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Odonata assemblages along an anthropogenic disturbance gradient in Ghana's Eastern Region

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Abstract. We assessed the effects of different levels of anthropogenic disturbance on Odonata species richness and assemblage composition in four different habitats in Ghana: mining sites, agricultural fields, human settlements, and primary forest habitat. A total of 992 individual adult Odonata representing 51 species (20 Zygoptera, 31 Anisoptera) in six families were recorded from 16 sites across these habitats. A majority of species (75 %) recorded across all sites were previously classified as habitat generalists, while 20 % represented specialists. The human settlement habitat exhibited the overall highest Odonata abundance (302 individuals), whereas the greatest species diversity was observed in the mining sites ($D = 4.59$). Agricultural fields had lowest abundance (n = 196 individuals), while primary forest sites exhibited the lowest diversity ($D = 2.75$), although these differences were not statistically significant. There was also no significant difference in adult Odonata richness D ($F_{3,59.72} = 2.48$, $p = 0.07$) among habitats. However, species composition differed significantly among the various habitats (ANOSIM: global $R = 0.73$, $p = 0.001$). A canonical correspondence analysis revealed that river flow rate, percentage of canopy cover and channel width were the key factors influencing Odonata assemblages. Generalist and heliophilic dragonflies dominated in human-altered habitats, while the matured forest habitat included more specialists and stenotopic damselflies. The results suggest that specialist dragonflies can be used as freshwater habitat quality indicators, and their habitat requirements also support the need to maintain the remnant primary forest in the East Akim District.

Further key words. Dragonfly, species richness, species composition, canonical correspondence analysis, multidimensional scaling, habitat types

Introduction

Human modification of natural habitats is a major threat to invertebrate populations worldwide (*e.g.*, Orr 2004; Todd & Rothermel 2006). Agricultural expansion, deforestation, urbanization, and mining activities can result in natural ecosystem depletion, with cascading impacts on invertebrate diversity (Strayer 2006; Dolný et al. 2011; Jeanmougin et al. 2014). Habitat disturbance may result in the reduction in native invertebrate diversity and abundance, and can also cause specialised native communities to be replaced by assemblages of generalist, wide-ranging, and disturbance-tolerant species with lower conservation value (Samways & Steytler 1996; Stewart & Samways 1998; Clausnitzer 2003; Cleary et al. 2005).

The influence of habitat disturbance and modification on invertebrate communities is often difficult to predict. However, several contrasting hypotheses have been proposed for the effects of such disturbance on invertebrate diversity and composition. Pulliam (1988) proposed that disturbance of natural ecosystems is a catalyst of ecological sinks, which results in local extinctions, reduced species diversity, and replacement of the native community by eurytopic and widespread species that exhibit wider distributions and fewer specialized habitat requirements. Conversely, Bock et al. (2008) suggested that an oasis effect can result from disturbances, whereby the disturbed habitat provides an alternative and favourable set of conditions and resources for exploitation by both native and colonizing species, resulting in an overall increase in species diversity. Similarly, Connell (1978) proposed a maximum number of species at an intermediate level of disturbance. Studies assessing the effects of human-led natural forest disturbance on species communities are urgently needed on a variety of invertebrate taxa to provide insight into how these novel disturbance regimes affect native, specialist, and total biodiversity.

Rapid assessments of the impact of human activities on biodiversity and ecosystems require the use of cost- and time-effective model systems. Indicator species are valuable for rapidly quantifying disturbance impacts on habitats and the biodiversity therein. Among the myriads of species being used as indicators of habitat quality, Odonata are particularly useful as they double as both aquatic and terrestrial environmental barometers (Clausnitzer 2003; Dolný et al. 2011). They are widely accepted as bio-indicator taxa owing to their conspicuous nature, high trophic position, relatively well-characterized diversity in both terrestrial and aquatic environments, and their previously-reported sensitivity to human-induced habitat change (Brown 1991; Clark & Samways 1996). Dragonflies have been extensively used as indicators of habitat quality in terms of species occurrence (Samways & Steytler 1996; Kadoya et al. 2008), diversity (Clausnitzer 2003; Sahlén 2006), distribution (Flenner & Sahlén 2008), morphology (Taylor & Merriam 1995; Hardersen & Frampton 1999), and dispersal (Jonsen & Taylor 2000).

In many tropical countries, including Ghana, human populations are growing rapidly. This is increasing pressure on freshwater resources, due to riparian deforestation, mining activities, human settlement encroachment, water abstraction for irrigation and domestic and industrial consumption, and damming to generate hydroelectric power. These processes can result in alteration and sometimes cessation of flow rates and also affect other properties of the water bodies (Stewart & Samways 1998). For Odonata communities especially, the specialist, resident species are expected to be particularly sensitive to such changes, and may become extirpated. Widespread and generalist species, which typically favour lentic systems, can then invade and become favoured in such disturbed lotic habitats (Harabiš & Dolný 2012). Odonata typically found in open and lentic areas are more agile and aggressive, and tend to outcompete the lotic specialist species. Competition with these species, combined with habitat degradation, can result in accelerated loss of lotic species and contribute to turnover in the entire Odonata community assemblage (Brasil et al. 2014).

The diversity, distribution, and ecology of the Odonata fauna of Ghana are currently poorly characterised. Most previous studies on Odonata in Ghana are primarily focused on species checklists (Neville 1960; Pinhey 1962; Frempong & Nijjhar 1973; Marshall & Gambles 1977; D'Andrea & Carfi 1994; O'Neill & Paulson 2001; Dijkstra 2007) with little emphasis on the community assemblage patterns in different land use matrices, with the exception of Dijkstra & Lempert (2003; see discussion). Obtaining information on Odonata diversity, distributions and assemblages from under-surveyed and human affected areas is a necessary first step for freshwater conservation efforts in Ghana. Such data on Odonata assemblages can inform conservation efforts and be used as baseline data for further monitoring of present and future effects of human activities on wetland quality and the local freshwater biodiversity.

Given these considerations, we sought to disentangle the impact of different land use disturbance patterns on Odonata species richness, diversity, and assemblage structure. We tested the hypothesis that Odonata communities will be significantly different among the different land use matrices, due to interspecific differences in sensitivity to structural habitat modification and human disturbance (Clark & Samways 1996; Samways & Steytler 1996). To test this hypothesis, we compared Odonata assemblages between mining sites, agricultural fields, human settlement habitats, and the natural primary forest habitat as reference habitat type, along seven major streams in the East Akim Municipal District in Ghana.

Material and methods

Study area

We surveyed seven different streams (Akoosi, Akokobenumsuo, Supon, Ayinasu, Twafour, Saaobeng, and Nantwikurom) located in the East Akim Municipal District in the Eastern Region of Ghana (06°04'–06°18'N, 00°38'–00°27'W). The streams passed through different land use matrices, making them ideal study locations for comparing Odonata assemblages according to different disturbance regimes (Fig. 1).

Akoosi (Asiakwa area) – The downstream reach was characterized by ongoing, small scale mining activities and included three sampling sites, while the upstream reach, where all of our forest sampling sites were located, was surrounded by primary forest vegetation of the Atewa Range Forest Reserve (Fig. 2).

Supon and Twafour (Asiakwa Township) – The Supon stream was affected by ongoing small scale mining activities while the Twafour stream was primarily affected by human settlements (Fig. 3). The Twafour stream was primarily used for agricultural irrigation and also supported a local, indigenous fishing industry.

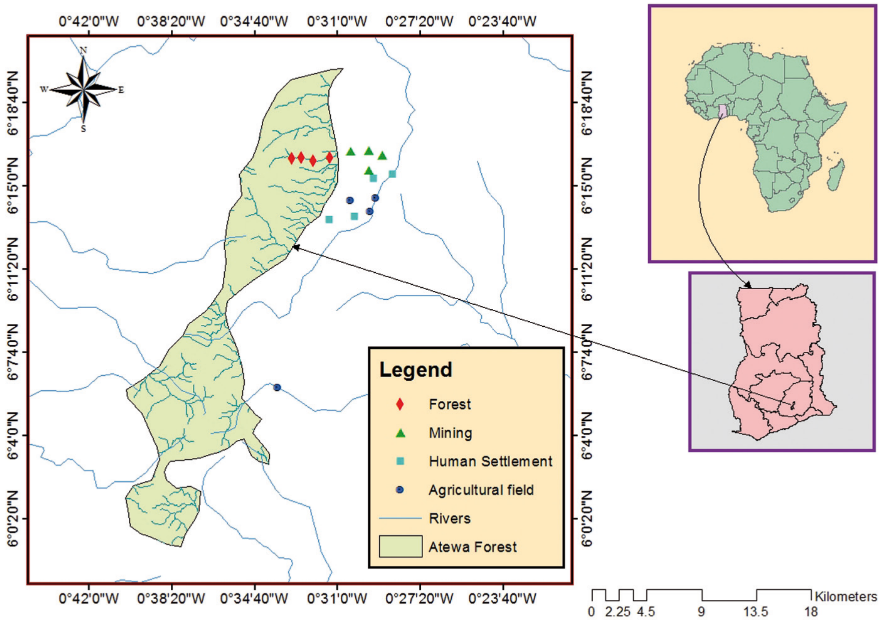

Figure 1. Map of the study area in and near the Atewa Forest, in the East Akim Municipal District in Ghana's Eastern Region, with the situation of the 16 sampling sites.

Figure 2. Primary forest habitat (S13) around the Akoosi stream in the East Akim Municipal District in Ghana's Eastern Region, characterized by dense vegetation and closed canopy cover (18-ii-2017). Photo: IS

Akokobenumsuo – Situated near the Protroase–Odumase road, the stream was heavily impacted by agricultural activities, with some patches of gallery forest left at both banks.

Ayinasu – The stream was located in the Sagyimase township of the East Akim District within the vicinity of human settlement (Fig. 4). There was evidence of community bathing and washing along the banks of the Ayinasu stream, likely impacting water quality.

Saaobeng and Nantwikurom – Both streams were located in the Sagyimase area of the District and were heavily impacted by agricultural cultivation, with cocoa plantations as the dominant crop.
Annual precipitation in the study area is between 1 200 and 1 800 mm, and the average temperature is 27°C (Abu-Juam et al. 2003). The soil types are primarily lithosols, red clays, and ochrosols from the Birimean rock formation (Hall & Swaine 1976). About 75 % of the area is hilly with elevation between 200 and 750 m a.s.l. (Hall & Swaine 1976).

Odonata sampling

Adult individuals of all Odonata species were sampled at 16 sites distributed across four land use types, namely; mining sites (4 sites), agricultural fields (4 sites), human settlement habitats (4 sites), and primary forest habitats (4 reference sites). At each site, we collected adult Odonata along a 100-m transect parallel to the stream bank. In the primary forest habitat, all four sites were sampled in the upstream segment of the Akoosi river. For the agricultural fields, we surveyed two sites along Saaobeng stream and one site each along the Akokobenumsuo and Nantwikurom streams. The mining sites were surveyed along the Supon (1 site) and Akoosi stream (3 sites, all located downstream). Two sites each were surveyed along the Ayinasu and Twafour streams to represent the human settlement habitat.

Sampling was done from August, 2016 to March, 2017 in both wet and dry seasons. Each site was visited at least once in each season. The wet season sampling was done from viii-2016 to x-2016 while the dry season survey occurred in ii-2017 and iii-2017. The sampling was done during the day, between 10 and 17 h GMT (UTC ± 0) following a standardized sampling pro-

Figure 3. Human settlement site (S12) along the Twafour stream in the East Akim Municipal District in Ghana's Eastern Region, characterized by completely open canopy cover (12-x-2016). Photo: IS

Figure 4. Human settlement site (S9) along the Ayinasu stream in the East Akim Municipal District in Ghana's Eastern Region, characterized by partial canopy cover resulting from a trace of gallery trees and shrubs and a nearby oil palm garden (15-ii-2017). Photo: IS

tocol of two researchers per hour for all the sampling sites. We captured all adult Odonata individuals where possible within this time period, using an entomological hand net of approximately 40 cm in diameter, with a 140 cm shaft. We identified each specimen to species level *in situ*, using Dijkstra & Clausnitzer (2014) identifiction keys. We photographed all species not mentioned in the key (which is for Eastern Africa), and then used the African Dragonflies and Damselflies Online database (ADDO; Dijkstra 2016) for further identification. When identification was not certain, we depended on expert knowledge and contacted K.-D. Dijkstra for further assistance and confirmation for the species identification. Using Dijkstra & Clausnitzer (2014), Clausnitzer et al (2012) and the ADDO database (Dijkstra 2016), we also recorded whether our identified species had been previously classified as habitat generalists (widespread in open habitats, with no significant habitat affinity), and habitat specialists (forest species with narrow range). We used these existing classifications as predictors in our models of habitat affinity.

Assessment of environmental variables

The canopy cover, flow rate, river width and depth, aquatic and bankside vegetation were recorded in all sampling sites. For each site, a measuring tape was used to measure the mean river width three times, at the beginning, midpoint, and the end of each sampling transect. The mean depth was assessed by submerging a pole in the water and the reading taken using a tape measure at three locations across the stream for each site. A Garmin GPS (eTrex 10; Garmin Ltd, Schaffhausen, Switzerland) was used to take the coordinates of each sampling site. The canopy cover was assessed using Spherical Crown Densiometer (Convex Model A). The flow rate of water was categorized according to Stewart & Samways (1998) as still (0), glide (1), and rapid (2). The percentage of clarity was qualitatively categorized as (1) highly turbid with bottom not visible (0–39 %), (2) turbid with bottom visible (40–69 %), and (3) clear (70–100 %). The plant species at each site along the various streams were recorded as aquatic vegetation (plants in stream channel, partly or fully submerged), marginal or bankside vegetation (shrubs, herbs, weeds, and trees) and algae (isolated and also in stones), following the Gerber & Gabriel (2002) classification system.

Data analysis

Species richness and diversity

We computed for Pielou evenness and Shannon Wiener index for all the sampling sites. Pielou evenness (J') was estimated as:

$$J' = H' / H'_{max} = H' / \log S$$

Where H'_{max} is the maximum possible value of Shannon diversity, *i.e.*, which would be achieved if all species were equally abundant (namely, logS) (Pielou 1969).

Shannon Wiener diversity index (H') for the individual sampling sites was also computed as:

$$H' = -\Sigma_I p_i \log(p_i)$$

Where p_i is the proportion of the total count arising from the i^{th} species (Shannon & Wiener 1963).

We also computed the Margalef index (D) of species diversity (Colwell & Coddington 1994) for each sampling site (Table 3) as well as separately for each habitat type (results in text). The index includes the total number of individuals (N), and estimates the total number of species (S) for a given number of individuals (Margalef 1968):

$$D = \frac{(S - 1)}{\log N}$$

Species richness was estimated simply as the number of species observed in a site. For analyses of relative abundances, we applied log (X + 1) to transform the abundances of each species at each site. General linear mixed models were used to test for the significant difference in species richness and diversity among the various habitats, since a priori test for normality, using Shapiro-Wilks test, showed that the data set was normally distributed (Zar 1999). We partitioned the variance in total abundance, richness, J', H', and D among the various habitat types, streams sampled and location along the streams (upstream *vs* downstream sites) using the lmerTest and lme4 packages (Bates et al. 2015) for R version 3.3.2 (R Core Team 2016), and fitting habitat type as a fixed effect and stream location and stream ID as random effects. We further ran a multi-factor analysis of variance to examine the variance in these response variables explained by each of: habitat, stream name, and stream location.

Similarity

We employed non-metric multidimensional scaling (nMDS) with Bray-Curtis similarity resemblance matrix to compare Odonata species composition among the various habitat types and streams (Fig. 5). For nMDS, we used an analysis of similarity with 999 permutations (ANOSIM; McCune & Grace 2002; Melo & Hepp 2008). We also employed Analysis of Similarity routine within the PRIMER package (ANOSIM; Clarke & Warwick 2001; McCune & Grace 2002; Melo & Hepp 2008; PRIMER 6.1.5), a modified version of the Mantel test based on rank correlation between two distance matrices, to determine the difference in species composition among (i) habitat types, (ii) the sampled streams, and (iii) the location of the various sites (upstream *vs* downstream stretches). Overall Log $(X+1)$ transformation was applied to the local (site-specific) abundance data for each species, prior to nMDS and ANOSIM analysis. This transformation is effective in focusing on patterns within the whole community, mixing contributions in the measure of similarity of habitats from common and rare species (Clarke & Warwick 2001).

To assess beta-diversity across habitat types, we also used the similarity percentage analysis (SIMPER) routine in PRIMER (Clarke & Gorley 2001) to measure the various Odonata species' contribution to dissimilarity between the four groups of habitat types. This method is useful in identifying species representative for one type of habitat, *e.g.*, typical forest species (Hofhansl & Schneeweihs 2008). In the results we present the species contributing the most to dissimilarity among each pair of habitats, measured using the Bray-Curtis dissimilarity index. All multivariate analyses were done using PRIMER 6.1.5 package (Clarke & Gorley 2001).

A canonical correspondence analysis (CCA) was performed to determine the environmental drivers of variation in Odonata assemblages across the study region (Ter Braak 1986). The CCA is a direct gradient analysis technique designed to detect the patterns of variation in species composition that can be explained best by the observed environmental variables. We implemented the CCA using Environmental Community Analysis (ECOM.

exe) ver. 1.4 packages (Henderson & Seaby 2000). A Monte Carlo test with 9 999 iterations was used to test for the significance of the eigenvalues generated by the first three axes of variation (Ter Braak & Verdonschot 1995) in Odonata assemblage structure and underlying habitat variables. This procedure allowed us to determine the significant contribution of each environmental driver of changes in Odonata assemblage structure. We included streams as a continuous environmental driver in this analysis by fitting dummy variables coded (0,1) indicating the presence or absence of each site within each stream. Only axes that were statistically significant ($\alpha = 0.05$) were interpreted.

Results

Species richness of Odonata among the various habitats

A total of 992 individual adult Odonata, representing 51 species from six families, were recorded at the seven streams, along the mining sites, agricultural fields, human settlement habitats, and primary forest habitats. Of the 51 Odonata species recorded, 20 were Zygoptera from five families (Calopterygidae, Chlorocyphidae, Lestidae, Coenagrionidae, and Platycnemididae), while 31 species were Anisoptera, all from the family Libellulidae. The majority of species (75 %) recorded in the study area were previously classified as generalists, while 20 % of the species, mostly from the primary forest habitat, had previously been described as specialists. Five Odonata families were identified in the primary forest, of which the Lestidae and Calopterygidae were found exclusively in this habitat. Four families occurred in both the mining sites and agricultural fields (Coenagrionidae, Chlorocyphidae, Platycnemididae, and Libellulidae), while three families were recorded in the human settlement habitat (Coenagrionidae, Platycnemididae, and Libellulidae; Tables 1 and 2).

Abundances and diversity of each habitat type are summarized in Table 3. The human settlement habitats exhibited the overall highest Odonata abundances (n = 302 captures across these 4 sites), followed by mining sites (n = 288 individual captures). The agricultural field had the lowest Odonata abundances (n = 169; Table 3). However, the primary forest habitat supported the highest abundance of zygopterans (n = 190), and the lowest abundance of anisopterans (n = 43). The mining sites, in contrast, exhibited highest anisopteran abundance (n = 256), and the lowest abundance of zygopterans (n = 32). Similarly, zygopteran species richness was highest in the primary forest habitat (n = 9), while the mining sites had the least number of zygopterans (n = 5). Conversely, the mining sites had the highest anisopteran species richness (n = 22), followed by human settlement habitat (n = 16), with the least numbers of anisopterans encountered in the primary forest habitat (n = 7; Tables 1, 2).

The greatest estimated species richness was observed in the mining site ($D = 4.59$), followed by the agriculture fields ($D = 4.48$). The primary forest habitat had the lowest estimated species richness ($D = 2.75$; Table 4). Despite these intriguing trends in the data, our general linear mixed models, which controlled for effects of stream and stream location, indicated that there was no significant difference in log(abundances) ($F_{3,6.18} = 1.18$, $p = 0.39$), D ($F_{3,59.72} = 2.48$, $p = 0.07$), H' ($F_{3,6.00} = 0.76$, $p = 0.56$), J' ($F_{3,78.19} = 0.49$, $p = 0.69$), or S ($F_{3,5.96} = 1.78$, $p = 0.25$) among the various habitat types. Pairwise comparisons between each of the degraded habitats and the forest habitat in these models also showed no significant differences between individual pairs of habitat types (all $p > 0.05$). We further partitioned the variance in S, D, and abundance among the three factors: habitat, stream name, and stream location. This analysis revealed that 2 % of the variance in Odonata abundance among sites was explained by habitat type, while 25 % was explained by stream name, 0 % explained by stream location, and 73 % is residual (unexplained by these factors). Similarly, 16 % of the variance in D among sites was explained by habitat type, 21 % explained by stream name, 0 % explained by stream location, and 64 % is residual (unexplained by these factors). For species richness (S), 17 % of variation was explained by habitat type, 33 % was explained by stream, 0 % by stream location, and 50 % was residual.

Similarity

The Non-metric Multi-Dimensional Scaling (NMDS) ordination test, based on Bray-Curtis similarities, identified three ecologically significant Odonata assemblages structure. The primary forest habitat (Akoosi 4, Akoosi 5, Akoosi 6, and Akoosi 7), mining sites (Akoosi 1, Akoosi 2, Akoosi 3, and Supon), and agricultural habitat (Saaobeng 1, Saaobeng 2, Nantwikurom,

Table 1. Abundance and relative abundance (% RA) of Zygoptera species recorded in mining sites (MS), agriculture fields (AF), human settlement habitats (HS), and primary forest habitats (PF) in the East Akim Municipal District in Ghana's Eastern Region. Species classified as forest specialists are represented by an asterisk (*), and generalist species are represented by a hash symbol (#) following Dijkstra & Clausnitzer (2014), Clausnitzer et al (2012), and ADDO database (Dijkstra 2016)

Zygoptera species	MS	AF	HS	PF	Total	% RA
Lestidae						
Lestes dissimulans Fraser, 1955*	0	0	0	5	5	1.35
Calopterygidae						
Phaon camerunensis Sjöstedt, 1900*	0	0	0	20	20	5.41
Phaon iridipennis (Burmeister, 1839)*	0	0	0	13	13	3.51
Sapho ciliata (Fabricius, 1781)*	0	0	0	59	59	15.95
Umma cincta (Hagen in Selys, 1853)*	0	0	0	11	11	2.97
Chlorocyphidae						
Chlorocypha curta (Hagen in Selys, 1853)#	7	0	0	0	7	1.89
Chlorocypha luminosa (Karsch, 1893)*	0	0	0	26	26	7.03
Chlorocypha radix Longfield, 1959*	0	0	0	3	3	0.81
Chlorocypha selysi Karsch, 1899*	0	3	0	29	32	8.65
Platycnemididae						
Allocnemis sp.	0	8	5	0	13	3.51
Elattoneura nigra Kimmins, 1938#	5	3	0	0	8	2.16
Coenagrionidae						
Africallagma vaginale (Sjöstedt, 1917)#	0	5	0	0	5	1.35
Africallagma glaucum (Burmeister, 1839)#	0	0	12	0	12	3.24
Agriocnemis sp.#	0	22	7	0	29	7.84
Ceriagrion glabrum (Burmeister, 1839)#	3	5	11	0	19	5.13
Ceriagrion rubellocerinum Fraser, 1947#	0	6	4	0	10	2.70
Ceriagrion corallinum Campion, 1914#	0	4	0	0	4	1.08
Pseudagrion hamoni Fraser, 1955#	9	0	0	0	9	2.43
Pseudagrion melanicterum Selys, 1876#	8	15	32	24	79	21.35
Pseudagrion isidromorai Compte Sart, 1967	0	6	0	0	6	1.62
Abundance	7	3	0	161	171	100
Number of species	5	10	6	9		

Table 2. Abundance and relative abundance (% RA) of Anisoptera species recorded in mining sites (MS), agriculture fields (AF), Human settlement habitats (HS) and primary forest habitats (PF) in the East Akim Municipal District in Ghana's Eastern Region. Species classified as forest specialists are represented by asterisk (*****) and generalist species are represented by a hash symbol (**#**) following Dijkstra & Clausnitzer (2014), Clausnitzer et al (2012) and ADDO database (Dijkstra 2016).

Anisoptera species	MS	AF	HS	PF	Total	% RA
Libellulidae						
Acisoma inflatum Selys, 1882**#**	15	0	27	0	42	6.75
Aethriamanta rezia Kirby, 1889**#**	2	0	0	0	2	0.32
Brachythemis lacustris (Kirby, 1889)**#**	5	0	2	0	7	1.13
Brachythemis leucosticta (Burmeister, 1839)**#**	3	0	10	0	13	2.09
Chalcostephia flavifrons Kirby, 1889**#**	11	0	12	0	23	3.69
Diplacodes lefebvrii (Rambur, 1842)**#**	3	0	0	0	3	0.48
Diplacodes luminans (Karsch, 1893)**#**	3	0	0	0	3	0.48
Micromacromia zygoptera (Ris, 1909)*****	0	0	0	3	3	0.48
*Neodythemis klingi (*Karsch, 1890)**#**	0	13	9	9	31	4.98
Olpogastra lugubris (Karsch, 1895)**#**	14	0	0	0	14	2.25
Orthetrum abbotti Calvert, 1892**#**	4	0	0	0	4	0.64
Orthetrum africanum (Selys, 1887)*****	0	2	0	0	2	0.32
Orthetrum angustiventre (Rambur, 1842)**#**	0	2	2	0	4	0.64
Orthetrum austeni (Kirby, 1900)**#**	10	2	14	0	26	4.18
Orthetrum chrysostigma (Burmeister, 1839)**#**	2	2	8	1	13	2.09
Orthetrum guineense Ris, 1909**#**	0	5	0	0	5	0.80
Orthetrum icteromelas Ris, 1910**#**	0	2	0	0	2	0.32
Orthetrum julia Kirby, 1900**#**	17	20	37	9	83	13.34
Orthetrum microstigma Ris, 1911**#**	0	8	3	0	11	1.77
Orthetrum monardi Schmidt, 1951**#**	0	5	0	0	5	0.80
Orthetrum stemmale (Burmeister, 1839)**#**	6	15	3	11	35	5.63
Orthetrum trinacria (Selys, 1841)**#**	0	7	0	0	7	1.13
Orthetrum sp.	8	0	3	6	17	2.73
Palpopleura lucia (Drury, 1773)**#**	55	7	51	0	113	18.17
Palpopleura portia (Drury,1773)**#**	18	2	34	0	54	8.68
Pantala flavescens (Fabricius, 1798)**#**	9	0	0	0	9	1.45
Rhyothemis semihyalina (Desjardins, 1832)**#**	6	0	0	0	6	0.96
Trithemis aconita Lieftinck, 1969**#**	8	0	14	4	26	4.18
Trithemis arteriosa (Burmeister, 1839)**#**	41	0	0	0	41	6.59
Trithemis dichroa Karsch, 1893**#**	11	0	2	0	13	2.09
Trithemis grouti Pinhey, 1961**#**	5	0	0	0	5	0.80
Abundance	256	92	231	43	622	100
Number of species	22	14	16	7		

Table 3. Summary of Odonata richness (S), Abundance (N), Margalef index (*D*), Pielou evenness (*J'*) and Shannon Wiener diversity index (*H'*) in the various sampling sites in the East Akim Municipal District in Ghana's Eastern Region. Stream location, Down – downstream, Up – upstream.

Site N°	Stream name	Stream location	Habitat type	S	N	*D*	*J'*	*H'*
S1	Akoosi 1	Down	Mining site	14	52	3.29	0.9128	2.409
S2	Akoosi 2	Down	Mining site	14	83	2.942	0.828	2.185
S3	Akoosi 3	Down	Mining site	16	108	3.204	0.9228	2.558
S4	Supon	Down	Mining site	10	45	2.364	0.893	2.056
S5	Akokobe-numnsuo	Down	Agriculture habitat	11	51	2.543	0.9303	2.231
S6	Nantwiku-rom	Down	Agriculture habitat	9	34	2.269	0.931	2.046
S7	Saaobeng 1	Down	Agriculture habitat	11	44	2.643	0.8822	2.115
S8	Saaobeng 2	Down	Agriculture habitat	8	40	1.898	0.8906	1.852
S9	Ayinasu 1	Down	Human settlement	7	47	1.558	0.809	1.574
S10	Ayinasu 2	Down	Human settlement	9	48	2.067	0.8592	1.888
S11	Twafour 1	Down	Human settlement	10	86	2.02	0.8871	2.043
S12	Twafour 2	Down	Human settlement	14	121	2.711	0.9334	2.463
S13	Akoosi 4	Up	Primary forest	12	53	2.771	0.8772	2.180
S14	Akoosi 5	Up	Primary forest	13	37	3.323	0.965	2.475
S15	Akoosi 6	Up	Primary forest	12	98	2.399	0.8628	2.144
S16	Akoosi 7	Up	Primary forest	9	45	2.102	0.8677	1.906

Table 4. Summary of Odonata richness in the various habitats in the East Akim Municipal District in Ghana's Eastern Region. Note that observed and estimated Margalef indices (*D*) decline from the mining to the primary forest habitats.

Habitat	Total Odonata abundance	Observed species richness	Estimated species richness	Estimated Margalef index (*D*)
Mining site	288	27	13.3±1.5	4.59
Agricultural field	169	24	9.8±0.8	4.48
Human settlement	302	22	10.0±1.5	3.68
Primary forest	233	16	11.5±0.9	2.75

and Akokobenumsuo) each occupy distinct clusters at 20 % cut off maximum similarity (Fig. 5). However, the human settlement sites were less ecologically distinct, and overlapped significantly in assemblage structure with some of the other habitat types. Two of the human settlement sites (Twafour 1 and Twafour 2) grouped with the mining sites, while the remaining two human settlement sites (Ayinasu 1 and Ayinasu 2) grouped with the agriculture sites (Fig. 5). The Similarity percentage (SIMPER) analysis reinforced this trend, suggesting that sites in the mining and human settlement habitats (70.87 %) and agricultural fields and human settlement habitats (67.72 %) were most similar to one another. The mining sites and primary forest habitats (92.55 %) were the least similar in Odonata species composition (Table 5), despite being located on the same stream (Fig. 1).

The most dissimilar species between the mining and agricultural habitats were *Trithemis arteriosa* (8 %) and *Agriocnemis* sp. (5 %), while those species contributing most to dissimilarity between mining and human settlement habitats were *T. arteriosa* (8 %) and *Orthetrum julia* (6 %). *Palpopleura portia* (7 %) and *Pseudagrion melanicterum* (6 %) were the most dissimilar species between agricultural field and human settlement habitats, and *Sapho ciliata* (7 %) and *T. arteriosa* (7 %) contributed most to the dissimilarity between the mining and primary forest habitats. In the agricultural field and the primary forest habitats, *S. ciliata* (10 %) and *Chlorocypha luminosa* (7 %) contributed the highest dissimilarity percentage, while between sites in the human settlement and the primary forest habitats, *S. ciliata* (9 %) and *P. lucia* (7 %) contributed the most to dissimilarity.

The species composition of Odonata differed significantly among the various habitat types (ANOSIM: global $R = 0.73$, $p < 0.001$). Pairwise comparison tests revealed significant differences between sites in the mining and agricultural habitats ($R = 0.89$, $p = 0.029$). Similarly, primary forest habitats differed significantly in the pairwise comparison with mining sites ($R = 0.99$, $p = 0.029$), agricultural fields (R = 0.92, p = 0.029), and the human settlement habitats ($R = 0.88$, $p = 0.029$). Conversely, pairwise test between mining sites and human settlement habitats ($R = 0.29$, $p = 0.14$) and between agricultural fields and human settlement habitats ($R = -0.05$, $p = 0.57$) did not differ significantly. When we compared the composition of Odonata between the site locations (upstream *vs* downstream) and the various streams sampled, we

Table 5. Dissimilarity [%] in species composition among the various habitat types in the East Akim Municipal District in Ghana's Eastern Region.

Habitat types	Mining sites	Agricultural fields	Human settlement	Primary forest
Mining sites		86.66	70.87	92.55
Agricultural fields	86.66		67.72	82.71
Human settlement	70.87	67.72		84.29
Primary forest	92.55	82.71	84.29	

found a significant difference in species composition between the upstream and downstream stretches of the sampled sites ($R = 0.94$, $p = 0.001$), which reflects differences in habitat types found upstream (forest only) *vs* downstream (all other habitat types). However, Odonata species composition did not differ significantly among the various streams sampled ($R = 0.133$, $p = 0.213$).

Environmental predictors of Odonata assemblage structure and distribution

Out of the five biophysical factors and the six streams analyzed, CCA ordination showed that % canopy cover ($r = -0.81$, $p < 0.01$), river width ($r = 0.94$, $p < 0.01$), % clarity ($r = -0.71$, $p < 0.01$) and flow rate ($r = -0.94$, $p < 0.01$), were the only key determinants of Odonata distributions, and these factors all strongly correlated with axis I (Fig. 6, Table 6). However, on axis II, almost all the factors including the stream types showed a weak correlation with community composition. The first two axes jointly explained 50.75 % of the cumulative variance in Odonata structure and spatial distribution across the streams sampled. In the primary forest, flow rate was observed to be high, especially in streams where the % canopy cover along the fringes was abundant. The predominantly specialist species of primary forest (*Sapho ciliata*, *Umma cincta, Chlorocypha luminosa*, *Ch. selysi*) responded to these environmental drivers of their spatial distribution.

In streams running through degraded habitats, % clarity tended to be turbid, as canopy cover along the fringes became less pronounced. Generalists and specialist heliophiles (*e.g.*, *Ceriagrion*, *Olpogastra lugubris, Orthetrum*

Table 6. Canonical coefficients and the correlations with the first three axes of the environmental variables of the canonical correspondence analysis (CCA) for the four habitat types in the East Akim Municipal District in Ghana's Eastern Region. Inter-set correlations were significant (p <0.05) for the three axes.

	Axis II	Axis II	Axis III
Canonical Eigen value	0.965	0.540	0.344
Variance explained	32.54	18.21	11.59
Cumulative % variance	32.54	50.75	62.33
Pearson correlation species/environment scores	0.973	0.979	0.991
Kendal rank correlation of species/environment scores	0.833	0.95	0.883
Correlation			
% Canopy cover	-0.812	0.136	-0.029
Flow rate	-0.944	0.029	-0.045
% Clarity	-0.708	0.212	0.042
Width	0.937	-0.138	-0.002
Depth	0.417	-0.216	-0.061
Akoosi	0.201	-0.395	-0.102
Supon	0.207	-0.221	-0.189
Akokobenumnsuo	-0.108	0.236	0.369
Saaobeng	-0.185	0.305	-0.070
Ayinasu	-0.093	0.360	-0.061
Twafour	0.351	0.047	0.239

julia, and *Neodythemis klingi*) were thus favoured in these habitat types. Species like *Trithemis arteriosa*, *Palpopleura lucia*, *Ellatoneura nigra*, *Acisoma inflatum*, and *Chalcostephia flavifrons* were predominant in more extremely degraded communities with even lower clarity and canopy cover, representing mining and human settlement areas (Fig. 6). *Brachythemis leucosticta* and *Agriocnemis* sp. with a relative abundance of 2.09 %, and 7.84 %, respectively, were the only outlier species that appeared not to be influenced by any of the environmental factors assessed in this study.

Discussion

Species richness

Our findings show that the presence of opportunistic generalist dragonflies resulted in substantial species richness in degraded habitats. This suggests

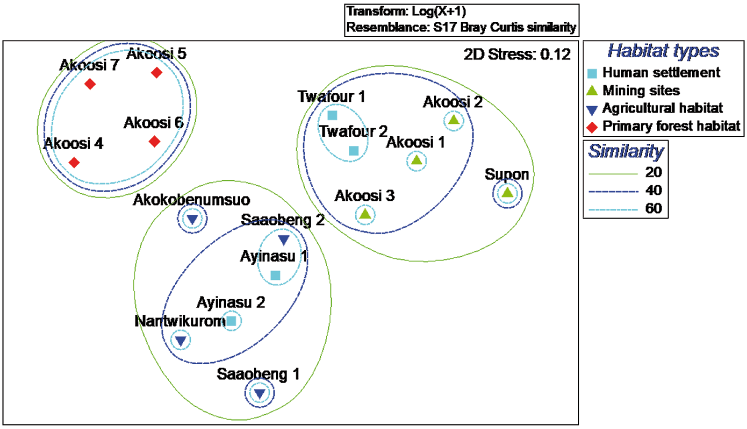

Figure 5. Multidimensional scaling (MDS) ordination plot of Odonata assemblage structure in the East Akim Municipal District in Ghana's Eastern Region, based on Bray-Curtis similarity of log (x + 1) transformed species abundances. Notice that species from the primary forest (red diamonds) were clustered separately from the rest of the habitats and are considered specialists.

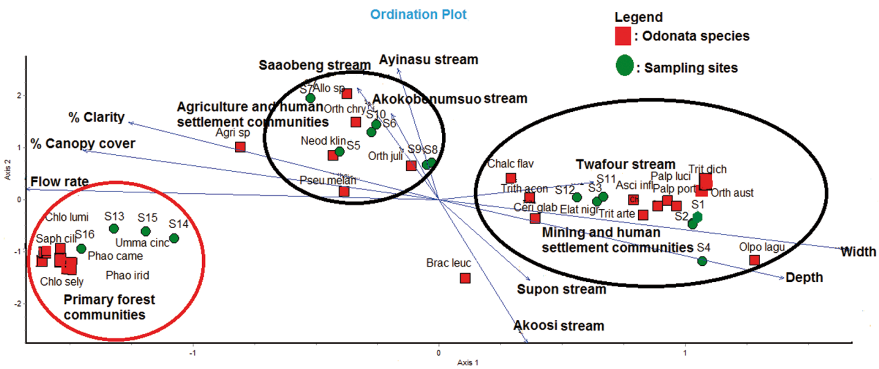

Figure 6. Canonical correspondence analysis (CCA) ordination diagram, showing the relationship between environmental variables and Odonata species across four habitat types in the East Akim Municipal District in Ghana's Eastern Region. Species names are abbreviated with the first four letters of the genus and the first four letters of the species (*e.g.*, *Orthetrum Julia* – *Orth juli*). The blue arrows represent each of the environmental variables plotted pointing in the direction of maximum change of explanatory variables across the habitat type. Red and black ovals represent specialists and generalist/heliophilic species in the primary forest and degraded habitats, respectively.

that Odonata species richness per se is a potentially misleading indicator of habitat quality in species monitoring and environmental studies (Monteiro-Júnior et al. 2013). Furthermore, there is a general consensus that when a natural habitat is subjected to disturbance, it may be colonized by species which can tolerate the disturbed landscape, while rendering the habitat unsuitable for the native community (Dijkstra & Lempert 2003). The Odonata generalists typically found in open areas are more aggressive and tend to outcompete the forest specialist species, which can result in accelerated loss of forest species and contribute to turnover in the entire Odonata community assemblage (Brasil et al. 2014). This contributes to the niche partitioning of Odonata community between the forest specialists and generalists which occupy more open habitats (Dijkstra & Clausnitzer 2006), and when forest habitats are altered, the forest specialists tend to lose ecological space (Brasil et al. 2014). It is therefore not unexpected to see higher numbers of generalist dragonflies in the mining, agricultural and human settlement habitats, resulting in equal or higher species richness in these degraded habitats. Increases in species richness in deforested landscapes (Ferreira-Peruquetti & De Marco 2002) and agricultural habitat (Ferreira-Peruquetti & Fonseca-Gessner 2003) have also been documented in Brazil, and were attributed to the increased primary productivity and occurrence of eurytopic generalist species in open and more lentic habitats.

The primary forest habitat with dense canopy cover harboured the highest number of specialist damselfly species. Tropical specialist damselflies have limited dispersal and competition ability outside their preferred habitats and are particularly sensitive to modifications of the riparian vegetation (Samways & Steytler 1996). Most Zygoptera are perchers in nature and utilize the forest structure as oviposition, emergence, and as perching substrates for thermoregulation. The high species richness of Zygoptera in primary forest habitat is linked to this dense canopy cover, which provides both substrate and shading for these species. However, the low species richness of Anisoptera in primary forest habitat may be linked to the quantitative transect methodology used in this study, which favours more lentic and common species than rare dragonflies from the Gomphidae or Macromiidae and some species from the Libellulidae. Our methodology was designed with the purpose of surveying only adult Odonata that can effectively be used as bio-indicators without considering larvae or target sampling of rarer and more secretive species. Such species, which are far more difficult to survey, are not advisable as indicators of habitat quality in rapid ecological assessments. This finding corroborates HOFHANSL & SCHNEEWEIHS (2008), who also reported lower species richness of dragonflies in streams embedded in the forest sites as compared to the cultivated areas in Costa Rica. STEWART & SAMWAYS (1998) also produced results in line with our findings, with more Anisoptera recorded in the degraded flanks of the various streams.

Similarity

We found dissimilar Odonata assemblages among the various habitat types, demonstrating differing effects of human disturbances. The primary forest and mining habitats were most dissimilar in Odonata species composition, likely due to differences in disturbance magnitude. The mining sites were associated with intensive mining regimes which led to disruption of flow in the main water bodies and the formation of numerous mined pools adjacent to the main river channel. This created diverse habitats, which were mostly exploited by generalist and heliophilic dragonfly species that dominated the mining community and caused the observed dissimilarity in species composition between mining habitats and primary forest or agricultural habitats.

The human settlement habitat type encompassed two different disturbance regimes. Sites S11 and S12 were associated with complete open canopy cover, whereas the other two human settlement sites (S9 and S10) were characterized by partial canopy cover resulting from a trace of gallery trees and shrubs and a nearby cocoa and oil palm garden along the Ayinasu stream. This explains why the Odonata assemblages in the human settlement habitat overlapped with the mining sites characterized by total open canopy cover, and the agricultural field which was also associated with some canopy cover, owing to the adjacent cocoa planation. These disturbances along the streams provided environmental and habitat conditions favouring eurytopic generalist species with wide dispersal ability. Accordingly, generalist and heliophilic species (*Acisoma inflatum*, *Chalcostephia flavifrons, Olpogastra lugubris*, *Trithemis aconita*, *T. arteriosa*) dominated in mining and human settlement assemblages whereas other generalist species, which were associated with some form of shading (*Pseudagrion melanicterum*, *Neodythemis klingi*, *Orthetrum julia*), were abundant in the agriculture and human settlement habitats. None of these assemblages represents suitable indicators of pristine habitats in Ghana.

Our findings largely concur with the study by Dijkstra & Lempert (2003) in Ghana and Liberia. They classified Odonata species according to their occurrence at small streams, intermediate streams, large streams, small rivers and large rivers. Consequently, Odonata species such as *P. melanicterum* and *O. julia*, which predominated in the agriculture and human settlement sites in our study, were categorized by Dijkstra & Lempert (2003) as characteristic of small and intermediate streams. Similarly, large rivers were commonly associated with open canopy cover, and these sites included species which overlapped with the mining and human settlement sites in our study (*O. lugubris*, *T. aconita*, *T. grouti*). On the other hand, Dijkstra & Lempert (2003) found *Chlorocypha pyriformosa* Fraser, 1947, *Pseudagrion camerunense* (Karsch, 1899), *Pseudagrion sjoestedti* Förster, 1906, *P. sublacteum* (Karsch, 1893), *Mesocnemis singularis* Karsch, 1891, or *Eleuthemis buettikoferi* Ris, 1910 in large rivers, but these species were not detected in our study. Conversely, *Ch. flavifrons, N. klingi, A. inflatum, Orthetrum austeni*, and *Trithemis dichroa*, which dominated in the mining and human settlement communities in our study, had not been recorded by Dijkstra & Lempert (2003).

Forest specialist species from the Chlorocyphidae (*Chlorocypha selysi, Ch. radix*) and Calopterygidae (*Sapho ciliata*, *Umma cincta*), which utilize the forest vegetation for numerous activities, have been listed according to Dijkstra & Lempert (2003) as typical of small and intermediate streams, associated with dense vegetation cover. Similarly, these species dominated in the primary forest habitats in our study. On the other hand, *Prodasineura villiersi* Fraser, 1948, *Sapho bicolor* Selys, 1853, *Chlorocypha dispar* (Palisot de Beauvois, 1807), *Heliaeschna fuliginosa* Selys, 1883, and *Notiothemis robertsi* Fraser, 1944 were recorded by Dijkstra & Lempert (2003) in small and intermediate streams in Ghana and Liberia but are also missing in our study. Our mining sites harboured generalist species such as *O. lugubris* or *Pantala flavescens*, which are more widespread and have a general affinity to disturbances (Dijkstra 2016). Similar to our findings, Dijkstra & Lempert (2003) characterized Libellulidae like *Palpopleura lucia, P. flavescens*, or *T. arteriosa* as having strong affinity to stagnant and temporary waters as well as to large rivers. Most species within the Libellulidae are heliothermic in nature and thus depend on direct sunlight for thermoregulation and flight behaviour (De Marco & Peixoto 2004). The heliothermic species are favoured directly by the removal of forest cover as well as interspecific competition, where they achieve dominance in the degraded habitat, thus excluding specialist species (De Marco & Peixoto 2004).

The observed pattern of Odonata composition is linked to the location of the downstream and upstream stretches of the various rivers sampled as well as to habitat type. For example, all sampling sites of the primary forest habitat were located upstream of the Akoosi River while mining sites, agricultural and human settlement sites were also located downstream. It can prove difficult to distinguish location from habitat type in these analyses, because human activities in Ghana have largely overtaken all downstream localities adjacent to waterways. However, our analysis has identified distinct differences among habitats that are robust to effects of locality. Accordingly, the forest community exhibited a distinctive Odonata assemblage while Odonata compositions in the degraded habitats overlapped. It is also possible that some random factors and other environmental variables not considered in our study may influence the pattern of Odonata assemblages. Generally, environmental factors (canopy cover, riparian vegetation, bank vegetation, altitude, flow rate, substrate type, channel width and depth, sunlight regime, and physicochemical variables), may serve as filters for Odonata species (Monteiro-Júnior et al. 2013). Depending on the sensitivity to different environmental parameters, species can be divided into two groups: eurytopic or generalist species that are widespread and tolerant to a wide range of environmental variables, and stenotopic or specialist species having narrow ranges of environmental tolerances (Kinvig & Samways 2000). Degraded habitats have fewer stenotopic species and are notably dominated by Anisoptera (Stewart & Samways 1998). On the other hand, the Zygoptera comprise more specialist species (Dolný et al. 2012), which has been confirmed by our study, as more Zygoptera apart from Coenagrionidae were recorded exclusively in primary forest habitat.

Overall our findings suggest that specialist damselfly guilds are better indicators of riverine ecosystem health in Ghana than Odonata as a whole. We recognize that this pattern is preliminary and generally recommend caution in equating Odonata assemblages to a healthy ecosystem, and suggest the development of region-specific Odonata bio-indicators, based on investigation on a larger spatial scale and a careful study of species-environment correlations. Moreover, we recommend the imminent collection of baseline riverine biodiversity data in any remaining pristine, lowland habitat worldwide, as these lowlands as an undisturbed reference sites are already unfortunately lost in the East Akim Municipal Region of Ghana.

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