

# Banderillas: Effects of deforestation on dragonflies (Insecta, Odonata) in the Pacific lowland of Costa Rica

## Banderillas: Efectos de la deforestación sobre libélulas (Insecta, Odonata) en la tierra baja Pacífica en Costa Rica

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**Abstract:** Deforestation in the past is responsible for the loss of large forest areas in all tropical regions and this process is ongoing. The reclamation of cultivated land reinforces the disappearance of natural habitats and reproductive sites for many species typical for pristine forests. Lotic waters may remain when the trees are gone, but their characteristics will have changed dramatically and species tied to these water bodies face different challenges maintaining self-sustaining populations. This study contributes to the question of whether changes in land use affect species assemblages and their ability for recruitment, and whether streams embedded in cultivated landscapes provide viable reproductive habitats for dragonflies.

We surveyed dragonflies at four forest sites, two sites at forest margins and four sites at streams in an agricultural landscape. At each site, adult dragonflies were recorded twice along a 50 m transect in January and February 2007. We found significant differences in species richness, species assemblages and proportion and number of widespread species between forest and cultivated area. Only 3 of 11 species found in forests were also observed at streams in agricultural areas. Our results indicate that rivers in agricultural environment do not represent suitable reproductive habitats for the majority of 'forest species'. Therefore, deforestation poses an enormous threat for these species.

**Key words:** biodiversity, conservation, land-use, species composition, species richness.

**Resumen:** En Costa Rica y otros países tropicales, la deforestación es responsable de la pérdida de grandes áreas de bosque que son hábitats naturales de varias especies. Con la explotación de madera y el cultivo de áreas antes forestadas van desapareciendo los lugares donde viven y se reproducen estas especies. En el caso de las libélulas los hábitats de reproducción se encuentran cerca y dentro del agua, donde también viven sus larvas. Los adultos se encuentran generalmente en las orillas para aparearse y finalmente las hembras ponen sus huevos cerca del agua o directamente dentro. A pesar de la deforestación aún permanecen los arroyos en las zonas cultivadas. Sin embargo sus características cambian y las libélulas enfrentan situaciones totalmente diferentes.

Se investigaron las diferencias entre las comunidades de libélulas de arroyos del bosque y zonas cultivadas, y si las aguas en zonas cultivadas sirven como lugares de reproducción para libélulas.

Se observaron libélulas adultas en cuatro puntos de un arroyo en el bosque, en dos arroyos situados al borde del bosque y en cuatro arroyos en la zona cultivada. Se visitaron cada sitio dos veces a lo largo de un transecto de 50 metros, durante enero y febrero de 2007. La composición de libélulas variaba significativamente entre el bosque y la zona cultivada, en la cual había más diversidad de especies. En la zona cultivada había también un porcentaje más alto de especies de distribución amplia y un mayor número de individuos de esas especies. Solo 3 de las 11 especies encontradas en el bosque se encontraron también en los arroyos de la zona cultivada. Los resultados señalan que las especies sensibles del bosque no pueden utilizar las aguas en zonas cultivadas para su reproducción y que por tanto la deforestación representa una gran amenaza para estas especies.

**Palabras clave:** biodiversidad, conservación, uso del suelo, composición específica, riqueza de especies.

### Introduction

Banderillas, the local name for dragonflies (including damselflies) in southern Costa Rica, are among the most common and attractive groups of insects. Their aerial acrobatics, beautiful colours and relatively large size capture everyone's attention. Despite a widespread ignorance about these creatures, they might easily be used as indicators to quantify effects of changing envi-

ronmental parameters in freshwater habitats (e.g. oxygen concentration, nutrient accommodation and pollution), since dragonflies in all stages of their life cycle are closely bound to aquatic habitats (ESQUIVEL 2006).

Odonata inhabit a variety of habitat types: larvae are capable to develop along the whole course of fluvial systems, from headwaters to estuaries, and in lentic water bodies, both perennial and temporary (CORBET

1999). However, among dragonflies habitat requirements can vary significantly. Some species show preferences for a certain habitat type and can only persist within narrow niches of biotic and physical factors. In contrast, other species are eurytopic and therefore relatively tolerant to a broad range of environmental variables and thus inhabit different types of freshwater habitats. Usually, the physiological and morphological constraints of the larvae determine the presence of a species at a given location. Nonetheless, it is the adults that oviposit and their habitat selection acts as a filter on species composition (MCCAULEY 2006, HOFMANN & MASON 2005). However, reproductive and foraging habitats of dragonflies are affected by human activities and changes in land use. In Costa Rica, like in most tropical countries, deforestation converts forested areas into open and fragmented landscapes (SÁNCHEZ-AZOFEIFA 2001). When forest is converted into agricultural landscape, the characteristics of terrestrial and aquatic habitats (e.g. flow modification, nutrient and pesticides influx, sediment deposition, invasion of alien species in riparian vegetation and isolation due to landscape fragmentation) change (DUDGEON et al. 2005). Such severe alterations in environmental parameters are likely to have a remarkable impact on dragonflies and their occurrence in modified landscapes.

Deforestation and fragmentation obviously have a major impact on ecological systems. The composition and configuration of countryside habitats strongly influence the diversity and composition of native plant and animal communities (SWEENEY et al. 2004, DAILY et al. 2003). The consequences of forest modification and habitat conversion on species richness have been the subject of intensive research at a multi-taxon level (LAWTON et al. 1998, SCHULZE et al. 2004). In forests, slight disturbance may increase species richness, but can also cause a shift in species assemblage and extinction of sensitive species (BROWN 1997). However, in strongly modified landscapes, species diversity usually declines significantly and sensitive forest species are replaced by a few generalists and geographically widespread species (SIGEL et al. 2006). For tropical (CLAUSNITZER 2003, SAMWAYS 2003) and subtropical (STEWART & SAMWAYS 1998) regions, studies on dragonflies reported similar results. In Costa Rica, studies have focused on mammals (DAILY et al. 2003), birds (DAILY et al. 2001, MATLOCK et al. 2002), butterflies (HORNER-DEVINE et al. 2003), moths (RICKETTS et al. 2001) and other arthropod groups (GOEHRING et al. 2002), but knowledge of dragonflies is scarce. In this preliminary study, we present initial data on the response of dragonfly communities to forest modification and conversion in Costa Rica.

Particularly the following life-history traits of Odonata may be responsible for their sensitivity against habitat disturbance:

(1) Species often depend on certain types of macrophyte vegetation or even single plant species (SCHINDLER et al. 2003, RANTALA et al. 2004).

(2) Thermoregulatory responses to open or closed and shaded habitats may differ between the two suborders. Smaller Zygoptera have lesser thermoregulatory efficiency than Anisoptera which can adjust their heat balance by wing motion or body posture in relation to the sun (DE MARCO et al. 2005).

This study addresses the question of how much a changing environment modifies dragonfly assemblages in the Pacific lowlands of Costa Rica. Our assumptions are that sensitive semi aquatic insects like Odonata divide into species that cannot live or reproduce in disturbed habitats, and species overruling previously dominant species in abundance in these new, artificially shaped niches.

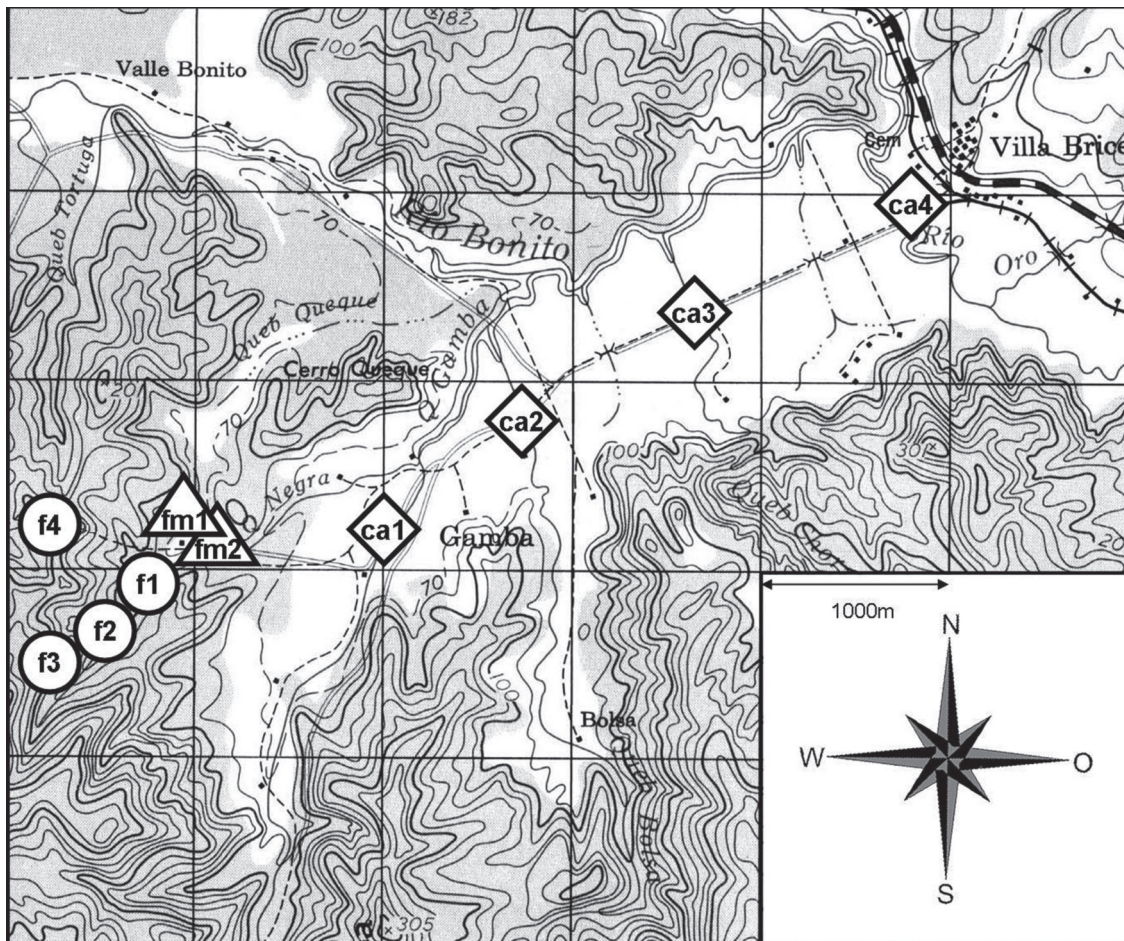
## Material and Methods

### Study Area

Dragonfly surveys were conducted in the vicinity of the Tropical Research Station La Gamba (8°42'46"N, 83°12'09"W) in the south of Costa Rica, in the 'Parque Nacional Piedras Blancas', a protected area in the Golfo Dulce region comprising one of the last remnants of lowland rainforest on Costa Rica's Pacific coast, and adjacent cultivated areas. Average annual precipitation in the region is 5000-6000 mm with no month receiving less than 180 mm. The rainy season lasts from September until November, the driest months are between January and March. Average monthly temperature ranges between 22°C and 28°C (WEBER et al. 2001). The Golfo Dulce region with its high richness of vascular plants (e.g. 700 tree species) is a biodiversity 'hot spot' and a high degree of endemism corresponds with the region's status as a refuge during glacial periods (WEBER et al. 2001). Beyond the borders of the national park, human impact on the environment becomes obvious as the landscape changes dramatically from forest to a matrix of agricultural areas consisting of cultivated fields, plantations and pastures. The main cultivated plants are rice (*Oryza* sp.) and oil palm (*Elaeis guineensis*). In these cultivated areas, trees have almost completely vanished and often only gallery forests of several metres width remained, accompanying bigger streams as 'forest like' structures.

### Study sites

To investigate differences in species assemblages between pristine and modified habitats, we surveyed drag-



**Fig. 1:** Position of rivers and survey sites. Dark areas are covered with forest, pale areas are open landscapes.

onflies along streams at four pristine forest (f1-4), two forest margin sites (fm1-2) and four sites within the cultivated area (ca1-4) (Fig. 1).

Pristine forest sites were situated along first to second order streams. Three sites were located along the river 'Quebrada Negra' (Fig. 9) and one at a small stream in a narrow and shaded ravine.

The two forest margin sites were situated at streams close to the garden of the field station. Fm2 at the Quebrada Negra was surrounded by the garden of the field station and an old agroforest with *Theobroma cacao*. Tall trees (e.g. *Tectona grandis*) provided a high degree of shading. In contrast, fm1 was located at a small stream supplying an artificial reservoir. This stream runs through a meadow that is occasionally mown, without any trees in the riparian vegetation.

Cultivated area sites were located along four different streams: Rio La Gamba, Rio Bolsa, Rio Chorro & Rio Oro in the hinterland of La Gamba village, running through flat, human altered landscape (Fig. 8). Riparian vegetation consisted of gallery forest strips with tall shading trees (e.g. *Luehea seemanii* & *Inga* sp.) and various macrophytes covering the banks.

## Survey Methods

Between January 16<sup>th</sup> and February 17<sup>th</sup> 2007, each site was surveyed two times by pacing the riverbed for one hour within 50 metres of the shoreline. Dragonflies, either flying by or perching on vegetation at both sides of the stream, were caught with a sweep net (mesh-width 3 mm, diameter 45 cm) fixed on a stick (1.5 m).

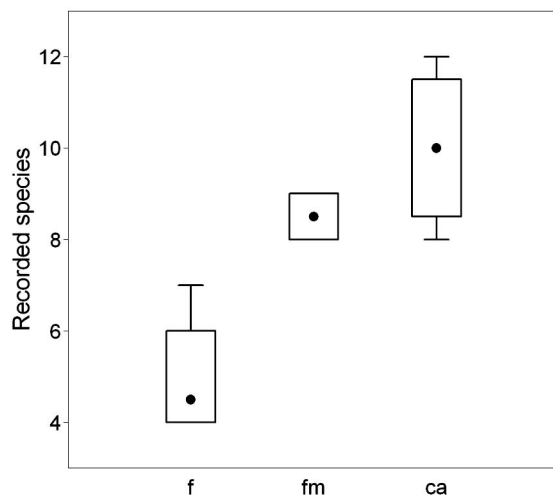
Dragonflies were identified according to FÖRSTER (1999) and afterwards released to their former territories. Identification was always possible to genus level but sometimes not to species level. In such cases, we assigned individuals to 'morphospecies' (KRELL 2004). Carlos Esquivel (Universidad Nacional Costa Rica, Heredia) kindly provided help in species identification.

## Statistical analysis

### Species richness

To assess species inventories of habitats we conducted observation units. These observation intervals are temporary and therefore only represent a snapshot of species occurring at a given location. Results are strongly influenced by the mobility of species, external factors (e.g. weather conditions) and stochastic events (BROSE & MARTINEZ 2004, ROUQUETTE & THOMPSON 2007) and

**Fig. 2:** Box plots of recorded species in forest (f:  $n = 4$ ), forest margin (fm:  $n = 2$ ), and cultivated area sites (ca:  $n = 4$ ) habitats. Dots show median species number per habitat type, boxes show 25-75% of recorded species per habitat type and whiskers show minima and maxima of species recorded at sites within one habitat type.



it is very likely that they underestimate species richness at the surveyed sites. Species richness estimators that predict true species richness more accurately are useful tools that help to correct this bias. We calculated estimated species richness using the non-parametric ACE estimator. Species richness was not estimated for forest margin sites due to the small number of spatial replicates ( $n = 2$  sites). Species accumulation curves (Mao Tao) were calculated to show the number of observed species per habitat type dependent on sampling effort. Estimators and species accumulation curves were calculated with the EstimateS 7.0 package (COLWELL 2006).

To identify habitat characteristics influencing species richness, we measured three habitat parameters and ran a multiple ridge-regression model to correct for multi-collinearity between explanatory variables. Habitat parameters were canopy closure 'cc' (as surrogate for shade), slope 'sl' (as surrogate for flow velocity) and stream width 'sw' (we decided to measure above bank-full, as this factor integrates over a longer period than single measurements of water line). Data for slope were arcsine transformed before analysis to give a normal distribution. Several other parameters (dissolved oxygen, pH, conductivity) measured during prior studies showed little variance among streams (ph  $\sim 8$ , dissolved oxygen  $\sim 8$  mg/L) (TSCHELAUT 2005, TSCHLAUT et al. 2005) and were therefore excluded from the model. Statistical analyses were performed with Statistica 7.0 (StatSoft 2005) and Primer v5 (CLARKE & GORLEY 2001).

### Similarity

We used Bray-Curtis similarity indices and non-parametric multidimensional scaling (NMDS) to visualise relationships of species composition between sampling sites. Sample data were square root transformed before analysis. Whether habitat groups had an effect on species composition was tested by a one-way analysis of similarities (ANOSIM) with Bray-Curtis similarities as

dependent and the two habitat types f and ca as independent factor. Forest margin sites were excluded from the ANOSIM because of the small number of spatial replicates ( $n = 2$ ). To examine the potential influence of spatial distribution of sites on species composition, we performed a Spearman matrix rank correlation for Bray-Curtis similarities and distances between sites.

To test the effects of habitat variables (cc, sl, sw) on species composition after exclusion of the influence of spatial arrangement of sites, we conducted partial Mantel tests, using zt software (BONNET & VAN DE PEER 2002).

Similarity percentage analysis (SIMPER) was used to quantify species' contribution to similarity within a habitat and dissimilarity between the three groups of habitat types. This method can identify species representative for one type of habitat e.g. typical 'forest species'.

Numbers of individuals and relative species richness of widespread and range-restricted species were compared between habitat types using t-tests. Range-restricted (restricted) species were defined as distributed only in Central America. Species distributed in Central America and additional regions were classified as widespread. Information on the distribution of species was extracted from the book 'Dragonflies and damselflies of Middle America and the Caribbean' (ESQUIVEL 2006).

## Results

### Species richness

We recorded 902 individuals of adult dragonflies representing 32 species belonging to 20 genera and 7 families (5 Zygoptera, 2 Anisoptera, see Table 1).

More species were observed in the cultivated landscape (18) than at forest sites (11) (t-test:  $N = 4$ ,  $t = 4.6$ ,  $df = 3$ ,  $p = 0.02$ ; Fig. 2) which was also proved by the estimated species richness. Species accumulation curves show highest species richness in forest margin habitats, although number of observation units was low ( $n = 4$ ). Additional sampling effort may lead to a higher number of species in fm habitats than in other habitat types (Fig. 3). Estimated species richness indicates that additional sampling effort would add species to the respective species inventories (Table 1). However, completeness of species inventories was high for f (92%) and ca (90%). Estimation of total species richness (53 species) provided an appraisal of the species inventory that can be expected in the whole study area representing 19% of 286 species known for Costa Rica (RAMIREZ et al. 2000).

The total number of observed individuals was higher in cultivated area (638) than in forest (62). Number

of observed individuals per site was also higher in cultivated area (mean = 159.5, sd = 63.4) than in forest (mean = 15.5, sd = 3.9) (t-test: N = 4, t = 4.7, df = 3, p < 0.02). A complete list of observations is given in Table 2.

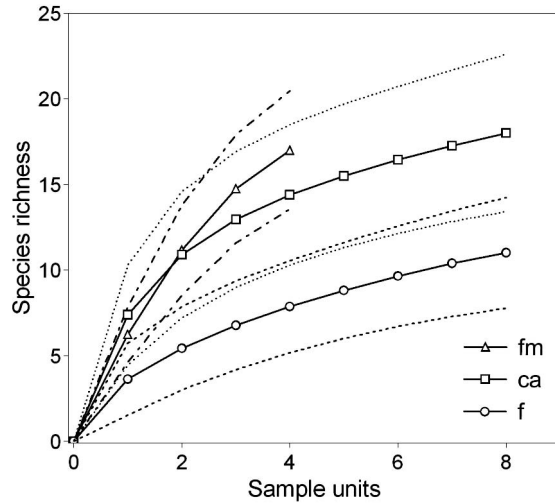
In the multiple ridge-regression model (lambda = 0.1, multiple r = 0.94, r<sup>2</sup><sub>corr</sub> = 0.82, F<sub>3,6</sub> = 17.7, p < 0.004) canopy closure, as a surrogate for shade, best accounted for variance in species richness (cc: r<sub>part</sub> = -0.77, p = 0.03). Slope and stream width were not significantly related to species richness (sw: r<sub>part</sub> = 0.62, p = 0.1; sl: r<sub>part</sub> = -0.46, p = 0.3, see Fig. 4).

**Similarity**

The NMDS plot based on Bray-Curtis similarities showed that forest and cultivated area sites form two distinct clusters with forest margin sites situated in between (Fig. 5). Species composition differed significantly between forest and cultivated area (ANOSIM: global R = 0.70, p = 0.003; pairwise tests for cultivated area and forest: R = 0.99, p = 0.03).

Spearman matrix rank correlation with Bray-Curtis similarities and geographic distance (Rho = 0.39, p = 0.01) outlined the ascending dissimilarity with increasing distance of sites. Partial Mantel tests proved that habitat parameters cc and sl significantly influenced similarities of dragonfly assemblages (corrected for spatial distribution of sites), (cc: r = -0.62, p < 0.001, sw: r = -0.02, p = 0.45, and sl: r = -0.44, p = 0.001) (Fig. 6).

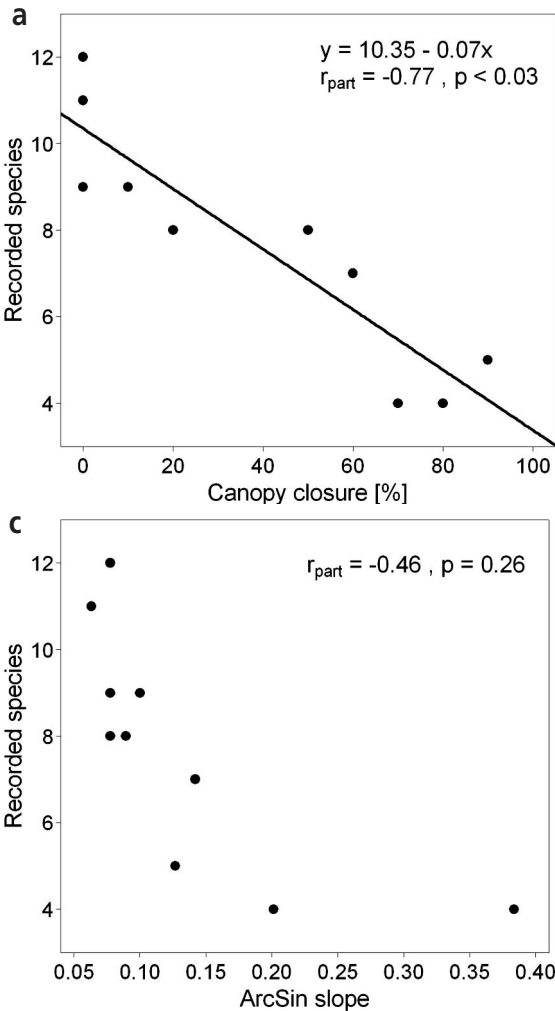
SIMPER analysis revealed average similarities within groups for forest (39%), cultivated area (36%) and forest margin (all similarities were zero). Species contributing most to similarity of habitats were *Heteragrion erythrogastrum* (with 53% contribution to similarity of forest), *Argia* sp. 1 (22%), *Hetaerina occisa* (15%) for



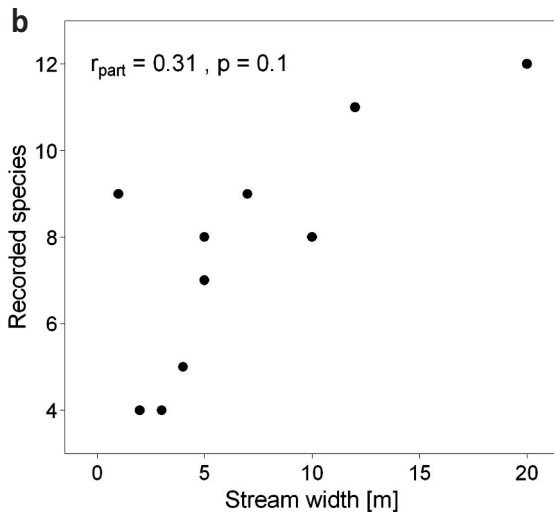
**Fig. 3:** Species accumulation curves (Mao Tao) for habitat types forest margin (fm), forest (f) and cultivated area (ca). Dotted and dashed lines without objects show 95% confidence intervals.

**Table 1:** Recorded and estimated (ACE) species for forest (f), cultivated area (ca), forest margin sites (fm) and the total survey area.

Habitat	Species observed	Estimated species	Coverage%	Families	Genera
f	11	12	92	5	7
ca	18	20	90	4	13
fm	17	-	-	5	11
total	32	53	60	7	20



**Fig. 4:** Habitat parameters used in the multiple ridge regression model to account for variance in species richness between sites. (a) Canopy closure was found to be a relevant predictor for species richness. (b) Stream width was not significantly correlated with species richness but showed a trend to more diverse assemblages in broader streams. (c) Correlation between slope and species richness was not significant.



**Table 2:** List of species and number of individuals observed at sampling sites.

Family	Species	Sites									
		f1	f2	f3	f4	fm1	fm2	ca1	ca2	ca3	ca4
Calopterygidae	<i>Hetaerina fuscoguttata</i> (Selys 1878)	-	-	-	1	-	7	6	20	20	40
	<i>Hetaerina occisa</i> (Hagen 1853)	4	2	2	-	-	42	33	-	65	-
	<i>Hetaerina vulnerata</i> (Hagen 1853)	-	-	-	-	-	-	10	16	40	5
Coenagrionidae	<i>Acanthagrion</i> (Selys 1876) sp.	-	-	-	-	-	-	-	-	-	1
	<i>Argia cupraurea</i> (Calvert 1902)	3	3	-	-	-	-	-	-	4	2
	<i>Argia</i> (Rambur 1842) sp. 1	2	5	6	-	6	-	-	-	-	-
	<i>Argia</i> (Rambur 1842) sp. 2	-	-	-	2	-	4	-	-	-	-
	<i>Argia</i> (Rambur 1842) sp. 3	-	-	-	-	-	1	24	39	60	4
	<i>Argia</i> (Rambur 1842) sp. 4	-	-	-	-	-	-	-	-	-	1
	<i>Enallagma novaehispaniae</i> (Calvert 1907)	-	-	-	-	-	-	3	-	1	11
Megapodagrionidae	<i>Ischnura capreola</i> (Hagen 1861)	-	-	-	-	-	-	-	3	-	-
	<i>Heteragrion erythrogastrum</i> (Selys 1886)	6	4	8	2	-	4	-	-	-	-
Polythoridae	<i>Cora semiopaca</i> (Selys 1878)	-	-	-	5	-	-	-	-	-	-
Protoneuridae	<i>Neoneura esthera</i> (Williamson 1917)	-	-	-	-	-	-	-	-	-	1
	<i>Protoneura amatoria</i> (Calvert 1907)	-	-	-	-	-	-	-	5	2	-
Gomphidae	<i>Aphylla obscura</i> (Kirby 1899)	-	-	-	-	1	-	-	-	-	-
Libellulidae	<i>Cannaphila insularis</i> (Kirby 1889)	-	2	-	-	-	-	-	-	-	-
	<i>Cannaphila vibex</i> (Hagen 1861)	-	1	-	-	-	-	-	-	-	-
	<i>Dythemis multipunctata</i> (Kirby 1894)	-	-	-	-	-	3	-	-	-	-
	<i>Dythemis sterilis</i> (Hagen 1861)	-	-	-	-	-	1	1	12	11	26
	<i>Erythrodiplax connata</i> (Burmeister 1839)	-	-	-	-	1	-	-	-	-	-
	<i>Erythrodiplax fervida</i> (Erichson 1848)	-	2	-	-	1	-	-	-	-	-
	<i>Erythrodiplax fusca</i> (Rambur 1842)	-	-	-	-	100	-	3	106	7	20
	<i>Erythrodiplax kimminsi</i> (Borror 1942)	-	-	-	-	-	-	-	2	-	-
	<i>Libellula foliata</i> (Kirby 1889)	-	-	-	-	7	-	-	-	-	-
	<i>Macrothemis imitans</i> (Karsch 1890)	-	-	-	-	-	-	-	-	-	2
	<i>Macrothemis</i> (Hagen 1868) sp. 2	1	-	1	-	-	-	-	-	-	-
	<i>Nephepeltia phryne</i> (Perty 1834)	-	-	-	-	2	-	-	-	-	-
	<i>Orthemis ferruginea</i> (Fabricius 1775)	-	-	-	-	14	-	-	3	-	22
<i>Perithemis mooma</i> (Kirby 1889)	-	-	-	-	-	1	-	5	-	-	
<i>Rhodopygia</i> (Kirby 1889) sp.	-	-	-	-	7	-	-	-	-	-	
<i>Uracis imbuta</i> (Burmeister 1839)	-	-	-	-	-	-	1	1	-	-	

forest; and *Argia* sp. 3 (28%), *Hetaerina fuscoguttata* (22%) and *Hetaerina vulnerata* (15%) for cultivated area.

Average dissimilarity for forest & cultivated area was 98% with the most dissimilar species being *Argia* sp. 3, *Erythrodiplax fusca* and *Hetaerina occisa*. Average dissimilarity for forest & forest margin was 90% with the most dissimilar species being *Erythrodiplax fusca*, *Hetaerina occisa* and *Orthemis ferruginea*. Average dissimilarity for cultivated area & forest margin was 75% with the most dissimilar species being *Erythrodiplax fusca*, *Argia* sp. 3 and *Hetaerina occisa*.

The importance of widespread species increased towards more disturbed habitats (Fig. 7), as mean number of individuals and proportion of widespread species were significantly higher at sites in cultivated area than in forest (t-test; number of species:  $N = 4$ ,  $t = 21$ ,  $df = 3$ ,  $p < 0.001$ ; number of individuals:  $N = 4$ ,  $t = 4.6$ ,  $df = 3$ ,  $p = 0.02$ ).

## Discussion

### Species richness

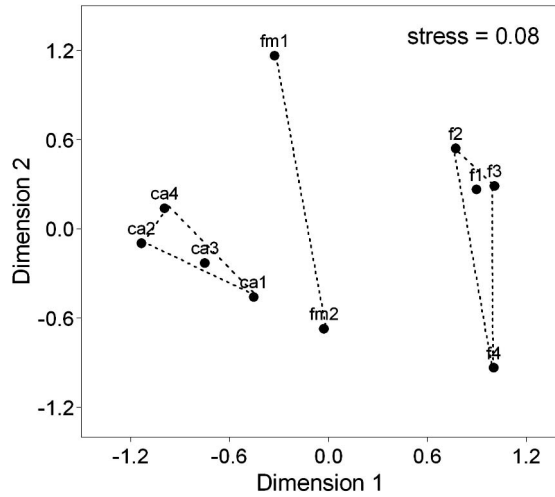
The findings of our study parallel the results of comparable research on this issue. Our survey sites located in cultivated areas were significantly richer in species and had a higher number of individuals overall than forest sites. Estimates indicate that a high completeness of species inventories was achieved in both habitat types. Therefore, we expect a higher sampling effort not to affect the general conclusions drawn from our results. Estimation of total number of species provides an initial assessment of species richness for the area around La Gamba but supplementary sampling during the rainy season will probably improve this relatively low estimate.

An increase of species richness from primary towards slightly disturbed sites has been found in various studies from the subtropics (SAMWAYS & STEYTLER 1996) and tropics (CLAUSNITZER 2003), and has been

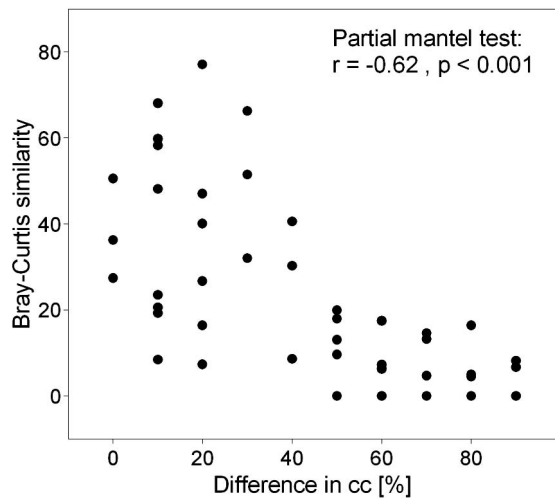
explained by the increased habitat diversity created by disturbance. Shade and exposed macrophytes are mentioned to be the most important environmental parameters accounting for variable species composition. Fewer species are resident in shaded forests than in habitats with a light/shade mosaic or open sunny locations. In La Gamba we found canopy closure to be the relevant influence on species richness. Canopy closure will directly influence the shading of water surface and banks and thus other biotic and abiotic conditions (e.g. temperature and level of dissolved oxygen in the water) as important parameters for larvae. Polythorid larvae for instance are the only dragonfly larvae in Mesoamerica with additional lateral gills on the abdominal segments and apparently require well oxygenated water (ESQUIVEL 2006). In this family we found *Cora semiopaca*, a species endemic to Costa Rica and Panama, at forest site 4, a small, steep stream at the bottom of a shaded ravine.

Disturbed habitats were mostly inhabited by opportunistic and common species that populate habitats in higher densities. Their presence in particular is responsible for the higher species richness at disturbed habitats, while sensitive species vanish. The high species number at forest margin habitats may not derive from a potential ecotone state of these habitats, combining elements of pristine and altered areas, but is likely to be explained by the two different types of surveyed forest margin sites. Site fm2 was relatively undisturbed whereas fm1 showed a high degree of bank degradation with respect to shading trees and was more resembling cultivated area sites.

Although our study has the disadvantages of a low sampling effort, a temporal restriction to the dry season and an uneven spatial distribution of forest and cultivated area sites, we do not expect this to affect our general conclusions. Most species, however, are known to repro-

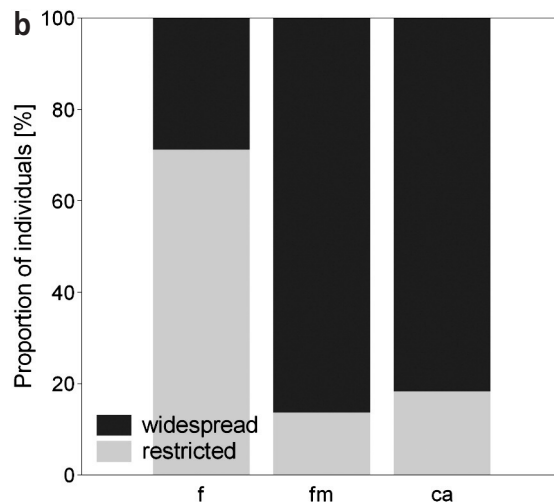
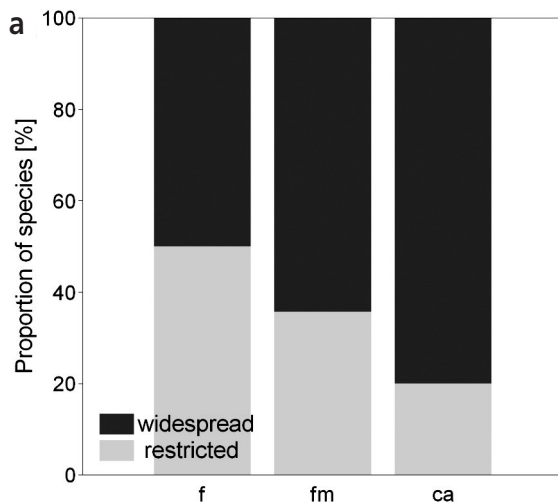


**Fig. 5:** NMDS plot based on Bray-Curtis similarities. Sites belonging to the same habitat category (f = forest, fm = forest margin, ca = cultivated area) are connected by lines.



**Fig. 6:** Relationship between faunal similarities and canopy cover over streams. Similarity of species inventory is negatively correlated to difference in canopy closure (cc) between sites.

duce typically during the rainy season showing high abundances and some species do not appear as adults during dry season. So it is likely that additional species not recorded in our study will be found in the survey during the wet season. The potential of other not investigated factors influencing the occurrence of species will be discussed later on.



**Fig. 7:** Proportion of species (a) and individuals (b) of widespread and range-restricted dragonflies in different habitat types. Species not identified to species level are not included (3 species for each habitat respectively). Forest (f): n = 4; forest margin (fm): n = 2; cultivated area (ca): n = 4. Range restricted (restricted) species are distributed in Central America only.



**Fig. 8:** Cultivated area site 4 at Rio Oro, a broad stream with low flow velocity. Beyond the adjacent strip of gallery forest the stream is surrounded by cattle pastures and paddy fields.



**Fig. 9:** Forest site 3 at the stream Quebrada Negra embedded in pristine forest. The rapid stream velocity, steep slope and riverine vegetation affect inhabiting fauna.

## Similarity

As expected, we found dissimilar dragonfly communities at streams in forests, at forest margins and in cultivated areas, representing a gradient in human disturbance. Communities in forests and cultivated areas were clearly distinct and forest margin sites acted as a link between the former communities. On the one hand, we found few species that tended to occur very specifically at pristine forest sites (e.g. *Heteragrion erythrogastrum*), and on the other hand many species that were not restricted to distinct habitats and could be encountered nearly everywhere (e.g. *Hetaerina occisa*, Fig. 10).

Species compositions of three forest sites were very similar, most probably because all the sites were situated along the same stream. Forest site 4 is characterised by different conditions, since there the narrow stream falls down a cascade of rocks and then fades in a thin runlet into shaded ravine forest. This site is worthy of mention for the presence of *Cora semiopaca* (Fig. 11). SIMPER revealed the species responsible for these differences. *Heteragrion erythrogastrum* was frequently found at forest streams and forest margin site 2. This species is reported to prefer shaded habitats, where it perches for hours in the dark (ESQUIVEL 2006). Although all cultivated area sites provided shaded patches and cultivated area 1 had relatively dense canopy cover, *Heteragrion erythrogastrum* was completely absent from these habitats. It is unknown to what extent fragmentation and isolation from closed forest prevents the colonisation of such streams running through small patches of gallery forest by species such as *Heteragrion erythrogastrum*.

The dragonfly communities of cultivated areas were characterised by a significantly higher proportion than in forest communities of species with a wide distribution (i.e. exceeding the boundaries of Central America). Forest sites were inhabited by species specialised to the prevailing conditions, but not able to establish populations in cultivated area, dominated by common and widespread species.

The presence of *Erythrodiplax fusca* strongly discriminated forest margin habitats from others. We found this species in large quantities at forest margin 1. This site, although it is situated next to the forest, in some way represented the highest degree of degradation of all sites, because it was strongly artificially shaped and no trees covered its banks. *Erythrodiplax fusca* is a common element of open landscapes on both American continents (ESQUIVEL 2006).

Differences between habitats remained on higher taxonomic levels since we observed certain families in respective habitats exclusively. Polythoridae only occurred at forest streams, Protoneuridae in cultivated area



and Gomphidae at forest margin streams. Members of Polythoridae and Gomphidae are inhabitants of streams and rivers in forests. Especially species of Polythoridae are not very common and only species of the genus *Aphylla* (Gomphidae) are reported to live in open areas (ESQUIVEL 2006). The differences between dragonfly ensembles on species and genus level and the absence of some species in the disturbed secondary forest, accompanying forest margin stream, demonstrate the close relation of some species to specific forest conditions.

The composition of species assemblages and similarities between habitat types was significantly influenced by differences in habitat characteristics, clearly overriding the effects deriving from the spatial arrangement of sites.

Even though we obtained a clear pattern, some concerns have to be mentioned, since some factors not investigated in this study may have an additional impact on dragonfly communities:

(1) We conducted our survey for a relatively short period of four weeks during the dry season only. The likelihood of observing further species during the rainy season was mentioned above.

(2) PICHLER (2006) reported 23 fish species for the Quebrada Negra, some of them insectivorous. Fish predation on dragonfly larvae is one additional factor shaping the structure of larval composition and distribution (JOHANSSON et al. 2006). We have no knowledge of the fish fauna in cultivated area streams, but the occurrence of insectivorous fish is very likely. A different composition of predatory fish species in cultivated area sites may, therefore, have a different effect on the community of aquatic insects.

(3) Forest streams were low order streams (1-2) and the Quebrada Negra was a tributary of the Rio La Gamba where the site ca1 was situated. Cultivated area streams were of higher stream order and therefore differences between sites maybe not only be related to habitats but the type of investigated stream and river. Cultivated area streams were broad and showed low flow velocities as they ran through a flat landscape, whereas forest streams were situated in a mountainous landscape. Odonate assemblages usually vary along a watercourse (HAWKING & NEW 1999, CHOVANEC et al. 2004, HOFMANN & MASON 2005) in response to changing physical and biotic parameters. Stream width and slope gave us no significant response when investigating species richness variance between habitat types; however, these parameters at least show clear trends when related to species richness, as mentioned before. Furthermore, they are linked to the characteristics of current water bodies in plains or mountains, and a part of the



**Fig. 10:** *Hetaerina occisa*, male. This species was encountered in all habitat types but was most abundant at streams in cultivated area.



**Fig. 11:** *Cora semiopaca*, male. This endemic species typically lives at shaded streams in pristine forests.

different community members may be elucidated not by deforestation but by a lowland/upland dualism.

This study focused on dragonfly communities of streams, thereby representing only a certain proportion of the total species ensemble. However, some species living away from flowing waters are not encountered in open habitats, including dragonflies specialised to using phytotelmata exclusively (i.e. water-filled tree holes and tanks of epiphytes) for oviposition and larval development. Within the study area, we observed individuals of *Mecistogaster modestus* in the forest. This species is a member of the South and Central American distributed family of Pseudostigmatidae, whose larvae live in tank bromeliads (YANOVIK 2001) and are described as living exclusively in forests. Thus, the occurrence of *Mecistogaster modestus* stresses the importance of forests as habitats for sensitive species.

Agricultural land use combined with deforestation changes important biotic and abiotic parameters of riverine habitats, which strongly influence site selection of adult dragonflies and the persistence of larvae (shade, macrophyte and riparian vegetation) as well as the structure of the surrounding landscape in which adults may disperse and forage. These factors determine the presence of species and shape community composition. The pattern of species distribution we found strengthens the assumption that streams in agricultural areas do not serve as suitable habitats for many sensitive species that are typically found in forests, and that deforestation poses a severe threat to these species. When habitats in degraded and open landscapes such as agricultural areas are unsuitable as reproductive habitats for sensitive forest species, it becomes evident that deforestation endangers not only dragonflies but all aquatic biodiversity, implying that the conservation of native habitats deserves immediate priority and attention.

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