictly nocturnal moths. We here suggest four potential reasons for higher moth diversity at ridges are (a) higher local plant species richness, (b) higher nutritional quality of plant resources, (c) breakdown of vertical stratification of the fauna, and (d) sampling artifacts.

(a) For the Golfo Dulce region, several studies reported plant species richness to be higher on ridges compared to slopes and creeks (Hofhansl et al., 2014; Morera-Beita et al., 2019; Weissenhofer, Huber, Koukal, et al., 2008). Higher plant species richness could promote species richness of herbivorous insects because a wider variety of larval host plant species are available and therefore a greater number of herbivore species with different ecological requirements might be able to coexist (Lewinsohn & Roslin, 2008; Novotný & Weiblen, 2005; Novotný et al., 2006). (b) Due to the exposed position of ridges, there are far more treefall gaps and the forest is overall much more open and less tall (Balzotti et al., 2017). It has been hypothesized that higher light availability in forest gaps might increase plant resources and therefore might decrease the resource limitation of herbivores, relative to the less productive understory of dense forest (Bugmann, 2001). This way, small-scale disturbances could foster higher animal species richness in rain forest gaps (Richards & Coley, 2007; Spitzer et al., 1997). However, lower soil nutrient availability at ridges could lead to growth limitation of trees, lower quality of foliage and litter, and a higher level of chemical defense by phenolics (Hofhansl et al., 2011, 2012; Homeier et al., 2010; Werner & Homeier, 2015). All these factors exert negative influences on herbivore abundance and diversity, rendering the relaxation of resource limitation unlikely. (c) Usually, moth communities show a clear vertical stratification in tropical forests (Ashton et al., 2016; Brehm, 2007), which may be less pronounced at more disturbed forest sites (Fermon, Waltert, Vane-Wright & Mühlenberg, 2005). Due to the topographic position of ridge and slope sites, which also showed a higher density of the understory vegetation, a larger fraction of canopy species might have strayed into the lower vegetation strata than in creek sites. In addition, some widespread species of more open and disturbed habitats may occur in the rather open ridge forest sites but are not expected to show up in more densely vegetated creeks. (d) Due to the more open structure of ridge forest sites, the effective radius of the light trap might have been larger and thus could have attracted more moths than in more occluded creek forest.

Why are there are so few moths at the creeks? While in-depth information on life history traits of Neotropical moths is still rather incomplete, potential reasons for the lower moth density in creeks are (a) overall hostile conditions for caterpillar development, (b) a lower plant species richness at creeks, and (c) the absence of canopy species probably present in the other habitats. (a) Creek forests seem to provide an unfavorable habitat for most moth species of the regional species pool. The less mobile early stages may even more strongly depend on suitable microclimatic conditions than adults. Massive rainfalls during the wet season repeatedly cause waterlogging, floodings (D. Rabl, personal observations), and a constantly high relative humidity in forest sites at creeks, while precipitation can run off quickly from slopes and ridges. This can directly affect lesser mobile stages (eggs, caterpillars, pupae) of lowest vegetation strata by drowning and reduce moth abundance. Moreover, due to the high relative humidity in the forest understory along the creeks, leaves are very quickly overgrown by epiphylls (lichens, algae, and fungi) and hence not acceptable to many herbivores which predominantly prefer fresh leaves (Coley & Barone, 1996; Coley, Kursar & Machado, 1993; Toomey, Roberts & Nelson, 2009). Recent studies have shown that, in tropical mountain forests, caterpillars that feed on dead plant parts or graze on epiphylls play a very substantial role (Bodner, Brehm & Fiedler, 2015; Seifert, Lehner, Bodner & Fiedler, 2016), but it remains to be shown how important these particular caterpillar guilds are in tropical lowlands. Furthermore, the moist microclimate of the creek forests might facilitate the activity and spread of pathogens, thereby increasing early life stage mortality and finally leading to a lower moth abundance (Hilt, Brehm & Fiedler, 2007; Intachat, Holloway & Staines, 2001): (b) Lower plant species richness at creek sites might constrain moth species richness. However, this argument does not offer a causal link to low moth abundance at creeks because in habitats with low plant species richness (e.g., plantations, monocultures), a small number of herbivore species can markedly raise total herbivore abundance. (c) It is a common observation of entomologists that light trapping on slopes or on ridges is more effective than at the bottom of valleys and creeks, possibly because moths are more attracted by light from above than from below. For example, moth abundance at downslope collection sites close to the San Francisco River in southern Ecuador was lower than at nearby slope or ridge forests (Brehm et al., 2016), similar to the pattern presented in this study.

The huge differences in moth activity density independently of the phylogenetic lineage may indicate that the functional significance of moths in the food webs differs between the forest types, as herbivore communities are shaped by biotic interactions such as bottom-up and top-down control (e.g., Power, 1992; Richards & Coley, 2007; Walker & Jones, 2001). Low moth density at creeks means (a) a lower amount of food resources is available for their predators (e.g., birds, bats, spiders, other insects) and parasitoids (e.g., ichneumonids, tachinids), (b) vegetation of creeks would be expected to experience lower herbivory rates and less defoliation due to a lower number of caterpillars, and (c) an altered investment of plants in chemical defense mechanisms due to the absence of common herbivores (Coley, Bryant & Chapin, 1985; Lamarre et al., 2012). Hence, these repercussions on both lower and higher trophic levels might strongly influence ecological networks of the three forest types and deserve closer scrutiny in forthcoming studies.

Regional species richness with 145 Arctiinae and 202 Geometridae species was very similar to other lowland rain forest areas in Costa Rica. For example, Alonso-Rodríguez et al. (2017)

altogether observed 142 arctiines and 170 geometrid species in oil palm plantations, secondary forests, and old-grown forests in the same study area. Brehm and Axmacher (2006) collected 162 arctiine and 196 geometrid species, and Brehm (2007) 146 arctiine and 140 geometrid species with similar sampling effort in an Atlantic lowland rain forest in Costa Rica. Yet, the complete bombycoid complex has not been addressed in earlier diversity studies in Costa Rica, so it is not possible to compare results on this moth taxon with other studies. Overall, the study area around La Gamba can be considered as a moderately species-rich Neotropical area, in comparison with much higher regional and local moth richness observed in the biodiversity hot spot of the Ecuadorian Andes (Brehm, Pitkin, Hilt & Fiedler, 2005; Brehm et al., 2016; Hilt & Fiedler, 2005) and some areas in Brazil (Hawes et al., 2009; Zenker et al., 2015).

4.2 | Moth species composition

The three forest types under study differed markedly in their floristic composition (Morera-Beita et al., 2019; Weissenhofer, Huber, Koukal, et al., 2008). As expected, this was clearly reflected by differences among moth communities regarding their species composition. Similar observations have been made in other tropical regions where local moth communities reflected habitat gradients at sometimes strikingly small spatial scales (e.g., Alonso-Rodríguez et al., 2017; Hawes et al., 2009; Ricketts et al., 2001). It has been suggested that in tropical lowland forests, local alpha diversity exceeds beta diversity (Condit et al., 2002; Tuomisto, 2010), such that locally co-existing species, if sufficiently covered through sampling, represent a large proportion of the regional species pool (Novotný & Weiblen, 2005; Novotný et al., 2007). If this concept were to apply to the forests around La Gamba, then only weak differentiation of assemblages would have been expected to occur. Assemblages of creek sites with low species richness seem to represent nested subsets of more species-rich assemblages found at other sites. Nearly all moth species observed at the species-poor creeks also occurred in one of the other two forest types. Creeks showed a much more erratic moth assemblage composition than slopes and ridges, indicating a higher degree of stochastic site-to-site variation. Moths may tend to fly along the open ridges and are less able to reach unconnected creek forests. Local differentiation of moth assemblages was largely due to differences in the abundances of species shared between different forest sites and less so driven by species turnover. Several other studies analyzing more extensive habitat gradients (e.g., disturbance gradients) found a marked differentiation through species turnover (Alonso-Rodríguez et al., 2017; Axmacher et al., 2009; Kitching, Ashton, Nakamura, Whitaker & Khen, 2013). Accordingly, independently of the taxonomic unit there was only a very small number of unique species at the creeks, mostly represented by singletons.

Our indicator species analysis corroborated the impoverished nature of moth communities at creeks, which harbored no single unique indicator species. The vast majority of indicator species was significantly associated with ridges or both ridges and slopes. Only species with similar habitat requirements can exist in any particular

forest type. One would therefore conclude that local habitat conditions filter those species from the regional pool whose requirements are best met at the respective sites (e.g., Kraft, Cornwell, Webb & Ackerly, 2007). Unfortunately, for the vast majority of Neotropical moth species there is still insufficient information about habitat requirements and niche dimensions (Kraft et al., 2007). Hence, for the time being, it was not feasible to assess whether moth assemblages associated with the three forest types differ consistently with regard to relevant functional traits during either their adult or larval stages.

Only for 33 of the 92 recognized indicator species (35.9%) could we trace any information on larval host plant affiliations, mostly from Web-based repositories (http://janzen.sas.upenn.edu/cater pillars/database.lasso; http://www.nhm.ac.uk/our-science/data/ hostplants/search/index.dsml; http://www.caterpillars.org). If congeneric moth species are considered as well, this fraction increases to 80%. However, the clear majority of our indicator species turned out to be host plant generalists, whereas only 23 species (25%) have taxonomically restricted host plant ranges. Among the few indicator species with narrow larval host ranges (one plant family or even one plant genus), affiliations to Moraceae, Urticaceae (*Cecropia*), or Fabaceae (*Inga*) recurred several times, but we did not recognize any clear patterns in relation to habitat preferences of the more prevalent tree species in the topographic gradients under study (Morera-Beita et al., 2019). This tentative survey indicates rather unspecific host–plant associations to predominate among indicator moth species found in the three forest habitat types.

A foregoing study conducted in the same region reported similarly strong differences in plant community composition among forest plots in relation to topography, successional stage, and disturbance regime (Morera-Beita et al., 2019). Based on a subset of the most abundant plant species, especially creek forests exhibited a plant species composition very distinct from forest plots located on ridges and slopes. Although in general lowland forests in the region are characterized by a high abundance of palms, certain trees that serve as hosts for some of our indicator moth species, such as *Brosimum* or *Inga*, are abundant alongside creeks (Table S9). Yet, indicator species whose larvae feed on exactly these trees predominantly occurred not in creek forest, but rather at slopes or ridges. Hence, there is at present no solid evidence that the clear community patterns observed in moths in relation to topography are directly mediated by local habitat preferences of their larval host plants. Accordingly, other factors such as gradients in microclimate, enemy pressure, or availability of nectar resources might be more important for shaping moth assemblages at the small spatial scale of our study.

5 | CONCLUSION

Our data demonstrate that moth assemblages of a perhumid lowland rain forest landscape in southwestern Costa Rica show strong concordant responses to small-scale topographic habitat differentiations into creek, slope, and ridge forests. These differences likely result from local habitat filtering processes due to varying

ecological conditions along topographic gradients and with regard to species diversity and composition patterns were broadly similar to those observed in the same region for plants, butterflies, or birds. The reasons for the unexpectedly low moth abundance and diversity in creek forests deserve further scrutiny. From a conservation perspective, the clear faunal differentiation also calls for efforts to maintain the entire diversity of forest types found in the region, which reflect the topographic heterogeneity of Mesoamerican lowland forests in nature reserves such as the Piedras Blancas National Park. Since topographic relief shapes tropical forests all over the world, our findings should be relevant for future biodiversity studies by highlighting the importance of small-scale spatial heterogeneity, which might be crucial to accurately estimate biodiversity. Further studies should now assess whether similar biodiversity patterns as reported here for southwestern Costa Rica also recur in other biogeographical regions of different historical origin and how they are linked to ecological traits of the respective organisms.

DATA ABILITY

Data Availability: The data used in this study are archived at the Dryad Digital Repository (https://doi.org/:10.5061/dryad.783p8m2) and GenBank under accession numbers MK585624–MK585626, MK612137–MK612313, MK612314–MK612398.

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