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Ecomorphology of an Odonata community in the southern Pacific lowlands of Costa Rica

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Acknowledgements

Abstract

Tropical ecosystems, especially tropical freshwater habitats are under threat of human-made disturbances. Odonata are known to qualify for assessing the integrity of freshwater ecosystems. To gain knowledge about potential drivers of Odonata community assemblages, this study aims to shed light on the interplay of differing habitat types and morphological traits of Odonata species shaping the community composition in the southern Pacific lowlands of Costa Rica. The study took place from October 2016 to February 2017 around La Gamba. Adult Odonata were sampled along streams in four different habitat types, forest interior, forest margin, gallery forest and openland. Measurements of morphological traits known to influence flight characteristics were taken from voucher specimens. The study found no habitat preferences among the sampled species on a family level. Community-weighted means of the measured traits revealed morphological differences of the Odonata communities along the gradient from forest interior to openland habitats, but a fourth corner analysis failed to link certain morphological traits to the assessed habitat variables.

Keywords: Dragonflies, damselflies, wing morphology, morphological traits, habitat filter, tropical lowland rainforest

Introduction

Freshwater ecosystems are among the most endangered ecosystems in the world as they are exposed to many man-made threats such as pollution, overexploitation, habitat destruction or climate change (Buss et al., 2002; Dudgeon et al., 2006; Reidl et al., 2019). Globally, the result is a sharp decline in the biodiversity of aquatic organisms, including taxonomic groups such as the Odonata (Insecta), which already lost a substantial proportion of species (Sánchez-Bayo & Wyckhuys, 2019).

When assessing the integrity of freshwater ecosystems, Odonata have proven to be valuable bioindicators due to their semiaquatic lifestyle, and – compared to other aquatic invertebrates – their easy accessibility and species identification of the adults (Chovanec et al., 2015; Adu et al., 2019). Besides their value when assessing freshwater ecosystems, Odonata communities are also sensible to terrestrial habitat alterations (Dolný et al., 2012).

Odonata consist of two suborders, Anisoptera (dragonflies) and Zygoptera (damselflies), with both using a variety of waterbody types for reproduction. The larvae have an aquatic lifestyle, while the adults are terrestrial. Odonata are predatory in all life stages (Colbert, 2004). Because of their semiaquatic lifestyle with exclusively aquatic larval stages and adults hunting prey along water bodies and in adjacent terrestrial habitats, Odonata represent an important link between aquatic and terrestrial environments (Chovanec & Raab, 1997). Furthermore, Odonata hold a socio-economic value for suppressing aquatic insect larva, especially the larva of Culicidae (Insecta: Diptera), hence influencing the spread of diseases important to humans, like dengue for instance (Saha et al., 2012; Samanmali et al., 2018).

To date, the Catalogue of Life lists more than 5900 Odonata species worldwide (Tol, 2021), the estimated total species number is around 7000 (Kalkman et al., 2008). Kalkman et al. (2008) lists 1636 Odonata species for the Neotropics; 285 species are so far recorded from Costa Rica, not including 5 species, which have yet to be formally described (Paulson & Haber, 2021). Despite this fact, only a few studies have been published on Costa Rican dragonflies and damselflies, causing an information deficit on the ecology of certain Odonata species (Ramírez et al., 2000).

When assessing a community structure, the concept of niche theory still remains one of the most important approaches to explain the occurrence of species in a given area. Following the theory, species occur in habitats with suitable niches. Those niches are defined as an n-dimensional space, shaped by biotic and abiotic variables (Hutchinson & MacArthur, 1959). Furthermore, the co-occurrence of a set of species might be influenced by environmental filtering, leading to communities sharing certain traits (Webb et al., 2002; Cornwell et al., 2006; Lebrija Trejos et al., 2010), or biotic factors like competition (MacArthur & Levins, 1967).

Besides abiotic factors, the submerged macrophyte vegetation and the state of riparian vegetation in different habitats were recognised as important factors, when assessing the Odonata assemblages in lentic and lotic water bodies (Schindler et al., 2003; De Oliveira-Junior et al., 2017). De Marco et al. (2005) explained differences in the assemblage of Odonate communities with different thermoregulatory strategies, stating that the larger species of the suborder Anisoptera are bound to sunny openland habitats. In contrast, smaller species belonging to the suborder Zygoptera can rely on the ambient temperature for heat management, enabeling them to thrive in habitats with dense canopy cover restricting radiation from the sun. Odonata are categorized into three groups, depending on their thermoregulatory strategies: ectotherms, heliotherms and endotherms. Ectotherms are depending solely on the ambient air temperature for thermoregulation (usually Zygoptera). Heliotherms, species intermediate in size, need to warm up in sun spots (May, 1991; De Marco et al., 2005). Thermoregulatory strategies of heliotherms are known to be mostly behavioral, since they are regulating their body temperature by changing the microhabitat (sun spots vs shaded areas) or adjusting the body posture, to increase or decrease the surface exposed and hence heated by the sun (May, 1976). The third type of Odonates, endothermic species, can utilize excess heat from their flight muscles to warm up and the hemolymph flow to regulate the body temperature (Heinrich & Casey, 1978). Ectothermic Odonates are considered *perchers*, species that spend a significant time of the day at their perching site, while endothermic Odonates are classified as *fliers*, species that are strong on their wings, continuously patrolling their habitat (Corbet & May, 2008).

These effects are the basis of the ecophysiological hypothesis (EH), proposing that temperature (influenced by forest cover) acts as a filter on Odonate communities in the tropics. Furthermore it is expected that species-specific traits like life history, behavior or morphological traits

potentially play an important role when Odonate species interact with this environmental filter, since e.g. some Zygoptera can be found in openland habitats (De Marco Junior et al., 2015). Several morphological traits were linked to thermoregulation, flight agility, dispersal ability or the classification into *fliers* and *perchers* in general in Odonata. Since flight is the energetically most demanding activity that Odonata perform (Norberg, 1995; Corbet and May 2008), it is likely that wing dimensions in relation to body dimensions can be linked to flight performance, needed for certain behaviors of Odonata (Sacchi & Hardersen, 2013). For example, long wings in Zygoptera increase flight speed, but reduce the ability for quick flight maneuvers to avoid avian predators (Svensson & Friberg, 2007). Morphological differences between *fliers* and *perchers* are known to be associated to differences in body weight, with fliers being usually heavier (Grabow & Rüppel, 1995), wing shape (Johansson et al., 2009) or the allometry between body length and wing length (Sacchi & Hardersen, 2013). Aspect ratio has been shown to vary within the geographical range of *Calopteryx maculata* (Zygoptera: Calopterygidae), with higher aspect ratios being associated with lower temperatures, allowing *C. maculata* to fly with greater efficiency in colder habitats (Hassall, 2015). A larger thorax potentially offers more space for flight muscles and bigger flight muscles have a greater power output (Schilder & Marden, 2004). Furthermore, wing size, wing shape and thorax size differ among species with different dispersal behavior (McCauley, 2013).

Mesoamerica is recognized an important biodiversity hotspot. Unfortunately, the region already lost more than 80% of its primary forests (Myers et al., 2000). In Costa Rica, great efforts are made to preserve pristine habitats, with a system of national parks and smaller protected areas and biological corridors aiming to connect these remaining forest fragments (Boza, 1993). With Odonata linking aquatic and terrestrial habitats, that are potentially under the threat of being diminished in size or capacity, and their socio-economic value to humans, Odonata are an important asset to ecosystems and generating knowledge about them seems to be important and worth the effort.

Since Odonata show differences in morphological traits and behavior, in respect to environmental factors like canopy closure or stream width, to cope with requirements on flight or thermoregulation, this study aims to shed light on the interplay of morphology and habitat structure in an Odonata community in the southern Pacific lowlands of Costa Rica.

The following hypotheses were tested:

(1) Differences in habitat utilization of species are related to differences in morphological traits known to influence flight characteristics. Hence, we expect that morphological traits of forest-dependent species forced to maneuver in the dense understory differ those of species preferably occurring at open sites in the human-dominated landscape.

(2) Certain morphological traits of the sampled Odonata are expected to correspond with different habitat characteristics.

Materials and methods

Study area and sampling sites

The study was conducted around the Tropical Research Station La Gamba (8.700962°N, 83.201718°W, 70 m.a.s.l.), situated in the southern Pacific lowlands of Costa Rica. Odonata were sampled at lotic water bodies of different dimensions, all belonging to the Rio Esquinas water catchment area (Tschelaut et al., 2008) in vicinity of the Piedras Blancas National Park. Selected sites belonged to one of the following four habitat types: (1) forest interior, (2) forest margin, (3) gallery forest and (4) openland. For every habitat type eight transects were selected, each of which had a length of 50 meters. All transects were located at least 200 meters apart from each other (Fig. 1).
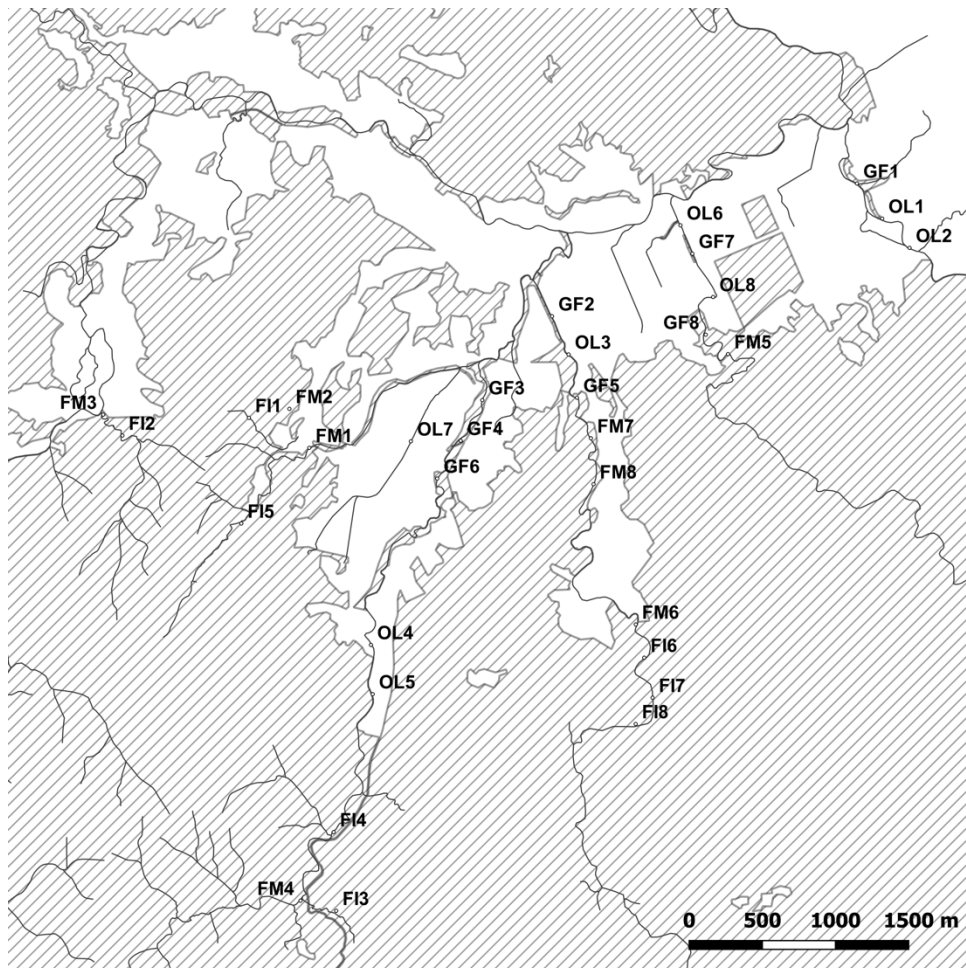

Figure 1*: Map of the study area around La Gamba, showing the location of the transects along the streams and their habitat classification. Forest interior (FI), forest margin (FM), gallery forest (GF) and openland (OL). Dashed areas symbolize forest, unfilled areas symbolize agricultural land-use systems.*

Habitat variables

Several variables were utilized to describe differences between sites and habitat types. Besides habitat variables known to influence the solar radiation received at a site (stream width [m] and canopy closure at the river margins [%]), the study also included the amount of sand [%], small gravel [%] and leaf litter [%] to describe the substrate composition found at the river banks, as well as the amount of deadwood [0-3] and the number of protruding rocks within the water body. As landscape variables, the cover of oil palm plantations [%] and old-growth forest [%], within a 150 meter buffer on both sides of the waterbody, were used. All habitat variables were assessed by Degenhart (2017).

Dragonfly survey

The surveys took place between October 23rd 2016 and February 10th 2017. The sampling was executed from 9 am to 4 pm, or until it started to rain. Each site was surveyed for one hour per sampling round and a total of four sampling rounds for each site were realized. For the sampling, a simple sweep net was used and only adult specimens were caught. The length of the sweep net handle allowed to sample up to a height of about three meters. The sampled Odonata were killed with Acetic Ether, photographed, dried and stored in paper envelopes for a later measurement of various morphological traits in the laboratory. For identification, several monographs were used (Förster, 2001; Esquivel, 2006; Schneeweihs et al., 2009). Species purely bound to lentic water bodies for reproduction, based on information gathered from the available literature, were not considered in this study.

Morphological measurements

For the morphological measurements (Fig. 2), for each species, a maximum of ten males were randomly drawn as a subsample. If a species was represented by less than ten male individuals, the measurements were taken from all available male specimens. Detailed photographs of each individual and their right front and hind wing were taken. For measuring the length of the abdomen, wing area as well as length and width of the wings, ImageJ was used (Schneider et al., 2012). The width of the thorax was measured using a digital caliper. The sample specimens were dried for seven hours, until no further weight loss was detectable. For drying, a Binder FED 400 drying cabinet was used. After the specimens were dry, they were weighted using a laboratory scale. Aspect ratio was calculated as wing length^2/wing area for front and hind wings separately and wing loading as dry weight/(area front wing + area hind wing).
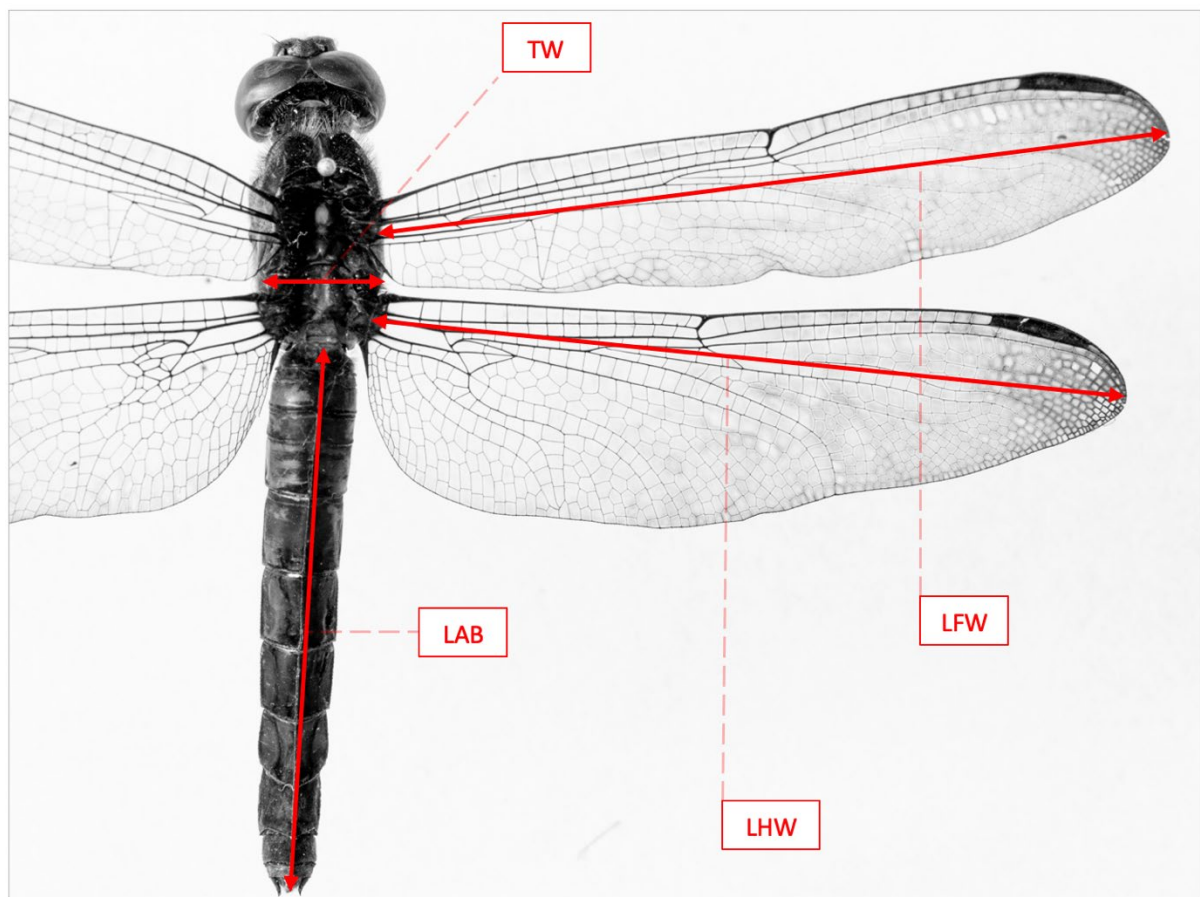

Figure 2: *The red arrows are showing the different measurements taken. The length of forewing and hindwing (LFW/LHW), as well as length of the abdomen (LAB) were measured with ImageJ. The width of the thorax (TW) was measured using a caliper.*

Data analysis

For the analysis, species records from this study were combined with records assessed one year earlier, at the same sites and in the same months, by Degenhart (2017). After combining the species records, all species represented by four or less individuals, as well as species known to reproduce in lentic water bodies were excluded from the analysis. For the morphological traits used in the analysis, only the measurements from male individuals were used, since the number of females recorded was substantially lower compared to the number of recorded males (a total of 533 females compared to 1921 males for the 29 species used in the analyses).

NMDS ordinations were calculated to visualize (1) the morphological similarity of species (quantified as Euclidian distances calculated using a trait matrix with six morphological measurements; see Table 1) and (2) similarity of habitat utilization (quantified using Bray-Curtis similarities based on a species x habitat type matrix). The NMDS plots were calculated using the R package Vegan (Oksanen et al., 2017; R Core Team, 2017). To test for differences in habitat use on a family level, a one-way ANOSIM was performed, using Primer 5 for Windows V5.2. Furthermore, a Spearman matrix rank correlation was calculated to test for a relationship between similarities in habitat use and morphological traits of the sampled Odonata. Also the Spearman matrix rank correlation was performed with Primer 5 for Windows V5.2. Several one-way ANOVAs were performed with community-weighted means of the traits to gain insight into the relationship of certain morphological traits of the Odonata communities found along the habitat gradient and the four different habitat types, using Past 4.02 (Hammer et al. 2001). Resulting p values were corrected for multiple testing by a False Discovery Rate (FDR) correction (Benjamini & Hochberg 1995).

Finally, a RLQ test (Doledec et al., 1996), followed by a Fourth-Corner analysis (Legendre et al., 1997), was performed using the R package ade4 (Dray & Dufour, 2007). The RLQ test works with three matrices (R= environmental traits/ site, L= abundance of species/ site, Q= morphological traits/ species), that together form a fourth matrix (Fourth-Corner matrix). The Fourth-Corner matrix reflects possible connections between environmental variables and the species morphological traits.

Results

Overview

The dataset used for the analysis includes 2454 records of Odonata, belonging to 29 species, comprised of four families (Libellulidae: N=8 species; Calopterygidae: N=4; Coenagrionidae: N=16; Megapodagrionidae; N=1; also see Appendix Table A1).

Similarity of traits and habitat use between species

The NMDS ordination visualizing morphological similarities (for considered traits see Table 1) between the 29 considered Odonata species shows a clear segregation of the families Libellulidae, Calopterygidae and Coenagrionidae. The single Megapodagrionidae species plotted within the Coenagrionidae cluster (Fig. 3). The strong morphological differences between the three families Libellulidae, Calopterygidae and Coenagrionidae were confirmed by the calculated one-way ANOSIM (Global $R = 0.742$, $p = 0.001$). Also all pairwise comparisons achieved a significant level (Libellulidae vs. Calopterygidae: $R = 0.39$, $p = 0.016$; Libellulidae vs. Coenagrionidae: $R = 0.767$, $p = 0.001$; Calopterygidae vs. Coenagrionidae: $R = 0.824$, $p = 0.001$).

Table 1: *Means and standard deviations (SD) for the measured traits of all measured Odonata.*

Trait	Mean	SD
Dry weight (g)	0.0215	0.0252
Thorax width (mm)	2.4864	1.1255
Abdomen length (mm)	26.7059	6.2252
Wing loading (g/mm²)	0.00009040	0.00003541
Aspect ratio forewing	6.3472	1.3264
Aspect ratio hindwing	5.9526	1.8061
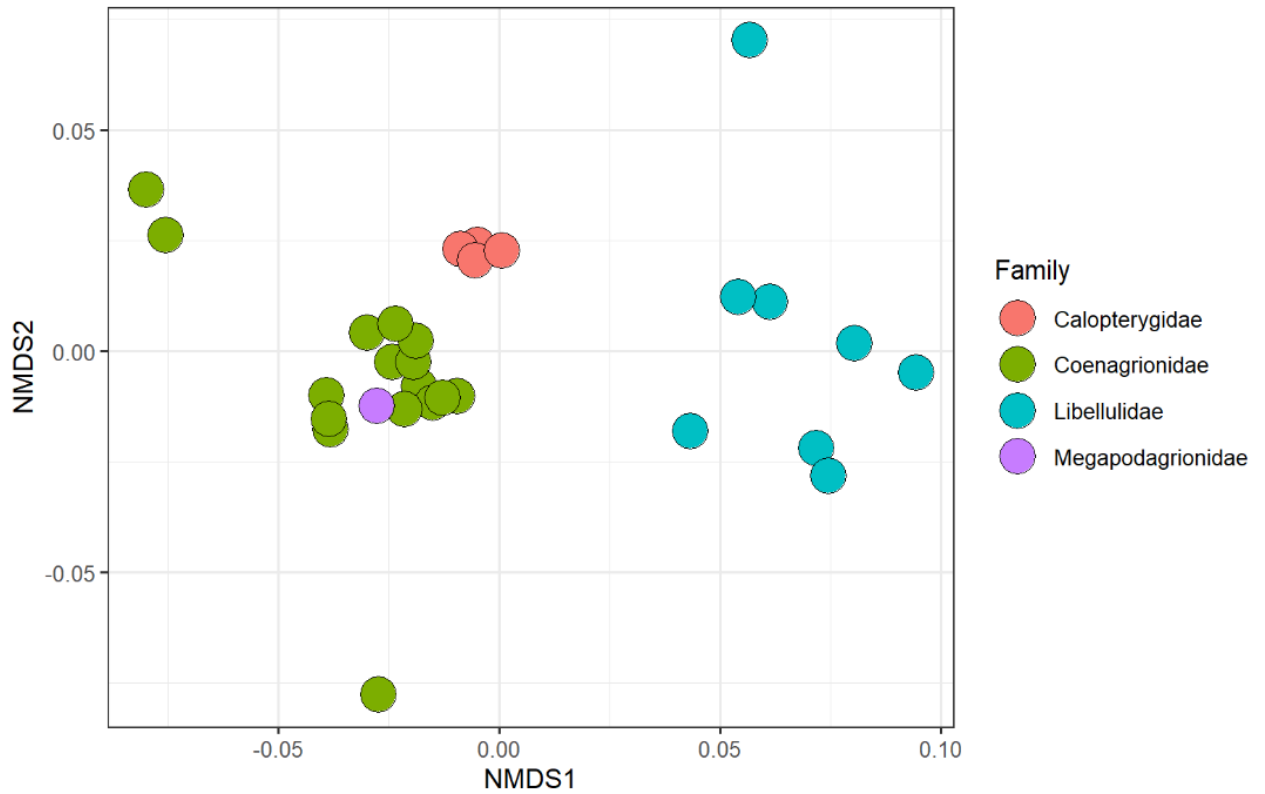
Figure 3: *NMDS plot, based on similarities of morphological traits between species, visualizing the segregation of sampled Odonata species on family level (stress = 0.04).*

The NMDS ordination visualizing the similarity relationships of habitat utilization of the 29 species shows the habitat preferences of the species following the gradient from forest interior to openland habitats along the x-axis (Fig. 4A). A further NMDS ordination based on figure 4A depicts the habitat preferences of the species on a family level, and shows that patterns of species' habitat use did not differ between families (one-way ANOSIM: Global R = -0.054, p = 0.723; not including the family Megapodagrionidae with only one species). However, a weak relationship between similarity of habitat use and morphological traits could be found (Spearman matrix rank correlation: Rho = 0.24, p = 0.013).
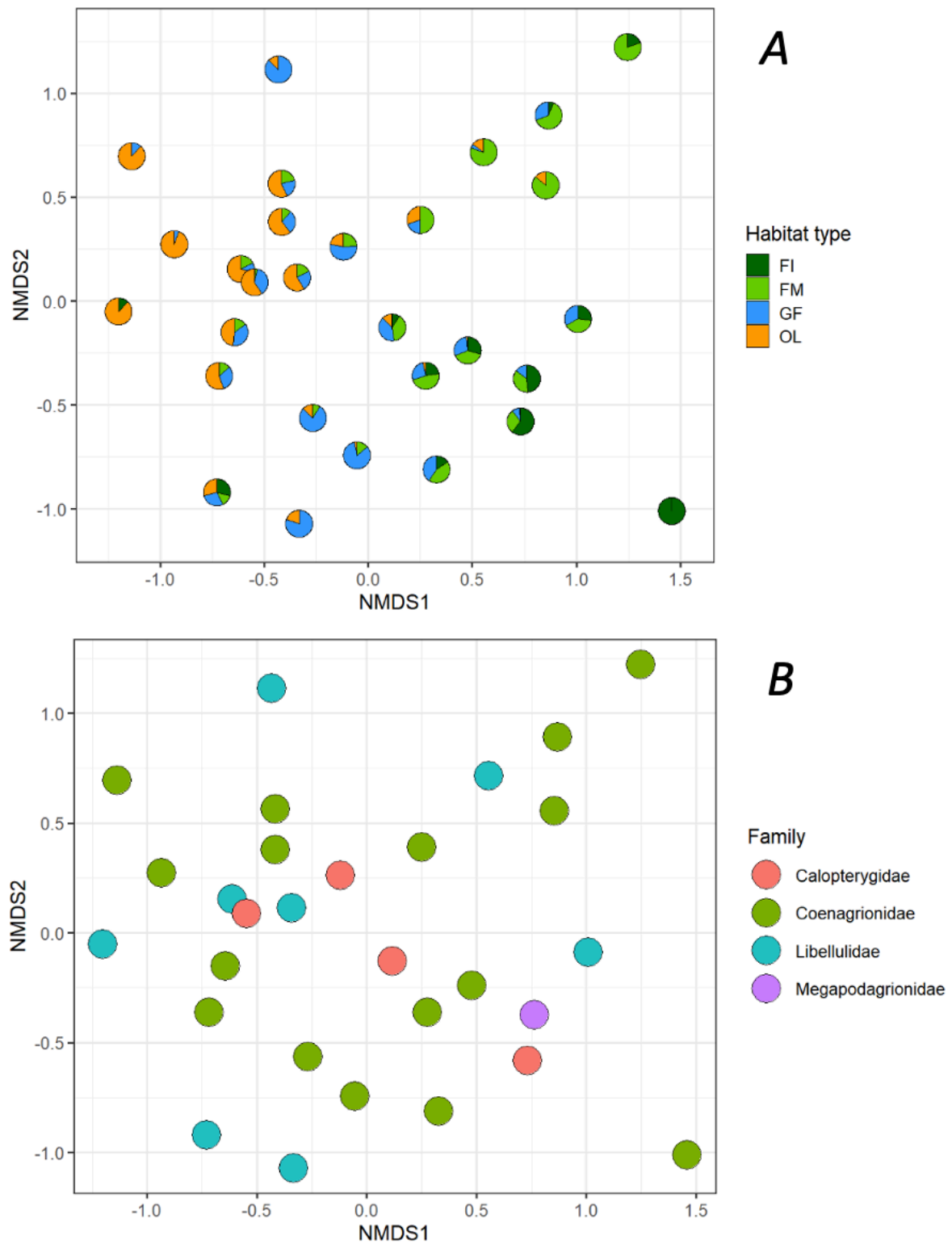
Figure 4: *NMDS plot showing similarity relationships of habitat use between the sampled Odonata species (stress = 0.18).* ***A****: For each species, pie charts indicate the percentage of individuals sampled in each of the four habitat types.* ***B:*** *Different colors represent the family affiliation of species.*

Several one-way ANOVAs calculated for CWM traits proved differing significantly between sampled habitats (Fig. 5a-f). Openland sites showed a higher mean dry weight of recorded species than the habitats FM and GF ($F_{3,28} = 6.335$, FDR-adjusted $p = 0.0027$), mean thorax width was higher in OL habitats compared to FI habitats ($F_{3,28} = 3.257$, FDR-adjusted $p = 0.0363$), the mean abdomen length was longest in FI habitats and shortest in OL habitats ($F_{3,28} = 27,14$, FDR-adjusted $p < 0,0001$), the mean wing loading was higher in FI habitats compared to FM, GF and OL habitats ($F_{3,28} = 6,664$, FDR-adjusted $p = 0.0024$) and forewing aspect ratio ($F_{3,28} = 20,91$, FDR-adjusted $p < 0,0001$) as well as hindwing aspect ratio ($F_{3,28} = 25.97$, FDR-adjusted $p < 0.0001$) proved to be significantly higher in FI habitats compared to the other habitats, with OL habitats showing the lowest aspect ratios for the community weighted means.

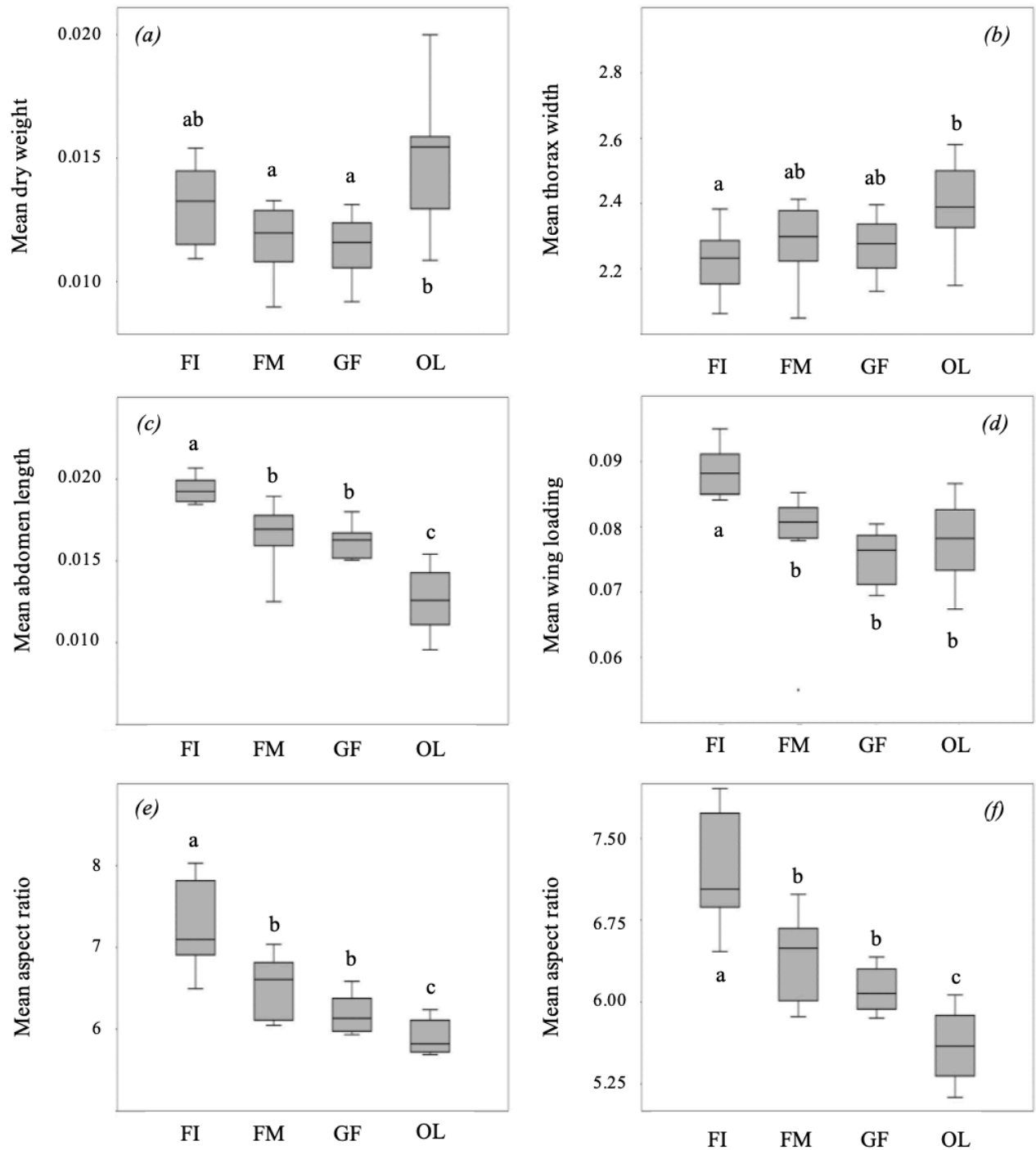Figure 5: *Community-weighted means of (a) dry weight, (b) thorax width, (c) abdomen length, (d) wing loading and (e) forewing aspect ratio and (f) hindwing aspect ratio of species recorded per site for the four sampled habitats (FI, FM, GF, OL). Boxes show interquartile ranges, whiskers indicate the minimum-maximum values. Different letter codes indicate significant differences between habitats (Tukey HSD tests).*

However, a calculated fourth-corner / RLQ analysis did not identify any morphological traits clearly related to any of the considered environmental variables. The first two axes of the calculated RLQ tests explained 92.40% and 6.13% of the variation of our data. However, the tests did not show any significant relationships between individual habitat variables or Odonata traits with one of the two axes (all p values > 0.22). Further, no significant relationships could be detected between any of the habitat variables and the morphological traits of the Odonata (all p values > 0.13). The fourth-corner analysis also emphasizes that there is no strong relationship between habitat variables and morphological traits of the considered Odonata species (p = 0.1472).

Discussion

Habitat utilization

When having a look at the habitat utilization of the Odonata communities found around the tropical research station in La Gamba, the data shows that the species are forming communities alongside the gradient, rather than assembling in distinct communities. Most species were caught predominantly in one or two habitat types, usually when the habitats were adjacent to each other, with *Orthemis ferruginea* (Anisoptera) being one exception. *O. ferruginea* specimens were mostly observed and caught in OL habitats, but were also encountered once at an FI site, showcasing the high dispersal ability of this rather big Libellulid species.

On a family level, the pattern reveals that the three main families represented in the data set (Coenagrionidae, Libellulidae and Calopterigidae) are well distributed along the habitat gradient from forest interior to the open land sites and habitat utilization does not differ between the three main families. For the most abundant family assessed in this study, the Coenagrionidae (Odonata, Zygoptera), the NMDS plot shows that species belonging to the family are found in all four habitat types, with some species mainly occurring at FI and FM sites, while other species prefer more open habitats, but generally Coenagrionids are found all over the habitat gradient.

Although Anisoptera are often recognized to prefer more open habitats due to physiological reasons (De Marco et al., 2015), the family of Libellulidae seem to be an exception to this concept based on differences in thermoregulatory strategies (May, 1991; De Marco et al., 2005). Although Zygoptera are dominating the communities encountered at forest interior sites, the data shows that some species of Libellulidae are regularly found in habitats with a denser vegetation.

The four species of Calopterigidae (Zygoptera) all belong to the genus *Hetaerina*. Although the morphological traits are found to be quite similar among the four species, they are equally spaced along the habitat gradient, with *Hetaerina titia* and *Hetaerina caja* utilizing more open habitats, gallery forests or forest margins, *Hetaerina occisa* staying closer to gallery forests and the forest margin and *Hetaerina fuscoguttata* occurring mainly at FI sites, but also FM habitats. The only species belonging to the Zygoptera family Megapodagrionidae, *Heteragrion erythrogastrum*, known to be a forest specialist, was found in big numbers at FI sites but also at FM sites and also, albeit in lesser numbers, in habitats formed by gallery forests. The only species exclusively found in a single habitat type was *Argia carolus* (Zygoptera, Coenagrionidae), a species that can truly be deemed a forest specialist in our study area.

Differences in morphological traits among the communities

Our study indicates only a weak relationship between species' habitat utilization and their morphology. Several ANOVAs were calculated to gain a better understanding of how morphological traits are represented within the communities found in the different habitat types, using community weighted means for the different traits, a method that proved valuable when assessing ecosystem community dynamics (Garnier et al, 2004). All tests showed significant differences between the habitats. Dry weight and thorax width were found to be highest in open land habitats, suggesting that communities found in more open space consist of more robust species, evolved for higher flight speeds (Schilder & Marden, 2004) and less for maneuverability, compared to communities living in habitats with denser vegetation. Abdomen length, wing loading and aspect ratio showed to be highest in communities located in forest interior sites. A higher aspect ratio is related to a higher maneuverability (Hedenström & Möller, 1992) and could hint in this case to a selective pressure towards higher maneuverability in denser vegetated habitats (Pereira et al., 2019), whereas shorter wings, with a lower aspect

ratio could be selected for in open land habitats, e.g. due to pressure from avian predators for flight characteristics that allow for quick turns (Svensson & Friberg, 2007). Wing loading is found to be generally higher in Zygoptera compared to Anisoptera (Grabow & Rüppell, 1995), which would explain the higher wing loading found in communities of forest interior sites, since Zygoptera are encountered more often in densely vegetated areas compared to Anisoptera.

Relation between morphological traits and habitat variables

The RQL/Fourth Corner analysis shows no significant relationship between any morphological trait with any of the habitat variables. A similar study conducted in the Amazon by Pereira et al. (2019) found a significant relationship of thorax width, wing width, abdomen length and oviposition mode (endophytic/exophytic oviposition) with macrophyte cover and an habitat integrity index and therefore it was argued that open habitats filter for larger species (Anisoptera). One important clue to why the results of Pereira et al. (2019) differ quite strong from the results from the community in La Gamba could be due to differences in the composition of the sampled species. While the study from the Amazon included data from 52 species of Zygoptera and 60 species of Anisoptera, the data set from La Gamba has a significantly lower number of species (Zygoptera: N=21 species; Anisoptera N=8 species). Another possible interference in the data set from La Gamba is the absence of major Anisoptera families. Only one specimen belonging to the family of Gomphidae (*Progomphus pygmaeus*, Anisoptera) was caught, and no specimen belonging to the family of Aeshnidae. Concerning the number of sampled species, it is important to take into consideration that a uniform sampling effort does not guarantee for a complete set of species, because the detectability of individuals can vary significantly between habitats (Oppel, 2006). Subsequently, the data set only includes species that are classified as *perchers* in their foraging mode (Corbet & May, 2008) and thermal conductors (all Zygoptera) or heliotherms (Libellulidae, Anisoptera) in regards to the species thermoregulatory strategy (May, 1991; De Marco et al., 2005).

It is possible, that based on the close phylogenetic relationships of the sampled Odonata (with only four families) and therefore their more similar morphological traits, the RLQ/Fourth Corner analysis shows no connections between the morphological traits and the habitat variables, since the families are well distributed along the four habitat types, and the phylogenetic structure of Odonata communities is known to have a major impact on the

functional diversity of species assemblages (Díaz et al., 2013). Based on this, it is concluded that the species are morphologically too similar to detect corresponding habitat variables, even if the CWMs are significantly different for the assessed traits.

Although the RLQ/Fourth Corner analysis could not match any measured morphological traits to the assessed habitat variables, the CWMs still differ between the habitat types, showing that there are morphological differences between the Odonata communities, even if *fliers* are not included in the data set. The communities showed to differ on the habitat gradient from FI to OL sites (Fig. 5A), with all families sampled being evenly distributed throughout the habitat gradient (Fig. 5B), showing that Zygoptera as thermal conductors are well suited to occur in habitats with high solar radiation like the open land sites chosen for this study, a pattern predicted by the *Ecophysiological Hypothesis* (De Marco Junior, 2015). The data also shows that heliotherms like the family of Libellulidae are capable of occurring in denser vegetated areas in the forest, although in smaller numbers, a circumstance also described by Schmidt Dalzochio et al. (2018), who found heliotherms to be widespread among different habitat types.

The morphological traits showed to differ between the families and the communities sampled. These results hint towards a habitat filter effect for higher maneuverability of species found in the denser vegetated forest compared to more open sites. On the contrary, communities encountered at the less dense vegetated sites of open land seem to be filtered more towards being strong on the wing and less for maneuverability. Habitats in-between the extremes of forest interior and open land sites show to have communities with intermediate traits in terms of flight characteristics, underlining the gradient from FI to OL.

Other studies have come to similar conclusions about the morphological structure of Odonata communities alongside habitat gradients in the tropics, explaining differences in community assemblages also with different oviposition strategies (Pereira et al., 2019), coloration of species (Modiba et al., 2017) or the phylogenetic structure of Odonata communities (Costa Bastos et al., 2021), showing that functional diversity in Odonata assemblages goes beyond purely morphological traits influencing the flight characteristics of species and that community structures are influenced by several factors like behavior or history too.

Explaining differences in the composition of species assemblages across environmental gradients soley with environmental filters might oversimplify the situation, since it's merely impossible to exclude biotic factors in the field (Kraft et al., 2015). However, based on this study and studies conducted with similar questions on the interplay of morphological traits and the community structure of Odonates, the evidence hints towards filter effects on morphological traits being an important aspect influencing the communiy assemblage of Odonates.

Due to the circumstance that only *perchers* are included in the data set, it is concluded that not only differences in thermoregulation, and therefore a difference in morphological traits between thermal conductors, heliotherms and endothermic species and subsequently between *perchers* and *fliers* play a role in shaping communites, but that *perchers* themselves are facing varying requirements on flight abilities throughout the habitat gradient sampled in this study.

The study shows that different habitats require a different set of morphological traits influencing flight characteristics of Odonata on a community level, even when only looking at species classified as *perchers.* The knowledge about those differences in morphological traits could be of value when assessing conservation measurements in the region and are likely to positively inform about Odonata community structures within the landscape. Having deeper knowledge about the assembly rules shaping of Odonata communities can help to better understand the impact of de- or reforestation, the preservation of riparian forests or the facilitation of a landscape with a higher degree of permeability with the introduction of corridors.

Odonata are known to hold value when assessing the integrity of one of mankind's most important resources and therefore it should be the task of conservational efforts to have a close eye on them, and for science to further gain knowledge about those semiaquatic insects, to help to secure the integrity of our freshwater systems and adjacent terrestrial habitats.

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Appendix

Zusammenfassung

Tropische Ökosysteme, im Speziellen tropische Süßwasserhabitate sind durch menschliche Störungen bedroht. Odonata sind gut geeignet um die Integrität von Süßwasserhabitaten festzustellen. Die Studie hat das Ziel potentielle Ursachen für die Zusammensetzung von Odonata Gemeinschaften im südlichen pazifischen Tiefland von Costa Rica anhand von morphologischen Unterschieden der Artengemeinschaften in unterschiedlichen Habitattypen zu beleuchten. Die Studie wurde zwischen Oktober 2016 und Februar 2017 durchgeführt. Odonata wurden in vier verschiedenen Habitattypen gefangen. Messungen von morphologischen Eigenschaften, die bekannt für ihren Einfluss auf die Flugcharakteristik sind, wurden an Belegexemplaren durchgeführt. Die Studie hat keine Habitatpräferenzen für die gesammelten Arten auf dem Familienniveau feststellen können. Die „Community weighted means" der gemessenen Eigenschaften konnten morphologische Unterschiede der Odonata Gemeinschaften entlang des Gradienten von Waldhabitaten zu Offenlandhabitaten aufzeigen, allerdings hat eine „fourth corner" Analyse keine morphologischen Eigenschaften zu den aufgenommenen Habitatvariablen in Beziehung setzen können.

Table A1: Species list and number of specimens caught in 2016/2017.

Species	N specimens	Species	N specimens
Acanthagrion sp.	4	*Hetaerina fuscoguttata*	70
Acanthagrion trilobatum	14	*Hetaerina occisa*	326
Argia adamsi	11	*Hetaerina sp.*	5
Argia calida	1	*Hetaerina titia*	112
Argia cupraurea	69	*Hetaerina titia*	17
Argia esquivelensis	5	*Heteragrion erythrogastrum*	185
Argia frequentula	10	*Ischnura capreola*	32
Argia pulla	210	*Leptobasis vacillans*	7
Argia sp.	15	*Miathyria marcella*	4
Argia tezpi	2	*Micrathyria aequalis*	1
Argia translata	7	*Micrathyria ocellata*	2
Brechmorhoga nebecula	1	*Neoneura esthera*	13
Brechmorhoga sp.	1	*Nephepeltia phyrne*	28
Cannaphila insularis	1	*Orthemis biolleyi*	1
Dythemis multipunctata	18	*Orthemis ferruginea*	11
Dythemis sterilis	69	*Palthothemis sp.*	1
Elasmothemis cannacrioides	1	*Perithemis mooma*	14
Enallagma novaehispaniae	46	*Perithemis sp.*	4
Erythemis plebeja	2	*Philogenia zeteki*	3
Erythrodiplax berence	1	*Progomphus pygmaeus*	1
Erythrodiplax fervida	4	*Protoneura amatoria*	15
Erythrodiplax fusca	64	*Psairneura remissa*	8
Erythrodiplax kimminsi	3	*Rhodopygia hinei*	1
Erythrodiplax sp.	2	*Rhodopygia sp.*	1
Erythrodyplax connata	1	*Telebasis limoncocha*	7
Hetaerina caja	73	*Uracis imbuta*	6

Table A2: Species and according families used for morphological measurements and the number of specimens recorded for each species in 2015/2016 and 2016/2017.

Family	Species	2016/2017	2015/2016	Total
Libellulidae	*Dythemis multipunctata*	15		15
	Dythemis sterilis	64	60	124
	Elasmothemis cannacrioides	1	6	7
	Erythrodiplax fusca	38	42	80
	Nephepeltia phryne	7	1	8
	Orthemis ferruginea	8		8
	Perithemis mooma	4	1	5
	Uracis imbuta	5	15	20
Calopterygidae	*Hetaerina caja*	71	45	116
	Hetaerina fuscoguttata	70	72	142
	Hetaerina occisa	322	190	512
	Hetaerina titia	119	103	222
Coenagrionidae	*Acanthagrion trilobatum*	8	6	14
	Argia adamsi	11	21	32
	Argia carolus	6		6
	Argia cupraurea	61	138	199
	Argia frequentula	6	4	10
	Argia indicatrix	2	5	7
	Argia oculata	26	38	64
	Argia oenea	4	29	33
	Argia pulla	182	106	288
	Argia translata	10	35	45
	Enallagma novaehispaniae	46	43	89
	Ischnura capreolus	21	13	34
	Leptobasis vacillans	5	11	16
	Neoneura esthera	13	10	23
	Protoneura amatoria	13	23	36
	Psaironeura angeloi	5		5
Megapodagrionidae	*Heteragrion erythrogastrum*	188	106	294
	Total	**1331**	**1123**	**2454**

Table A3: Community weighted means for dry weight (g), thorax width (mm), abdomen length (mm), wing loading (dry weight/ (area front wing + area hind wing)) and aspect ratios for fore- and hindwings (wing length^2/wing area) for each site.

Plot	DryWeight_cwm	ThoraxWidth_cwm	AbdomenLength_cwm	WingLoading_cwm	FWAR_cwm	HWAR_cwm
FI1	0.010916667	2.0625	34.36	0.088333333	8.030833333	7.955833333
FI2	0.011415085	2.142033898	34.03864407	0.092033898	7.757457627	7.661186441
FI3	0.014	2.232745098	34.99392157	0.088431373	7.24627451	7.168235294
FI4	0.01540451	2.383333333	34.13745098	0.084117647	6.496862745	6.461960784
FI5	0.0125	2.19	35.68	0.095	7.8375	7.755
FI6	0.011756032	2.233492063	33.50095238	0.084444444	6.948888889	6.902539683
FI7	0.014184211	2.287105263	34.70157895	0.086578947	6.909736842	6.864473684
FI8	0.014582679	2.285178571	33.45321429	0.088035714	6.90875	6.884642857
FM1	0.011583488	2.212790698	33.95139535	0.085232558	7.038488372	6.986046512
FM2	0.008964844	2.04953125	27.51671875	0.055	6.82734375	6.54796875
FM3	0.011723218	2.256551724	32.01528736	0.082643678	6.73816092	6.63183908
FM4	0.012384217	2.264457831	31.8313253	0.083012048	6.775060241	6.689036145
FM5	0.013276286	2.413428571	32.337	0.077857143	6.050428571	5.950142857
FM6	0.010536232	2.332463768	32.93246377	0.07942029	6.477391304	6.438115942
FM7	0.013045393	2.381235955	30.63325843	0.079550562	6.046629213	5.865730337
FM8	0.012206095	2.370380952	31.87333333	0.081904762	6.293238095	6.194285714
GF1	0.011775253	2.27030303	30.44989899	0.079090909	6.387777778	6.325050505
GF2	0.009174386	2.130877193	30.05192982	0.069736842	5.958157895	5.916929825
GF3	0.011608286	2.328857143	31.73428571	0.076428571	6.188285714	6.114285714
GF4	0.011483523	2.34	33.00534091	0.076363636	6.076477273	6.043409091
GF5	0.011549135	2.224326923	30.06509615	0.0775	6.349423077	6.231057692
GF6	0.013116441	2.396440678	31.65915254	0.075423729	5.934576271	5.850508475
GF7	0.01024087	2.195326087	31.5501087	0.069456522	6.025	5.986304348
GF8	0.012574396	2.284065934	31.01208791	0.08043956	6.585494505	6.411648352
OL1	0.015058485	2.442222222	30.40727273	0.078585859	5.868686869	5.716464646
OL2	0.015882778	2.354111111	27.74588889	0.083555556	6.192111111	5.931555556
OL3	0.012635922	2.31776699	29.41563107	0.073106796	5.800097087	5.616601942
OL4	0.020000615	2.52	24.56661538	0.086615385	5.694153846	5.124307692
OL5	0.015849649	2.423684211	27.08561404	0.079824561	5.809298246	5.37877193
OL6	0.013871809	2.352978723	27.44138298	0.074042553	5.834893617	5.573404255
OL7	0.010853271	2.148878505	25.7771028	0.067383178	6.238878505	6.064579439
OL8	0.015847944	2.580747664	28.86373832	0.077850467	5.691214953	5.301495327

Table A4: Habitat variables for each site.

ID	habitat type	buffer of 150 m [%] - Oil Palm Plantation	buffer of 150 m [%] - Old Growth Forest	sand [%]	gravel small [%]	leaf litter layer [%]	deadwood [0=none, 1=few single branches, 2=many, 3=large tree stems]	protruding rocks > 30 cm [N]	stream width [m]	canopy closure margins [%]
FI1	FI	0.00	100.00	-	-	-	2	0	-	80.26
FI2	FI	0.10	96.18	0	40	20	3	22	3	75.86
FI3	FI	0.00	85.16	5	30	10	1	3	3.5	74.73
FI4	FI	0.00	97.52	5	a	5	1	0	11.5	79.10
FI5	FI	0.00	98.05	20	45	5	3	41	4	75.57
FI6	FI	0.00	76.93	0	45	5	3	35	14	77.99
FI7	FI	0.00	100.00	5	45	0	3	20	11	75.98
FI8	FI	0.00	100.00	5	30	10	3	17	18	78.54
FM 1	FM	0.00	54.09	10	10	5	1	0	3	77.47
FM 2	FM	0.00	61.84	10	50	40	3	0	2	67.51
FM 3	FM	9.96	68.32	0	20	60	2	0	3	68.27
FM 4	FM	0.00	90.10	20	10	5	1	3	12	68.03
FM 5	FM	0.00	67.04	30	30	10	3	1	14	62.46
FM 6	FM	0.00	32.03	0	20	10	1	5	10	69.68
FM 7	FM	0.00	38.51	0	0	5	3	0	17.5	66.25
FM 8	FM	0.00	43.77	0	45	5	1	1	16	75.54
GF 1	GF	41.46	0.00	5	0	0	3	6	15	65.55
GF 2	GF	0.00	0.00	5	10	5	1	0	10	71.53
GF 3	GF	29.78	27.28	5	30	10	3	0	14	76.06
GF 4	GF	36.28	25.98	5	15	10	3	0	13	78.00
GF 5	GF	0.00	28.93	30	30	5	3	0	14.5	62.23
GF 6	GF	0.00	15.97	5	60	5	1	0	13.5	68.44
GF 7	GF	1.52	0.00	10	40	10	1	0	10.5	80.50
GF 8	GF	12.36	15.41	0	70	5	3	0	13	76.99
OL1	OL	0.00	0.00	15	25	0	1	0	10	30.92
OL2	OL	0.00	2.93	5	5	0	0	0	16	20.01
OL3	OL	0.24	35.36	10	20	5	1	2	11.5	54.45
OL4	OL	0.00	0.10	10	60	0	3	0	12	0.00
OL5	OL	0.00	44.67	5	40	5	1	0	5.5	0.97
OL6	OL	0.00	0.00	5	50	5	1	0	8	31.03
OL7	OL	3.48	0.00	5	50	0	0	0	2.5	0.96
OL8	OL	21.06	0.00	10	10	0	2	0	5	30.72