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Comparison of two Odonata communities from a natural and a modified rainforest in Papua New Guinea

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Abstract

The Odonata fauna of Papua New Guinea is species-rich, but human population growth and resulting modification of primary rainforests may lead to a loss of valuable habitat and species diversity. In this study, I compared the odonate assemblages of a natural tropical rainforest and a modified forest in order to assess the loss that could result from human forest alteration. I collected odonates and recorded habitat use at both study sites for several weeks. The assemblages were compared with similarity indices, and total species richness was estimated using a jackknife procedure. The natural forest community, with 61 species, had both a higher diversity and evenness than the village community, with 38 species. Altogether I found 78 species of 13 families, of which 21 were shared between the two areas. Among the families with more than one species, Megapodagrionidae and Libellulidae had the highest similarity between the two sites, whereas Coenagrionidae and Platycnemididae had fairly dissimilar community composition. Three families occurred only in the natural forest. The most important habitats in the village were open sunny areas, artificial ditches, and small permanent creeks, compared to most running waters and the forest interior in the natural forest. Based on habitat preferences in the natural forest, species inhabiting temporary water sources under closed canopy rainforests are most vulnerable to forest modification. They comprised a third of the forest community, and I estimate that approximately 25% of natural rainforest species will disappear following human-induced forest alteration.

Introduction

Anthropogenic changes to tropical forest ecosystems have a large impact on native arthropod communities (Brown 1991). Deforestation is seen as a major threat to the conservation of odonate diversity in tropical forest landscapes worldwide (Clausnitzer 2004; Dijkstra & Vick 2004; Orr 2004; Paulson 2004; Rowe 2004).

In most cases, alteration or removal of the primary forest will lead to a reduction in species diversity and abundance, and communities in disturbed habitat will often be comprised of eurytopic and widespread generalists (Hill et al. 1995; Samways & Steytler 1996; Stewart & Samways 1998; Fermon et al. 2000; Willott et al. 2000; Clausnitzer 2003; Cleary et al. 2005). The influence of alterations on invertebrate communities is, however, difficult to predict. Disturbance may cause decreases or increases of species diversity in a certain area, as habitat modification may provide habitat for non-forest species (Owen 1971; Clausnitzer 2003; Ferreira-Peruquetti & Fonseca-Gessner 2003; Cleary et al. 2004; Hill & Hamer 2004). Furthermore, habitat modification may have different effects on species at different trophic levels (Petchey et al. 2004), and results of one taxon are generally imprecise predictors for effects on other taxa (Lawton et al. 1998). Studies on the impact of different forms of human forest modification on a variety of invertebrate groups are therefore urgently needed.

Papua New Guinea (PNG) is known for its very high biodiversity in many taxa, probably due to a rugged mountainous landscape that enhances local endemism (Lieftinck 1942, 1949; Heads 2001, 2002). The odonate fauna of PNG is poorly studied, and distribution and habitat requirements of many species are unknown (Brooks & Richards 1992; Polhemus 1995; Mack 1998; Rowe 2004). As in many other tropical countries the human population in Papua New Guinea is growing rapidly. This increases the pressure on the remaining natural areas and water sources (Henderson 1997). Human modification of the landscape usually results in deforestation and degradation of streams and rivers as a result of pollution and erosion, with negative consequences for stream-dwelling organisms (Timm et al. 2001; Buss et al. 2002).

In this study I compared the Odonata communities of a natural tropical rainforest and a nearby village. The village was characterised by subsistence gardening and small-scale forest clearing, and thus represented a typical modification of the forest landscape following human population growth and expansion. Besides comparing the communities as a whole and on the family level, I recorded habitat use of all species to determine which habitat types host assemblages most vulnerable to deforestation. The results are discussed to highlight habitats and species of the highest conservation concern.

Material and methods

Study location

The two study sites were situated in the Crater Mountain Wildlife Management Area (6°43’S, 145°05’E), a 2,700 km² tract of continuous rainforest on the southern scarp of the central mountain range of Papua New Guinea. The climate at the two sites was stable throughout the year, and both rainfall and temperature did not exhibit seasonal patterns. The natural study site (Crater Mountain Biological Research Station – CMBRS) covered ca 2.5 km², ranging from 850 m to 1,300 m a.s.l., with aseasonal rainfall of ca 6.5 m per annum (Wright et al. 1997). The site was entirely forested, except a small clearing for the research station and a helicopter landing pad. Water sources included one small, fish-free pond (0.25 ha), as well as innumerable streams and rivers with a high variability of flow rate, depending on rainfall. The forest floor was moist and muddy, and puddles formed quickly after rain and persisted for several days.

The village of Herowana was ca 10 km east of CMBRS, and consisted of a small grassy airstrip, subsistence gardens, small coffee plantations and scattered huts comprising an area of ca 4 km^2. Native primary and secondary forest was still present, but had been degraded by cutting. The village was ca. 1,300 m in elevation and featured several creeks and ditches, as well as a fish-free pond in semi-natural forest and a sedge swamp in abandoned gardens. The gardens were situated along a deep river valley, which descended to an elevation of 950 m a.s.l. Thus, the village site was on average at a slightly higher elevation. Open areas had mainly firm clay soil where puddles formed after rain and persisted for several days.

Sampling methods

I sampled odonates at CMBRS between November 2003 and August 2004, and in Herowana from July through August and in October 2004. Due to the aseasonal climate I assumed that the little temporal overlap of sampling periods did not significantly alter my results. The sampling period at CMBRS was about three times as long (112 days) as in Herowana (36 days). Due to a higher proportion of rare species the species richness of natural tropical forests is often underestimated at a given level of sampling effort (Morse et al. 1988; Godfray et al. 1999). Preliminary analysis suggested that the species accumulation curves of both sites showed a similar asymptotic tendency at the end of each sampling period (Oppel 2005). Species accumulation curves are useful tools to standardize results from areas with unequal sampling effort (Moreno & Halffter 2000; Willott 2001; Ugland et al. 2003; Colwell et al. 2004), and I conclude that the different sampling effort does not have a significant effect on the results.

Sampling was carried out by slowly walking through all habitat types. Specimens were collected with butterfly nets and killed in jars with ethanol. They were stored in paper envelopes and kept in a box filled with silica gel and naphthalene. J. Michalski (Morristown, USA) and T.W. Donnelly (Binghampton, USA) examined the specimens, and a number of species still awaits formal identification or description.

I defined 10 distinct habitat types to record habitat use: open sunny areas without water (habitat type 1); forest interior without obvious surface water (2); temporary puddles in the forest interior (3); temporary puddles in open sunny areas (4); fish-free permanent pond (5); large, open and sunny river > 8 m wide (6), small, partially shaded river 4-8 m wide (7); small, permanent, mostly shaded creek 1-4 m wide (8); small, temporary creek in the forest < 1 m wide (9); and artificial ditch (10). The water in all running water sources (habitat types 6-9) was normally clear, except after heavy rain when waters were murky due to the sediment load. For every encounter with an adult odonate the habitat type and the number of individuals were recorded.

Analysis

To estimate total species richness I used the first-order jackknife estimator (Heltshe & Forrester 1983), as this was the most accurate and least biased estimator in a comparison of several procedures (Palmer 1990). I divided the species list of each area into shared species (shared with the other area) and only species (not shared with the other area), and calculated the percentage of shared and only species per habitat type. I then compared the communities of both sites using a new derivative of Jaccard's similarity index that is robust towards unequal sampling size (Chao et al. 2005). This index uses the relative abundance of all shared species, and I calculated similarity indices for all families and all habitat types using the total number of individuals per family or habitat type to calculate relative abundances. I assigned every species to a 'preferred' habitat type, even though a measure of habitat availability, required for true preference analysis (Jones 2001), was not feasible in this study. I defined 'preferred habitat' as the habitat type where the species was most commonly found, and omitted species with equal proportions of observations in different habitat types. Similarity indices, evenness, and species richness estimators were calculated using the program EstimateS (Colwell 2004), using the first-order jackknife estimate procedure.

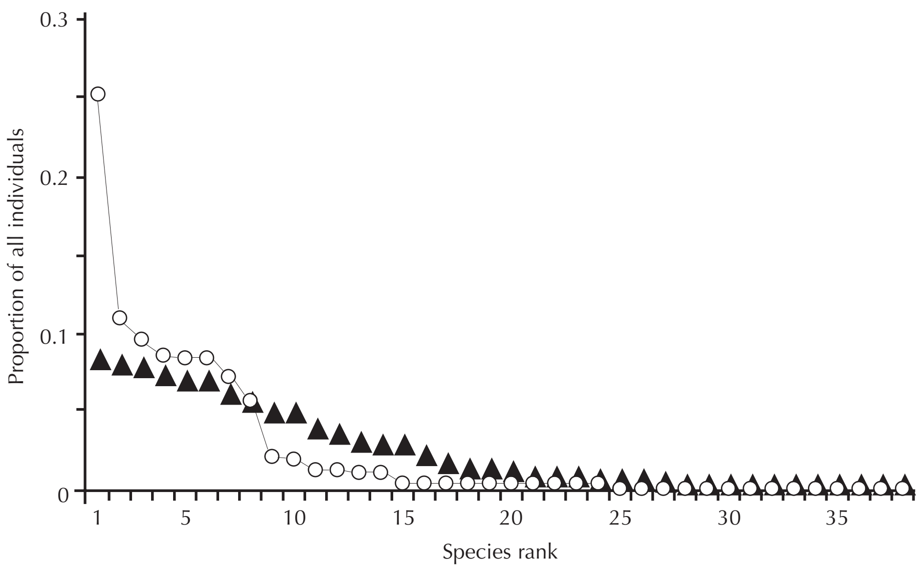

Figure 1: Rank-abundance curves for Odonata species — ▲ in natural rainforest (CMBRS: Crater Mountain Biological Research Station), and ○ in modified rainforest (Herowana) in the Crater Mountain Wildlife Management Area, Papua New Guinea, in 2004. Note that for simplicity only the first 38 species are shown at CMBRS. See Table 2 for species identities.

Table 1. Inventory data of the two odonate communities — from a natural rainforest (CMBRS: Crater Mountain Biological Research Station), and a modified rainforest (Herowana) in the Crater Mountain Wildlife Management Area, Papua New Guinea, in 2004.

	CMBRS	**Herowana**
Number species	61	38
Number families	13	10
Anisoptera	16 (27%)	9 (24%)
Zygoptera	45 (73%)	29 (76%)
Species total	78	
Shared species	21	
Species locally endemic	40	17
Jaccard Abd. (Chao et al. 2005)	0.477	
Simpson-Index	11.48	8.59
Evenness	0.804	0.715

Results

Community comparison

I recorded a total of 78 species from 13 families in both study areas together, with 21 species occurring both in Herowana and at CMBRS (Table 1). A complete species list of the two areas is given in Table 2. The natural rainforest site had a higher number of species and families, and a higher evenness. A rank-abundance curve showed that the eight most common species contained a higher proportion of individuals in Herowana than at CMBRS (Fig. 1). Both areas had about three times as many Zygoptera species as Anisoptera species.

The estimated species richness calculated was 73 (± 3.55 s.d.) species at CMBRS and 53 (± 4.14 s.d.) species in Herowana. The observed species richness was therefore 84% and 72% of the estimated species richness at CMBRS and in Herowana, respectively. The estimator of the Jaccard abundance index including shared unseen species was 0.503.

For any given individual from either community, the chance that it belonged to a shared species was 0.477 (Jaccard Abundance-Index, Table 1). The similarity of the two communities was marginally different for Anisoptera (0.449) and for Zygoptera (0.499), but differed widely between families. Four families with one member each occurred in both study areas and had therefore a similarity of 1.0 (Calopterygidae, Chlorocyphidae, Protoneuridae, and Aeshnidae). Three families occurred only at CMBRS (Lestidae, Platystictidae, and Synthemistidae), and one family (Isostictidae) did not have a species common between the two study areas. Among the remaining families the Megapodagrionidae had a very high proportion of shared species individuals (0.724), followed by the Libellulidae (0.491). Coenagrionidae, Platycnemididae, and Corduliidae had dissimilar assemblages in the two study areas with similarities of 0.193, 0.144 and 0.145, respectively.

Table 2. List of all Odonata species — recorded in natural rainforest (CMBRS: Crater Mountain Biological Research Station), and in modified rainforest (Herowana) in the Crater Mountain Wildlife Management Area, Papua New Guinea, in 2004. For every species the preferred habitat type, number of observed individuals (no.) and the abundance rank are given. See text for the definition of preference. Species without preferred habitat type occurred in equal proportions in different habitat types. Note that abundances result from different sampling periods in the two study areas and might not be comparable in absolute terms.

Species name	**CMBRS**			**Herowana**		
	Preferred habitat	No.	Rank	Preferred habitat	No.	Rank
Calopterygidae						
Neurobasis sp. nov.	8	207	1	8	52	7
Chlorocyphidae						
Rhinocypha tincta Rambur	8	58	13	8	66	4
Lestidae						
Indolestes tenuissimus Tillyard	5	132	7		0	
Megapodagrionidae						
Argiolestes kirbyi Förster	7	78	10	8	76	3
microstigma Lieftinck	8	23	19		0	
saltuarius Lieftinck		0		8	16	9
sidonia Martin	8	40	16	8	14	10
sp. nov. A	7	9	28	10	3	19
sp. nov. B	9	3	39		0	
sp. C	9	2	45	8	6	15
sp. D	2	45	1	1	26	
Podopteryx selysi Förster	2	3	39		0	
Coenagrionidae						
Palaiargia charmosyna Lieftinck		0		2	2	21
halcyon Lieftinck		0		6	1	26
sp. A	8	3	39	8	1	26
sp. B	0		10	2	21	
Papuagrion auriculatum Lieftinck		0		1	1	26
degeneratum Lieftinck		0		8	1	26
flavipedum Lieftinck		0		10	1	26
occipitale Selys		0		8	1	26
sp. nov. A	2	6	35		0	
sp. B	2	10	25	1	1	26
sp. C	7	2	45		5	17
sp. D	8	32	10	2	21	
Pseudagrion sp. A		7	1	53		0
sp. B	9	1	53		0	
sp. nov. C		0		8	13	11
Teinobasis dominula Lieftinck		0		4	1	26
scintillans Lieftinck	9	43	15	10	90	2
sp. A	8	1	53		0	
sp. B	7	34		0		
sp. C	5	85	9		0	
sp. D	3	1	53		0	
stigmatizans Lieftinck		0		10	2	21
Xiphiagrion cyanomelas Selys	5	151	6		0	
truncatum Lieftinck		0		5	10	12

Species name	**CMBRS**			**Herowana**		
	Preferred habitat	No.	Rank	Preferred habitat	No.	Rank
Isostictidae						
Selysioneura cornelia Lieftinck	7	17	21		0	
sp. A	1	53		0		
sp. nov. B		0		8	1	26
Platycnemididae						
Arrhenicnemis sp.	9	1	53		0	
Idiocnemis australis Gassmann	2	11	24		0	
leonorae Lieftinck		8	32		0	
obliterata Lieftinck	3	9	28		0	
strumidens Lieftinck	2	62	12		0	
Paramecocnemis stilla-cruroris Lieftinck	0		7	1	26	
Rhyacocnemis prothoracica Lieftinck	19	20	10	3	19	
Torrenticnemis filicornis Lieftinck		0			1	26
Gen. nov., sp. nov.	8	9	28		0	
Platystictidae						
Drepanosticta sp. A	2	12	23		0	
sp. B	7	2	45		0	
sp. C	7	4	38		0	
sp. D	6	3	39		0	
sp. E	9	5	37		0	
sp. F	7	1	53		0	
sp. G	9	1	53		0	
sp. H	9	9	28		0	
sp. I	7	2	45		0	
sp. J	8	2	45		0	
sp. K	2	1	53		0	
Protoneuridae						
Nososticta finisterrae Förster	7	190	5	8	44	8
Aeshnidae						
Anax selysi Förster	5	101	8	4	8	13
Corduliidae						
Macromia sp.	6	33	18	1	2	21
Procordulia leopoldi Fraser	5	194	2		0	
Synthemistidae						
Synthemis primigenia Förster	3	3	39		0	
Libellulidae						
Agrionoptera longitudinalis Selys	9	6	35		5	17
Bironides glochidion Lieftinck	8	3	39		0	
Diplacina callirrhoe Lieftinck	8	10	25	2	8	13
smaragdina Selys	6	36	17		0	
Huonia hylophila Lieftinck		0		10	59	6
epinephela Förster	6	194	3		0	
Nannophlebia amphicyllis Lieftinck	7	53	14		1	26
Neurothemis stigmatizans Fabricius	1	13	22		0	
Orthetrum glaucum Brauer	1	64	11	4	66	4
sp.	6	2	45		0	
villosovittatum Brauer	5	192	4	10	193	1
Pantala flavescens Fabricius		0		1	6	15
unidentified libellulid A	5	2	45		0	
unidentified libellulid B	5	10	25		0	

Habitat use comparison

In Herowana the most species-rich habitat types were ditches, small permanent creeks, and open sunny areas (Table 3). These three habitats also served as preferred habitat for 68% of all species (Fig. 2). At CMBRS, running water sources had the highest species richness, ranging from 18 species in small temporary creeks to 26 in small permanent creeks (Table 3). The distribution of preferred habitats was more balanced at CMBRS than in Herowana, with five habitat types being equally important (Fig. 2). These were the forest interior, the pond, small rivers, and small permanent and temporary creeks. They served as preferred habitat for 79% of all species.

The similarity of habitat specific odonate assemblages was generally smaller than the overall community similarity. In the forest interior and in sunny puddles, similarity was zero as no shared species occurred in those habitats in Herowana. Puddles in the forest and big rivers also had very low similarities of 0.090 and 0.145, respectively. The remaining habitat types had similarities ranging from 0.245 (pond) to 0.461 (small rivers).

In Herowana, more than half of the species preferring open sunny areas, the forest interior, sunny puddles, small permanent creeks and ditches also occurred at CMBRS. The remaining species in Herowana, showing a preference for the pond, large and small rivers did not occur at CMBRS. At CMBRS the distribution of shared and only species was different, and the highest ratio of shared species was found in small rivers (45%), small permanent creeks (50%), and in open sunny areas (50%). Only one (13%) and three (33%) of those species preferring the forest interior and small temporary creeks at CMBRS were shared with the site in Herowana.

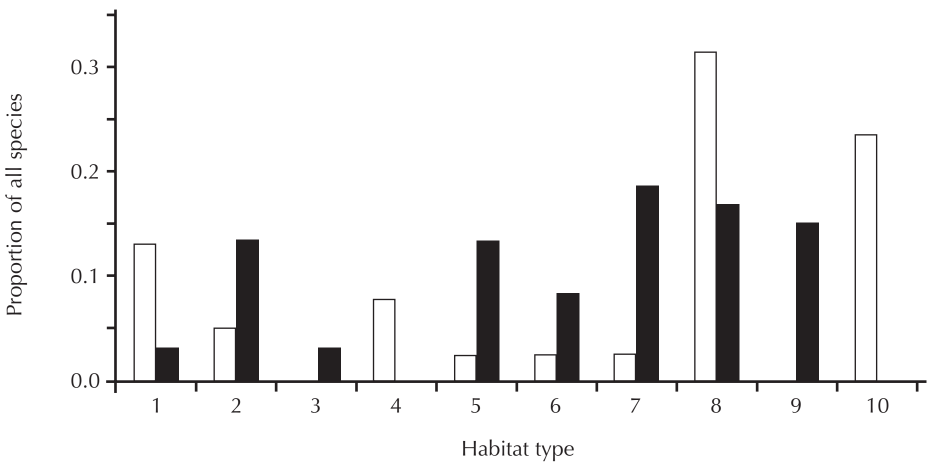

Figure 2: Proportion of all Odonata species preferring a particular habitat type — □ in modified rainforest (Herowana), and ■ in natural rainforest (CMBRS: Crater Mountain Biological Research Station), Crater Mountain Wildlife Management Area, Papua New Guinea, in 2004. See text for definition of habitat types and preference.

Table 3. Number of species occurring in and preferring each habitat type — in a natural rainforest (CMBRS: Crater Mountain Biological Research Station), and in a modified rainforest (Herowana) in the Crater Mountain Wildlife Management Area, Papua New Guinea, in 2004. Shared species indicates the number of identical species occurring in a particular habitat type in both study areas. Preferred habitat is defined as the habitat type in which the most individuals of a species were found (see text for details).

Habitat type		**CMBRS**		**Herowana**	
	Shared species	Occurring	Preferring	Occuring	Preferring
Open sunny areas (1)	2	5	2	16	5
Forest interior (2)	0	11	8	6	2
Puddles in the forest interior (3)	1	7	2	8	0
Puddles in open sunny areas (4)	0	2	0	9	3
Pond (5)	2	8	8	4	1
Big river (6)	4	13	5	10	1
Small river (7)	3	21	11	5	1
Small permanent creek (8)	5	26	10	17	12
Small temporary creek (9)	3	18	9	7	0
Ditch (10)	0	0	0	21	9

In Herowana, the two most species-rich habitat types (small permanent creeks and ditches) hosted 53% of the only species, whereas at CMBRS five habitat types (forest interior, forest puddles, pond, small rivers, small temporary creeks) had fairly equal proportions of only species and a total of 63%. The forest interior had the largest proportion of only species (18% of all only species).

Discussion

The odonate community in the natural rainforest at CMBRS is more diverse in species than in the modified forest and garden landscape in Herowana. Even though a longer sampling period in Herowana might have led to a higher number of recorded species, the estimated species richness suggests that the natural forest would still harbor substantially more species.

Overall species diversity of the two sites was high, especially when compared with studies of larger areas in Africa (Samways 1989; Clausnitzer 1999; Vick 1999, 2002; Dijkstra & Lempert 2003) and the Neotropics (Novelo Gutiérrez et al. 1988; de Marmels 1998; Ramírez et al. 2000; Paulson 2002). Species turnover between the sites was much lower than between the natural forest and another primary forest survey in the Lakekamu Basin in lowland PNG (Mack 1998), ca 200 km to the south-east. While decreasing similarity between distant sites is a common biogeographic pattern (Nekola & White 1999; Arita & Rodriguez 2002; Cleary & Genner 2004), it might also indicate that rates of local endemism in PNG could be equally high as in similar environments in South-East Asia (Orr 2003, 2004). This hypothesis might also be supported by the fact that species preferring larger watercourses in Herowana were absent from structurally very similar rivers at CMBRS, although anisopterans are generally good dispersers that should be able to colonize areas only 10-15 km apart.

The dominance structure of the community in Herowana was more skewed than at CMBRS, resulting in a lower evenness score. This indicates that the modification of the rainforest results in an altered species assemblage, where a few generalist species benefit from large open areas and achieve dominance in the odonate community (Samways & Steytler 1996; Stewart & Samways 1998; Clausnitzer 2003). Many libellulids are known to be eurytopic generalists occurring over large geographic ranges (Silsby 2001). The family Libellulidae had a fairly high proportion of shared species between the two study sites, and the two most common species in Herowana (*Orthetrum villosovittatum* and *O. glaucum*) were together with *Agrionoptera longitudinalis* also present in the survey at Lakekamu Basin (Mack 1998). Coenagrionidae and Platycnemididae had very low similarity scores. This might be a result of the high diversification within these families, which would confine most species to a very narrow ecological niche or geographic area. As a consequence, the ecological differences between CMBRS and Herowana will cause a relatively high species turnover within those families. The absence of the genus *Drepanosticta* from Herowana is, however, intriguing. While the species limits of this genus are currently unresolved (Orr 2004), the variety of habitats in which morphospecies of this genus were found suggests that the genus is adaptable to a broad spectrum of habitats.

Open sunny areas, artificial ditches, and temporary puddles in sunny areas were much more widespread and preferred by more species in Herowana than at CMBRS. In the natural forest the range of habitats preferred was wider and more evenly distributed, with species-rich assemblages found in running waters (rivers and creeks) as well as in the forest interior.

The species recorded in the forest interior away from obvious water sources might have been either foraging, or might depend on phytotelmata or water-filled tree-holes, as is known from other tropical regions (Lounibos et al. 1987; Kitching & Orr 1996; Louton et al. 1996; Clausnitzer 1997; Kitching 2000; Yanoviak 2001). *Podopteryx selysi* is known as a phytotelmata specialist (Kitching 2000), and this species was absent from Herowana. Most of the forest interior and small temporary water species at CMBRS did not occur in Herowana. Species depending on a closed canopy and temporary water sources are most susceptible to forest modification (Clausnitzer 2003), and the modification of the rainforest in Herowana might have led to drier conditions that do not meet the moisture requirements of certain species (Holdsworth & Uhl 1997; Silsby 2001; Cleary et al. 2004). Half of the species occupying the permanent creeks at CMBRS were also present in Herowana, indicating that these species are more tolerant to minor habitat modifications than species depending on temporary water sources.

Reduced shading of the water course may lead to an upward shift of certain species in disturbed landscapes (Korkeamäki & Suhonen 2002; Dijkstra & Lempert 2003). Species that are not dependent on a closed canopy may therefore tolerate habitat modification by moving upstream into shadier sections of the watercourse. Opening of the canopy along creeks may benefit species that are naturally limited by the availability of sunny areas along creeks. In Herowana, some creek species like *Rhinocypha tincta* were more abundant than in the natural forest, maybe as a result of extended creek sections being exposed to sunlight.

This study corroborates previous findings that deforestation and habitat disturbance lead to a lower β-diversity, and a species turnover towards more widespread generalists (Hill et al. 1995; Stewart & Samways 1998; Willott et al. 2000; Clausnitzer 2003; Samways 2003; Cleary et al. 2005). The higher dominance of generalist predators may furthermore cause a suppression of smaller species suffering from increased predation, especially in the larval stages (Cleary et al. 2004).

In this study, species associated with temporary puddles in the forest, small temporary creeks, and the forest interior comprised almost a third of the total odonate assemblage in the natural rainforest, and most of them could not be found in the modified forest. This suggests that modification of the forest caused by human subsistence gardening may lead to a loss of approximately 25% of the species associated with closed canopy forest habitats.

Given the potential for high levels of local endemism in PNG, forest modification might render many rainforest odonates vulnerable to extinction (Korkeamäki & Suhonen 2002). Conservation of these species will be difficult if only a few large nature reserves are set aside, which might be outside the natural range of many species. Conservation of odonates in PNG is therefore dependent on the preservation of natural rainforests in all parts of the country.

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