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The importance of tropical mountain forests for the conservation of dragonfly biodiversity: A case from the Colombian Western Andes

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Abstract: Forests have been widely recognized as key habitats for odonate (dragonflies and damselflies) biodiversity, but the importance of forests for holding odonate biodiversity remains understudied in tropical mountains, one of the most diverse ecosystems on the planet. Here we describe the odonate assemblage composition along the elevation gradient in the Tatamá Mountains (Colombian Cordillera Occidental). We analyzed the effects of elevation, habitat, and suborder on species richness and endemism. We found that the richest assemblage occurred in the foothills between 300 and 600 m, where the biotas of the Chocó biogeographic region and the Tropical Andes converge. Anisoptera richness was higher in open habitats, that of Zygoptera higher in forests. Richness and endemism decreased with elevation, and no relation between habitat and richness was found. However, the number of endemic species was strongly related to forests, which harbored 25 out of 28 endemic species. Also, forest odonates had narrower elevation ranges than open-habitat odonates. These patterns can be explained because tropical mountains were historically covered by forests, while open habitats derived from human activities (i.e., pastures) that have flourished in the past centuries. The forest odonate assemblages at different elevations have been evolving for millions of years, in relatively stable ecological conditions, which could promote the high number of forest endemics in the tropical mountains. Our results emphasize the role of tropical mountain forests in the conservation of Odonata diversity.

Keywords: beta diversity, dragonflies, damselfly, elevation gradient, endemism, habitat, species richness, Odonata, Tatamá Mountains.

Introduction

Tropical mountains are recognized for harboring great species richness in relatively small areas and therefore are considered biodiversity hotspots (Myers *et al.*, 2000; Perrigo, Hoorn, & Antonelli, 2020). The great biological diversity in tropical mountains has been related to their environmental stratification and relative climatic stability through time, constraining species altitudinal distribution to narrow elevation bands as a consequence of their thermophysiological adaptations to their local environments (Ghalambor et al., 2006; Graham et al., 2014; Janzen, 1967; Sheldon et al., 2018). Additional to elevation, vegetation structure plays an important role in microclimate stability, that also affects species composition, and forests have cooler and less variable environmental temperatures, higher humidity, and lower light intensity compared to open habitats (Cordero-Rivera, 2006a), affecting species distribution, assemblage structure, and species behavior (Cordero-Rivera 2017; Klinges &

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Scheffers, 2020). Tropical forests are recognized as some of the oldest ecosystems on the planet (Allen et al., 2020; Couvreur, Forest, & Baker, 2011), whereas most open habitats in tropical regions are due to human activities which have created new ecosystems mostly colonized by widespread and generalist species (Roberts, 2019).

The importance of forested habitats for odonate diversity is recognized in a synthesis on the association between odonates and forests from temperate regions through the tropics (Cordero-Rivera, 2006). This synthesis compiles studies exploring different aspects of the odonate-forest relationship, from simple facts such as microclimate variation related to differences in canopy cover to complex processes, such as cascade events originating the trophic networks of forests and the evolutionary history and role of forests in odonate speciation (Corbet, 2006; Dijkstra & Clausnitzer, 2006; Orr, 2006; Paulson, 2006; Sahlén, 2006; Watanabe, 2006). Despite this great research effort in the odonate-forest relationship, little is known about the odonates of tropical mountain forests (Maldonado *et al*., 2011).

Odonate diversity studies across tropical mountains show a high number of endemic species associated with forest habitats compared with open habitats. For instance, in the Afrotropical Mountain Archipelago, there are a greater number of endemic species compared with other African regions (Dijkstra *et al*., 2011; Dijkstra & Clausnitzer, 2006). In Borneo, mountain forests are recognized for their high endemism (Orr, 2006), and, inventories of Mount Kinabalu show that all the endemic species are forest dwellers (Hämäläinen, 1994). In Fiji, the genus *Nesobasis*, which shows the highest insular radiation of odonates (Lorenzo-Carballa et al., 2019), is mainly a group of forest specialists. In the Neotropics, along the eastern Peruvian Andes in Manu National park, evidence shows that endemic species are also mountain forest inhabitants (Louton, Garrison, & Flint, 1996). Furthermore, around 85% of the endemic species in Colombia, Ecuador, and Venezuela inhabit mountain forests (Bota-Sierra *et al*., 2016; Mauffray & Tennessen, 2019; Pérez-Gutiérrez & Palacino-Rodríguez, 2011; Vivas-Santeliz & De Marmels, 2017).

In contrast, open habitats such as natural savannas, wetlands, or agricultural lands, are usually inhabited by widespread and generalist species (Brasil et al., 2018; Calvão et al., 2020; Suhling, Martens, & Marais, 2009), most of them in the suborder Anisoptera due to their thermoregulatory abilities (Corbet & May, 2008; De Marco Jr, Latini, & Resende, 2005; May, 1976). These thermoregulatory abilities correlate also with their greater dispersal powers and the ease of dispersal in open habitats. Sahel nations are inhabited by pan-African species which can be easily found in open-habitat habitats from southern Sahara to South Africa and even into Eurasia (Dijkstra *et al.* 2011); in the Colombian savannas, at the Orinoco basin, all the odonate species have wide range distributions (Palacino *et al.* 2017, Palacino *et al.* 2020), and in Mexican arid regions, mainly covered by savannas and xerophytic vegetation, only one species has a narrow distribution (González-Soriano & Novelo-Gutiérrez, 2014; Ortega-Salas & González-Soriano, 2015). Hence, the composition of odonate assemblages in open-habitats varies less than in forest habitats, yet some differences in richness and species turnover are associated with land-use effects or ecosystem differences even for these generalist open-habitat species (Astudillo, Novelo-Gutiérrez, Vázquez, García-Franco, & Ramírez, 2016; Suhling *et al.* 2009; Veras, Lustosa, Moura, Ferreira, & Juen, 2020).

Here, we describe the changes in odonate assemblages along the Tatamá Mountains, in the western slope of the Cordillera Occidental of the Colombian Andes. We also analyze the effects of elevation and habitat on odonate species richness and endemism in damselflies (Suborder Zygoptera) and dragonflies (Suborder Anisoptera). We expect changes in the assemblage richness and composition with elevation, with the richest assemblages in the lowlands. Also, we expect endemism richness to be higher in forests than in open habitats, as the tropical mountains have been historically covered by forests (Allen *et al*., 2020; Herzog *et al*., 2011).

Methods

Study area: The Tatamá Mountains and its odonates

The Tatamá Mountains are located in the Cordillera Occidental of the Colombian Andes. This is the youngest among the three Andean ranges crossing the country (Gregory-Wodzicki, 2000; Hoorn *et al.*, 2010). With an average maximal elevation close to 3000 meters above sea level (Arias, 2011), it is the first great barrier for the great American biotic interchange, the mixture of Central American and South American biotas after the Panama isthmus uplift (Domingo *et al.*, 2020; Webb, 2006). There, two biodiversity hotspots converge: the Biogeographic Chocó, mainly lowlands covered by tropical rain forests, and the Tropical Andes (Myers *et al.*, 2000), making this region one of the richest biological areas on Earth (Callejas Posada, 2011; Sullivan *et al.*, 2009).

We sampled the western slope from the Bochoromá river, located in Chocó department at 140 m asl (5.29508° N, 76.39107° W) to the Montezuma Peak at 2550 m asl (5.25505° N, 76.11566° W, Figure 1). Along this elevation gradient we found a combination of agriculture, urban settlements, and forests from 140 to 1450 m asl, and from 1450 to 2550 m asl forests and natural open habitats. Odonate sampling was carried out between April 2014 and June 2019, including different seasons and different sampling efforts through the elevation gradient.

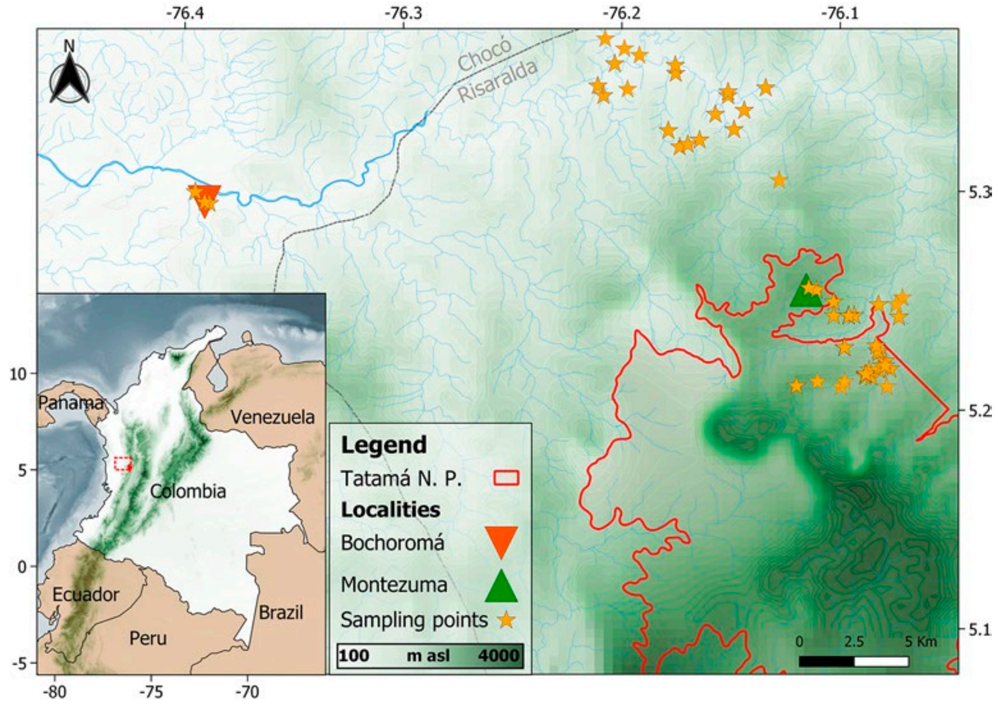

Figure 1. Map showing sampling sites along the elevation gradient from the lowest (Bochoromá) to the highest (Montezuma Peak). Tatamá National Park edge is marked.

To answer our question, we divided the elevation gradient into nine elevation ranges of 300 meters, from 0 to 2700. Since access to the elevation ranges differs, the ones with easier access were more exhaustively sampled than the difficult and isolated ones, but a minimum of 24 sampling events was accumulated for each elevation range, and toward the end of the sampling, only rarely were new species recorded (Supplementary Table 1). Sample coverage curves could not be calculated, as lists of all odonate species present were not done for every sampling event. A sampling event was considered as a visit to register the odonate species. It usually took four hours and was intended to explore all habitat types present in the sampled area by two observers. Sampling events were done between 800 and 1700 hours, always trying to observe and collect odonates in the peak activity hours at midday. The main sampling localities were mapped using QGIS v. 10.3.13 (Figure 1) (QGIS Development Team, 2020), and the map was composed with field geographic coordinates measured with a GPS (Garmin Etrex 20, ± 100 m, Garmin Ltd., Lenexa, Kansas, USA) and the GEBCO elevation grid (GEBCO, 2020).

A total of 121 odonate species were registered (Bota-Sierra *et al.,* 2019a). Following the classification proposed by Dijkstra *et al.* (2013), 64 of them are in the Anisoptera and 57 in the Zygoptera suborders. They are grouped into 14 families; the richest being Libellulidae (47 species) and Coenagrionidae (26 species). Four families are represented only by one species: Corduliidae, Synthemistidae, Megapodagrionidae, and an *incertae sedis* group (Supplementary Table 2). Seven species remain unidentified to the specific level (mainly because only females have been collected or belong to genera with tangled taxonomy). Five others have been described as new to science (Amaya-Vallejo *et al.* 2021; Bota-Sierra, 2017; Bota-Sierra & Novelo-Gutiérrez, 2017; Bota-Sierra *et al.* 2018; Bota-Sierra *et al.* 2019b), and four are in the process of description (Supplementary Table 2). Also, 28 of these species have restricted distributions: 16 are Colombian endemics, and 12 more are found only in the Biogeographic Chocó or the western slope of the Andes from Colombia to Ecuador (Bota-Sierra *et al.,* 2019a) and therefore were considered as endemics in our analysis.

The diversity of habitats and their use by the odonates at the Tatamá Mountains is high and complex: open habitat species can be specialized in ponds, wetlands, lakes, or running waters, some of them prefer habitats with a certain amount of shadow, others tolerate a certain degree of urbanization. Similarly, some forest inhabitants are specialized in the canopy, others in the understory, some patrol streams, others prefer small ponds or phytotelmata, usually males have different habitat use compared to females, and even the same species can use different habitats along its adult ontogeny: The immature adult males of *Erythrodiplax umbrata* use forest edges while the mature males are seen close to ponds in open pasture lands. To answer the main questions of this work, we divided the species into two groups, according to their habitat use, forest or open habitat species, simplifying the analysis according to the terrestrial habitat used by their males (since females were not always observed).

Data analysis

The species composition of each habitat was evaluated based on the Jaccard dissimilarity index which assigns values of 0 when all species are shared and 1 when no species are shared between a pair of assemblages. The pairwise beta diversity for dragonflies living in forested and open habitats was calculated using the Ensing and Pither (2015) approach, where the Jaccard's index of dissimilarity (β_{CC}) was computed between neighboring elevational assemblages and partitioned into two additive components: β_{REPL}, which measures species spatial turnover, and β_{RICH}, which measures the differences in species richness. Also, a dendrogram based on Jaccard's dissimilarity distances was done, and the bootstrap support values were calculated for the three main clusters. These analyses were implemented in R using the packages 'betapart' (Baselga & Orme 2012), 'vegan' (Wagner et al., 2019), 'fpc' (Hennig, 2020), and 'factoextra' (Kassambara & Mundt, 2020).

The species richness and endemic species richness were calculated using the species presences at each of the nine elevation ranges. These were used to fit generalized linear models using Poisson distribution to test for the effects of elevation, suborder, habitat, and the interaction between habitat and suborder in species richness and endemic species richness. The model validation was performed using the Shapiro-Wilk normality tests over the residuals. Wilcoxon tests were done to account for the effect of suborder and habitat used by the odonates and their elevation range, expecting forest odonates to have smaller elevation ranges due to their higher physiological specialization. The elevations ranges were calculated as the maximal elevation minus the minimal elevation recorded for each species at the Tatamá Mountains. All the analyses and graphs were performed in R (R Core Team, 2019; Wickham, 2016).

Results

Species distribution and composition

Among the 121 odonates recorded in the Tatamá Mountains we found that 23 Anisoptera species were forest specialists and 41 open habitat specialists; while in Zygoptera, 42 species were forest specialists and 15 open habitat specialists (Supplementary Table 2). Also, we found two Anisoptera endemic species specialized in forests and one specialized in open habitats; while 22 Zygoptera endemics are specialized in forests and one in open habitats (Supplementary Table 2).

Most odonate families recorded had lowland species representatives, except the family Synthemistidae and the *incertae sedis* group (Figure 3). For most of the families, the upper limit was around 1600 m, but the families Aeshnidae, Coenagrionidae, Libellulidae, Polythoridae, Synthemistidae, and the *incertae sedis* group have upper limits around 2400 m (Figure 2). Except for Synthemistidae, all families had forest-specialized species in the Tatamá Mountains; furthermore, Corduliidae, Heteragrionidae, Megapodagrionidae, Philogeniidae, Platystictidae, Polythoridae, and the *incertae sedis* group were represented only by forest specialists (Figure 2).

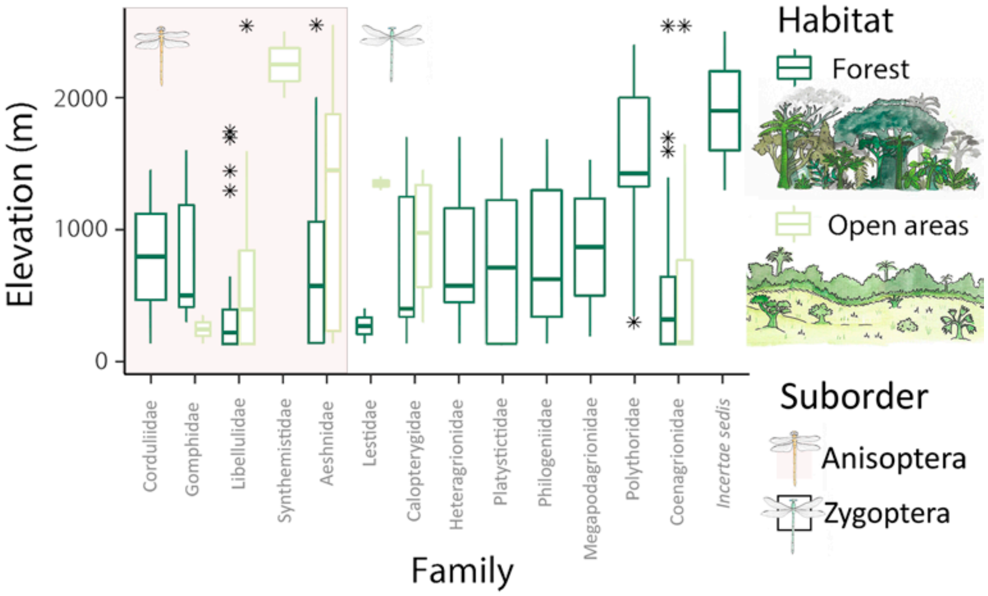

Figure 2. Elevation distribution of the 14 families recorded in the Tatamá mountains, divided by their habitat and suborder. Boxplots represent median, 3rd quartiles, and outliers.

The composition of species living in forest and open habitats exhibited similar variation in richness, but forest species showed a larger turnover along the elevation gradient (Figures 3–4, Table 1). The largest forest turnover occurred in the transition between the lowland plains and the foothills (300 – 600 m) where 34% of the forest species were replaced; this was not the case for open habitats where only 13% were replaced. Similarly, the beta diversity pattern showed a decrease of 49% in richness at 600 m, followed by an important turnover in both habitats at 900 m (46% of the species were replaced), between foothills and middle elevations. Then a plateau in richness was observed in the middle elevations, but a strong decrease in richness and a high turnover toward 1800 m was notable with only 14 species, 12% of the total richness, inhabiting the highest lands (Figures 3–4, Table 1). Congruently with the higher species turnover in forest species (Figure 4), the species elevation ranges of the odonates in the Tatamá Mountains were lower for forest odonates (mean ± SD = 463.8 ± 453.9) than for those of open habitats (mean ± SD = 616.3 ± 493.5; W = 1409.5, $P < 0.033$, Figures 3–4, Table 2).

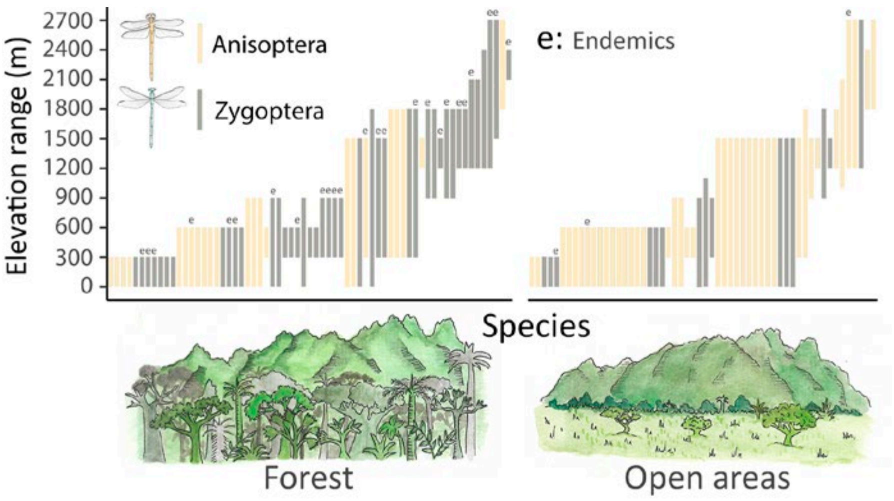

Figure 3. Elevation profiles of the odonate species along the Tatamá mountains separated by habitat and colored by suborder, endemic species are marked with an "e". Each bar represents the elevation range of a single species.

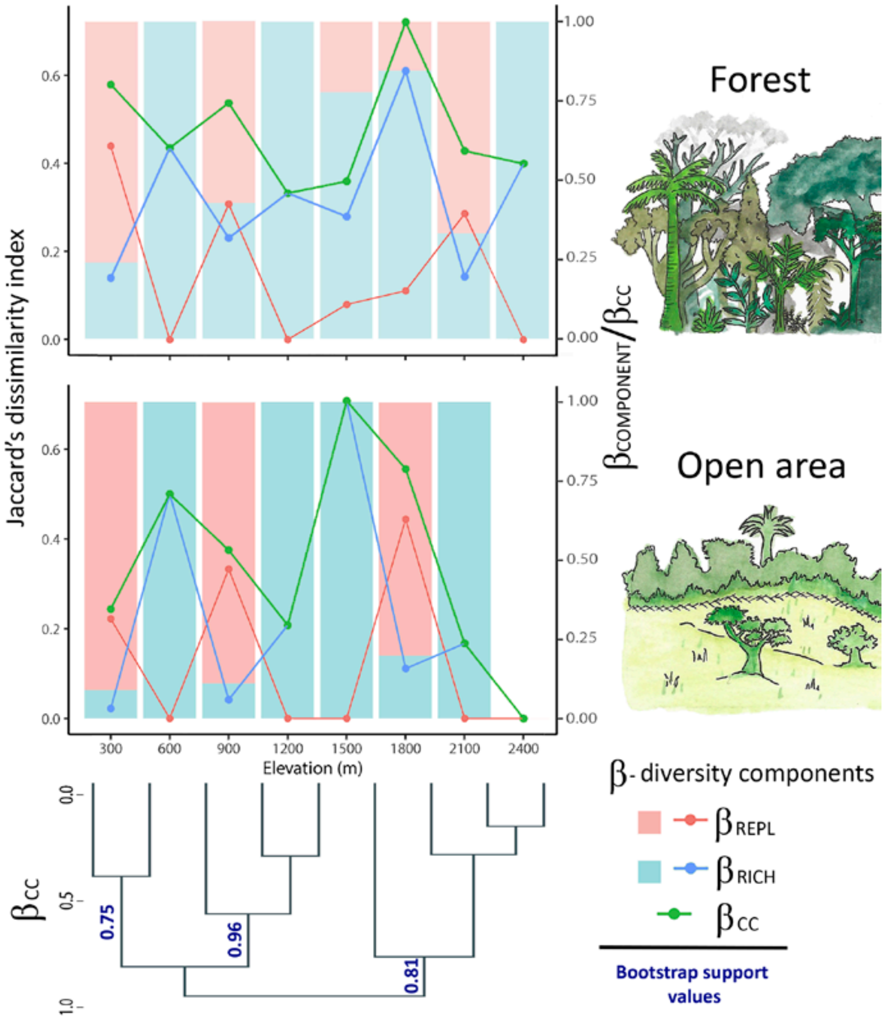

Figure 4. Beta-diversity components for dragonflies living in the forest and open habitats in the Tatamá mountains. Dissimilarity was computed between neighboring elevational communities. The bars show the proportion of the Jaccard's dissimilarity index (β_{CC}) explained by the species turnover (β_{REPL}) and by the species gain/loss (β_{RICH}). The dendrogram is based on Jaccard's dissimilarity distances for the whole community, the bootstrap support values of the three main clades are reported.

Table 1. Jaccard's index of dissimilarity (β_{CC}), and its components (β_{RICH} and β_{REPL}) between neighboring elevational communities. Calculated at forest, open areas, and their combination.

Elevation (m)	Forest			Open area			Combination		
	β_{RICH}	β_{REPL}	β_{CC}	β_{RICH}	β_{REPL}	β_{CC}	β_{RICH}	β_{REPL}	β_{CC}
0-300\\301-600	0.14	0.44	0.58	0.02	0.22	0.24	0.08	0.34	0.42
301-600\\601-900	0.44	0	0.44	0.5	0	0.5	0.47	0	0.47
601-900\\901-1200	0.23	0.31	0.54	0.04	0.33	0.38	0.14	0.32	0.46
901-1200\\1201-1500	0.33	0	0.33	0.21	0	0.21	0.27	0	0.27
1201-1500\\1501-1800	0.28	0.08	0.36	0.71	0	0.71	0.49	0.04	0.53
1501-1800\\1801-2100	0.61	0.11	0.72	0.11	0.44	0.56	0.44	0.22	0.67
1801-2100\\2101-2400	0.14	0.29	0.43	0.17	0	0.17	0.15	0.15	0.31
2101-2400\\2401-2700	0.4	0	0.4	0	0	0	0.2	0	0.2

Table 2. Analysis of variance for the species richness and endemic species richness logistic regressions, including the factors elevation, habitat, suborder, and the interaction between habitat and suborder. Also, the Elevation range vs Habitat Wilcoxon test statistics is shown.

	Factor	X^2	Df	*P-value*
Species richness	**Habitat**	0.08	1	0.7795
	Suborder	3.85	1	0.0498
	Elevation	148.25	8	< 0.0001
	Habitat : Suborder	43.46	1	< 0.0001
	Residuals	211.93	24	
Endemic species richness	**Habitat**	49.58	1	< 0.0001
	Suborder	28.88	1	< 0.0001
	Elevation	16.57	8	0.0349
	Habitat : Suborder	20.72	1	< 0.0001
	Residuals	132.21	24	
		W		
Elevation range	**Habitat**	1409.5		0.0326

The composition of species clustered in three groups of elevation ranges based on Jaccard's dissimilarity index (Table 1, Figure 4), the bootstrap support values for the three clusters were 0.75 or more (Figure 4). Lowland and mid-mountain clusters were more similar to each other than to the high-mountain cluster (Figure 4). The richest cluster was located at the lowlands (from 0 to 600 m), followed by the mid-mountain cluster (from 600 to 1500 m) and then the high-mountain cluster (from 1500 to 2700 m).

Species richness and the effects of elevation, habitat, and suborder

The species richness of the odonates in the Tatamá Mountains decreased with elevation ($X^2_{8,\,24}$ = 148.25, *P*< 0.0001, Figure 5, Table 2); the richest assemblage was found at the foothills between 300 and 600 meters (Figures 3, 5). The species richness differed between the suborders ($X^2_{1,\,24}$ = 3.84, *P*= 0.0498, Table 2). In the Anisoptera, there were more species in the lowlands, and they rapidly decrease with elevation (Figures 3, 5). In contrast, Zygoptera has two peaks of species richness, the richest at the lowlands and the other at mid-elevations (Figures 3, 5). The richness of each suborder at each habitat differed, Anisoptera were more speciose in open habitats, while Zygoptera were more speciose in forest habitats ($X^2_{1,\,24}$= 43.464, *P*< 0.0001, Figures 3, 5, Table 2). Nevertheless, the habitat did not affect the total richness of the odonate assemblage, presenting similar species numbers in forests and open habitats along the mountains (Table 2).

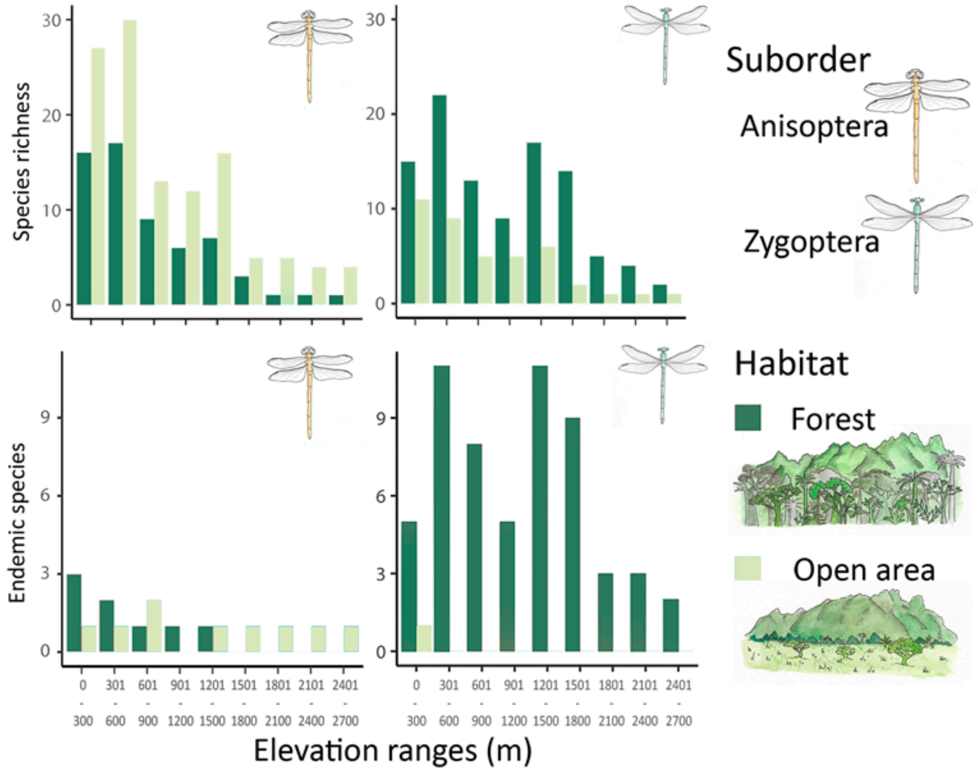

Figure 5. Odonata species richness and endemic species richness in the nine elevation intervals at the Tatamá mountains, divided by habitat and suborder.

Species endemism and the effects of elevation, habitat, and suborder

The richness pattern for endemic species showed some similarities to the richness pattern of the overall assemblage, decreasing with elevation ($X^2_{8, 24}$ =16.57, $P< 0.0349$, Figure 5, Table 2), but large differences between suborders were observed ($X^2_{1, 24}$ = 28.88, $P< 0.0001$, Figure 5, Table 2) as well as a significant interaction between habitat and suborder ($X^2_{1, 24}$ = 20.72, $P< 0.0001$, Table 2 and Figure 5). This was largely because 89% of the endemic species are forest Zygoptera, the habitat thus had a strong effect on the endemic species richness, different from the overall richness pattern ($X^2_{1, 24}$ = 49.58, $P< 0.0001$, Table 2, Figure 5).

Discussion

As expected, both richness and endemism of the odonate species decreased along the elevation gradient in the Tatamá Mountains, a pattern previously recorded for montane odonates in other geographic regions (Corbet, 1999); and a common pattern for many taxa inhabiting mountains around the globe (Peters *et al*., 2016; Rahbek *et al*., 2019). The assemblages of odonates differ between forested and open habitats, but we did not find differences in richness between forested and open habitat assemblages across the elevation gradient. However, forest odonates had narrower elevation ranges, increasing species turnover in forest assemblages across the mountain compared with open habitats.

The forest's high endemism richness can be explained because historically it was the prevalent habitat in montane ecosystems (Allen *et al*., 2020; Herzog *et al*., 2011). Allowing selection to act on forest specialists, promoting diverse evolutionary histories (Graham *et al*., 2014). In contrast, most open habitats in tropical mountains have been created by humans in the last few centuries (Roberts, 2019), allowing the range expansion of and colonization by tropical odonate generalists (Graham *et al*., 2014). These patterns of richness along the elevation gradient, with narrower distributions and a higher endemic species richness in the forest compared to open-habitats can be explained by thermal physiological limits of tropical taxa in mountains matching their local environment, promoting narrow elevational distribution and high species turnover (Ghalambor *et al*., 2006; Janzen, 1967; Peters *et al*., 2016; Polato *et al*., 2018; Sheldon, 2019).

Odonate richness in the Tatamá Mountains clustered in three groups and decreased with elevation. The richest assemblage is part of the lowland cluster, but it is not in the lower Chocó plains (0–300 m), the lowest elevation. In fact, it occurs in the foothills (300–600 m), where two of the most diverse biotas converge, the Chocó and the Andean, thus this high richness can be explained by the overlap of odonate assemblages from distinct biogeographical regions meeting there. This pattern is predicted by the mid domain hypothesis (Colwell, et al., 2004), and it is also observed with other taxa in other mountain systems where the convergence of two biogeographical regions promotes higher numbers of species (Joaqui *et al*., 2021; Morrone, 2020). At higher elevations, the species richness decreased, but the proportion of endemic species increased close to 40%, showing that despite the lower number of species inhabiting the highlands, these ecosystems are of great importance for the conservation of the Andean fauna. Comparable patterns of biological richness have been found in the Tropical Andes for bird, insect, and plant assemblages, which show similar patterns to odonates. Trees and lianas are more diverse from the lowlands through middle elevations (1500-1800 m), after which their richness begins to decrease (Jankowsky *et al.* 2012, Kessler *et al*., 2011). Many insect assemblages show a low- or mid-elevation peak in species richness, depending on the sampled group (Larsen *et al*., 2011; Ramos-Pastrana *et al.,* 2021), and similar findings are reported for birds, in which the peak in species richness changes from low to middle-elevations depending on environmental conditions (Herzog & Kattan, 2011, Jankowsky *et al.* 2012). On the Afrotropical Kilimanjaro mountains, different predictors of elevation diversity appear depending on the taxa sampled, but when several taxa are grouped in the analysis, temperature, which is mainly shaped by elevation and vegetation coverage, is the main predictor of biodiversity (Peters *et al*., 2016).

The richness of Anisoptera is higher in open habitats, while the Zygoptera are richer in forest ecosystems. This is probably related to the physiological and behavioral thermoregulatory abilities of Anisoptera (Heinrich & Casey, 1978; May, 1976, 1978, 1995; Rocha-Ortega *et al.,* 2020), which can regulate their body temperature through body posture and the control of hemolymph circulation, allowing them to lose heat by convection, conferring them an advantage in warmer open habitats compared to Zygoptera, which are considered thermoconformers (May, 1976). Also, most of the Anisoptera species have heavier bodies than Zygoptera and more powerful flight, which is advantageous for colonization of new habitats and regions (Corbet, 1999; May & Matthews, 2008; McPeek, 2008).

Overall, our study supports the fundamental role of forests for the conservation of odonate biodiversity, adding evidence from the tropical montane forests, one of the most diverse and endangered ecosystems on our planet (Morueta-Holme *et al*., 2015; Raxworthy *et al*., 2008; Sheldon *et al*., 2018; Sheldon, 2019; Tognelli *et al.,* 2016). This study calls attention to the fact that elevation is an important factor shaping biodiversity, but at a fine-scale the type of habitat also makes an important contribution to the biological richness patterns (Klinges & Scheffers, 2020; Peters *et al*., 2016).

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