

PROTECTING AQUATIC DIVERSITY IN DEFORESTED TROPICAL LANDSCAPES

Clare Lucy Wilkinson

Division of Ecology and Evolution

Department of Life Sciences

Imperial College London

&

Department of Biological Sciences

National University of Singapore

A thesis submitted for the degree of Doctor of Philosophy

2018

COPYRIGHT DECLARATION

The copyright of this thesis rests with the author and is made available under a Creative Commons Attribution Non-Commercial No Derivatives licence. Researchers are free to copy, distribute or transmit the thesis on the condition that they attribute it, that they do not use it for commercial purposes and that they do not alter, transform or build upon it. For any reuse or distribution, researchers must make clear to others the license terms of this work.

ABSTRACT

Global biodiversity is being lost due to extensive, anthropogenic land-use change. In Southeast Asia, biodiversity-rich forests are being logged and converted to oil-palm monocultures. The impacts of land-use change on freshwater ecosystems and biodiversity, remains largely understudied and poorly understood. I investigated the impacts of logging and conversion of tropical forest in 35 streams across a land-use gradient on freshwater fishes, a useful biotic indicator group, and a vital provisioning ecosystem service. This research was extended to quantify the benefits of riparian reserves in disturbed landscapes, and examine the interaction of land-use change with extreme climatic events.

There are four key findings from this research. (1) Any modification of primary rainforest is associated with a loss of fish species and functional richness. (2) Streams in oil-palm plantations with riparian reserves of high forest quality, and a width of > 64m on either side, retain higher species richness and higher abundances of individual fish species. (3) Although relatively low in species richness, streams in oil-palm plantations retain high biomass of freshwater fish that is readily captured using cast nets (the primary method used by local people), providing an important protein source and supplementary income to local communities. (4) An extreme El Niño drought interacted antagonistically with land-use change, reducing the capture rate of *N. everetti*, one of the most common species in my study area.

These results illustrate the critical impacts of land-use change on tropical freshwater ecosystems, and highlight the need to ensure riparian reserves are retained and primary forested areas are protected. Such actions will be needed to maintain freshwater diversity in modified tropical landscapes. Despite the impacts on fish communities due to land-use change, abundant, tolerant species appear to be resilient to climate-based stressors, while fish in headwater streams represent a sustainable food-resource for communities in human-modified landscapes.

ACKNOWLEDGEMENTS

This research was funded by a Joint studentship scholarship between Imperial College London and the National University of Singapore. Additional funding for research activities was provided by: the Stability of Altered Forest Ecosystems (SAFE) Project, through their funder Sime Darby for logistical support in Borneo, Royal Geographic Society, Landmark Trust and Imperial College London's Department of Life Sciences Travel grants.

Permission, for which I am very grateful, was given to conduct this research and export samples from Sabah Biodiversity Council (SaBC), Maliau Basin Management Committee (including Waidi Sinun and Rose John Kidi), Danum Valley Management Committee, Royal Society Southeast Asia Rainforest Research Programme (RS-SEARRP), Yayasan Sabah, Sabah Forestry Department, Benta Wawasan, and the Stability of Altered Forest Ecosystems (SAFE) Project. I would also like to thank Henry Bernard and Arman Hadi Fikir for being my local collaborators in Sabah, Malaysia, and for their help and advice with permission applications and my research.

I am eternally grateful to all of the SAFE project staff and researchers who have helped me with my research. In particular: Ryan Gray who provided huge amounts of logistical support, delicious food, drinks and always a friendly face; Research Assistants: Kiel Jahuri, James Loh and Wash for their tireless work in the field, putting up with me for 18 months of field work and the blood (leeches), sweat and tears that tried to get in the way; and all the researchers at the SAFE project that make life at the field camp an enjoyable place to be, with extra mentions to Adam Sharp, Philip Chapman, Michael Boyle, Nichar Gregory, Elizabeth Telford, Victoria Kemp for all the laughs, drinks, running, yoga and badminton fun times. In addition, Sarah Luke, who provided invaluable help and advice about work on freshwater streams, and aided in the design of this project and who's work is cited in everything I have written.

I would like to acknowledge the enormous amount of help and support provided by my supervisors Rob Ewers, Darren Yeo and Tan Heok Hui. Thank you for all the ideas, discussions, and general life advice that you have provided over the last four years. Thanks to Heok Hui for a great week in the field that led to the development of the Brantian catchment checklist, and to Darren for supporting my time in Singapore. I am also grateful for the insightful feedback and advice from Guy Woodward, Cris Banks-Leite and David Orme during my PhD.

For everyone, past and present, in the Forest Ecology and Conservation lab group in London and the Freshwater and Invasive Biology lab group in Singapore, thank you for making my time in these two

places a wonderful experience, where I have made friends for life. It has been a pleasure to work with you all, and thank you so much for the advice with R code (Adam Sharp and Phil Chapman), discussions, debates, as well as the many group lunches and drinks that we have shared. In addition, thank you to Marion Pfeifer for providing all remotely sensed satellite imagery and processed files of above ground biomass.

Lastly, a huge thank you for my friends and family who are always there for me, through the highs and lows of PhD life, and tolerating the many months of absence while I am away doing fieldwork. I hope that the many exotic holiday locations make up for this in some way.

DECLARATION OF ORIGINALITY

I certify that all material within this thesis is solely the result of my own work, except for the following exceptions. I therefore refer to 'we' instead of 'I' throughout.

Chapter 1: R. M. Ewers and D. C. J. Yeo commented on an earlier draft of this chapter.

Chapter 2: R. M. Ewers, D. C. J. Yeo and Tan H. H. provided detailed comments on this chapter. C. Ng, an anonymous reviewer and P. Boon also greatly helped to improve the manuscript during submission to *Aquatic conservation: Marine and Freshwater*.

Chapter 3: R. M. Ewers, D. C. J. Yeo and Tan H. H. provided comprehensive comments on this chapter. X. Giam and an anonymous reviewer also provided significant helpful comments to improve the manuscript during submission to *Conservation Biology*.

Chapter 4: R. M. Ewers, D. C. J. Yeo, Tan H. H. and C. D. J. Orme provided extensive comments on an earlier version of this chapter.

Chapter 5: R. M. Ewers, D. C. J. Yeo, and Tan H. H. provided helpful comments on an earlier version of this chapter. P. Chapman provided helpful insights into the analysis using spatially explicit mark recapture models.

Chapter 6: R. M. Ewers and D. C. J. Yeo provided comments on this chapter.

Appendix 1: Tan H. H. has commented on and put considerable amount of work into this manuscript.

TABLE OF CONTENTS

COPYRIGHT DECLARATION.....	iii
ABSTRACT.....	iv
ACKNOWLEDGEMENTS.....	v
DECLARTION OF ORIGINIALITY.....	vii
TABLE OF CONTENTS.....	viii
LIST OF TABLES.....	xi
LIST OF FIGURES.....	xii
CHAPTER 1: INTRODUCTION: IMPACTS OF LAND-USE CHANGE ON AQUATIC BIODIVERSITY	1
1.1. FRESHWATER ECOSYSTEMS	1
1.1.1. THE IMPORTANCE OF FRESHWATER ECOSYSTEMS	1
1.1.2. THREATS TO FRESHWATER ECOSYSTEMS.....	2
1.2. AGRICULTURAL EXPANSION AND LAND-USE CHANGE.....	4
1.2.1. GLOBAL EXPANSION AND CHANGE	4
1.2.2. LAND-USE CHANGE IN SOUTHEAST ASIA.....	5
1.3. IMPACTS OF LAND-USE CHANGE ON FRESHWATER ECOSYSTEMS	7
1.3.1. IMPACT OF SELECTIVE-LOGGING	7
1.3.3. IMPACT OF CONVERSION TO OIL-PALM PLANTATION	8
1.4. MITIGATING THE IMPACTS OF LOGGING AND OIL-PALM ON FRESHWATER ECOSYSTEMS.....	9
1.4.1. RIPARIAN RESERVES	9
1.4.2. THE ROUNDTABLE ON SUSTAINABLE PALM OIL (RSPO)	12
1.5. FRESHWATER FISH.....	13
1.5.1. FISH AS A FOCAL TAXA	13
1.5.2. IMPACT OF LAND-USE CHANGE ON FRESHWATER FISH.....	16
1.6. SAMPLING METHODS, DESIGN AND STUDY SITE	17
1.6.1. STUDY SITE: THE STABILITY OF ALTERED FOREST ECOSYSTEMS (SAFE) PROJECT	17
1.6.2. LAND USE GRADIENT	17
1.6.3. FISHING METHODS AND SAMPLING DESIGN	19
1.7. RESEARCH AIMS AND OBJECTIVES	22
1.8. THESIS CHAPTER OUTLINE.....	22
CHAPTER 2: FRESHWATER FISH RESOURCE AVAILABILITY IS MAINTAINED ACROSS A LAND-USE GRADIENT IN SABAH, BORNEO	24
ABSTRACT	24
2.1. INTRODUCTION	25

2.2. METHODS	29
2.2.1. STUDY SITE	29
2.2.2. FISH SAMPLING.....	29
2.2.3. FISH COMMUNITY METRICS	31
2.2.4. FOCAL FOOD SPECIES.....	31
2.2.5. ANALYSIS.....	32
2.3. RESULTS	35
2.3.1. FISH COMMUNITY METRICS	35
2.3.2. FOCAL FOOD SPECIES.....	37
2.4. DISCUSSION	39
CHAPTER 3: LAND-USE CHANGE IS ASSOCIATED WITH A SIGNIFICANT LOSS OF FRESHWATER FISH SPECIES AND FUNCTIONAL RICHNESS IN SABAH, MALAYSIA	44
ABSTRACT.....	44
3.1. INTRODUCTION	45
3.2. METHODS	48
3.2.1. STUDY SITE	48
3.2.2. FISH SAMPLING	50
3.2.3. ENVIRONMENTAL VARIABLES.....	51
3.2.4. FISH COMMUNITY METRICS	51
3.2.5. DATA ANALYSIS	52
3.3. RESULTS	54
3.4. DISCUSSION	59
CHAPTER 4: RIPARIAN RESERVES: RETAINING HIGH FOREST QUALITY IS ESSENTIAL FOR FRESHWATER FISH	64
ABSTRACT.....	64
4.1. INTRODUCTION	65
4.2. MATERIALS AND METHODS.....	68
4.2.1. STUDY SITE	68
4.2.2. RIPARIAN VARIABLES	70
4.2.3. FISH SAMPLING	71
4.2.4. FISH COMMUNITY AND SPECIES ABUNDANCE RESPONSE VARIABLES	72
4.2.5. DATA ANALYSIS	72
4.3. RESULTS	74
4.3.1. RIPARIAN VARIABLES	74
4.2.3. COMMUNITY LEVEL	74
4.2.4. SPECIES LEVEL	77

4.4. DISCUSSION	79
CHAPTER 5: RESILIENCE OF A TROPICAL FRESHWATER FISH SPECIES (<i>NEMATABRAMIS EVERETTI</i>) TO SEVERE, DROUGHT-INDUCED DISTURBANCE OVER A LAND-USE GRADIENT IN SABAH, MALAYSIA.....	83
ABSTRACT	83
5.1. INTRODUCTION	84
5.2 METHODS	87
5.2.1. STUDY SITE	87
5.2.2. FISH SAMPLING	88
5.2.3. ENVIRONMENTAL VARIABLES	90
5.2.4. RESPONSE METRICS	90
5.2.5. ANALYSIS	92
5.3. RESULTS	92
5.3.1. ENVIRONMENTAL VARIABLES	92
5.3.2. EFFECTS ON <i>N. EVERETTI</i>	93
5.4. DISCUSSION	99
CHAPTER 6: GENERAL DISCUSSION: IMPACTS OF LAND-USE CHANGE ON AQUATIC BIODIVERSITY	103
OVERVIEW	103
6.1. PRIMARY RAINFORESTS ARE IRREPLACEABLE	104
6.2. EFFICACY OF RIPARIAN RESERVES AND OTHER MANAGEMENT OPTIONS	106
6.3. RESILIENCE OF FRESHWATER FISH TO MULTIPLE STRESSORS.....	109
6.4. RECOMMENDATIONS FOR FUTURE MANAGEMENT.....	111
6.5. LIMITATIONS & FUTURE RESEARCH	113
6.6. CONCLUSIONS	114
BIBLIOGRAPHY.....	115
APPENDIX	135
APPENDIX 1 – RASBORA PYCONOPIZA, A NEW SPECIES OF CYPRINID FISH FROM EASTERN SABAH, WITH AN ANNOTATED CHECKLIST OF THE FISHES OF THE BRANTIAN DRAINAGE, KALABAKAN, SABAH, MALAYSIA.....	135
APPENDIX 2 – FOR CHAPTER 2	165
APPENDIX 3 – FOR CHAPTER 3	167
APPENDIX 4 – FOR CHAPTER 4	179
APPENDIX 5 – FOR CHAPTER 5	198

LIST OF TABLES

CHAPTER 2

TABLE 2.1. FULL SPECIES LIST	35
------------------------------------	----

CHAPTER 3

TABLE 3.1. RESULTS OF REDUNDANCY ANALYSIS	58
-------------------------------------------------	----

CHAPTER 5

TABLE 5.1. SUMMARY OF STREAM ENVIRONMENTAL VARIABLES BY YEAR.....	95
-------------------------------------------------------------------	----

TABLE 5.2. MIXED MODEL OUTPUTS OF ENVIRONMENTAL MODELS BY LAND-USE, DROUGHT & INTERACTION	96
-------------------------------------------------------------------------------------------------	----

LIST OF FIGURES

CHAPTER 1

FIGURE 1.1. INTERACTIONS AMONG FRESHWATER ECOSYSTEMS	4
FIGURE 1.2. PHOTOS OF SAMPLING TRANSECTS ACROSS A LAND-USE GRADIENT	19
FIGURE 1.3. SCHEMATIC AND MAP SHOWING STUDY AREAS IN SABAH	21

CHAPTER 2

FIGURE 2.1. SCHEMATIC AND MAP SHOWING STUDY AREAS IN SABAH	33
FIGURE 2.2. PHOTOS OF SAMPLING RANSECTS ACROSS A LAND-USE GRADIENT	34
FIGURE 2.3. EFFECT OF LAND COVER ON SPECIES RICHNESS AND BIOMASS	36
FIGURE 2.4. EFFECT OF LAND-USE ON FIVE FOCAL SPECIES	38

CHAPTER 3

FIGURE 3.1. SCHEMATIC AND MAP SHOWING STUDY AREAS IN SABAH	49
FIGURE 3.2. EFFECT OF LAND-USE ON SPECIES AND FUNCTIONAL RICHNESS.....	55
FIGURE 3.3. ORDINATION OF FISH COMMUNITY COMPOSITION	57
FIGURE 3.4. RELATIONSHIP BETWEEN SPECIES RICHNESS AND LEAF LITTER OR GRAVEL	58

CHAPTER 4

FIGURE 4.1. RELATIONSHIPS OF COMMUNITY VARIABLES WITH RIPARIAN VARIABLES	74
FIGURE 4.2. SUMMARY OF REGRESSION TREES.....	75
FIGURE 4.3. RELATIONSHIP OF FOREST QUALITY ON ABUNDANCE OF 20 SPECIES.....	77

CHAPTER 5

FIGURE 5.1. PHOTOS OF STREAMS ACROSS THE LAND-USE GRADIENT, BEFORE, DURING & AFTER DROUGHT.....	89
FIGURE 5.2. THE IMPACT OF LAND-USE, DROUGHT & INTERACTION ON FISH DENSITY, BIOMASS & DISTANCE MOVED.....	97
FIGURE 5.3. IMPACT OF TIME SINCE LAST CAPTURE ON MOVEMENT OF FISH	98

CHAPTER 1

1 INTRODUCTION: IMPACTS OF LAND-USE CHANGE ON AQUATIC BIODIVERSITY

2 This chapter provides an overview of the current state, ideas and research to date of the research
3 topic. I discuss the importance of freshwater ecosystems and the threats that they face, in particular
4 in relation to land-use change and agricultural expansion at the regional and local scales. I then
5 explore the possible protection mechanisms to safeguard freshwater ecosystems during
6 disturbance, and how these impact freshwater biodiversity. Lastly, I discuss the use of freshwater
7 fish as a focal taxon for studying the impacts of land-use change on freshwater ecosystems. I
8 conclude with an outline of the thesis and provide an overview of each chapter.

9 This thesis aims to understand the spatial and temporal impacts of logging and conversion of forest
10 to oil-palm plantation, climatic stressors and other disturbances to freshwater ecosystems, using fish
11 as a focal taxon in Sabah, Malaysia. Understanding these impacts, allows me to then determine if,
12 and how current mitigation strategies (e.g., riparian reserves) protect freshwater ecosystems, and
13 explore what needs to be done for the future conservation of these streams and rivers.

14

15 **1.1. FRESHWATER ECOSYSTEMS**

16 **1.1.1. THE IMPORTANCE OF FRESHWATER ECOSYSTEMS**

17 Freshwater ecosystems are among the world's most transformed, degraded and thus endangered
18 habitats on Earth (Tockner & Stanford 2002; Rood et al. 2008; Perry et al. 2012; Thomsen et al.
19 2012). Freshwater ecosystems make up only 0.01% of the world's water, approximately 0.8% of the
20 earth's surface, and yet disproportionately contain more than 100,000 aquatic species including one
21 third of all vertebrate species. This amounts to 6% of global biodiversity (Dudgeon et al. 2006; Balian
22 et al. 2008; Laurance et al. 2014), with thousands of freshwater or freshwater-dependent species

23 known to be threatened or already extinct (Thomsen et al. 2012). Fresh waters and freshwater
24 biodiversity provide valuable ecosystem services (MEA 2005) and natural resources in economic,
25 cultural, scientific, aesthetic and educational terms (Dudgeon et al. 2006). At the simplest level,
26 rivers, streams and lakes that constitute freshwater ecosystems provide food and water, and are
27 widely regarded as the most essential of natural resources (Vörösmarty et al. 2010).

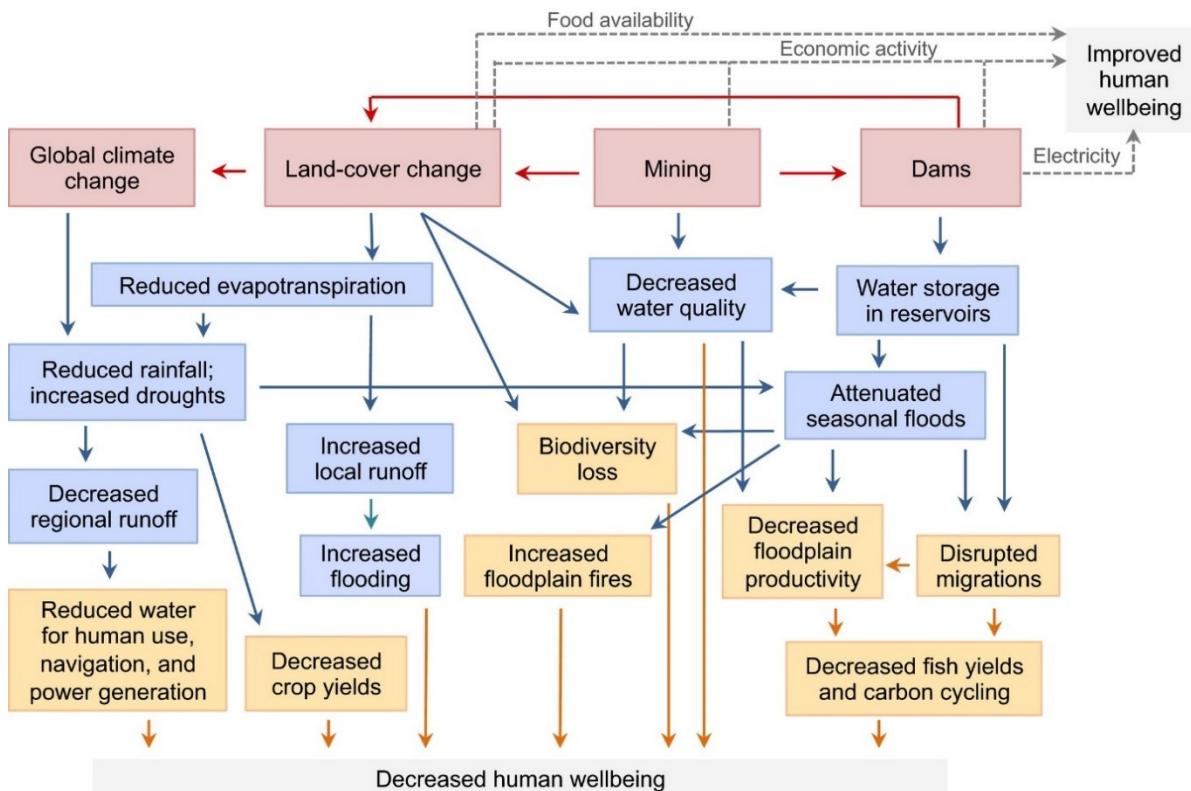
28 **1.1.2. THREATS TO FRESHWATER ECOSYSTEMS**

29 Freshwater ecosystems are directly threatened by a myriad of anthropogenic impacts, ranging from
30 over-exploitation, pollution, poor management, over-abstraction, barriers to migration (dams,
31 reservoirs and large scale engineering projects), fishing, invasive species and habitat change
32 (Dudgeon et al. 2006; Vörösmarty et al. 2010). Humans now utilise more than 50% of available
33 freshwater runoff (Jackson et al. 2001) and more than one million dams around the world have
34 caused river systems to become fragmented and disconnected (Nilsson et al. 2005) and facilitated
35 biological invasions (Liew et al. 2016). This has caused 25% of global sediment to be trapped in
36 reservoirs before it reaches the oceans (Syvitski et al. 2005), and over-exploitation is leading to many
37 inland fisheries being vulnerable to collapse. Declines in biodiversity in freshwater ecosystems are
38 greater than those in most terrestrial ecosystems (Sala et al. 2000), due to anthropogenic habitat
39 modifications that cause severe impacts (Cheng et al. 2012). Freshwater biodiversity is described as
40 being in a state of crisis, and estimates suggest that at least 10,000–20,000 freshwater species are at
41 risk or already extinct (IUCN 2009; Strayer & Dudgeon 2010), as species populations have fallen by
42 an average of 76%, which is more rapid than either marine (39%) or terrestrial (39%) populations
43 (LPR 2014).

44 Environmental change and its consequences for ecosystems worldwide has been extensively
45 documented (Brooks et al. 2002; Fahrig 2003; MEA 2005). In freshwater ecosystems, stream physical
46 habitat is strongly influenced by the catchment scale land-use, and streams are in a complex position
47 as they have their own specific aquatic threats, accumulate terrestrial threats, e.g., pollution from

48 land-use effluents, and are affected by terrestrial land-use change (Dudgeon 2000a; Dudgeon et al.
49 2006; Woodward et al. 2012). This disturbance to the whole ecosystem has knock on effects on
50 freshwater biodiversity, by possible reductions in fish catch, water quality and an increased risk of
51 natural disaster which all affect human wellbeing (Figure 1.1). Thus, disturbance to freshwater
52 ecosystems can lead to habitat loss and homogenisation (Allan 2004), which affects the structural
53 complexity of aquatic ecosystems (Allan 2004; Diana et al. 2006; de Paula et al. 2013). This is coupled
54 with a woefully incomplete knowledge of freshwater diversity (particularly among invertebrates and
55 microbes in the tropics; Balian et al., 2008) and the fact that freshwater hotspots receive less
56 attention scientifically than their terrestrial counterparts, due to the lack of data about many
57 freshwater species (Myers et al. 2000). Balian et al. (2008) have compiled the only comprehensive
58 global freshwater animal biodiversity assessment, examining global diversity of all major taxonomic
59 groups. Freshwater biodiversity declined by ~55% between 1970 and 2002, while that of terrestrial
60 systems and marine systems, each declined by ~32% (MEA 2005).

61 Habitat loss or degradation (within the riparian reserve and the catchment as a whole), water
62 pollution, over-exploitation, and alien species are the main processes predominantly threatening
63 freshwater species (Wilcove et al. 1998; Dudgeon et al. 2006). Alien species, and the diseases that
64 they carry, can outcompete or predate upon native flora and fauna leading to significant changes to
65 the food web (Wilcove et al. 1998). Over-exploitation is primarily limited to vertebrates for human
66 consumption, with fish making up the majority, but with reptiles, amphibians, and invertebrates
67 (e.g., crustaceans and molluscs) also being exploited (Dudgeon et al. 2006). Water pollution, for
68 example through mining or agriculture, can range from a pandemic to small scale and although
69 industrialised countries have made progress in reducing pollution from point source and domestic
70 sources, threats are increasing from nutrient enrichment and chemicals (Dudgeon et al. 2006).



72

73 **Figure 1.1.** Interactions among freshwater ecosystems, drivers (Red rectangles), hydrological
 74 alterations (Blue rectangles), and ecosystem impacts (Yellow rectangles) (from Castello & Macedo,
 75 2015).

76

77 1.2. AGRICULTURAL EXPANSION AND LAND-USE CHANGE

78 1.2.1. GLOBAL EXPANSION AND CHANGE

79 As stated above, agricultural expansion is one of the biggest and most pervasive threats to global
 80 and tropical biodiversity loss (Phalan et al. 2013; Eisner et al. 2016), and in recent decades, increases
 81 in agriculture and urban development have led to unprecedented losses of tropical forest (Lewis et
 82 al. 2015). This has resulted in forests becoming smaller, more fragmented (as~70% of forest area is
 83 now less than 1 km from the nearest forest edge; Haddad et al. 2015), and reaching critical
 84 thresholds of fragmentation for biodiversity (Taubert et al. 2018). This burgeoning human footprint
 85 (Venter et al. 2016) has caused a significant decline in global wilderness areas (Watson et al. 2016)
 86 and half of biodiversity hotspots having only 3–10% of intact vegetation remaining (Sloan et al.
 87 2014). Annual tropical deforestation rates have remained at around 8.0 million ha yr⁻¹ since the

88 1990s (Achard et al. 2014), but rates of deforestation and conversion vary across the globe, with
89 two major hotspots, in Southeast Asia and Brazil (Lewis et al. 2015).

90 This level of agricultural expansion is due to the increasing human population, which is predicted to
91 reach 10–11 billion by the end of this century (Lutz et al. 2010; Laurance et al., 2014), with the
92 greatest increase in tropical developing nations (Laurance et al., 2014). Subsequently, there is a
93 rising demand for food, water and resources causing further agricultural expansion and land-use
94 change (FAO 2010; Pereira et al. 2010; Phalan et al. 2011). Agriculture has resulted in the conversion
95 of 27% of the tropical forest biome and covers around 38% of the world's terrestrial surface (Foley et
96 al. 2011). However, the expansion of agriculture has slowed over the last 50 years due to
97 intensification, through the use of fertilisers (Eisner et al. 2016), but this has not stopped the
98 majority of recent expansion in the tropics, with around 80% of new croplands replacing tropical
99 forests (Gibbs et al. 2010), and expanding by c. $48,000 \text{ km}^2 \text{ yr}^{-1}$ from 1999–2008 in tropical forest
100 biomes (Phalan et al. 2013).

101 **1.2.2. LAND-USE CHANGE IN SOUTHEAST ASIA**

102 The forests of Southeast Asia have among the highest biodiversity and also the highest rates of
103 forest loss on the planet (Cushman et al. 2017). By 2010, the region had lost 70% of its lowland
104 forest (Wilcove et al. 2013). Malaysia has the highest degree of forest loss compared to land area,
105 while Indonesia has had the largest recent increase in the annual rate of forest loss (Hansen et al.
106 2013a). Forest loss and conversion increases carbon emissions with South and Southeast Asia
107 accounting for 32% of tropical carbon emissions from land-use change (Harris et al. 2012). This loss
108 of tropical forest is changing the outlook of biodiversity conservation, from monitoring the effects of
109 land disturbance (Shea et al. 2004) and land-use change on biodiversity to determining how species
110 can use changing landscapes. For example, it has been demonstrated that with the continued loss of
111 primary forests, secondary forests will play an increasing role in conservation of forest biodiversity
112 (Chazdon et al. 2009). Preventing conversion of logged forests is essential to conserving the

113 biodiversity in Southeast Asia as logged forests have been shown to support the majority of the
114 fauna in the region (Berry et al. 2010; Wilcove et al. 2013).

115 In Southeast Asia, and Borneo in particular, the widespread disturbance and degradation of
116 rainforest by logging activities and conversion of forest to cropland is predominantly for palm oil
117 (from oil-palm, *Elaeis guineensis*), forestry plantation and for the production of rubber (from rubber
118 plants, *Hevea brasiliensis*). Oil-palm is one of the most rapidly expanding crops due to its high
119 economic value (Phalan et al. 2013). The palm oil product, is used for a huge variety of products,
120 from food to detergents and more recently biofuels, leading to increasing demand for oil-palm (Wich
121 et al. 2014). Global production of palm oil is now over 70 million tonnes a year, in a cultivated area
122 of approximately 16.3 million hectares (Ferreira & Begot 2018), with Malaysia and Indonesia
123 producing over 80% of global palm oil (FAO 2010). Oil-palm in Malaysia covered 5.2 million hectares
124 or 16% of total land area (in 2010), with a constant growth rate since 1990. However, 40% of new
125 plantations expanded directly into forested areas, with the highest rates of conversion in Sabah,
126 Malaysia (62%, 714,000 ha) from disturbed and undisturbed forest (Gunarso et al. 2013). This level
127 of palm oil production brings in billions of Malaysian Ringgit in revenue (approximately RM 30 billion
128 a year in 2007 (Basiron 2007)). Increasing demand for oil-palm, is expected to cause expansion of
129 plantations within Southeast Asia, as well as in the Neotropics (Lees & Vieira 2013) and the
130 Afrotropics (Wich et al. 2014), increasing the need to find strategies that maintain biodiversity in
131 plantations.

132 Oil-palm monoculture supports less biodiversity, causing reduced species richness and changes the
133 composition of terrestrial and aquatic fauna because of its greatly simplified vegetation structure
134 compared to tropical forest (Fitzherbert et al. 2008; Mercer et al. 2014; Gray et al. 2014; Konopik et
135 al. 2015). Oil-palm landscapes have a large ecological impact, due to the growth of the industry into
136 the most biodiverse areas of the planet, but these landscapes are also an arena in which scientific
137 evidence can be incorporated into policy and used to inform management guidelines. It is crucial to

138 understand how impacts of habitat loss and land-use change can be mitigated or reduced, and if
139 existing reserves and protected areas can sustain their biodiversity.

140 **1.3. IMPACTS OF LAND-USE CHANGE ON FRESHWATER ECOSYSTEMS**

141 **1.3.1. IMPACT OF SELECTIVE-LOGGING**

142 The most widespread and destructive threat to aquatic ecosystems is habitat modification that
143 results from logging, deforestation and converting natural areas (Allan & Flecker 1993; Laurance et
144 al. 2014). Extensive logging and deforestation across the tropics (Hansen et al. 2010a; Achard et al.
145 2014) has caused direct biodiversity loss (Brook & Sodhi 2003) and indirect effects through large
146 scale modifications to catchments, resulting in changes in water quantity, quality, de-regulation in
147 stream hydraulics and increased sedimentation levels (Iwata et al. 2003a,b; Inoue & Nunokawa
148 2005). These effects on stream flow, complexity, depth, temperature, substrate composition, stream
149 bank stability, and structural complexity contribute to widespread changes in aquatic diversity (Cruz
150 et al. 2013; Luke et al. 2017a, b), by changing the microhabitats that they inhabit (e.g., Newcombe &
151 Macdonald 1991; Jones et al. 1999; Sazima et al. 2006). In addition, the type of logging is important,
152 more destructive logging practices can have a bigger impact. The practice of slash and burn
153 agriculture led to long term degradation of streams because of its greater impact on vegetation and
154 soil conditions than selective-logging regimes (Iwata et al. 2003a).

155 The time frame over which logging and disturbance occurs is an important factor determining
156 stream and catchment diversity (Harding et al. 1998; Iwata et al. 2003a, b; Burcher et al. 2008).
157 Significant lag times between deforestation and impact on aquatic diversity may be exhibited, due to
158 the time for the resultant impacts of deforestation such as habitat simplification and
159 homogenisation to occur, and for aquatic diversity to respond to these habitat changes (Brejão et al.
160 2018). Patterns of biodiversity can therefore vary between catchments, and logging history, as well
161 as the current landscape structure, all of which should be considered in analyses when studying the
162 impacts of land-use change.

163 In addition, freshwater biodiversity may not respond to deforestation in a simple linear relationship
164 (Smucker et al. 2013; Rodrigues et al. 2016; Brejão et al. 2018), but with threshold levels of logging
165 or deforestation at the riparian or catchment scale. In the Amazon, negative threshold responses to
166 deforestation have been shown at very low levels of deforestation (< 20%) and within 10 years since
167 the disturbance (Brejão et al. 2018). Across the tropics, sensitive species are usually endemic,
168 functionally unique, and associated with specific complex habitats and structures of allochthonous
169 origin found in undisturbed forested catchments (Brejão et al. 2018; Martin-Smith 1998b; Zeni et al.
170 2017). Environmental changes typically jeopardise the long-term persistence of specialist stream
171 species by reducing the diversity and quality of suitable habitats (Scott & Helfman, 2001), and
172 therefore can also disproportionately influence the functional structure of communities. However,
173 taxonomic and functional approaches can show different responses to the same environmental
174 gradient (Hoeinghaus et al. 2007; Pool et al. 2014), but it is crucial to understand how these changes
175 impact freshwater ecosystems.

176 **1.3.3. IMPACT OF CONVERSION TO OIL-PALM PLANTATION**

177 Numerous studies suggest that oil-palm plantations have mainly negative effects on tropical aquatic
178 biodiversity and support reduced biodiversity compared to tropical forests (Fitzherbert et al. 2008;
179 Gray et al. 2014; Konopik et al. 2015). As described in the impacts of logging (Section 1.3.2), changes
180 in land-use throughout the catchment result in the loss of structural complexity, which affects
181 stream habitat structure (Clapcott et al. 2012; Luke et al. 2017a), both directly and indirectly, due to
182 bank erosion, silting, or to changes in the type of energy source in the system—from allochthonous
183 to autochthonous (Dayang Norwana et al. 2011; Senior et al. 2013). The result of these impacts has
184 been shown in reduced biodiversity of fish (Giam et al. 2015; Ferreira & Begot 2018), frogs (Konopik
185 et al. 2015), and macroinvertebrates (Luke et al. 2017b; Mercer et al. 2014).
186 The impacts of conversion of forest to oil-palm monoculture can be mitigated by the retention of
187 forest patches and riparian reserves. Aquatic diversity was maintained at pre-conversion species

188 richness and functional diversity within oil-palm monocultures in the Indo-Malay region when
189 riparian reserves were present (Giam et al. 2015). By contrast, stream sites within plantations lacking
190 riparian reserves exhibited an average 42% reduction in aquatic species diversity (Giam et al. 2015).
191 Despite this, there is considerable variation in the impacts of land-use change on freshwater
192 ecosystems, leading to renewed calls to better understand the potential interactions of land-use
193 change with other stressors specific to certain regions such as dams, drought or invasive species
194 (Macedo et al. 2013; Taniwaki et al. 2017). Thus regional studies are needed to uncover local
195 impacts of varying land-use on freshwater diversity in order to safeguard freshwater ecosystems in
196 the long term.

197

198 **1.4. MITIGATING THE IMPACTS OF LOGGING AND OIL-PALM ON FRESHWATER ECOSYSTEMS**

199 A variety of management strategies may be employed to protect biodiversity in freshwater and
200 terrestrial ecosystems during land-use change. Riparian reserves (discussed below; 1.4.1) are the
201 default tool to protect freshwater ecosystems in changing landscapes, but additional legislation and
202 management is also implemented. These range from oil-palm certification schemes, that
203 recommend appropriate widths of riparian reserves, the proximity of using fertiliser to water
204 courses, and guidelines on road development (Barclay et al. 2017; RSPO 2013), to state and national
205 level legislation. In Malaysia, for example, there are National and State level legislations that prohibit
206 the expansion of oil-palm into steep or riparian areas (e.g., Waters Act 1920), although the extent to
207 which this is enforced may vary (e.g., Gomi et al. 2006; Ligtermoet et al. 2009). Below, I discuss the
208 use of riparian reserves and the major certification scheme, in protecting freshwater ecosystems, as
209 they have the greatest relevance to this thesis.

210 **1.4.1. RIPARIAN RESERVES**

211 The default conservation tool for protecting freshwater ecosystems is to protect the strip of land
212 either side of a stream or river, creating riparian reserves. Historically, riparian reserves were
213 created to control hydrological flow (e.g. reducing flooding and erosion) and protect water quality

214 from pollution. Over the last few decades, it has been accepted that riparian vegetation is a major
215 determinant in maintaining stream biodiversity and function (Lorion & Kennedy 2009; Wantzen &
216 Mol 2013), so reserves are increasingly implemented in an attempt to maintain natural processes
217 and functions in running water ecosystems, and they consequently help protect native aquatic fauna
218 (Naiman et al. 2000; Richardson et al. 2005).

219 Riparian reserves maintain hydrological dynamics, reducing flood risk and maintain water supplies
220 (Salemi et al. 2012), and regulate aquatic food webs by mediating the impacts of land-use change.

221 Riparian reserves help maintain water quality and buffer against the impacts of deforestation
222 through: controlling temperature, light and habitat structure (Inoue & Nakano 1998; Pusey &
223 Arthington 2003; Iwata et al. 2003a; Zeni et al. 2017), facilitating sediment filtration that reduces
224 suspended sediment and turbidity rates (Tabacchi et al. 1998), limiting pollution and contamination
225 from surrounding areas (Osborne & Kovacic 1993) and maintaining in-stream habitat heterogeneity,
226 by regulating flow and bank stability (Naiman and & Décamps 1997). Riparian vegetation can directly
227 influence the flow of allochthonous energy and materials from terrestrial ecosystems into the
228 aquatic system in the form of leaf litter and/or terrestrial invertebrate prey, which in turn influence
229 the size of predatory fish, and aquatic trophic interactions (Pusey & Arthington 2003; Chan et al.
230 2008). Therefore, riparian vegetation has a multi-scale influence on aquatic community composition
231 and trophic dynamics (Gregory et al. 1991; Rabeni & Smale 1995; Allan & Castillo 2007; Lorion &
232 Kennedy 2009).

233 Riparian reserves provide habitat for both terrestrial (Marczak et al. 2010; Gray et al. 2014) and
234 aquatic (Giam et al. 2015; Konopik et al. 2015) species which would otherwise not persist in human-
235 modified landscapes. Reserves have therefore, become an integral component of management
236 strategies for stream biodiversity conservation (Naiman and & Décamps 1997). The RSPO stipulate
237 that a reserve of 30 m needs to be retained during land conversion, and riparian reserves are
238 required by law in Indonesia and Malaysia (Republic of Indonesia 1990; Government of Malaysia

239 1965). For example, Sabah law stipulates that all permanent water courses over 3 m wide should
240 have 20 m wide riparian buffer strips (Sabah Water Resources Enactment 1998; ECD 2002). However
241 a major issue is that they are often not retained (Lajuin 2013) due to a lack of enforcement.

242 The importance and efficacy of riparian reserves is well studied in temperate zones (Pusey &
243 Arthington 2003; Rykken et al. 2007) but less so in the tropics (Chan et al. 2008). Available evidence
244 suggests that the geography and land-use in catchments affect the degree to which riparian reserves
245 protect aquatic biodiversity, as the features (vegetation width, composition and density) of riparian
246 reserves necessary for effectively conserving aquatic communities are still poorly understood
247 (Broadmeadow & Nisbet 2004; Lee et al. 2004). For example riparian reserves protect fish in streams
248 running through pasture in Brazil (Casatti et al. 2012), Costa Rica (Lorion & Kennedy 2009), and
249 Indonesia (Giam et al. 2015) but do not protect fish in pine monocultures in New Zealand (Rowe et
250 al. 2002). One difficulty for research, on freshwater ecosystems in particular, is the scale over which
251 you examine the impact of land-use change and riparian reserves. Land-use change occurs at the
252 catchment scale, but legislation and research is often at the smaller, riparian scale. However, Leal et
253 al. (2018), show that there is often little variation explained at either scale, as land-use change has
254 already caused modifications within the stream that have a greater effect on freshwater biodiversity.
255 The incoherence about the consistency of riparian reserves protecting aquatic diversity has led to: i)
256 the recommended width of reserves varying globally, ranging from 5–200 m depending on the water
257 body or species aiming to be protected (Northcote & Hartman 2008; Hansen et al. 2010b; Moraes et
258 al. 2014); ii) questioning of the utility of riparian reserve legislation in protecting freshwater diversity
259 (Leal et al. 2018).

260 It is suggested that the ideal width of riparian reserves varies globally and depends upon the aim of
261 the reserve. For biological conservation, the width of a riparian reserve can have a direct impact on
262 the value of riparian forests, but managers are pressurised to maximise economic exploitation from
263 environments by reducing the width of reserves (Marczak et al. 2010). Despite the inconsistent

264 approaches to informing policy on the effects and impacts of reserves, a width of 30 m has become
265 standard in many jurisdictions globally (Lee et al. 2004). In tropical countries, little information is
266 available to inform policy, as the majority of literature on riparian reserves is biased towards
267 temperate ecosystems (Gray et al. 2014). Views on riparian reserves are continually evolving in
268 terms of design, width, implementation and what they are designed to protect. In Brazil, legislation
269 has changed negatively for biodiversity, originally stipulating riparian reserve widths based on the
270 size of the water body, controversially it now states that the plot size of individual land owners
271 dictates the required area of riparian vegetation (Lees & Peres 2008; Viegas et al. 2014). In
272 comparison, North America has been progressing towards whole catchment based management
273 approaches, including head water reserves to protect larger areas at the confluence of rivers
274 (Rykken et al. 2007; Olson et al. 2007). The emphasis placed on protecting riparian zones may
275 increase in the future, as freshwater as a resource becomes a limiting factor in human growth and
276 development. Further research is needed to understand the ecological roles of riparian reserves in
277 Southeast Asia.

278 **1.4.2. THE ROUNDTABLE ON SUSTAINABLE PALM OIL (RSPO)**

279 The negative impacts of oil-palm are beginning to be accounted for and limited, as consumers
280 demand sustainability due to concern over deforestation and greenhouse gas emissions. Most
281 mitigation efforts are centred around voluntary certification schemes, by which signatories agree to
282 implement management recommendations. Chief among these is the Roundtable for Sustainable
283 Palm Oil (RSPO). The RSPO is an international palm oil certification scheme, set up in 2004 that now
284 includes > 570 oil-palm growers, traders, manufacturers, conservation NGO's and investors in the
285 production of palm oil. The RSPO has ten certification criteria including protection of any habitat
286 that provides key ecosystem services, such as riparian reserves which help to preserve water quality
287 (criterion 4.4) (RSPO 2013). In addition to riparian reserves, the RSPO criteria state that practices
288 need to be taken to minimise and control erosion, there will be a water management plan providing

289 a strategy for treatment of mill effluent, water abstraction and protection of water courses, palm
290 trees cannot be planted on steep slopes (location and context specific), and an environmental
291 impact assessment will have been undertaken. However, the RSPO has been criticised for
292 complications in the certification process or failing to reprimand member organisations for
293 transgressions (Nesadurai 2013). Work is needed to confirm that this legislation is adequate to
294 protect ecosystems and to ensure that it is adhered to.

295

296 **1.5. FRESHWATER FISH**

297 **1.5.1. FISH AS A FOCAL TAXA**

298 Freshwater fish are highly diverse in size and form, ranging from bony fish to sharks (Lévéque et al.
299 2007), and more than 13,000 species had been documented on Fishbase in 2005. However,
300 freshwater fish are among the most imperilled vertebrate taxa worldwide (Olden et al. 2010; Poos et
301 al. 2012). Conservation of fishes extends beyond preserving taxonomic diversity and uniqueness.
302 Fish are an important component in regulating ecosystem structure and functioning (Holmlund et al.
303 1999; Flecker 1992). For example, fish foraging behaviour can alter water turbidity, which affects the
304 abundance of phytoplankton, periphyton, and macrophytes, plus plankton and benthic communities
305 through influencing predator-prey interactions (Lévéque 1995). Therefore, fish help to regulate food
306 web dynamics, nutrient cycling and transport of materials in aquatic ecosystems (Lévéque 1995;
307 Holmlund et al. 1999; Small et al. 2011). In addition, fish are an essential provisioning ecosystem
308 service and resource worldwide as a source of protein (Chan et al. 2012; MacKinnon et al. 1997), and
309 some species are highly sort after and traded by aquarists (Ng & Tan 1997), which when sustainably
310 harvested can provide local communities with supplementary income (Giam 2014). The conservation
311 of fish and freshwaters is therefore essential for human wellbeing (Campos-Silva & Peres 2016).

312 Fish are a useful indicator taxon for the health of aquatic environments (Harris 1995) in at least three
313 ways. First in the sensitivity of fish to most forms of human disturbance; fish have been used in

314 many ways for assessing river health, monitoring responses to remedial action and can be used to
315 detect or sense water quality or environmental change on large scales (Chovanec et al. 2003).
316 Second, in their trophic importance via direct and indirect interactions; fish can affect aquatic
317 invertebrate assemblages by modifying the distribution and abundance of resources available to
318 them through the processes of detritivory and algal grazing (Flecker 1992). And third, in the
319 favourable benefit-to-cost ratio of fish assessment programmes. Fish are relatively easy and
320 affordable to catch, and identify to species level in the field (in comparison to invertebrates, for
321 which the taxonomy is much more poorly resolved, and all individuals are retained for identification)
322 as the species are relatively limited in number, with only minimal quantities needing to be retained
323 for positive identification or for vouchers. Fish can therefore be used as indicators over wide
324 temporal and spatial ranges; at the local scale, fish may be a good umbrella taxonomic group for the
325 conservation of other freshwater taxa.

326 The utility of monitoring freshwater fish is dependent on whether other freshwater taxa respond in
327 the same way to instream environmental parameters as fish. Aquatic macroinvertebrates track basal
328 food resources including leaf litter (Benstead et al. 2003) and have been shown to be sensitive to the
329 associated changes in sedimentation and siltation (Iwata et al. 2003a) and are therefore likely to
330 respond to riparian degradation in a similar way to fishes. Fish assemblages have therefore been
331 recognised as reliable indicators in reflecting aquatic ecosystem health (Ibarra et al. 2003; Rashleigh
332 2004), and the ecological integrity of aquatic systems at different scales from microhabitat to
333 catchment (Chovanec et al. 2003). To use fish as bio-indicators a comprehensive knowledge of
334 taxonomy, habitat requirements and physiology is a pre-requisite.

335 The freshwater ecosystems of Southeast Asia harbour some of the greatest freshwater fish diversity,
336 with the Indo-Malayan region ranking third in the world in terms of known numbers of species
337 (Darwall & Freyhof 2016). Asia has the highest number of freshwater fish families (> 105), five out of
338 the six most species rich basins and the largest number of range restricted species found only within

339 a single drainage (Giam et al. 2015). Sundaland is a global hotspot for freshwater diversity, with
340 ichthyofaunal endemism and diversity especially high in Borneo (Kottelat & Whitten 1996; Tan &
341 Sulaiman 2006 - introduction chapters cover endemic fish fauna of Borneo, which suggest a 50%
342 endemism rate). Unfortunately, approximately 24% of known freshwater fish species in the Indo-
343 Malayan region are threatened, which is a conservative estimate owing to the significant shortfall in
344 research and highlights the urgency for increased research effort within these threatened habitats
345 (Closs et al. 2016). Despite the recognised high diversity, knowledge of the biology and ecology of
346 freshwater fishes in tropical Asia, and Borneo in particular, is limited.

347 Within the Malaysian state of Sabah, taxonomic lists have been compiled for several water
348 catchments and localities, including Danum Valley (Martin-Smith and Tan 1998) and the
349 Kinabatangan (Lim and Wong 1994). Martin-Smith and Tan (1998) recorded 65 different species in
350 the Danum Valley, Lower Segama and Upper Kuamut Rivers, and demonstrated that there are
351 significant differences between regions and catchments separated by small geographical distances
352 (Martin-Smith 1998a). New species have consistently been discovered over the last century (Ng &
353 Tan 1999; Tan & Leh 2006; Tan & Sulaiman 2006, Kottelat & Tan 2008; Kottelat & Tan 2011),
354 indicating the need for more and more intensive sampling within this region. The Family Cyprinidae
355 dominate the communities in Borneo, as they have a wide range of size and feeding strategies. For
356 example benthic algal grazers e.g., *Crossocheilus elegans*; to surface feeding insectivores e.g.,
357 *Nematabramis everetti*. A group of endemics dominate the lower order headstreams e.g., in the
358 genera *Gastromyzon*, *Glaniopsis*, *Katibasia*, *Parhomaloptera*, *Protomyzon* and *Neogastromyzon*
359 (Inger & Chin 2002; Tan & Sulaiman 2006), feed on the algae and have evolved to thrive in these
360 fast-flowing, rocky streams. High rates of algal growth and primary productivity in chaotic tropical
361 headstream ecosystems have led to detrital and algal feeding fish being widespread (Kottelat &
362 Whitten 1996), in contrast to temperate streams where insectivorous fish predominate (Flecker

363 1992). This results in these algal feeding fish often being used as indicator species, as they are
364 affected by anthropogenic disturbance that alters stream ecosystems.

365 **1.5.2. IMPACT OF LAND-USE CHANGE ON FRESHWATER FISH**

366 As discussed above, deforestation and land-use change causes significant changes to freshwater
367 ecosystems. The type and intensity of disturbance affects the impact on freshwater communities,
368 with more destructive logging practices often having a bigger impact. The practice of slash and burn
369 agriculture led to long term degradation of streams because of its greater impact on vegetation and
370 soil conditions than selective-logging regimes (Iwata et al. 2003a). However, the effects of
371 deforestation on the species richness of fish are highly variable. Species richness can be increased
372 (Lorion & Kennedy 2009), decreased (Brook et al. 2003; Toham & Teugels, 1999), or unaffected
373 (Bojsen & Barriga 2002) by tropical deforestation, with equally variable impacts on fish community
374 composition (Bojsen & Barriga 2002; Giam et al. 2015). In Borneo, freshwater fish community
375 composition is thought to be structured more strongly by local, mesohabitat structures (pool, riffle
376 or run) than larger, catchment scale processes such as logging history, although time since logging
377 activity was shown to positively affect the abundance of common cyprinids (Martin-Smith 1998a). In
378 comparison, Iwata et al. (2003a) showed different fish guilds or community metrics responded
379 differently to deforestation. For example, the abundance of benthic fish and other taxa was lower in
380 deforested catchments, which was attributed to increases in sedimentation, but nektonic (free-
381 swimming) fish did not suffer reductions. It is suggested that deforestation or habitat alteration can
382 affect fish communities by changing the taxonomic identities and functional diversity of
383 communities, whereas mesohabitat differences affect the functional composition of communities
384 (Casatti et al. 2012), causing reductions in functionally distinct species (Villéger et al. 2010).

385 The impact of land-use change for agriculture is predominantly negative for biodiversity (Gray et al.
386 2014; Giam et al. 2015; Konopik et al. 2015; Luke et al. 2017a). However, the negative impact of
387 conversion of forest to oil-palm culture can be mitigated by the retention of forest patches and

388 riparian reserves. For example, when riparian reserves were present within oil-palm monocultures in
389 the Indo-Malay region, aquatic diversity was maintained at pre-conversion species richness and
390 functional diversity (Giam et al. 2015). By contrast, stream sites within plantations lacking riparian
391 reserves exhibited an average 42% reduction in aquatic species diversity (Giam et al. 2015). Similar
392 results are seen in the Neotropics. Ryan & Kelly-Quinn (2015) showed there is a strong link between
393 riparian cover and aquatic diversity. It is this considerable variation in impacts, that leads to renewed
394 calls to better understand the potential interactions of land-use change with other stressors, such as
395 dams, drought or invasive species (Macedo et al. 2013; Taniwaki et al. 2017). Thus regional studies
396 are needed to uncover local impacts of varying land-use on freshwater fish communities in order to
397 determine and validate protection mechanisms to safeguard freshwater ecosystems in the long
398 term.

399

400 **1.6. SAMPLING METHODS, DESIGN AND STUDY SITE**

401 **1.6.1. STUDY SITE: THE STABILITY OF ALTERED FOREST ECOSYSTEMS (SAFE) PROJECT**

402 All the field research for this thesis was carried out at the Stability of Altered Forest Ecosystem
403 (SAFE) Project and surrounding landscape, made up of a mosaic of protected, primary forest areas,
404 logged forest and oil-palm plantations (Figure 1.2). The SAFE Project is located in the Southeast of
405 Sabah, Malaysian Borneo and is carrying out a large-scale fragmentation experiment (117.43°E to
406 117.70°E and 4.57°N to 4.76°N), which will take advantage of salvage-logging and conversion to oil-
407 palm plantations. The SAFE Project is currently collecting data within Logged Forest (LF) and is
408 conducting the world's first tropical riparian reserve experiment (Ewers et al. 2011), presenting a
409 unique opportunity to determine the effects of deforestation and land-use change on freshwater
410 fish through space and time. The SAFE project experimental area (~ 8,000 ha) was twice-logged
411 forest (average above ground biomass (AGB) = 122 t ha⁻¹), but has undergone salvage-logging from
412 April 2013 until June 2016 (resulting in an average AGB ~ 95 t ha⁻¹), excluding logging in experimental
413 riparian reserves and defined forest fragments (Pfeifer et al. 2016). Riparian reserves of

414 experimental streams vary from 0–120 m, and will revert to 20 m, the current Malaysian legislation
415 (Sabah Water Resources Enactment 1998), below the experimental catchment, enabling the optimal
416 width of riparian reserves to protect freshwater ecosystems to be determined.

417 The experimental streams within the project area were chosen to be similar in size (length ~2 km,
418 and catchment area $260 \text{ ha} \pm \text{SD } 10$) and slope ($16^\circ \pm \text{SD } 2$; Ewers et al., 2011), and where possible all
419 other streams match these. Six experimental streams within the experimental area were sampled.

420 **1.6.2. LAND-USE GRADIENT**

421 We also sampled across a land-use gradient from primary rainforest, twice-logged forest and oil-
422 palm plantations, with and without riparian reserves, surrounding the SAFE project. We sampled two
423 different areas of primary rainforest: Danum Valley Conservation and the Brantian Tantulit Virgin
424 Jungle Reserve (VJR). Danum valley covers 43,800 hectares (438 km^2), and is situated in Lahad Datu
425 District, South-eastern Sabah, to the Northeast of the SAFE project (117.80°E and 4.96°N). Danum
426 Valley is approximately 70 km inland from the town of Lahad Datu in Sabah, and is one of the
427 largest, most important and best-protected expanses of pristine, lowland, dipterocarp forest
428 remaining in Southeast Asia. Four protected, primary (PF) forest control streams are sampled within
429 the area (catchment average AGB = 350 t ha^{-1}), in the Segama catchment. The Brantian Tantulit VJR
430 is located adjacent to the Southeast corner of the experimental area (Figure 1.3). VJRs are areas of
431 old growth forest that have been protected and are intended for research and conservation by the
432 Sabah Forest Department (<http://www.parks.it/world/MY/Eindex.html>). This reserve has been
433 established as a control for old growth forest and has a catchment average AGB = 350 t ha^{-1} .

434 We also sampled three streams in the Ulu Segama Forest Reserve (126,846 ha) and 17 streams the
435 Benta Wawasan Oil-Palm Plantation (covers 45,601 ha). The forest reserve is a large area of
436 continuous twice-logged forest (AGB = 122 t ha^{-1}) that extends between the SAFE project and Danum
437 Valley Conservation Area, and is now protected so that no further logging or deforestation would
438 occur in this area. The Benta Wawasan oil-palm plantation (average AGB 19.7 t ha^{-1}) is adjacent to

439 the SAFE project experimental area has 10 estates with oil-palm varying in age
440 (<http://www.bentawawan.com.my>). The estates of Selangan Batu, Merbau, Gaharu, Keruing and
441 Binuang have become established as control sites for oil-palm catchments within the SAFE project
442 framework.



443
444 **Figure 1.2.** Photos of four sampling transects across the land-use gradient, illustrating the streams
445 and land-uses as they are referred to in this paper: (A) oil-palm plantation with no riparian buffer, (B)
446 oil-palm plantation with a riparian buffer, (C) logged forest, and (D) primary forest.
447

448 **1.6.3. FISHING METHODS AND SAMPLING DESIGN**

449 Streams were chosen across a land-use gradient of primary forest, logged forest and oil-palm
450 plantation with and without riparian reserves. Streams were, where possible, matched in length,
451 slope and catchment size, to avoid confounding effects of the river continuum concept (Vannote et
452 al. 1980), and in independent tributaries to ensure spatial independence of data (Giam et al. 2015).
453 Streams were located in three catchments: Brantian, Kalabakan and Segama. Transects were created

454 on 16 ‘core’ streams that were sampled every year 2015–1017, and 8 of which had previously been
455 sampled in 2011 and 2013, across the land-use gradient. We used a Before-After-Control-Impact
456 study design to monitor the impact of salvage-logging that occurred during this research at a subset
457 of six streams, and an El Niño induced drought in 2016 across all streams. In addition, we sampled an
458 extra 18 streams across the land-use gradient, to determine the spatial changes in fish communities.

459 Fish communities were sampled using two different active sampling methodologies to answer
460 different questions.

461 1. Fish were caught along 200 m transects using a 2.75 m diameter cast net with 1 cm mesh (c.
462 20 throws per transect) and baited, funnel traps (20 traps per transect, alternating bread or
463 fish bait, 2.6 cm opening to trap) to determine the relative diversity, abundance of
464 freshwater fish (as done by others in Sabah; Rahim et al. 2002; Martin-Smith & Tan 1998a, b,
465 c), and explore local fishing techniques. Streams were sampled for 4–6 consecutive days in
466 all sampling seasons (2011, 2013, 2015, 2016, and 2017), and all Cyprinid fish > 6 cm (from
467 2013 onwards) were tagged with uniquely coded PIT tags for use in Capture-Mark-Recapture
468 models (Pine et al. 2003; Cunjak et al. 2005; Adams et al. 2006)

469 2. Complete sampling of fish communities was achieved using a combination of three sampling
470 at 100 m transects (the first 100 m of the 200 m transects). Fishes were sampled at each
471 transect on clear-weather days, in the following order: (1) three-pass electrofishing (model
472 EFGI 650), (2) cast netting (2.75 m diameter net with 1 cm mesh), and (3) tray (push) netting
473 (dimensions 60 x 45 cm, 2 mm mesh). At the start of sampling, stop nets (2 mm mesh) were
474 placed at 0 m and 100 m on the transect to prevent fish immigration or emigration during
475 the sampling period. The combination of these sampling methodologies target all major fish
476 groups and microhabitats in order to achieve comprehensive and unbiased metrics of fish
477 communities (Kennard et al. 2006; Giam et al. 2015).

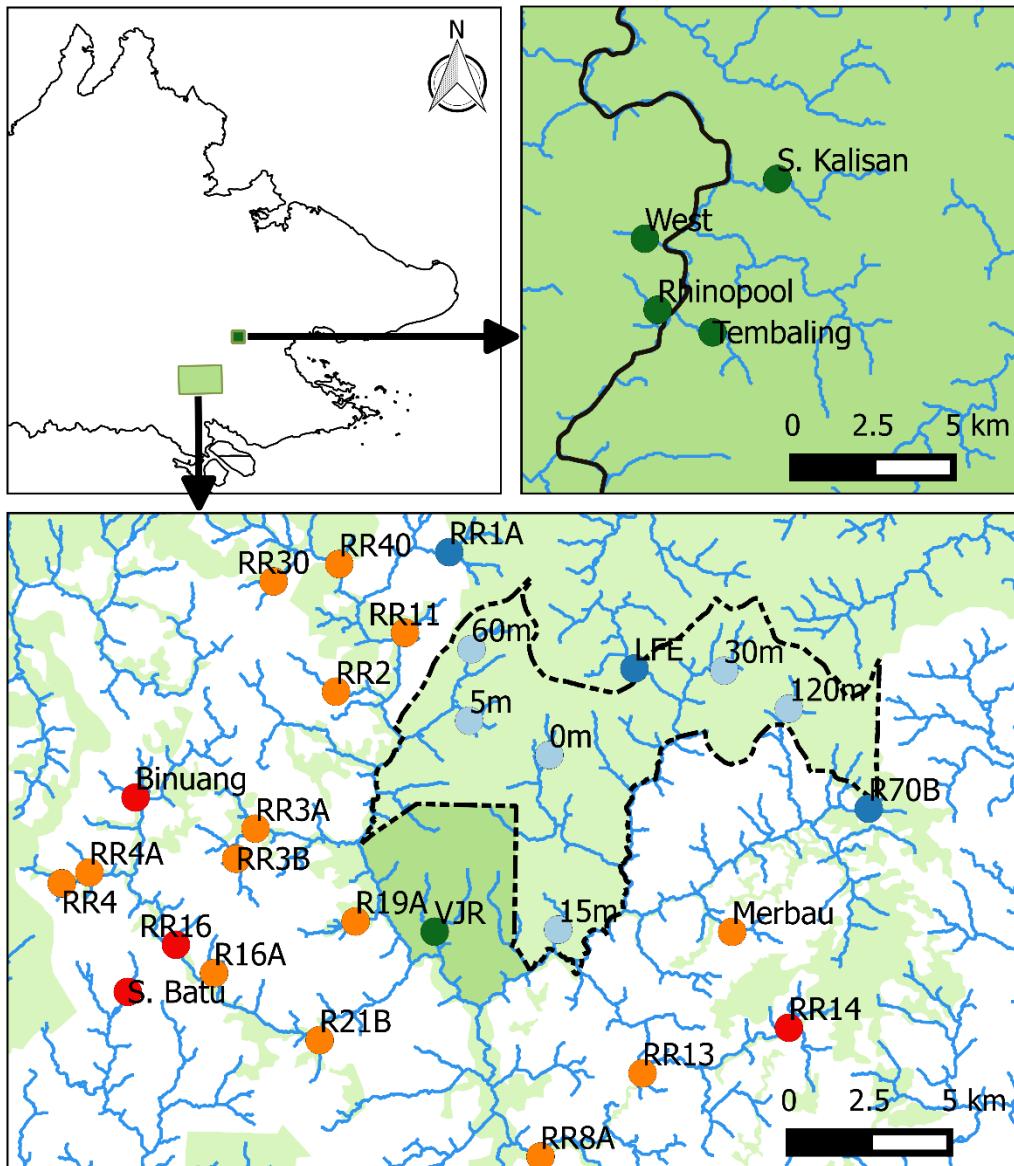


Figure 1.3. Schematic and map showing the study areas in Sabah, Malaysian Borneo, and the location of the thirty four stream sites that were used in this study. Protected forest is darker green (within Danum Valley Conservation Area to the left of the black line in the top right map), logged forest in paler green and oil-palm plantations in white. Stream sampling locations vary in colour by land-use: protected areas (green), twice-logged forest (dark blue), three times & salvage-logged forest (pale blue), oil-palm plantation with riparian reserve (orange), and without riparian reserve (red).

478

479

480 **1.7. RESEARCH AIMS AND OBJECTIVES**

481 In this thesis, I aim to determine the spatial and temporal impacts of land-use change on tropical
482 freshwater ecosystems in Southeast Asia.

483

484 I have four specific objectives:

- 485 1. Assess the availability of freshwater fish biomass as a resource to local communities across a
486 land-use gradient.
- 487 2. Determine the impact, and mechanisms of change associated with logging, deforestation
488 and conversion of land to palm oil plantation on freshwater fish communities, with a focus
489 on species richness, functional diversity and community composition.
- 490 3. Investigate the efficacy of riparian reserves in protecting freshwater ecosystems, and
491 determine the necessary conditions to maximise this protection to enable maintenance of
492 freshwater biodiversity at pre-conversion levels.
- 493 4. Measure the impact on and resilience of freshwater fish to multiple stressor events: land-
494 use change and extreme climatic events.

495

496 **1.8. THESIS CHAPTER OUTLINE**

497 In *Chapter 2*, I consider the availability and use of freshwater fish biomass as a resource to local
498 communities in Sabah. Using local fishing techniques, I quantify species richness, biomass and
499 abundance of commonly eaten species across the land-use gradient at the SAFE project and
500 surrounding area to determine changes in resource availability to local people.

501 In *Chapter 3*, I investigate the associated impacts on fish communities, spatially, across the land-use
502 gradient encompassing primary forest, twice-logged and salvage-logged forest and oil-palm
503 plantations with and without riparian reserves. I use electrofishing techniques to achieve a complete
504 sample of each transect, and compare the fish communities across the land-use gradient, and

505 associated environmental factors, to determine how the mechanism of land-use changes influences
506 stream ecosystems.

507 In *Chapter 4*, I consider the efficacy of riparian reserves, the default tool for protecting freshwater
508 ecosystems, on maintaining freshwater biodiversity during land-use change. I explore the
509 relationship between riparian conditions (forest quality, width and time since disturbance) and
510 freshwater fish communities, to be able to inform legislation on how to mitigate the impacts of
511 deforestation and agricultural conversion in Southeast Asia.

512 In *Chapter 5*, I assess the impact and resilience of land-use change and a severe, El Niño induced
513 drought on a common and abundant fish species, *Nematabramis everetti*. Using mark-recapture
514 data we investigate if drought and land-use change impact the biomass, density and movement of
515 the species, and how resilient they are to recover from multiple stressor events.

516 In *Chapter 6*, I synthesise the results of Chapters 2–5 in relation to each other and current literature.
517 I consider the implications of my results for freshwater diversity, and how management activities
518 and legislation around logging activities and oil-palm plantations can play a role in mitigating their
519 impact, along with possible directions for future research.

520 The *Appendix* includes a manuscript that is currently in review on which I am the lead author, which
521 provides a checklist of the fish species within the Brantian catchment, and describes a species of
522 cyprinid fish new to Science that I discovered during the course of my research. While not directly
523 addressing my research objectives, this is nevertheless an important scientific output, and therefore
524 included as an appendix.

525

CHAPTER 2:

526 **FRESHWATER FISH RESOURCE AVAILABILITY IS MAINTAINED ACROSS A LAND-USE GRADIENT IN**
527 **SABAH, BORNEO**

528 This chapter was published at the following location:

Wilkinson, C. L., Yeo, D. C. J., Tan, H. H., Hadi Fikir, A. & Ewers, R. M. (2018) Freshwater fish
resource availability is maintained across a land-use gradient in Sabah, Borneo. Aquatic
Conservation: Marine and Freshwater, 1-11.

529 **ABSTRACT**

530 Freshwater fish are a vital resource for local communities across the rural tropics. In Southeast Asia,
531 biodiversity-rich forests are being logged and converted to extensive oil-palm monocultures. This
532 clearly impacts associated freshwater ecosystems, but the impact on their biodiversity remains
533 largely understudied and poorly understood, despite the important provisioning service that
534 freshwater fishes provide for human well-being. We quantified the biomass stocks of freshwater fish
535 across a land-use gradient encompassing primary forest, twice-logged forest and oil-palm
536 plantations in Sabah, Malaysia, in an area where local communities are known to harvest freshwater
537 fish. Stream fish were sampled using a cast net, the dominant technique used by local fishermen, in
538 200 m long transects in 16 streams over three sampling years (2011, 2013 and 2015). Unexpectedly,
539 no impact of land-use on total fish availability was detected. There were no significant differences in
540 fish species richness, or most importantly, biomass per unit fishing effort across the land-use
541 gradient. There was variation in the responses of five known food species (*Tor tambra*, *Hampala*
542 *sabana*, *Barbodes sealei*, *Barbonymus balleroides* and *Gastromyzon lepidogaster*), and these small
543 differences are attributed to variation in species habitat selection that co-vary with land-use change.
544 Despite evidence to suggest freshwater fish communities are resilient to land-use change, they still
545 face risks associated with disturbance such as invasion by alien species; furthermore, several of the

546 more stenotopic species were only present in primary forest catchments. Nonetheless, freshwater
547 fish in small headwater streams appear to represent a sustainable food resource for villages
548 established in human-modified forests or developed oil-palm plantations.

549

550 **2.1. INTRODUCTION**

551 Freshwater ecosystems are the most threatened ecosystems globally (Thomsen et al. 2012), as they
552 have been severely affected by anthropogenic impacts, affecting riverine ecosystem services and
553 resources (Allan & Flecker 1993; Collen et al. 2008). Fishes are an important component of
554 freshwater ecosystems as a resource widely exploited for consumption and trade (Duncan &
555 Lockwood 2001), but also in terms of biomass and key positioning in trophic networks. The
556 widespread degradation of these ecosystems threatens aquatic biodiversity at both local and
557 regional scales (Richter et al. 1997; Vörösmarty et al. 2010). It follows, then, that conserving fish
558 populations and fish stocks is an important aspect of river conservation (Duncan & Lockwood 2001;
559 Dudgeon et al. 2006), nested within the wider global challenge of protecting freshwater ecosystems
560 and biodiversity (Collen et al. 2008; Vörösmarty et al. 2010).

561 Habitat modification as a result of converting land for agriculture is the most widespread and potent
562 threat to aquatic ecosystems (Allan & Flecker 1993; Laurance et al. 2014). Widespread logging and
563 deforestation in the tropics (Hansen et al. 2010a; Achard et al. 2014) has caused large scale
564 catchment alterations, triggering changes in water quantity and quality including changes to
565 regulation of stream hydraulics and increased sedimentation levels (Iwata et al. 2003a; Inoue &
566 Nunokawa 2005). Despite growing concern about how anthropogenic impacts, including land-use
567 change, will affect freshwater ecosystems globally, few studies have focused on small tropical
568 streams, leaving the impacts on resource availability and freshwater biodiversity poorly understood
569 (Ramirez et al. 2008).

570 The island of Borneo is a particularly high priority area for researching these questions due to its rich
571 aquatic biodiversity (in the Sundaland diversity hotspot) and high levels of forest loss (Fugère et al.
572 2016). Land-use change is driven primarily by the rapid expansion of oil-palm plantations (Gaveau et
573 al. 2014), with the plantations now being essential components of the economies of countries such
574 as Malaysia and Indonesia (Sheil et al. 2009; Meijaard & Sheil 2013). The process of converting forest
575 to oil-palm plantation results in an influx of people (particularly migrants in Borneo; Cramb & Curry
576 2012) into areas that were previously sparsely populated, primarily due to the mass migration of
577 labourers into plantation areas. It also stimulates investment in infrastructure, including roads and
578 facilities to house and care for plantation workers (Susanti & Burgers 2013; Schoneveld 2014). This
579 rise in population results in increased hunting intensity for bush meat in forests adjacent to, and
580 forest patches located within, plantations as migrant workers can bring with them a preference for
581 wild meat over other protein sources (Wilkie & Carpenter 1999; Cramb & Curry 2012; Dewi et al.
582 2013; Luskin et al. 2014). Freshwater fish are often not thought of as bush meat, rather a potential
583 alternative to the bush meat crisis (e.g., Brashares et al. 2004), but are a vital source of cheap and
584 readily obtainable protein nonetheless. If policy makers focus solely on reducing unsustainable
585 consumption of wildlife, adverse impacts will be seen on fisheries, especially if fisheries
586 management is not improved (Inogwabini 2014).

587 In Sabah, and more widely across Borneo, threats to aquatic biodiversity include not only loss of
588 forest cover and conversion, but also pollution, introductions of alien species, and fishing for either
589 food or for the aquarium trade (Kottelat et al. 1993; Kottelat & Whitten 1996). The combined
590 demand on fish supplies for subsistence and commerce mean the majority of the freshwater fishes
591 in Malaysia are being overfished (Chong et al. 2010), and in particular the large, long-lived and/or
592 migratory riverine species (Dudgeon et al. 2006). This overfishing, combined with the degradation of
593 freshwater environments by pollution and siltation from land-use change, has already led to the

594 demise of several riverine fisheries, for example those of mahseers and pangasiids (Chong et al.
595 2010).

596 Reports from the sites where this study takes place, and more broadly across the region,
597 demonstrate the reliance and dependence of local people upon freshwater fish as a source of
598 protein or supplementary income (Martin-Smith 2004; Rachmatika et al. 2005; Chong et al. 2010;
599 Fitzmaurice 2014). For example, in the flooded forest system of Danau Sentarum, Kalimantan, only
600 two of more than two hundred recorded species of fish are not used in some way by the several
601 thousand people dependent on the system (Martin-Smith 2004). Communities in the Malinau region
602 of North Kalimantan ranked fish as the fourth most important “species” for selling, and the 11th
603 most important food “species” with much of the catch being eaten (Rachmatika et al. 2005). Some
604 fishes, such as *Tor tambra* and *Anguilla* species, fetch good market prices in the food trade and are
605 therefore fished predominantly for sale (Rachmatika et al. 2005). Up to 2,000 tonnes (~ US\$5
606 million) of *Anguilla* species are exported from Indonesia and the Philippines every year (Jacoby and
607 Gollock 2014), and *Tor tambra* can reach prices of US\$420 per kg in markets or restaurants
608 (Mysinchew 2010; M. Kottelat Pers. Comm. 2011, in Kottelat 2012).

609 The ornamental fish trade is dominated by freshwater species and the global trade is worth
610 approximately USD 278 million (FAO 1996–2005). Malaysia is the third largest exporter of
611 ornamental fish (next to Singapore and Indonesia) with an 8% share of the global market in 2000
612 (Rani et al. 2014). It is difficult for collectors to know where fish have come from (farm or wild
613 caught). In the wild, most freshwater aquarium fish are caught primarily in rivers and streams using
614 artisanal fishing methods and are typically collected in remote fishing sites (Livengood & Chapman
615 2007).

616 Previous studies on freshwater fish biodiversity in the tropics have thus far focused on comparing
617 either previous logging regimes, or the efficacy of riparian reserves in oil-palm (Giam et al. 2015).
618 Across the tropics, the species richness of fishes in rivers from different sites can be increased

619 (Lorion & Kennedy 2009), decreased (Toham & Teugels 1999; Brook & Sodhi 2003), or unaffected
620 (Bojsen & Barriga 2002) by deforestation. Community composition has been shown to be more
621 sensitive to habitat variables at the local, mesohabitat scale (pool, riffle or run) rather than at the
622 larger, catchment scale at which tropical logging regimes occur (Martin-Smith 1998a, b), suggesting
623 logging has little direct effect on fish communities. In temperate ecosystems, by contrast, freshwater
624 fish populations are not resilient to logging unless deliberate actions are put in place to mitigate the
625 impacts (Detenbeck et al. 1992). More regional studies are thus needed to uncover local impacts of
626 land-use on freshwater fish communities. Moreover, understanding the potential interactions of
627 land-use change with other stressors specific to certain regions, such as fishing, dams or drought
628 (e.g., Macedo et al. 2013), and developing ways to design optimal management strategies that
629 explicitly consider features of the local landscape (e.g., Iñiguez-Armijos et al. 2014), are also essential
630 to protect freshwater ecosystems in the long term.

631 We aimed to determine the impact of land-use on freshwater fish resource availability in Sabah,
632 Malaysia. Although freshwater fish are routinely caught across the study area, no catch data is
633 available to directly quantify the importance of freshwater fish provisioning as an ecosystem service.
634 Local fishing methods were therefore used to quantify instead the freshwater fish resource that is
635 available to local communities. Previous studies have suggested that freshwater fish communities
636 may not change as a result of deforestation or conversion of land to oil-palm plantations (Martin-
637 Smith 1998a; Giam et al. 2015), but this does not necessarily reflect the availability of fish to local
638 communities. The explicit assumption was made that fishing pressure on streams in oil-palm
639 plantations is higher than on streams in logged and primary forest due to increasing human
640 populations. Increased fishing in the area can alter fish community structure and composition
641 through targeted removal of preferred species, for subsistence where large individuals of target
642 species will be preferred, or for trade, targeting economically important species (for example *Tor*

643 *tambra*). A decline in the average length, abundance and biomass of targeted fish species was thus
644 expected in streams arising from oil-palm plantation compared to streams from forest catchments.

645

646 **2.2. METHODS**

647 **2.2.1. STUDY SITE**

648 The study focussed on small, headwater streams (3–10 m wide, ≤ 1.2 m depth) in Southeastern
649 Sabah, Malaysian Borneo. The landscape is a mosaic of twice-logged lowland dipterocarp rainforest
650 (LF), oil-palm plantations (OP; planted between 1998 and 2011), and primary rainforest (PF; Danum
651 Valley Conservation Area and Brantian Tantulit Virgin Jungle Reserve). The sites form part of the
652 Stability of Altered Forest Ecosystems (SAFE) project (Ewers et al. 2011) (SAFE project: 4° 38' N to 4°
653 46' N and 116° 57' E to 117° 42' E, and Danum Valley Conservation Area: 5° 01' N and 117° 48.75' E).
654 The landscape is drained by tributaries of the Brantian and Segama Rivers, both of which empty into
655 the Celebes Sea. Data was collected from 16 stream catchments: seven in continuous, twice-logged
656 forest located adjacent to oil-palm communities (forests were logged in the 1970's and again in the
657 1990s–2000s), five in oil-palm plantations (varying in age since planting from 7–12 years), and four in
658 primary forest (three at Danum Valley Conservation Area, and one in the Brantian Virgin Jungle
659 Reserve; Figure 1; Figure 2). A 200 m transect was located in each stream, and all streams were
660 independent tributaries to ensure spatial independence of data.

661 **2.2.2 FISH SAMPLING**

662 Data was collected over three sampling seasons: September–October 2011, April–June 2013, and
663 March–August 2015, with 8–10 of the 16 streams sampled each year across the land-use gradient
664 (Appendix 2.1). Seasonal changes at our study site are very limited (Walsh & Newbery 1999;
665 Kumagai et al. 2005) suggesting little effect of the differences in timing of the sampling within years.
666 However droughts do occur in Sabah, and the latest El Niño induced drought affected Sabah in 2015–

667 16. Despite this, rainfall data from the SAFE project field camp (R. Walsh, Pers. Comm. 2016) during
668 the sampling period suggests that rainfall is highly variable, both spatially as well as temporally, and
669 that the 2015 period was not unusual. We believe that the conditions when we were sampling
670 during all sampling periods were comparable, and that there was no significant difference to stream
671 conditions.

672 Fishes were sampled using a 2.75 m diameter cast net with 1 cm mesh, which is the most common
673 method used by local communities in small streams. Cast netting alone does not provide a complete
674 sample of the freshwater fish community, which is best described using methods such as
675 electrofishing followed by cast and tray netting (Martin-Smith 1998a, b; Beamish et al. 2003; Iwata
676 et al. 2003a; Giam et al. 2015). Nonetheless, given our specific aim of investigating changes in
677 stream fish resource availability to local communities, our choice of method was appropriate
678 because cast netting is preferentially used by the local (subsistence and artisanal) fisherman to catch
679 fish in these streams (pers. obs, Fitzmaurice 2014).

680 Each stream transect was sampled for between four and six consecutive days (mean = 5.26), with
681 around 20 throws of the net per day in 2013 and 2015 (mean = 18, range = 10 to 32), and with
682 around 10 throws of the net per day in 2011 (mean = 10, range = 8 to 16). The number of throws per
683 transect varied with the number and size of pools. Species accumulation curves were generated
684 using iNEXT (Chao et al. 2014; Hsieh et al. 2014) to determine the sample completeness at each
685 stream, using the aggregated daily catch for the transect as the sample unit. These curves
686 demonstrated this level of sampling effort was appropriate to catch > 90% of species in each stream
687 transect.

688 Captured fishes were identified to species (Inger & Chin 2002; Kottelat 2013), measured (2013 and
689 2015 sampling), weighed (2015 sampling only) using a portable balance, and returned to the stream
690 at the point of capture. Fish over 6 cm total length were also tagged with a passive integrated
691 transponder (PIT) tag (Biomark). A small sample of voucher specimens were euthanized with MS-

692 222, fixed in 10% formalin, and transferred to 75% ethanol for identification and storage in the Lee
693 Kong Chian Natural History Museum, National University of Singapore. Fish capture, handling and
694 euthanisation protocols were ethically reviewed and approved by the Animal Welfare and Ethical
695 Review Body at Imperial College London.

696 **2.2.3 FISH COMMUNITY METRICS**

697 Species richness was calculated as the total number of fish species caught in each stream in a
698 sampling season. Fish biomass was calculated by regression equations. For species with at least 30
699 weighed specimens, the mass of unweighted fish was interpolated from their total length using
700 regression models built from the weighed individuals (Appendix 2.2). For rarer species with less than
701 30 specimens, general regression equations depending on body morphology were used to determine
702 mass (Martin-Smith 1996). Total biomass for all unique fish (excluding recaptured fish) was divided
703 by number of times the cast net was thrown per day, providing biomass per unit cast effort.

704 **2.2.4. FOCAL FOOD SPECIES**

705 Focal species known to be widely eaten or sold (pelagic species: *Tor tambra*, *Hampala sabana*,
706 *Barbodes sealei*, *Barbomyrus balleroides*, and benthic species: *Gastromyzon lepidogaster*, in
707 descending order of popularity; Rachmatika et al. 2005) were analysed individually. Catfish and eels
708 were not analysed individually due to the low catch rate in a cast net. Unsurprisingly, four of our five
709 target species (the exception being *G. lepidogaster*), grow to large sizes (>190 mm TL) and are
710 relatively “less bony”. Biomass per cast effort, abundance and average length of each of these
711 species were calculated at each stream in each sampling season. These metrics provide possible
712 explanations for differences in fish community composition or structure.

713

714

715

716 **2.2.5. ANALYSIS**

717 Fish community metrics (species richness and biomass per cast, per stream per sampling year
718 (n=26)) and those for each focal species (biomass per cast, abundance and mean length, per stream
719 per sampling year) were analysed as the response variables across the land-use gradient with levels
720 primary forest, logged forest, or oil-palm. Generalised linear mixed models (GLMMs; Bates et al.
721 2014) including differences in intercept between streams and sampling years as independent
722 random effects were used. For the species richness model a Poisson error distribution was applied,
723 for all other models a Gaussian error distribution was applied (Zuur et al. 2009), and log-likelihood
724 ratio tests were used to assess model significance. The relative importance of fixed and random
725 effects was ascertained using the methods of Nakagawa & Schielzeth (2013). Multiple tests were
726 applied to the same datasets, so for focal species analyses a Bonferroni correction was applied to all
727 p-values.

728 Each stream was sampled intensively, meaning only a small number of independent streams were
729 sampled equating to relatively low sample sizes (for species richness: n = 27 streams; 6 x PF, 13 x LF,
730 and 8 x OP; for biomass: n = 18 streams: 5 x PF, 6 x LF, 7 x OP). Power analysis (two sample T test)
731 was therefore used to determine our ability to detect effects for each community metric (species
732 richness and biomass per cast). The minimum difference that could reliably be detected between
733 primary forest and oil-palm for species richness and primary forest and logged forest for biomass
734 was estimated given our sample size.

735

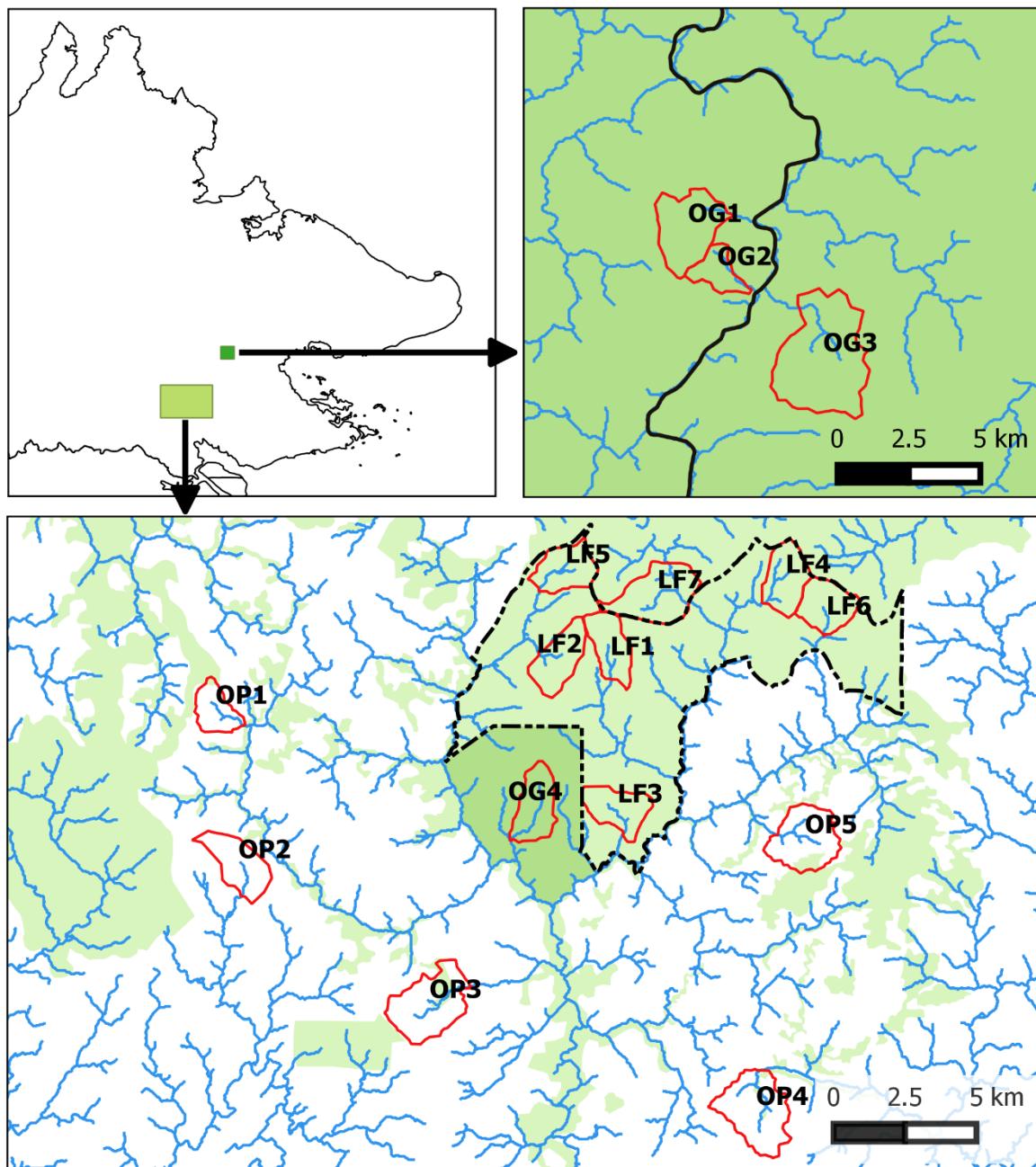


Figure 1. Schematic and map showing the study areas in Sabah, Malaysian Borneo, and the location of the sixteen stream sites that were used in this study. All maps were drawn in the program QGIS with the use of map layers developed from Landsat imagery (Ewers et al. 2011) and SRTM digital elevation model (Jarvis et al. 2008).

736

737



Figure 2. Photos of four sampling transects illustrating the streams and land-uses as they are referred to in this paper: (A) oil-palm plantation with no riparian reserve, (B) oil-palm plantation with a riparian reserve, (C) logged forest, and (D) primary forest.

738

739

740 **2.3. RESULTS**741 **2.3.1. FISH COMMUNITY METRICS**

742 In total, 25 species from 6,048 fish captures were identified (see Table 1 for a species list). Species
743 accumulation curves showed thorough sampling, with on average 93% (range = 80.8 to 100%) of
744 species sampled at each site. The most commonly captured species, in terms of abundance and
745 presence across all land-uses, were *Tor ticta*, *Barbodes sealei*, *Nematabramis everetti* and
746 *Rasbora cf. sumatrana*, which collectively accounted for 78% of all captures. Several species were
747 only detected in a single type of land-use, some of which were also rare: *Crossocheilus elegans*,
748 *Garra borneensis*, *Lobocheilos erinaceus*, and *Luciosoma pellegrini* (N = 1) (only in primary
749 rainforest); *Anguilla marmorata* (N = 1), *Barbonymus collingwoodi* (N = 1), *Leptobarbus*
750 *melanotaenia* (N = 2), *Nemacheilus olivaceus* (N = 1) and *Osteocheilus ingeri* (only in logged forest);
751 and *Hemibagrus baramensis* (N = 5) and *Hemibagrus fortis* (N=1; only in oil-palm).

752

Table 1. Full species list of the 25 species present in this study.**Family Anguillidae***Anguilla marmorata* Quoy & Gaimard, 1824**Family Cyprinidae***Barbodes sealei* (Herre, 1933)*Barbonymus balleroides* (Valenciennes, in Cuvier & Valenciennes, 1842)*Barbonymus collingwoodi* (Günther, 1868)*Crossocheilus elegans* Kottelat & Tan 2011*Garra borneensis* (Vaillant, 1902)*Hampala sabana* Inger & Chin, 1962*Leptobarbus melanotaenia* Boulenger, 1894*Lobocheilos erinaceus* Kottelat & Tan 2008*Luciosoma pelligrini* Popta 1904*Nematabramis borneensis* Inger & Chin 1962*Nematabramis everetti* Boulenger, 1894*Osteochilus chini* Karnasuta, 1993*Osteochilus ingeri* Karnasuta, 1993*Rasbora einthovenii* (Bleeker, 1851)**Family Cyprinidae (cont.)***Rasbora hubbsi* Brittan, 1954*Rasbora cf. sumatrana* Tan, 2013*Tor ticta* (Valenciennes, in Cuvier & Valenciennes, 1842)**Family Gastromyzontidae***Gastromyzon ingeri* Tan, 2006*Gastromyzon lepidogaster* Roberts, 1982*Parhomaloptera microstoma* (Boulenger, 1899)*Protomyzon griswoldi* (Hora & Jayaram, 1952)**Family Nemacheilidae***Nemacheilus olivaceus* Boulenger, 1894**Family Bagridae***Hemibagrus baramensis* (Regan, 1906)*Hemibagrus fortis* (Popta, 1904)

753

754 No significant effect of land-use on freshwater fish rarefied species richness (Figure 3a; $\chi^2_{(2)} = 1.86$,
 755 $P = 0.39$) or total biomass per cast effort (Figure 3b; $\chi^2_{(2)} = 0.76$, $P = 0.68$) was found. Stream as a
 756 random effect explained a considerable proportion of the variance in the model for species richness
 757 (conditional R^2 (R^2_c) = 0.85, marginal R^2 (R^2_m) = 0.06) and biomass (R^2_c = 0.90, R^2_m = 0.05), whereas
 758 year had no explanatory effect in either model.

759 Power analysis showed the power of the test for species richness to be moderate (power = 0.43), but
 760 to be low for biomass per cast (power = 0.07). Given our sample sizes, a difference of three species
 761 could be detected with power = 0.8; as opposed to the two species mean difference observed
 762 between oil-palm (5.5 species) and primary forest (7.5 species). For biomass, a difference of 19.6 g
 763 per cast could be detected with power = 0.8; this was much larger than the mean difference of 3.8 g
 764 per cast observed between primary (15.2 g per cast) and logged forest (11.8 g per cast).

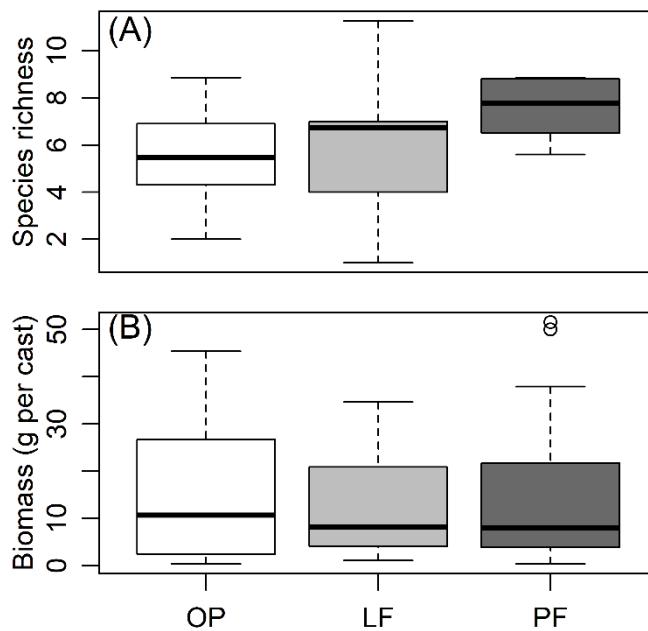


Figure 3. Effect of land cover (oil-palm plantation (OP), logged forest (LF) and primary forest (PF)) on freshwater fish (A) rarefied species richness, and (B) total biomass per casting effort. All panels show box and whisker plots indicating the means, second and third quartiles within the rectangle, upper and lower quartiles in the ‘whiskers’ and outliers as unfilled circles.

765

766

767 **2.3.2. FOCAL FOOD SPECIES**

768 There was no impact of land-use on biomass or abundance per cast effort for any of the focal species
769 (Figure 4; *Tor tambera*: biomass $\chi^2_{(2)} = 2.51$, $P = 0.840$, abundance $\chi^2_{(2)} = 0.72$, $P = 1.000$; *Barbodes*
770 *sealei*: biomass $\chi^2_{(2)} = 1.63$, $P = 1.000$, abundance $\chi^2_{(2)} = 3.50$, $P = 0.510$; *Barbonymus balleroides*:
771 biomass $\chi^2_{(1)} = 0.90$, $P = 1.000$, abundance $\chi^2_{(2)} = 2.00$, $P = 1.000$; *Hampala sabana*: biomass $\chi^2_{(2)} =$
772 1.92, $P = 0.76$, abundance $\chi^2_{(2)} = 2.50$, $P = 0.58$; *Gastromyzon lepidogaster*: biomass $\chi^2_{(2)} = 0.91$, $P =$
773 1.000, abundance $\chi^2_{(2)} = 0.79$, $P = 1.000$). Mean length of fish captured was significantly higher in
774 logged forest streams than in primary forest or oil-palm streams for two of the five species
775 (*Barbodes sealei*: $\chi^2_{(2)} = 8.12$, $P = 0.017$; *Tor tambera*: $\chi^2_{(2)} = 7.38$, $P = 0.025$). For all focal species
776 models, both random effects, stream and year, explained substantial amounts of the variation (all
777 $R^2m < 0.13$, and $R^2c > 0.26$, with the exception of *Barbonymus balleroides* and *Hampala sabana*
778 biomass where R^2m and R^2c equalled 0.05 and 0.10, respectively).

779

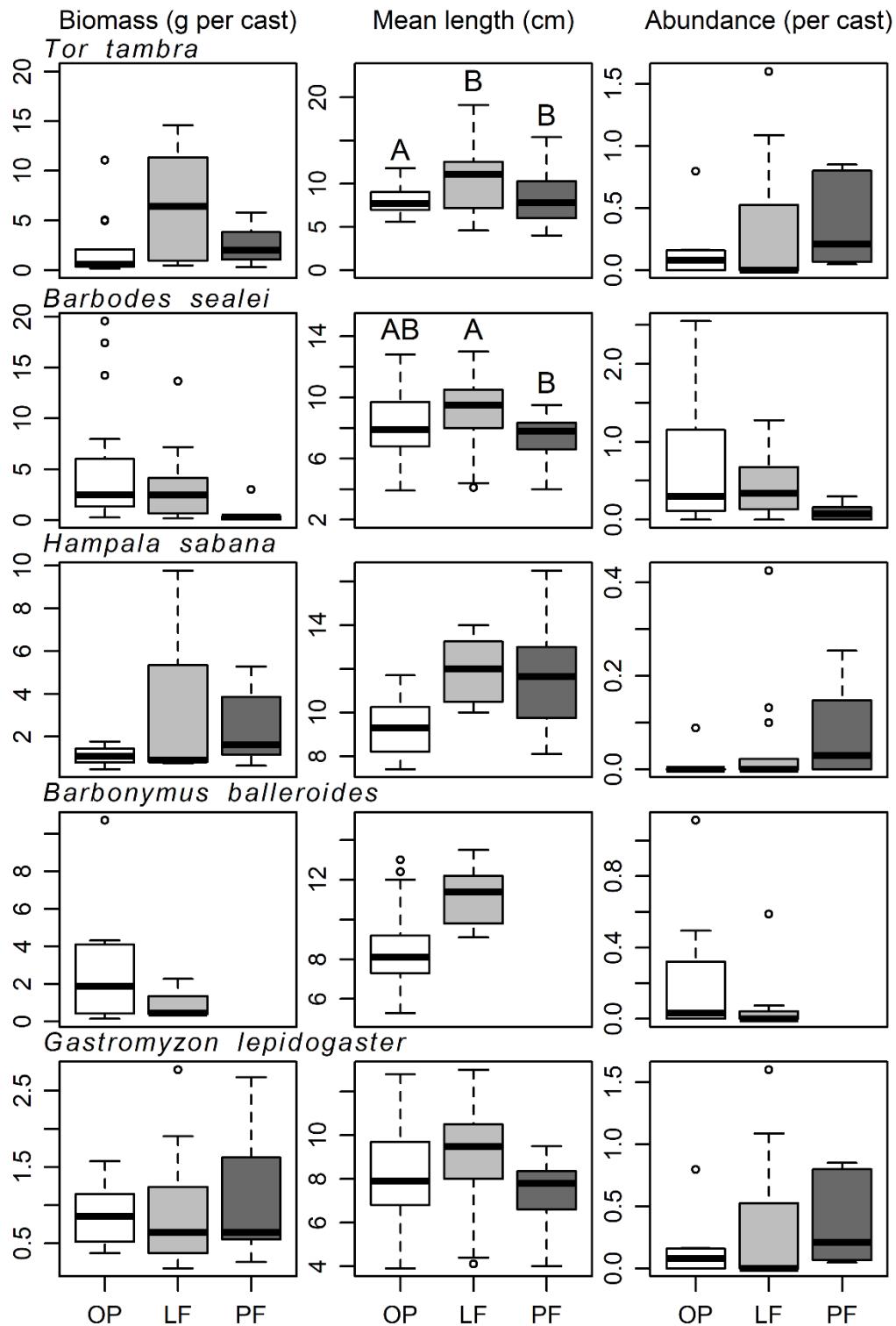


Figure 4. Effect of land-use (oil-palm plantation (OP), logged forest (LF) and primary forest (PF)) on five focal species, shown in five rows (*Tor tmbra*, *Barbodes sealei*, *Hampala sabana*, *Barbomyrus balleroides*, and *Gastromyzon lepidogaster*). Columns represent measures of species' biomass per fishing effort, length and abundance. All panels show box and whisker plots indicating the means, second and third quartiles within the rectangle, upper and lower quartiles in the 'whiskers' and outliers as unfilled circles. Letters within graph panels (A and B) represent significant differences between land-uses.

780 **2.4. DISCUSSION**

781 As far as we are aware, this study is the first to examine the impact of land-use change on
782 freshwater fish resource availability for rural communities in Southeast Asia. Land-use within
783 catchments (primary forest, logged forest and oil-palm plantation) had no significant impact on
784 freshwater fish community species richness or biomass per unit effort. This indicates that there is no
785 change in freshwater fish resource availability to local communities. From a conservation
786 perspective, however, although species richness doesn't change across this land-use gradient,
787 changes in composition, i.e. the turnover of species is important (Banks-Leite et al. 2012). Several
788 stenotopic, fast flowing hill stream specialists were found only in forested catchments and not in oil-
789 palm catchments, as isolated and fragmented habitats typically present the most challenging
790 environments for small, specialised fish (Arthington et al. 2016), suggesting these species are likely
791 to be threatened by land-use change.

792 Quantitative studies of the impact of land-use on freshwater fish communities in Borneo to date
793 have indicated that with sustainable land-use conversion, the impact on freshwater communities is
794 minimal. Selective-logging is thought to be more benign to freshwater fish (Martin-Smith 1998a;
795 Iwata et al. 2003a, b) than clear cutting and agricultural conversion (Beamish et al. 2003; Giam et al.
796 2015), although the impact of agricultural conversion is mitigated by the retention of forest patches
797 and riparian reserves (Giam et al. 2015). This possibly explains why no impact of land-use was seen
798 within this study. The logged forest was last logged more than 10 years ago (1990s–2000s) allowing
799 for substantial regrowth in the catchments, although the sites did still show signs of disturbance 10–
800 15 years after selective-logging (Luke et al. 2017a). In addition, three out of the five oil-palm streams
801 had substantial riparian reserves (on average > 28 m either side of the stream). These reserves
802 provide some protection to waterways, but not enough to maintain fully forest-like stream
803 conditions (Luke et al. 2017a). However, it is important to note that this study targets desirable food
804 fish caught in cast nets (pelagic, insectivorous or omnivorous fish), and does not sample the full fish

805 community, as previous studies have (Beamish et al. 2003; Iwata et al. 2003a; Giam et al. 2015). It is
806 possible some impacts of land-use change on the entire fish community are thus missed, limiting our
807 ability to understand species interactions and food web structure within these streams, which may
808 become important to sustainable fish catches valued by local peoples in the future. We advocate
809 caution in using our data to make conclusions about the ecological impact of land-use on freshwater
810 fish biodiversity.

811 Some differences from other studies were found in how our focal species respond to land-use
812 change. For example, in contrast to Iwata et al. (2003a), who detected a higher catch per unit effort
813 in primary forest than in logged forest for benthic fish species and no difference for pelagic fish, no
814 such trend was apparent in this study. It was expected that the biggest impact of land-use would be
815 seen for *T. tmbra*, as it is a widely sought after, and threatened, food fish in other parts of Asia
816 (Rachmatika et al. 2005). However, although the mean length of *T. tmbra* was higher in forested
817 compared to oil-palm streams, there was no significant change or impact on biomass and
818 abundance. The higher mean length in forested ecosystems is attributed to greater availability of
819 macroinvertebrate prey that the species predominantly feeds on (Luke 2016), increased habitat
820 complexity and thus cover provided by allochthonous inputs reducing predation (Hagen et al. 2010;
821 Luke et al. 2017a), and a potential decrease in fishing pressure in logged forest streams relative to
822 those in oil-palm.

823 The lack of impact of land-use change and local human communities living in oil-palm plantations or
824 in close proximity to logged forest streams demonstrates an unexpected resilience of freshwater fish
825 communities to even severe disturbance from land-use change. Fishing occurs in all land-uses, but it
826 is expected to be higher in logged forest and oil-palm plantation catchments due to the proximity of
827 villages and human populations. These communities, however, are known to hunt bush meat within
828 the study area (Fitzmaurice 2014), and have access to fresh fish at nearby local markets (C. Wilkinson

829 Pers. Obs.). This availability of other sources of protein and supplementary income may lead to
830 lower than expected fishing pressure in these streams.

831 No significant threat of land-use change to freshwater fish and the resource availability in small
832 headwater streams was detected. More streams were sampled, and the majority with repeated
833 sampling, in this study (16 streams, with up to 3 sampling seasons) than in other freshwater stream
834 studies (8–17 streams; Jones et al. 1998; Martin-Smith 1998a, b; Mercer et al., 2014; Giam et al.,
835 2015). All model random effects indicated there is large, among-stream variation in response metrics
836 (also shown by Luke et al. 2017a), suggesting catchment land-use is not the most important factor in
837 determining fish community differences between streams. We are confident that these data and
838 analyses adequately represent the situation, despite power analysis suggesting the sample sizes
839 were relatively low. The power analysis suggested a mean difference of three species, and 19.6 g per
840 cast biomass, could reliably be detected between land-uses. The species richness difference
841 observed was near this threshold, suggesting there is a chance that land-use exerts a significant, but
842 small, effect on species richness that was not detected. Biologically, however, such an effect would
843 likely make very little difference to the resource availability of freshwater fish to local communities.
844 By contrast, a difference of 19.6 g per cast is considerably higher than the mean catch rates
845 observed (11.8 g for logged forest and 15.2 g for primary forest), and much larger than the observed
846 difference between land-uses (3.8 g per cast). This reflects the high variability in biomass among
847 stream transects within land-uses (range 3.29–23.6 g in logged and 5.18–30.4 g in primary forest).
848 We are therefore confident that our results are correct in showing no statistically significant effect of
849 land-use change on fish biomass.

850 The lack of change in fish resource availability may be due to a time lag effect, or a lack of difference
851 in fishing pressure between land uses. Changes in the fish community in response to land-use
852 change and increasing human populations may only become significant over time. This is unlikely,
853 however, because the oil-palm plantation sample sites are in fully developed, mature oil-palm

854 plantations which are already in full production. For the logged forest sites, there has been no
855 change since the last round of logging more than 10 years previously. There is a possibility of a
856 prolonged time lag for fish communities to be impacted by land-use change, or alternatively that fish
857 communities underwent an immediate decline after logging and conversion to oil-palm plantations,
858 and have subsequently recovered, or are recovering, in the intervening years between the
859 disturbance and our sampling. It was also expected that a difference in fishing pressure may become
860 apparent, through the targeted removal of species for food or sale, although this is not seen in this
861 study. Further research at the SAFE project during deforestation and conversion to palm oil-
862 plantation will monitor for a lag time impact; however, differences in fishing pressure would have to
863 be addressed through monitoring and questionnaires to the local communities.

864 Something that might lead to a dramatic change in the fish community or change fish resource
865 availability in the future could be the introduction and/or establishment of invasive alien species,
866 which is generally more likely in human modified landscapes (Leprieur et al. 2008; Kwik & Yeo 2015).
867 The Mozambique tilapia (*Oreochromis mossambicus*), for example, has been discovered breeding in
868 one nearby stream running through oil-palm plantation in the local area (Pers. Obs.). Tilapia are
869 widely reported to exclude native fish from prime breeding grounds, are reproductively active for
870 long periods, have short reproductive cycles, and can quickly colonise new areas (Canonico et al.
871 2005). The pathway by which tilapia was introduced is unknown, but it is likely to have been
872 deliberately introduced for aquaculture, as has been commonplace across mainland Southeast Asia
873 (e.g., Bilio 2007; Arthur et al. 2010; Liew et al. 2012). It will be important to monitor for spread or
874 impacts of the species in the study area.

875 This study focuses on the value of freshwater fish as a resource to benefit human wellbeing, as
876 opposed to examining fish community changes due to, and the ecological impact of, land-use
877 change. There is wide debate between the provision of ecosystem services and the need to protect
878 biodiversity for its intrinsic value, especially in the freshwater context. Protected areas are the main

879 conservation strategy worldwide, but have had limited effectiveness for freshwater biodiversity
880 (Hermoso et al. 2016). To protect fresh waters it is essential to preserve upstream–downstream and
881 lateral linkages (including land-based activities in the wider catchment both for biophysical
882 functioning and biodiversity (Hermoso et al. 2016)). However, protected areas in Sabah, Malaysia,
883 are to date designed for terrestrial biodiversity. Riparian reserves are required by law in Sabah (20 m
884 either side of rivers wider than 3 m, Sabah Water Resources Enactment 1998) predominantly for
885 protection of water quality and to act as corridors for terrestrial species, but these reserves are not
886 automatically considered protected areas (Payne et al. 2007). As freshwater fish represent a vital
887 provisioning ecosystem service and are at the same time highly biodiverse, it is essential to monitor
888 and protect them, as threats such as land-use change, climate change, and alien species are likely to
889 increase within the tropics (Gardner et al. 2009; Strayer & Dudgeon 2010; Laurance et al. 2012;
890 Taniwaki et al. 2017).

891 Our study only examined fish communities in catchments where land-uses that had not changed for
892 more than seven years since disturbance, and therefore makes no conclusions about possible short
893 term impacts that might arise during or immediately after the process of logging and conversion to
894 oil-palm. Nonetheless, freshwater fish in small headwater streams appear to represent a sustainable
895 resource, and thus we infer a vital sustainable provisioning ecosystem service for villages established
896 in developed oil-palm plantations.

897

CHAPTER 3:

898 LAND-USE CHANGE IS ASSOCIATED WITH A SIGNIFICANT LOSS OF FRESHWATER FISH SPECIES AND 899 FUNCTIONAL RICHNESS IN SABAH, MALAYSIA

900

901 This chapter was published at the following location:

902 Wilkinson, C. L., Yeo, D. C. J., Tan, H. H., Hadi Fikir, A. & Ewers, R. M. (2018) Land-use change
903 is associated with a significant loss of freshwater fish species and functional richness in
904 Sabah, Malaysia. *Biological Conservation*, 222, 164-171.

905 ABSTRACT

906 Global biodiversity is being lost due to extensive anthropogenic land cover change. In Southeast
907 Asia, biodiversity-rich forests are being extensively logged and converted to oil-palm monocultures.
908 The impacts of this land-use change on freshwater ecosystems, and particularly on freshwater
909 biodiversity, remains largely understudied and poorly understood. We assessed the differences
910 between fish communities in headwater stream catchments across an established land-use gradient
911 in Sabah, Malaysia (protected forest areas, twice-logged forest, salvage-logged forest, oil-palm
912 plantations with riparian reserves, and oil-palm plantations without riparian reserves). Stream fishes
913 were sampled using an electrofisher, a cast net and a tray net in 100 m long transects in 23 streams
914 in 2017. Local species richness and functional richness were both significantly reduced with any land-
915 use change from protected forest areas, but further increases in land-use intensity had no
916 subsequent impacts on fish biomass, functional evenness, and functional divergence. Any form of
917 logging or land-use change had a clear and negative impact on fish communities, but the magnitude
918 of that effect was not influenced by logging severity or time since logging on any fish community
919 metric, suggesting that just two rounds of selective impact (i.e., logging) appeared sufficient to cause
920 negative effects on freshwater ecosystems. It is therefore essential to continue protecting primary
921 forested areas to maintain freshwater diversity, as well as to explore strategies to protect freshwater

922 ecosystems during logging, deforestation, and conversion to plantation monocultures that are
923 expected to continue across Southeast Asia.

924 **3.1. INTRODUCTION**

925 Anthropogenic land cover change through agricultural expansion and intensification is currently a
926 major driver of global biodiversity loss (Phalan et al. 2013; MEA 2005). The destruction of tropical
927 forests is of particular significance owing to the disproportionately high levels of biodiversity present
928 in the tropics (Bradshaw et al. 2009; Laurance et al. 2012); marked declines in biodiversity when
929 tropical forest is converted to other land-use types (Phalan et al. 2013); and the unabated levels of
930 deforestation due to increasing human demands for food, timber and other products (Sodhi et al.
931 2004; Wilcove et al. 2013). Large areas of logged forest and agriculture will be key features of future
932 tropical landscapes. Primary forests are critically important for conserving tropical biodiversity
933 (Gibson et al., 2011) and once-logged forests in Southeast Asia have high conservation value for
934 terrestrial taxa (Edwards et al. 2014), but focussing on these habitats alone is not sufficient. The
935 impacts of this large scale land-use change and other anthropogenic activities on freshwater
936 ecosystems and biodiversity in tropical streams remains largely understudied and poorly understood
937 (Ramirez et al. 2008). It is important to understand how these changing landscapes impact upon
938 aquatic as well as terrestrial biodiversity, and to devise strategies that provide protection
939 mechanisms.

940 The most widespread and destructive threat to aquatic ecosystems is habitat modification that
941 results from converting natural areas to agricultural land (Allan & Flecker 1993; Laurance et al.
942 2014). Extensive logging and deforestation across the tropics (Hansen et al. 2010a; Achard et al.
943 2014) has caused large scale modifications to catchments, resulting in changes in water quantity,
944 quality, de-regulation in stream hydraulics and increased sedimentation levels (Iwata et al. 2003a;
945 Inoue & Nunokawa 2005). The effects of deforestation on the species richness of fish are variable.
946 Species richness can be increased (Lorion & Kennedy 2009), decreased (Brook et al. 2003; Toham &

947 Teugels 1999), or unaffected (Bojsen & Barriga 2002) by tropical deforestation, with equally variable
948 impacts on fish community composition (Bojsen & Barriga 2002; Giam et al. 2015).

949 In Borneo, freshwater fish community composition is thought to be structured more strongly by
950 local, mesohabitat structures (pool, riffle, or run) than larger, catchment scale processes such as
951 logging history, although time since logging activity was shown to positively affect the abundance of
952 common cyprinids (Martin-Smith 1998a, b). In comparison, Iwata et al. (2003a) showed different fish
953 guilds or community metrics responded differently to deforestation. For example, the abundance of
954 benthic fish and other taxa was lower in deforested catchments, which was attributed to increases in
955 sedimentation, but nektonic (free-swimming) fish did not suffer reductions. It is suggested that
956 deforestation or habitat alteration can affect fish communities by changing the taxonomic identities
957 and functional diversity of communities, whereas mesohabitat differences affect the functional
958 composition of communities (Casatti et al. 2012), causing reductions in functionally distinct species
959 (Villéger et al. 2010).

960 Land-use change causes alterations in sediment load, nutrient runoff (e.g., from fertilisers), canopy
961 cover and thus temperature, leaf litter and woody debris, to name but a few environmental
962 variables (Luke et al. 2017a). All of these impacts change the microhabitats that fish inhabit and can
963 affect taxonomic or functional groups differently (e.g., Jones et al. 1999; Newcombe & Macdonald
964 1991; Sazima et al. 2006). Moreover, more destructive logging practices can have a bigger impact.
965 The practice of slash and burn agriculture led to long term degradation of streams because of its
966 greater impact on vegetation and soil conditions than selective-logging regimes (Iwata et al. 2003a).
967 The impacts of conversion of forest to oil-palm monoculture, however, can be mitigated by the
968 retention of forest patches and riparian reserves. Aquatic diversity was maintained at pre-conversion
969 species richness and functional diversity within oil-palm monocultures in the Indo-Malay region
970 when riparian reserves were present (Giam et al. 2015). By contrast, stream sites within plantations
971 lacking riparian reserves exhibited an average 42% reduction in aquatic species diversity (Giam et al.

972 2015). Despite this, there is considerable variation in the impacts of land-use change on freshwater
973 ecosystems, leading to renewed calls to better understand the potential interactions of land-use
974 change with other stressors specific to certain regions such as dams, drought or invasive species
975 (Macedo et al. 2013; Taniwaki et al. 2017). Thus regional studies are needed to uncover local
976 impacts of varying land-use on freshwater fish communities in order to determine and validate
977 protection mechanisms to safeguard freshwater ecosystems in the long term.

978 The aim of this study was to determine how freshwater fish communities change in headwater
979 stream catchments that vary over an established land-use gradient from protected forest areas,
980 twice-logged forest, and oil-palm plantations with and without riparian buffers, in Sabah, Malaysia.
981 This is among the first studies in Southeast Asia comparing freshwater fish diversity across this suite
982 of land-uses, and in such a close geographical space. We expected to see a decline in fish species
983 richness (following the 42% decline previously reported by Giam et al., 2015), biomass, and all
984 metrics of functional diversity, as forest is logged or converted to oil-palm plantations, in comparison
985 to protected forest catchments (Martin-Smith 1998a, b, c; Iwata et al. 2003a; Mercer et al. 2014;
986 Giam et al. 2015; Juen et al. 2016; Pye et al. 2017). Community composition is expected to change in
987 disturbed habitats (Iwata et al. 2003a; Kwik & Yeo 2015), reducing to a subset of species present in
988 protected forests. In addition, oil-palm streams with a forested riparian buffer (~ 30 m wide on both
989 sides of the stream) were expected to have a higher richness, biomass and functional diversity than
990 those without riparian buffers (Lorion & Kennedy, 2009; Giam et al. 2015). We predicted this would
991 be due to changes in canopy cover over the streams, impacting for example, water temperature,
992 litter fall and litter retention within the stream. With ongoing deforestation and conversion to oil-
993 palm plantations in Southeast Asia, it is crucial to understand how these processes impact
994 freshwater biodiversity in order to develop strategies to protect freshwater ecosystems and
995 maintain the ecosystem services they provide.

996

997 **3.2. METHODS**998 **3.2.1. STUDY SITE**

999 Study sites were located on small, headwater streams (3–10 m wide, ≤ 1.2 m maximum depth) in
1000 Southeastern Sabah, Malaysian Borneo (117.5°N, 4.6°E). The landscape is a mosaic of protected
1001 forest (PF) areas consisting of primary lowland dipterocarp rainforest (Danum Valley Conservation
1002 Area and the Brantian Tantulit Virgin Jungle Reserve; catchment above ground biomass (AGB)
1003 average 165 T Ha⁻¹), twice-logged forest (LF2; AGB average 96.3 T Ha⁻¹) and salvage-logged forest
1004 (LF3; AGB average 65.8 T Ha⁻¹), and oil-palm plantations with (OPB) and without riparian reserves
1005 (OP; planted between 1998 and 2011; AGB average for all oil-palm streams is 19.7 T Ha⁻¹) (Pfeifer et
1006 al. 2016). The sites form part of the Stability of Altered Forest Ecosystems (SAFE) Project (Ewers et al.
1007 2011). The landscape is drained by tributaries of the Brantian, Kalabakan and Segama rivers, all of
1008 which empty into the Celebes Sea.

1009 We collected data from 23 headwater stream catchments that were, where possible, matched to the
1010 SAFE project experimental streams (length ~2 km; catchment area ~260 ha; slope ~16°; (Ewers et al.
1011 2011)). Five catchments were in protected areas (four at Danum Valley Conservation Area, and one
1012 in the Brantian Tatulit Virgin Jungle Reserve; Fig. 1). Three catchments were in continuous twice-
1013 logged forest (selectively-logged in the 1970s and again in the 1990s-2000s) and six in recently
1014 salvage-logged forest in the SAFE project experimental area (selectively-logged in the 1970's and
1015 1990s-2000s, and salvage-logged between 2013 and 2015). Another five catchments were in oil-
1016 palm plantations with riparian reserves of approximately 30 m width, and four oil-palm catchments
1017 without riparian reserves. Oil-palm catchments had palms that varied in time since planting from 4–
1018 11 years. Each catchment was an independent tributary, ensuring spatial independence of data.
1019 Within each catchment, a 100 m transect was established.

1020

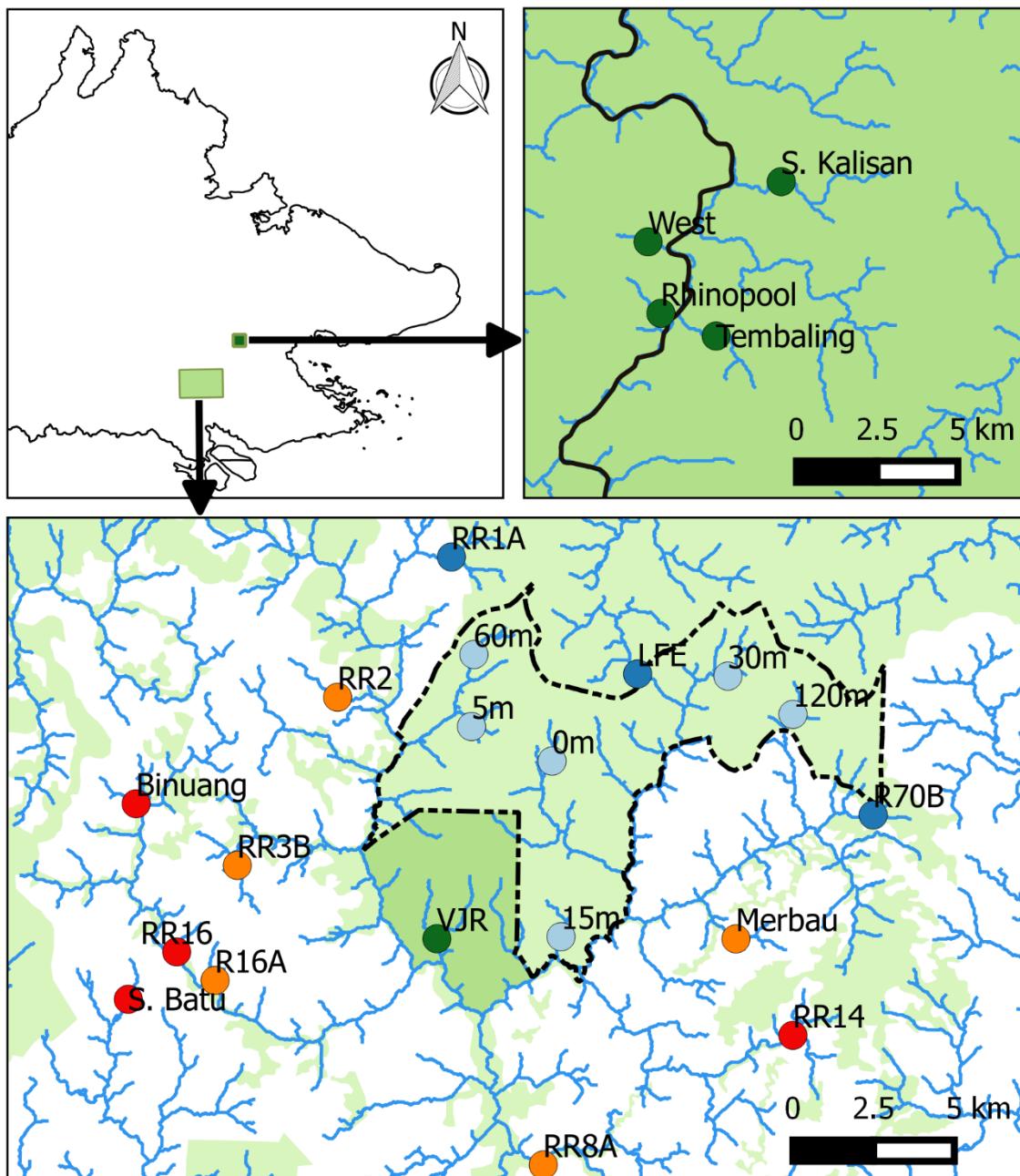


Figure 1. Schematic and map showing the study areas in Sabah, Malaysian Borneo, and the location of the twenty three stream sites that were used in this study. Protected forest is darker green (within Danum Valley Conservation Area to the left of the black line in the top right map), logged forest in paler green and oil-palm plantations in white. Stream sampling locations vary in colour by land-use: protected areas (green), twice-logged forest (dark blue), salvage-logged forest (pale blue), oil-palm plantation with riparian reserve (orange), and without riparian reserve (red).

1021

1022

1023

1024 **3.2.2. FISH SAMPLING**

1025 Field work was conducted between February–July 2017. We sampled fishes on clear-weather days
1026 using three capture methods, performed in the following order at each transect: (1) three pass
1027 electrofishing (model EFGI 650; Bretschneider Spezialelektronic), (2) cast netting (2.75 m diameter
1028 net with 1 cm mesh), and (3) tray (push) netting (dimensions 60 x 45 cm, 2 mm mesh). Tray (push)
1029 netting involves capturing fish by placing a rectangular steel-framed net downstream of possible
1030 habitat (undercut banks, leaf litter and rocky areas) while disturbing the habitat, e.g., by kicking. In
1031 each transect, before sampling began, we placed stop nets (2 mm mesh) at upstream and
1032 downstream boundaries to prevent immigration and emigration of fish during our sampling period.
1033 We employed these methods to target all major fish microhabitats so as to obtain comprehensive
1034 and unbiased descriptions of fish communities (Kennard et al. 2006; Giam et al. 2015).

1035 Captured fishes were identified to species (Inger & Chin 2002; Kottelat 2013), measured and
1036 uncommon species (< 30 individuals previously weighed; 9% of individuals) weighed using a portable
1037 balance, and most (85%) were returned to the stream at the point of capture. Prior to this study,
1038 5,136 fish had been weighed at these stream transects for other studies (C. Wilkinson, Unpub. data),
1039 so for common species we recorded their length only and used length-mass regressions to estimate
1040 weight (Appendix 3.2.1). A subset of fish (up to three individuals of each species from each stream)
1041 were preserved as vouchers for proof of identification. These fish specimens were euthanized with
1042 MS-222, fixed in 10% formalin, and transferred to 75% ethanol for storage in the Lee Kong Chian
1043 Natural History Museum, National University of Singapore. Fish capture, handling and euthanisation
1044 protocols were approved by the Animal Welfare and Ethical Review Body at Imperial College
1045 London.

1046

1047

1048 **3.2.3. ENVIRONMENTAL VARIABLES**

1049 Twelve stream scale and four riparian vegetation scale variables were measured at every transect.

1050 Instream variables were: temperature ($^{\circ}\text{C}$), dissolved oxygen (mg L^{-1}), conductivity ($\mu\text{S cm}^{-1}$), pH, and

1051 turbidity (NTU) measured with a YSI Professional Plus, wetted width (m), depth (cm), mean surface

1052 current speed (m s^{-1} ; measured by timing a tennis ball travelling 2 m, repeated three times),

1053 substrate (%; sand, gravel, pebbles, large rocks, bedrock), littoral leaf cover (%; measured in a 50 cm

1054 transect across the stream and recorded to the nearest 10%), sedimentation (presence or absence),

1055 canopy cover (densiometer readings oriented upstream, downstream, and to the left and right

1056 banks), and each was measured every 10 m along the 100 m transects. Riparian vegetation

1057 measurements of canopy cover (densitometer readings upstream, downstream, towards stream and

1058 away from stream), density of trees (relascope), percentage vine cover (assessed visually and

1059 recorded to the nearest 10%) and a general forest quality score (0–5, 0 = oil-palm; 1 = no trees, open

1060 canopy with ginger/vines or low scrub; 2 = open with occasional small trees over ginger/vine layer; 3

1061 = small trees fairly abundant/canopy at least partially closed; 4 = lots of trees, some large, canopy

1062 closed; 5 = closed canopy with large trees, no evidence of logging) (Ewers et al. 2011) were

1063 measured visually every 50 m, starting at the 0 m point on the transect, 10 m away from the stream

1064 edge and on both sides of the stream for 500 m.

1065 **3.2.4. FISH COMMUNITY METRICS**

1066 Fish catch data was collated per stream, combining the three sampling methods. In addition to local

1067 species richness per stream, we calculated functional diversity and fish biomass. Functional diversity

1068 is defined as the variation in species traits that influence ecosystem function (Petchey & Gaston,

1069 2006). We focussed on one aspect: energy flow (Giam et al. 2015; Viole et al. 2007). Functional

1070 traits known to affect energy flow in stream ecosystems through their impact on a species' life

1071 history, feeding strategy, habitat use, and locomotion were compiled from the literature (e.g.,

1072 Roberts 1989), FishBase (www.fishbase.org), and field observations of behaviour, form and function

1073 of freshwater fishes within the SAFE project, in other parts of Borneo as well as Southeast Asia by
1074 the authors over the past seven years (C. Wilkinson, H. H. Tan, Unpub. data). The traits were average
1075 body size, body shape, trophic position, mouth position, presence of jaw teeth, gregariousness,
1076 presence of barbels, vertical position in water column, and air-breathing capability (Appendix 3.1.2,
1077 3.1.3). Fish biomass and biomass per functional trait were calculated using regression equations
1078 (Appendix 3.2.1). These were calculated where enough individuals ($N > 30$) of each species had been
1079 caught and weighed. Fish total length was then extrapolated to calculate the mass of all individual
1080 fish of that species that had not been weighed. General regression equations that varied according
1081 to body morphology (heavy-bodied or flattened) were calculated for species with low catch rates to
1082 determine body mass.

1083 **3.2.5. DATA ANALYSES**

1084 We quantified functional diversity with three complementary metrics: functional richness (F_{ric}),
1085 functional divergence (F_{div}), and functional evenness (F_{eve}) (Villéger et al. 2008). These metrics were
1086 chosen as they can be used to indicate whether species within a given habitat are performing similar
1087 (i.e. redundant) or different (i.e. complementary) roles for a given function or service. Functional
1088 richness is the volume of trait space occupied by a community (Laliberté & Legendre 2010).
1089 Functional divergence is the divergence in distribution of species in trait space. Functional evenness
1090 quantifies community evenness in trait space. Functional redundancy, the number of taxonomically
1091 distinct species that exhibit similar ecological functions, was also explored to determine the strength
1092 and shape of the relationship between taxonomic and functional richness (Lawton & Brown 1994;
1093 Naeem 1998). We used the FD package (Laliberté et al. 2011) in R 3.4.1 (R Core Development Team,
1094 2017) to calculate these metrics using presence-absence data of the fish in each stream. We used a
1095 null model to distinguish whether the observed change in functional richness was higher or lower
1096 than expected given the species richness observed (Petchey 2004). We used simulations to create a
1097 random (null) distribution of functional richness values for each given species richness per transect.

1098 Holding species richness constant for each land-use type, we randomly selected species from the
1099 species pool (the total number of species in the study) to calculate a null functional richness for each
1100 richness level. We used 1000 iterations to produce a null distribution of values and tested whether
1101 the actual, observed functional richness for each community was significantly higher or lower than
1102 the mean of the null functional richness distribution.

1103 We fitted and analysed generalised linear models (GLMs) of local species richness, the three metrics
1104 of functional diversity, total biomass, and biomass per functional trait across the land-use gradient.
1105 All data were compiled per transect, resulting in 23 data points per model. Biomass per functional
1106 trait was calculated for all traits, excluding mean length by assigning the biomass of each species to
1107 the functional trait of that species, at each transect. Functional redundancy at each stream was
1108 analysed using a generalised linear model, testing if the interaction between local species richness
1109 and land-use had a significant impact on functional richness.

1110 We then investigated the mechanisms that may be controlling local species richness by comparing
1111 univariate GLMs to identify the strongest instream environmental correlates of local species richness
1112 (Appendix 3.3). Multiple tests were applied to the same dataset of species richness, so a Bonferroni
1113 correction ($0.05/n$; $n = 21$; corrected $\alpha = 0.002$) was applied to all p-values. For all the species
1114 richness models a Poisson or Quasipoisson error distribution was applied (dependent upon the
1115 results of a test for over dispersion using the AER package (Kleiber & Zeileis 2017)). For all other
1116 models a Gaussian error distribution was applied (Zuur et al. 2009). Log-likelihood ratio tests were
1117 used to assess model significance.

1118 To determine whether each land-use supported different communities, and what environmental
1119 variables may be associated with these differences in fish communities, we used the vegan package
1120 (Oksanen et al. 2013) in R 3.4.1 to perform redundancy analysis (RDA). We chose to use RDA
1121 because Detrended Correspondence Analysis on the community composition data showed the
1122 gradient lengths to be <2 , indicating linear responses (Lepš & Šmilauer 2003). Euclidean distances of

1123 abundance data were maintained using the ‘Hellinger transformation’. Adonis permutational
1124 multivariate analysis of variance (perMANOVA) models from the package ‘vegan’ (Oksanen et al.
1125 2013) was performed to quantify differences between land-uses. We used p-values (generated by
1126 999 permutations) to assess significance and R² values to assess effect size of land-use in explaining
1127 community composition. Forward selection was used to rank all (instream and riparian)
1128 environmental variables in order of importance in terms of their association with differences in
1129 species composition (significant conditional effects set at p < 0.05).

1130

1131 **3.3. RESULTS**

1132 We identified 34 species from 2,902 fish captures (see Appendix 3.4.1 for species list). The most
1133 common species in terms of abundance and presence across all land-uses were *Barbodes sealei* (N =
1134 603, 21% of the total), *Nematabramis everetti* (N = 851, 29%), *Rasbora cf. sumatrana* (N = 528, 18%)
1135 and *Tor ticta* (N = 183, 6%). Sixteen species were only detected in a single land-use type, most of
1136 which were also rare (< 10 individuals; *): *Crossocheilus elegans*, *Garra borneensis*, *Lobocheilos*
1137 *erinaceus**, *Lobocheilos unicornis**, *Luciosoma pelligrinii**, *Betta unimaculata**, *Mastacembelus*
1138 *unicolor**, *Homolopteroides stephsoni*, *Magrognathus keithi** (only in protected rainforest);
1139 *Rasbora elegans* (only in twice-logged forest); *Protomyzon borneensis** (only in salvage-logged
1140 forest); *Barbonymus balleroides*, *Clarias anfractus**, *Cyclocheilichthys repasson**, and *Channa*
1141 *striata** (only in oil-palm streams with a riparian reserve); and *Oreochromis mossambicus* (only in oil-
1142 palm streams without a riparian reserve). Nine of these 16 species were found only in protected
1143 rainforest (see Appendix 3.4.1, 3.4.2 for species list and presence) in the Segama catchment. A
1144 further 10 species were found only in the Brantian catchment (Appendix 3.4.2), showing variability
1145 between catchments. Several of the species that we detected in just one or the other catchment
1146 have previously been observed in the other catchment (we captured *Barbonymus balleroides* and
1147 *Cyclocheilichthys repasson* only in the Brantian, and *Betta unimaculata* and *Mastacembelus unicolor*

1148 only in the Segama; but all four species are known to be present in both catchments; Pers. Obs.). We
 1149 detected one known introduced species, *Oreochromis mossambicus* (Mozambique tilapia), and one
 1150 possibly introduced, *Channa striata*, in the oil-palm sites.

1151 We found a significant impact of land-use on local species richness (Figure 2a; $\chi^2_{(4)} = 21.45$, $P <$
 1152 0.001), with richness highest in protected rainforest and lower in all other land-uses. There was no
 1153 significant difference between oil-palm and logged forest, or between streams with different logging
 1154 histories. Functional richness of protected forest streams was significantly higher than that of all
 1155 disturbed sites (Figure 2b; $\chi^2_{(4)} = 30.72$, $P < 0.001$), but this decline at disturbed sites was not
 1156 significantly different from that expected according to a random loss of species as determined by the
 1157 null model. Sites within each land-use showed different patterns in relation to the null model, but no
 1158 significant differences between land-use types (Figure 2b; $\chi^2_{(1)} = 1.18$, $P = 0.28$). There was no
 1159 significant interaction between local species richness and land-use in explaining functional richness
 1160 ($\chi^2_{(4)} = 2.06$, $P = 0.724$), suggesting the same level of functional redundancy in all land-uses.

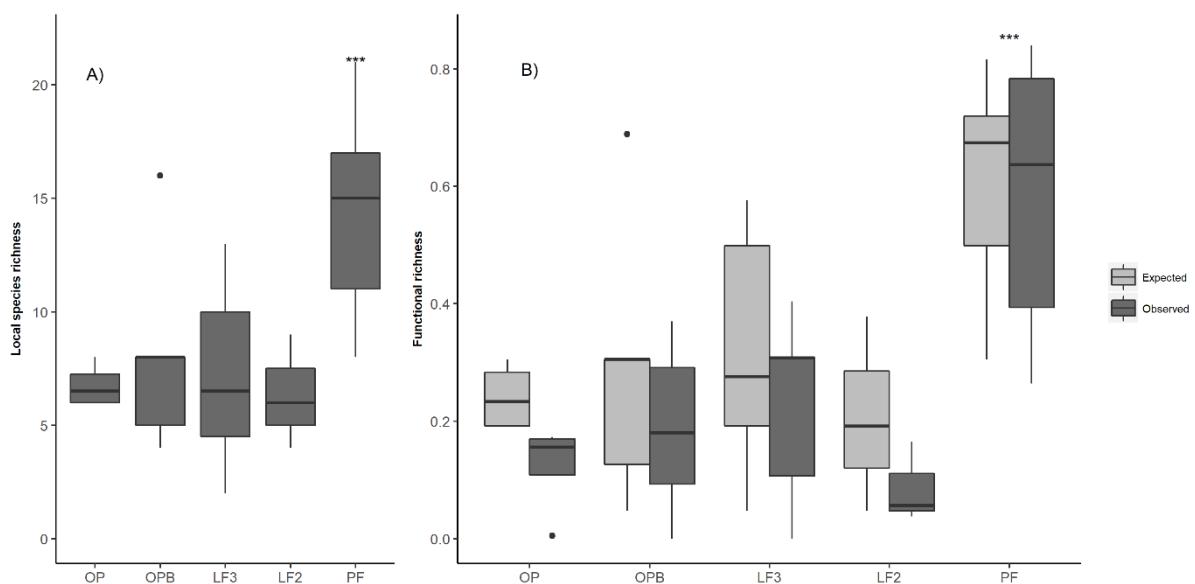


Figure 2. Box and whisker plots of local species richness (A), and the observed and expected functional richness across a land-use gradient (B). Box and whisker plots indicate the median (dark band), interquartile range (within each rectangle), and the highest and lowest values of the data, excluding outliers, in the whiskers, with outlying points as black dots. OP = oil-palm plantation without riparian buffer, OPB = oil-palm plantation with riparian buffer, LF3 = salvage-logged forest after the third round of logging, LF2 = twice-logged forest, and PF = protected forest catchments.

'*' indicate the significance of each model and which land-use is significantly different from the others (** = P < 0.001).

1161 There was no significant impact of land-use on functional evenness ($\chi^2_{(4)} = 3.18$, P = 0.528),
1162 functional divergence ($\chi^2_{(4)} = 6.53$, P = 0.163), or total biomass ($\chi^2_{(4)} = 0.84$, P = 0.933). Biomass per
1163 functional trait highlighted a significant difference across the land-uses in benthopelagic fish ($\chi^2_{(4)} =$
1164 10.49, P = 0.032) and fish with superior mouths ($\chi^2_{(4)} = 13.698$, P = 0.008). Biomass was higher in
1165 forested streams than in oil-palm streams for benthopelagic fish that are predominantly grazers, but
1166 lower in forested streams than oil-palm streams for fish with superior mouths that are surface
1167 feeding invertivores.

1168 Univariate generalised linear models (Appendix 3.3) showed that species richness increased with
1169 littoral leaf litter cover (Figure 4a; $\chi^2_{(4)} = 14.57$, P = 0.003) and was positively correlated with
1170 percentage gravel (Figure 4b; $\chi^2_{(4)} = 11.97$, P = 0.011), but was not correlated with other instream
1171 environmental variables (Appendix 3.3.1). Neither of the two variables that were correlated with
1172 species richness varied significantly among land-uses (leaf litter ($\chi^2_{(4)} = 4.83$, P = 1.000), percentage
1173 gravel ($\chi^2_{(4)} = 4.20$, P = 1.000)), whereas some other variables did: temperature ($\chi^2_{(4)} = 33.22$, P <
1174 0.001), stream canopy cover ($\chi^2_{(4)} = 21.338$, P < 0.001), sedimentation ($\chi^2_{(4)} = 50.87$, P < 0.001),
1175 riparian canopy cover ($\chi^2_{(4)} = 20.49$, P < 0.001), riparian vine cover ($\chi^2_{(4)} = 27.78$, P < 0.001),
1176 riparian tree density ($\chi^2_{(4)} = 35.78$, P < 0.001) and riparian forest quality ($\chi^2_{(4)} = 181.07$, P < 0.001).

1177 Freshwater fish community composition was similar between all land-uses (perMANOVA $R^2 = 0.20$, P
1178 = 0.282), but had the strongest associations with substrate (percentage of sand, gravel and bedrock),
1179 average depth and littoral leaf litter cover (Table 1; Figure 3). All disturbed sites with anthropogenic
1180 land-uses have a restricted number of species within each stream transect, but have high variability
1181 in species presence across the landscape, indicated by the large confidence interval ellipses in
1182 comparison to protected forest streams (Figure 3). The average depth and percentage of sand were
1183 strongly correlated with Axis 1 ($r = -0.587$ and 0.419, respectively), which represented a gradient
1184 from forest cover (negative values) through to oil-palm plantations with no riparian reserve (positive

1185 values). Pelagic or benthopelagic, invertivorous and omnivorous fish occurrence were correlated
 1186 with this gradient, with greater occurrence in forested streams. Littoral leaf litter cover and
 1187 percentage bedrock were correlated with axis 2 ($r = -0.375$ and 0.725 respectively), which comprised
 1188 a gradient of occurrence of benthic, algal feeding fish. Negative values indicating a greater
 1189 percentage of littoral leaf cover, lower percentage bedrock and higher numbers of benthic algal
 1190 feeders in protected forests, sensitive to changes in water quality, and positive values representing
 1191 disturbed catchments: logged or oil-palm plantations with and without riparian reserves.

1192

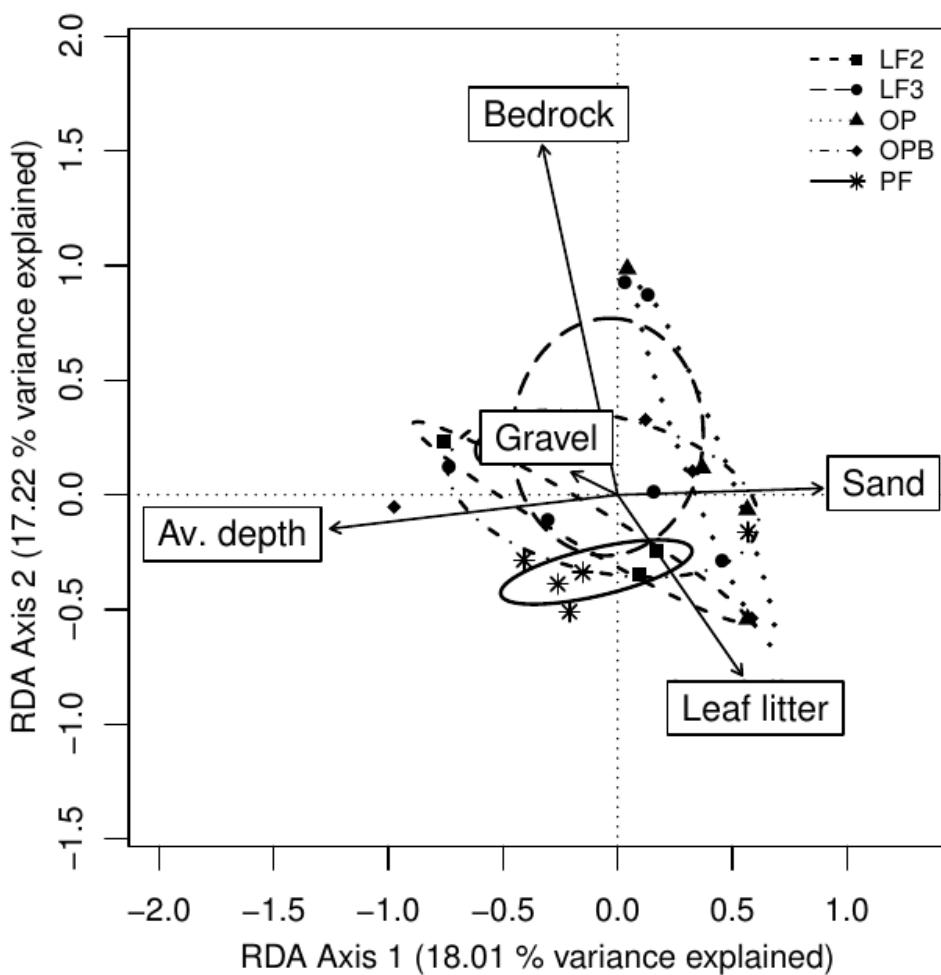


Figure 3. Ordination tri-plots showing redundancy analysis (RDA) of fish community composition and significant ($P < 0.05$) environmental variables across all land-uses. Points represent each stream community composition and ellipses show 95% confidence interval of each land-use.

Table 1. Results of redundancy analysis (RDA) forward selection to test the effects of environmental variables on fish communities across land-uses, listing all significant ($p < 0.05$) environmental variables (λ_2 variance explained and p value), and the resultant intraset correlation coefficients of significant environmental variables for the first two axes of the RDA for freshwater fish community composition.

Environmental variable	λ_2	p	Axis 1	Axis 2
% bedrock	0.07	0.001	-0.1769	0.82109
Average depth	0.05	0.004	-0.6752	-0.07969
% gravel	0.04	0.025	-0.1086	0.05352
% sand	0.04	0.013	0.4815	0.01541
Littoral leaf litter cover	0.03	0.030	0.2927	-0.42414

λ_2 shows the variation explained, and associated significance, for each variable as it was included into the model by forward selection. Significance of each environmental variable was calculated using Monte Carlo permutation tests with 999 random permutations.

1193

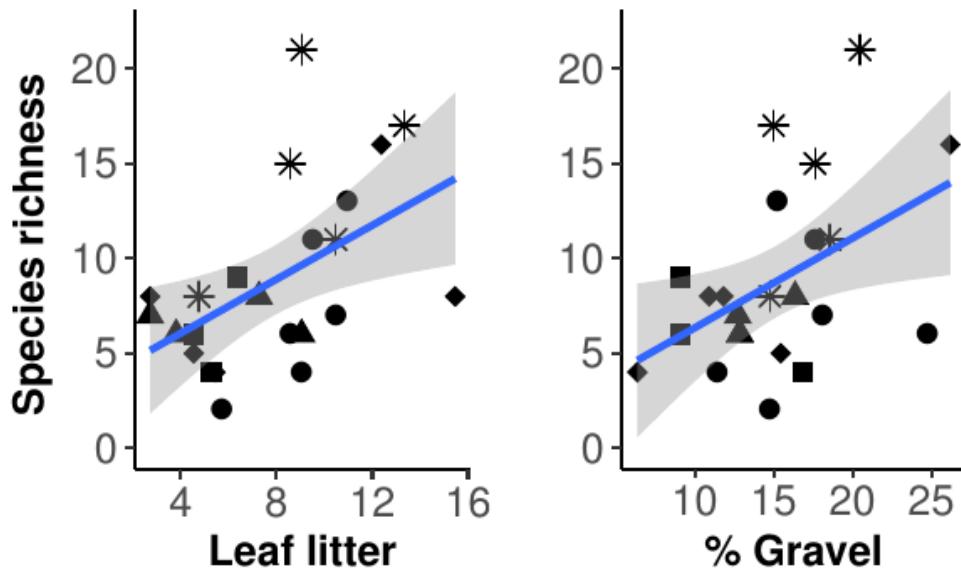


Figure 4. Relationship between local species richness and (a) littoral leaf litter cover, and (b) percentage gravel. Each point represents the local species richness and leaf litter cover/percentage gravel in a particular site. The land-use of the site are represented by the following symbols – star: protected forest; square: twice-logged forest; circle: salvage-logged forest; diamond: oil-palm with riparian buffer; and triangle: oil-palm with riparian reserve. Black line and shaded area are the Poissons generalised linear model and 95% confidence intervals.

1194

1195 **3.4. DISCUSSION**

1196 Catchment land-use has a significant impact on the species richness of freshwater fish communities,
1197 but not on community level biomass or composition. Any disturbance (logging or conversion) from
1198 protected forest catchments sees a significant loss of functionally distinct species and reduced
1199 functional richness of the communities, but there was no change in functional redundancy among
1200 land-uses. Several endemic, fast flowing, hill stream specialist species were only found in low
1201 numbers inside protected forest catchments, suggesting these range-restricted species are likely to
1202 be threatened by land-use change (Giam et al. 2011).

1203 Quantitative studies in Borneo show that with sustainable land-use conversion, the impact of land-
1204 use on freshwater communities is minimal. However each study has only compared different logging
1205 regimes (Martin-Smith, 1998a, b, c; Beamish et al. 2003; Iwata et al. 2003a) or oil-palm plantations
1206 with or without riparian reserves (Giam et al. 2015) to continuous or primary rainforest. The impact
1207 of land conversion for palm-oil or other agricultural plantation can be mitigated by the retention of
1208 forest fragments and riparian reserves (Giam et al. 2015), and the impact of selective-logging is
1209 suggested to be more benign to freshwater fish (Martin-Smith 1998a, c; Iwata et al. 2003a) than
1210 clear cutting and agricultural conversion (Beamish et al. 2003; Giam et al. 2015). This study suggests,
1211 however, that streams in all disturbed land-uses (selective-logging, salvage-logging and conversion
1212 to oil-palm plantation) suffer losses in species and functional richness relative to protected
1213 rainforest.

1214 We had expected to see a greater difference in species richness or community composition between
1215 protected or primary forest streams and oil-palm streams, than between logged forest and oil-palm
1216 streams. In addition, we had expected species richness to be lower in the recently, salvage-logged
1217 forest streams (logged from April 2013 to July 2016), than the twice-logged forest streams (last
1218 logged more than 10 years ago) due to the severity and time since logging activities. This logging
1219 timeframe is within the life span (2–5 years) of small, tropical freshwater fish (Ng & Tan 1997). Yet

1220 logging history was not included as a stand-alone factor in our statistical models. We had only a
1221 limited sample size to test for this effect, but visual inspection of Figure 2 suggested there was no
1222 difference among twice, selectively-logged forests, and three times-logged (with the third round
1223 being salvage-logging) forests for any fish community metric. This suggests that time since logging,
1224 type of logging and number of times the forest is logged have no additional impact on fish
1225 communities.

1226 Interestingly, there was also no significant difference in species richness or functional diversity
1227 between logged forest and oil-palm catchments (Figure 2), contrary to what we had expected. This
1228 indicates that all forms of disturbances have strong negative influences on fish communities. In
1229 contrast to Giam et al. (2015), however, local species richness in oil-palm streams with and without
1230 riparian reserves was very similar, and our data are not consistent with the expectation that oil-palm
1231 streams with riparian reserves can maintain ‘forest-like’ conditions within a stream. The differing
1232 results between this study and Giam et al. (2015) may be due to fewer microhabitats covered and/or
1233 a smaller metacommunity of fishes in the hill streams we sampled as opposed to the lowland
1234 streams sampled by Giam et al. (2015).

1235 Together, our results indicate that any land-use change has lasting, negative impacts on the
1236 freshwater ecosystem, and that undisturbed, protected forest areas are essential in protecting
1237 freshwater diversity. But how does disturbance, through logging or deforestation, and land-use
1238 change to oil-palm plantation, disrupt fish communities? Our data indicate that littoral leaf litter
1239 cover is the instream variable with the biggest influence on fish communities. The highest proportion
1240 of littoral leaf litter cover was seen in protected forests and cover decreased in logged and oil-palm
1241 streams. The diversity and composition of riparian derived leaf litter has previously been shown to
1242 exert strong influences on the community structure and functioning of stream ecosystems (LeRoy &
1243 Marks 2006; Kominoski & Pringle 2009; Kominoski et al. 2011). This likely occurs because leaf litter
1244 supports fish communities by providing cool and dark microhabitats, shelter from predators (Sazima

1245 et al. 2006), and increasing and spatially concentrating food resources such as macroinvertebrates,
1246 biofilm and algae (Pringle et al. 1988; Wallace et al. 1997).

1247 Sedimentation also had a substantial impact on species richness, with richness decreasing as
1248 sedimentation increased. Besides providing leaf litter inputs, less disturbed forests and forested
1249 riparian reserves can minimise soil erosion and substrate deposition from upstream within the
1250 catchment (Jones et al. 1999; McIntosh & Laffan 2005). Other results from our study site have
1251 indicated that as forest gets removed from the whole catchment, or riparian reserves get converted
1252 to oil-palm, streams become shallower, wider and have a greater proportion of sand and sediment
1253 influx due to reduced bank stability (Luke et al. 2017a). Higher levels of siltation and sedimentation
1254 can damage gill tissue, reduce fish spawning grounds and benthic food resources (Newcombe &
1255 Macdonald 1991; Jones et al. 1999), and thus reduce fish species richness. Our field data
1256 corroborate this, with a greater number of benthic or benthopelagic species occurring in protected
1257 forest streams that are dominated by gravel and larger substrates as opposed to those with greater
1258 proportions of sediment or sand substrate. Our results here are consistent with those of Giam et al.
1259 (2015), implicating the same environmental variables as local drivers of fish community richness
1260 despite working in quite different stream systems (e.g. hill streams vs. lowland and slightly alkaline
1261 vs. acidic streams, in this study vs. Giam et al. (2015), respectively). As Luke et al. (2017a) showed,
1262 there are clear differences in these variables across the land-use gradient.

1263 We did not record water chemistry, in particular concentrations of nitrates and phosphates, in our
1264 study despite their potential impact on fish species richness (Covich et al. 1999; Yule et al. 2009). At
1265 our study site, nitrate levels are known to be as much as 12x lower, and phosphorus levels up to 3x
1266 higher, in less disturbed forested streams than in oil-palm catchments (Luke et al. 2017a). All values
1267 of nitrate and phosphorus concentrations recorded at our study site were, however, lower than at a
1268 comparable study site in Sarawak (Mercer et al. 2014), and are within recommended limits for
1269 sensitive aquatic species on the basis of Malaysian National Water Quality Standards (Ministry of

1270 Natural Resources and Environment Malaysia 2014). We therefore discount the possibility that the
1271 differences in species richness we observed among land-uses are due to the small differences in
1272 nitrates and phosphates within this area.

1273 One potential confounding factor in our study is that the majority of protected rainforest
1274 catchments were located in a different catchment (Segama) to the majority of the modified land-use
1275 catchments (Brantian). However, seven out of the nine species only caught in the Segama catchment
1276 in this study are nevertheless known to occur within the Brantian catchment (Pers. Obs.) or have
1277 been recorded in other catchments across Eastern Sabah (Inger & Chin 2002). This observation
1278 provides support that the drop in species richness from protected rainforest to logged rainforest is a
1279 real effect of land-use rather than a correlative pattern arising from a study design encompassing
1280 multiple catchments.

1281 Despite reductions in species richness with habitat disturbance, community composition was not
1282 significantly different across the land-uses. This result indicates that disturbed stream catchments
1283 are more variable in fish composition, but that many species are retained in more than one land-use
1284 type, suggesting the community-level differences among land-use types are negligible. The
1285 relatively small gradients in community composition that we did observe in the RDA were driven by
1286 environmental variables that are consistent with our prior observations about the determinants of
1287 species richness, with leaf litter, substrate and stream depth all exerting an influence. Loach and
1288 catfish species that specialise in benthic microhabitats were absent or at a lower abundance in
1289 disturbed catchments. However, pelagic or benthopelagic species dominated in all landscapes with
1290 *Barbodes sealei*, *Nematobramis everetti*, *Rasbora cf. sumatrana*, and *Tor ticto* — the four most
1291 common species — all being pelagic invertivores or omnivores that do not appear to specialise in
1292 benthic habitats.

1293 Worryingly, two introduced species were captured in oil-palm streams without riparian reserves.
1294 Mozambique tilapia (*Oreochromis mossambicus*) and common or striped snakehead (*Channa striata*)

1295 are both common food fish that are routinely introduced to tropical streams (Diana 2009; Gozlan et
1296 al. 2010). The source of the introduced species at our study sites is unknown but they are likely to
1297 have been from aquaculture. Both species were present in low numbers and each was confined to a
1298 single stream, so we suggest these detections represent the early stages of a relatively new invasion
1299 event. It is becoming increasingly important to track how invasive or introduced species interact
1300 with native species in disturbed habitats, especially due to the ongoing expansion of agricultural
1301 frontiers in the tropics (Taniwaki et al. 2017), so our early detection of an invasion event may
1302 provide an important research opportunity.

1303 This study found that freshwater fish in small headwater streams appear to suffer significant losses
1304 in richness with any disturbance (logging or conversion to oil-palm) from protected forests.
1305 However, there was no significant difference between streams of different logging history despite
1306 twice-logged and salvage-logged forests varying in the number of times they had been logged, the
1307 cumulative severity of logging and in the time since logging. We had expected to see a further
1308 decrease in richness with a third, more recent round of logging, but did not detect any impact on top
1309 of the effects of the two prior rounds of selective-logging. However, in contrast to Giam et al. (2015),
1310 streams in oil-palm plantations with riparian reserves maintain the same levels of species richness
1311 than streams without riparian reserves. It is therefore essential to continue protecting primary,
1312 forested areas to maintain freshwater diversity, and explore strategies to protect freshwater
1313 ecosystems during logging, deforestation and conversion to plantation monocultures that are
1314 expected to continue across Southeast Asia.

1315

CHAPTER 4

1316 **RIPARIAN RESERVES: RETAINING HIGH FOREST QUALITY IS ESSENTIAL FOR FRESHWATER FISH**

1317 _____

1318

1319 **ABSTRACT**

1320 Global biodiversity is severely threatened by extensive land degradation and land-use change, and
1321 freshwater ecosystems are no exception. Riparian reserves are an important conservation tool for
1322 protecting lotic freshwater diversity and maintaining water quality during and after land-use change.

1323 However, the riparian reserve conditions necessary to protect freshwater diversity have seen little
1324 research, especially in the tropics. We assessed the difference in freshwater fish communities and
1325 individual species abundances across a land-use gradient in Sabah, Malaysia. Both regression trees
1326 and generalised linear models indicated a role for the width, forest quality and age of riparian
1327 reserves in predicting fish community metrics and individual species abundances. Regression trees
1328 were a better fit to the data and indicated threshold levels for fish tolerance to riparian reserve
1329 conditions. High riparian forest quality strongly increased species richness, functional richness, and
1330 the abundance of individual species. However, streams with low forest quality (e.g., oil-palm

1331 plantation streams with and without riparian reserves) sometimes had high richness and abundance,
1332 while the lowest levels of species richness, biomass and abundance were in recently salvage-logged
1333 streams. Overall, Simpson's diversity was highest in streams with riparian reserves more than 35 m
1334 in width, either side, and functional divergence was highest in streams with riparian reserves that
1335 were more than 10 years old. The abundance of individual species, also increased with riparian
1336 reserve threshold widths of 35–64 m, on either side of the stream, and reserves of 6–10.5 years old.

1337 Riparian reserves are vital in maintaining biodiversity and water quality for freshwater ecosystems
1338 and the wider environment. We advocate riparian reserves of 60 m width and of high forest quality
1339 (350 t ha^{-1}) to provide adequate protection of freshwater biodiversity. With the ever expanding

1340 global demand for palm oil, it is essential that sufficient riparian reserves are incorporated into
1341 plantations if we are to minimise biodiversity losses associated with land-use change.

1342

1343 **4.1. INTRODUCTION**

1344 Tropical forests have disproportionately high levels of biodiversity compared to other terrestrial
1345 ecosystems (Bradshaw et al. 2009; Laurance et al., 2012). A particular threat to Southeast Asia's
1346 biodiversity is the rapid conversion of forests to oil-palm plantations (Wilcove et al. 2013; Gaveau et
1347 al. 2014), which have become the primary global source of vegetable oil (Turner et al. 2008). Marked
1348 reductions in biodiversity are seen in plantations, but oil-palm is now an essential part of the
1349 economies of some of Southeast Asia's largest countries (Basiron 2007; Koh & Wilcove 2007).

1350 Finding ways to minimise the impact on biodiversity when forests are logged or converted to
1351 productive landscapes is a key challenge (Phalan et al. 2011).

1352 Riparian habitats are a vital component of previously forested landscapes converted to agriculture.
1353 They are among the most degraded ecosystems globally (Nilsson & Berggren 2000), despite being
1354 valuable for a wide range of terrestrial and aquatic biodiversity (Lorion & Kennedy 2009; Cruz et al.
1355 2013; Gray et al. 2014; Giam et al. 2015; Luke et al. 2017b; Wilkinson et al. 2018a). Riparian reserves,
1356 forested strips along the edges of streams and rivers, are the default conservation tool to protect
1357 aquatic biodiversity, water quality, and ecosystem services in logged and production landscapes
1358 (Naiman and & Décamps 1997). Despite this, riparian reserves vary widely in their quality of
1359 vegetation; they range from narrow, grassy banks in plantation landscapes to wide, forested
1360 reserves, and this quality can fluctuate longitudinally along watercourses (Wahl et al. 2013).

1361 Riparian reserves retain 'forest-like' conditions in and around streams within logged forests and
1362 production landscapes. They are expected to protect freshwater biodiversity through a wide variety
1363 of mechanisms: a reduction in sedimentation and runoff of fertilisers and pesticides (Naiman and &

1364 Décamps 1997), maintenance of temperature regimes and terrestrial subsidies (e.g. leaf litter,
1365 woody debris and terrestrial insects; Dudgeon 2000b), higher levels of dissolved oxygen (Heartsill-
1366 Scalley & Aide 2003), substantially reduced hydrological changes (Nagasaki & Nakamura 1999), and
1367 maintenance of water quality in a range of agricultural systems (Cruz et al. 2013; Luke et al. 2017a).
1368 The efficacy with which riparian reserves benefit aquatic communities are, however, strongly
1369 modulated by the geographic location and land-use context of reserves. For example, forested
1370 riparian reserves of > 15 m wide help to maintain forest-like communities of macroinvertebrates
1371 (Lorion & Kennedy 2009a) and fish (Lorion & Kennedy 2009b; Casatti et al. 2012) in pasture in Costa
1372 Rica and Brazil, but do not benefit fish communities in pine monoculture in New Zealand (Rowe et al.
1373 2002).

1374 Riparian reserves are a commonly implemented conservation tool in oil-palm plantations, and form
1375 a key criterion for determining the sustainability of a plantation (RSPO 2013). Despite their ubiquity,
1376 our knowledge of how effectively riparian reserves protect biodiversity in tropical agricultural
1377 systems remains poor (though see Giam et al. 2015 and Luke et al. 2016). In addition, riparian
1378 habitats are considered predominantly in production agriculture landscapes but rarely in degraded
1379 natural landscapes, despite activities such as logging having a significant, negative impact on tropical
1380 freshwater communities (Wilkinson et al. 2018a) and deforestation being a primary driver of
1381 biodiversity change (Brajão et al. 2018). Logging and deforestation have been shown to have
1382 negative, threshold responses on aquatic biodiversity in the Amazon, and consistently occurred at
1383 low levels of deforestation (< 20%) and soon after impact (< 10 years) (Brajão et al. 2018). Within
1384 production landscapes, oil-palm plantation streams with a riparian reserve in Indonesia were shown
1385 to support 42% more fish species than streams with no reserve, through increased levels of littoral
1386 leaf cover, maintenance of coarse substrates and decreased sedimentation (Giam et al. 2015; Brajão
1387 et al. 2018).

1388 There are, however, no established guidelines or global recommendations on the legal status or
1389 recommended width of reserves, or on how much forest should be retained or replanted in riparian
1390 zones and surrounding catchments to maintain or re-establish instream ecological integrity (Death &
1391 Collier 2010). Minimum widths of riparian reserves to stabilise banks and protect water quality are
1392 thought to be 10–30 m (Sweeney & Newbold 2014), whereas protection is expected to need > 30 m
1393 for aquatic diversity (Sweeney & Newbold 2014) and up to 200 m for terrestrial biodiversity (e.g.
1394 Barclay et al. 2017). In Malaysia and Indonesia, retention of riparian reserves is required by law
1395 (Government of Malaysia 1965; Republic of Indonesia 1990), although they are often not retained in
1396 oil-palm plantations (Lajuin 2013). The Malaysian state of Sabah requires that all permanent water
1397 courses over 3 m wide should have 20 m wide riparian reserves, but also recommends the
1398 protection of smaller streams during oil-palm planting, and retention of 50–100 m reserves in either
1399 steep areas or areas important for wildlife (Sabah Water Resources Enactment 1998). Riparian
1400 reserves are also mandatory for growers who opt to join the Roundtable for Sustainable Palm Oil
1401 (RSPO, www.rspo.org) certification scheme: a voluntary program whereby growers agree to employ
1402 best management practices aimed at improving environmental and social outcomes in exchange for
1403 recognition of the “greenness” of their products. The RSPO criteria state that all permanent water
1404 bodies in plantations should be surrounded by natural vegetation, with reserves of > 10 m on both
1405 sides for water course 1–5 m wide (at the highest water level), whilst watercourses over 5 m wide
1406 should have 50 m wide reserves. (RSPO 2013).

1407 We are also not aware of any regulations that specify the quality of vegetation required for riparian
1408 reserves to be effective. For the regulations that do exist, for retention of reserves, there is a lack of
1409 evidence about whether the required riparian reserves actually conserve freshwater biota in tropical
1410 logged forests and/or oil-palm monoculture. It is vital, therefore, to identify and understand how
1411 stream biota respond to the presence and quality of riparian forest after logging, deforestation and
1412 conversion to plantation (Wahl et al. 2013). Our intention was, therefore, to be able to better inform

1413 legislation on the ‘conditions’ of riparian reserves (width and quality of vegetation) necessary to
1414 protect freshwater ecosystems and maintain freshwater fish community diversity and abundance,
1415 whilst accounting for the time since disturbance, in Sabah, Malaysian Borneo. We hypothesized a
1416 positive correlation between the width and forest quality of a riparian reserve, and that there would
1417 be higher freshwater fish species richness, biomass, and functional richness in streams where the
1418 surrounding riparian vegetation is of higher forest quality and wider riparian reserves, because
1419 stream conditions will be the most similar to pre-conversion conditions. We also examined the
1420 impact of riparian reserve features on individual species abundances, to understand how different
1421 life history characteristics affect presence and abundance under different riparian conditions. We
1422 expected that stream biodiversity may respond to logging and conversion with threshold responses
1423 rather than linear relationships (Smucker et al. 2013; Rodrigues et al. 2016). Threshold responses of
1424 fish and aquatic invertebrate diversity in temperate aquatic environments have been observed once
1425 catchment thresholds, that can be < 50% habitat loss, have been passed (Baker & King 2010;
1426 Smucker et al. 2013). With ongoing conversion of tropical forests for oil-palm plantations across
1427 Southeast Asia, the Afrotropics (Wich et al. 2014) and Neotropics (Lees & Vieira 2013), it is globally
1428 relevant and essential to understand what riparian reserve conditions are relevant for maintaining
1429 freshwater diversity, and to identify any critical disturbance thresholds that might impede effective
1430 conservation and management.

1431

1432 **4.2. MATERIALS AND METHODS**

1433 **4.2.1. STUDY SITE**

1434 Study sites were located in southeastern Sabah, Malaysian Borneo at Danum Valley Conservation
1435 Area (117.80°E and 4.96°N), and in and around the Stability of Altered Forest Ecosystems (SAFE)
1436 Project (117.43°E to 117.70°E and 4.57°N to 4.76°N) (Ewers et al. 2011). All sampling sites were

1437 located on small first or second order, headwater streams (3–10 m wide, ≤ 1.2 m deep). The
1438 landscape is drained by tributaries of the Brantian, Kalabakan and Segama Rivers, all of which empty
1439 into the Celebes Sea.

1440 We collected data from 34 headwater streams (23 of which are shown in Wilkinson et al. 2018a)
1441 across a heterogeneous landscape with highly variable amounts of above ground biomass (AGB)
1442 removed via logging and conversion to oil-palm plantation (Pfeifer et al. 2016). Where logistically
1443 possible, we sampled streams similar to those already selected for long term monitoring at the SAFE
1444 project: length ~2 km, catchment area ~260 ha and average gradient ~16° (Ewers et al. 2011). Each
1445 transect was located inside an independent tributary, and divided among five categories:

- 1446 i) Five streams were in primary lowland dipterocarp rainforest in protected areas (PF; AGB
1447 average 350 t ha⁻¹) with four in the Danum Valley Conservation Area, and one in the
1448 Brantian Tantulit Virgin Jungle Reserve.
- 1449 ii) Three streams were in continuous twice-logged forest (LF_{cont}; average AGB 122 t ha⁻¹).
1450 Catchments were logged in the 1970's and again in the 1990s-2000s.
- 1451 iii) Six catchments were in recently salvage-logged forest (LF_{salv}; average AGB 95 t ha⁻¹) in
1452 the SAFE project experimental area. Catchments were logged between 2013 and 2015,
1453 as well as at the same times as the continuous twice-logged catchments.
- 1454 iv) Sixteen catchments were oil-palm plantation streams with riparian reserves (OP_{rip};
1455 average AGB 38 t ha⁻¹). Oil-palms were planted between 1998 and 2011. Within this
1456 land-use category, we selected streams with riparian reserves that differed widely in
1457 width and forest quality. Riparian reserves comprised selectively-logged and secondary
1458 forests, but were irregular in shape, and varied from 10 to 1000 m wide on each side of
1459 the stream.

1460 v) Four catchments were in oil-palm catchments without riparian reserves (OP_{minus} ;
1461 catchment average AGB and palm ages same as for OP_{rip} streams, average AGB 38 t ha^{-1}).
1462 In these catchments, oil-palms were planted right up to the stream edge.

1463 **4.2.2. RIPARIAN VARIABLES**

1464 At all streams, we established a 500 m transect along which riparian reserve quality was quantified.
1465 We focussed on three variables for this analysis: mean riparian width, riparian forest quality and the
1466 time since disturbance in the surrounding catchment. Riparian width was measured for all oil-palm
1467 plantation streams within a riparian reserve using PLEIADES remotely sensed satellite imagery.
1468 Width measurements were taken every 50 m along the transect, orthogonal to the stream bed, and
1469 across the whole riparian reserve (both sides of the stream and including the stream bed itself). We
1470 then subtracted the bank-full stream width, took the mean width over the 11 point measurements
1471 and divided by two to give an average riparian reserve width for each stream. The riparian reserve
1472 width was set as 0 m for oil-palm plantation streams with no riparian reserve, and we used an
1473 arbitrary value of 1000 m for protected and logged forest catchments. This value was chosen as it
1474 approximates the maximum catchment width ($\sim 2000 \text{ m}$) for the sampled streams.

1475 For streams in all land-uses, riparian reserve forest quality was measured visually every 50 m at sites
1476 located 10 m away from the stream edge and on opposite sides of the stream ($n = 22$ sites per
1477 stream). At each site we recorded an ordinal forest quality score that ranged from 0 to 5: (0 = oil-
1478 palm; 1 = very poor—no trees, open canopy with ginger or vines, or low scrub; 2 = poor—open with
1479 occasional small trees over ginger or vine layer; 3 = moderate—small trees fairly abundant or canopy
1480 at least partially closed; 4 = good—lots of trees, some large, and canopy closed; 5 = very good—
1481 closed canopy with large trees, no evidence of logging (Ewers et al. 2011). We used modal forest
1482 quality score to provide an average measure of forest quality for each stream. This rapid, qualitative
1483 metric of forest quality has been demonstrated to correlate well with quantitative metrics of forest
1484 disturbance that are considerably more time consuming to implement in the field (Pfeifer et al.

1485 2015). Roughly 80% of high quality forest sites (scores of 4 or 5) have AGB > 240 t ha⁻¹, whereas
1486 medium quality forest (scores of 2 and 3) have AGB ranging from 23 to 175 t ha⁻¹, and low quality
1487 forest (scores of 0 and 1) have AGB ranging from 13 to 63 t ha⁻¹ (Pfeifer et al. 2015; Pfeifer et al.
1488 2016).

1489 Time since disturbance (years) was dependant on land-use and measured at the catchment scale.
1490 For logged forest streams, we recorded the time since the last round of logging within each
1491 catchment (LF_{salv} – two years, C. Wilkinson, Pers. Obs.; LF_{cont} – 20 years, Ewers et al., 2011; Fisher et
1492 al., 2011). For oil-palm plantation streams, we used year of planting of oil-palm seedlings within each
1493 catchment provided by the estate managers (Benta Wawasan Sdn. Bhd). Primary forests are
1494 undisturbed, and were assigned an arbitrary value of 100 years since disturbance.

1495 **4.2.3. FISH SAMPLING**

1496 All sampling was conducted between February–July 2017. Freshwater fishes were sampled in the
1497 downstream 100 m section of each transect. Sampling took place on clear-weather days using three
1498 methods in the following order: (1) three pass electrofishing (model EFGI 650), (2) cast netting (2.75
1499 m diameter net with 1 cm mesh), and (3) tray (push) netting (dimensions 60 x 45 cm, 2 mm mesh).
1500 At the start of sampling, we placed stop nets (2 mm mesh) at 0 m and 100 m on the transect to
1501 prevent fish immigration or emigration during the sampling period. The combination of these
1502 sampling methodologies target all major fish groups and microhabitats in order to achieve
1503 comprehensive and unbiased metrics of fish communities (Kennard et al. 2006; Giam et al. 2015).

1504 For each transect, captured fishes were held in tanks until sampling was complete. The species
1505 identity (Inger & Chin 2002; Kottelat 2013) and total length (mm) of all fish were recorded before
1506 being returned to the stream. More than 5,000 fish from 31 species have previously been measured
1507 and weighed at many of these stream transects for other studies (Wilkinson et al. 2018a, b), from
1508 which length-mass regressions were constructed and used to estimate the body mass for all

1509 individuals of common species (Appendix 4.1.1). This approach significantly reduced handling time in
1510 the field. Uncommon species (< 30 individuals previously weighed, 4.5% of fish caught) were
1511 weighed in the field using a portable electronic balance. A subset of fish was preserved for proof of
1512 identification. These fish specimens were euthanized with MS-222, fixed in 10% formalin, and
1513 transferred to 75% ethanol for identification and storage in the Lee Kong Chian Natural History
1514 Museum, National University of Singapore. Fish capture, handling and euthanisation protocols were
1515 approved by the Animal Welfare and Ethical Review Body at Imperial College London.

1516

1517 **4.2.4 FISH COMMUNITY AND SPECIES ABUNDANCE RESPONSE VARIABLES**

1518 For each stream, we calculated local species richness, fish biomass, three complementary metrics of
1519 functional diversity (functional richness, evenness and divergence; Villéger et al. 2008) and
1520 Simpson's diversity index from the standardised equation (Simpson 1949). Abundance was analysed
1521 individually for fifteen species deemed as common (> 10 individuals, caught at > 3 streams, and > 1
1522 land-use category). An additional five species were abundant (> 10 individuals) only in four protected
1523 forest streams and are only included in a final mixed model. The remaining 14 species had
1524 insufficient data to be included in the species level abundance analyses.

1525 **4.2.5 DATA ANALYSES**

1526 We use R 3.4.1 for all analysis (R Core Team 2017). We first analysed the correlation of the three
1527 explanatory riparian environmental variables (mean width, forest quality and time since disturbance)
1528 using the robust Kendall's correlation (τ , Kendall 1938). Riparian width was square root transformed
1529 and time since disturbance was log transformed prior to analysis to ensure model assumptions
1530 would be met. We then fitted both generalised linear models (GLMs) and regression trees (tree
1531 package; Ripley 2016) separately for each of the six community response variables, and using the
1532 three riparian variables and all two-way interactions as predictors. This combination of statistical

1533 methods allowed us to contrast linear relationships with non-linear relationships that include
1534 threshold values (break points within regression trees) for each variable. GLMs were backward
1535 stepwise simplified using Akaike's information criterion (AIC) for model selection. For the species
1536 richness model, a Poisson error distribution was used; for all other models, a Gaussian error
1537 distribution was used. Log-likelihood ratio tests were used to assess model significance on the most
1538 parsimonious model. For regression trees, data was randomly split into training and test data ($n = 17$
1539 for each) to perform tree pruning and cross validation. We recorded the occurrence of each variable
1540 in the pruned tree, which variable was the first node, and the threshold value (break point) of the
1541 variable in the decision tree. Regression trees were compared to linear models (the most
1542 parsimonious model was re-run using only the training data) using root mean standard error (RMSE)
1543 of all models for the training datasets.

1544 Subsequently, we investigated how the abundances of individual species changed among streams.
1545 First, we used a Poisson generalised linear mixed model (GLMMs; Bates et al. 2014) of abundance of
1546 all 20 species , including differences in intercept between species as an independent random effect,
1547 to examine the overall community differences of the three riparian variables and all two-way
1548 interactions as predictors. We performed backwards stepwise model simplification using AIC, and
1549 log-likelihood ratio tests were used to assess model significance. The relative importance of fixed
1550 and random effects was ascertained using the methods of Nakagawa & Schielzeth (2013), and
1551 Tukey's multiple comparison of mean ranks was used to differentiate among forest quality scores.
1552 Secondly, we repeated the modelling framework above, of GLMs and regression trees, to predict the
1553 abundance of 15 common fish species (present across multiple land-uses), in order to determine
1554 what is driving the overall fish community differences, and look at threshold points from regression
1555 trees.

1556

1557

1558 **4.3. RESULTS**

1559 A total of 4,304 fish comprising 34 species were captured and identified (see Appendix 4.2 for
1560 species list). Four species were highly abundant and present across the land-use gradient:
1561 *Nematabramis everetti* ($N = 1440$, 33%), *Barbodes sealei* ($N = 859$, 20% of the total), *Rasbora* cf.
1562 *sumatrana* ($N = 620$, 14%) and *Tor tambra* ($N = 314$, 7%). In contrast, 13 species had < 10 individuals
1563 across all streams, eight species were found only in primary rainforest, five species only in oil-palm
1564 plantation streams with a riparian reserve and one species only in twice-logged forest.

1565 **4.3.1. RIPARIAN VARIABLES**

1566 As expected, riparian forest quality and width were correlated ($\tau = 0.66$, $df = 32$, $p < 0.001$), with
1567 wider riparian reserves having a higher forest quality. Time since disturbance had no correlation with
1568 riparian width ($\tau = 0.07$, $df = 32$, $p = 0.619$) or riparian forest quality ($\tau = 0.20$, $df = 32$, $p = 0.144$),
1569 suggesting it should be feasible to detect any independent impact on the fish communities.

1570 **4.3.2. COMMUNITY LEVEL**

1571 Both regression trees and generalised linear models indicated a role for all three riparian variables in
1572 predicting community variables. For linear models (Appendix 4.3.1), we found a significant and
1573 highly explanatory impact of riparian forest quality on local species richness (Figure 1a; $\chi^2_{(28)} =$
1574 35.77, $P < 0.001$, $R^2 = 0.50$) and functional richness (Figure 1b; $\chi^2_{(28)} = 20.52$, $P < 0.001$, $R^2 = 0.42$),
1575 with both richness metrics increasing as forest quality increases. Functional divergence significantly
1576 increased with a greater time since disturbance (Figure 1c; $\chi^2_{(32)} = 4.81$, $P = 0.028$, $R^2 = 0.13$) and
1577 Simpsons diversity index was significantly higher with wider riparian reserves (Figure 1d; $\chi^2_{(32)} =$
1578 6.01, $P = 0.014$, $R^2 = 0.16$), but the explanatory power of these relationships was relatively low. No
1579 model was significant in explaining functional evenness or biomass.

1580 Riparian forest quality was the first node split in regression trees of species richness, biomass,
1581 functional richness, and functional evenness (Figure 2a; Appendix 4.3.2, 4.3.3). Forest qualities of 2

1582 and 3 (logged forest or oil-palm with a buffer) with lower species and functional richness, biomass
 1583 and evenness were split from the other forest quality scores that had higher species and functional
 1584 richness, biomass and evenness. Time since disturbance was the first node for functional divergence,
 1585 with a threshold at 10.5 years, with higher functional divergence in streams with higher time since
 1586 disturbance (Figure 2c), whilst riparian width was the first node split for Simpson's diversity index,
 1587 with a threshold at 37 m width. Simpson's diversity was greater in streams with wider riparian
 1588 widths, and this pattern was repeated in the tree for functional divergence (Figure 2b).

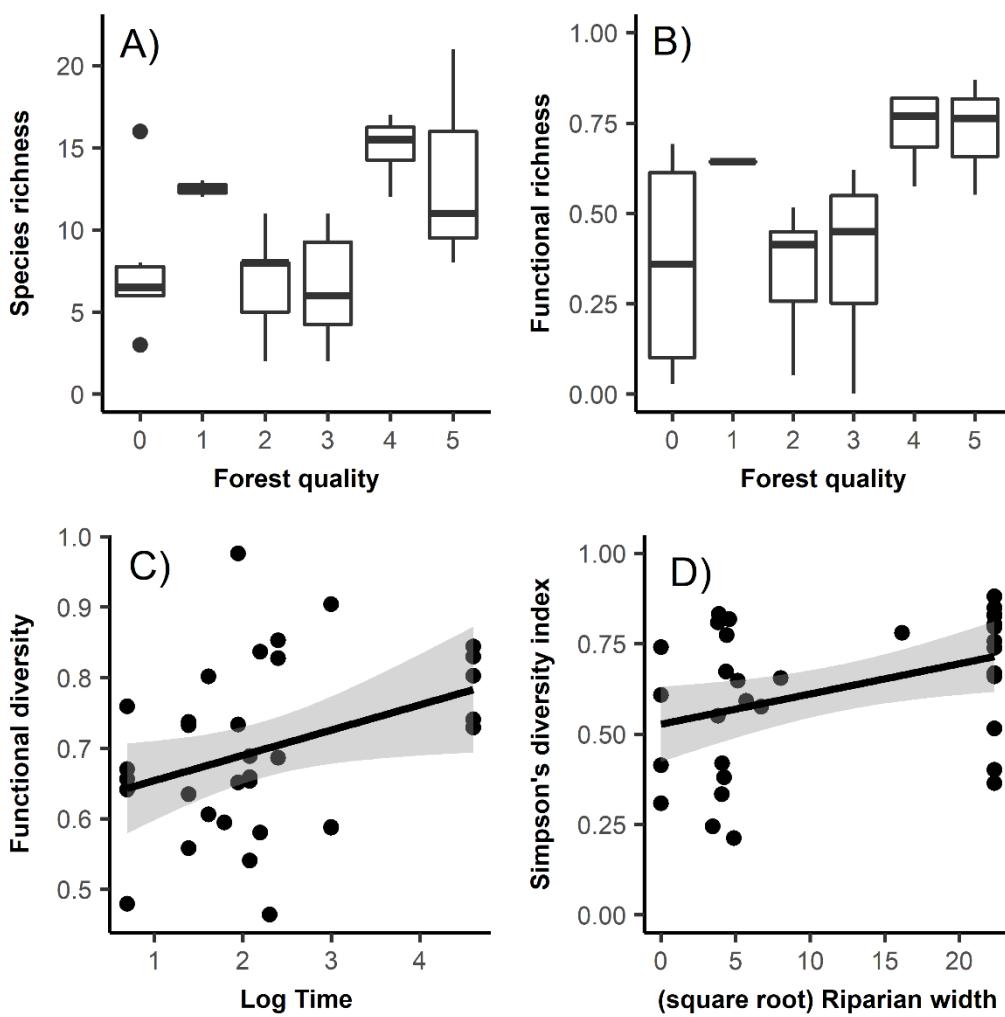


Figure 1. Relationship between local species richness (a), and functional richness (b), with riparian forest quality. Relationship between functional diversity and time since disturbance (c), and Simpson's diversity index and riparian width (d). Lines and 95% confidence intervals show results of generalised linear models.

1589

1590

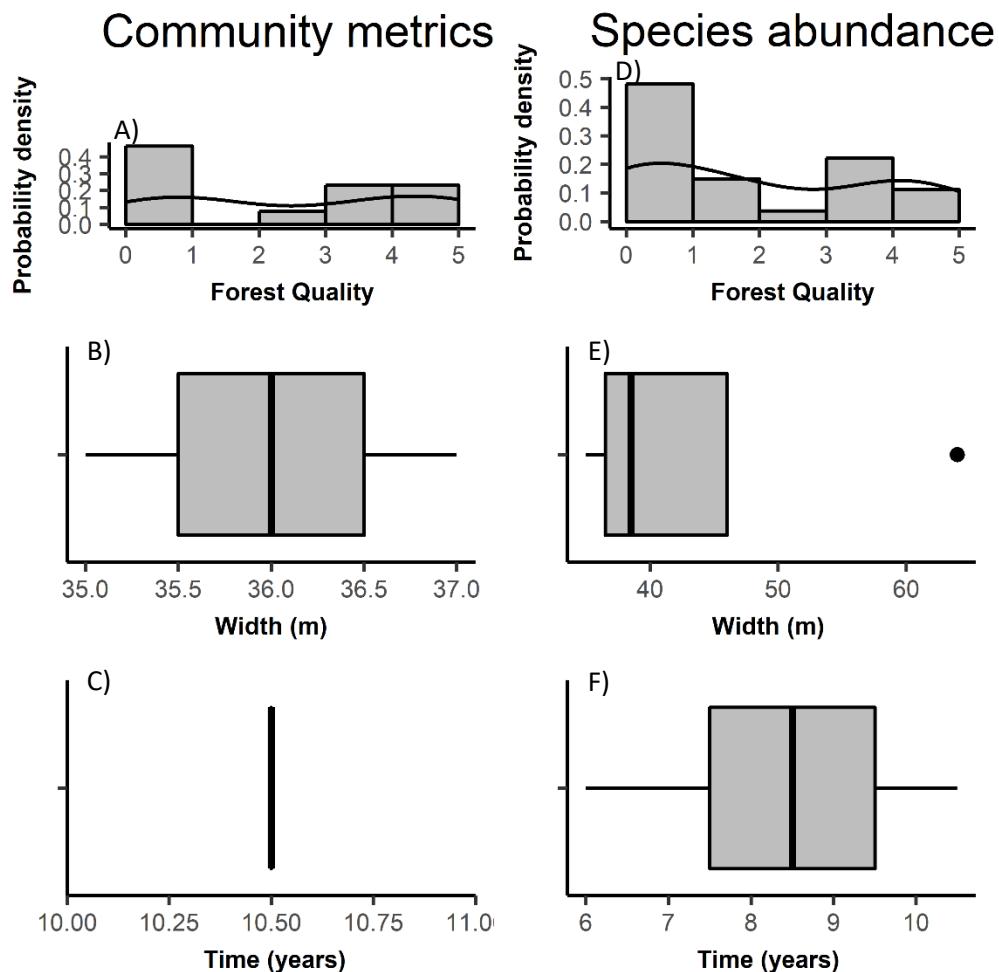


Figure 2. Figure 2. Summary of regression trees of freshwater fish community metrics (A-C) and individual species abundances (D-F) for three riparian reserve variables. Values represent the break point in the regression trees (six for six community variables, and 15 for individual species abundances), graphs collate these variables for each variable as follows. Graphs A and D show histograms and probability density of the break point falling on that score of forest quality. Graphs B, C, E and F show a box and whisker plot, illustrating the means, second and third quartiles (within the rectangle), upper and lower quartiles in the ‘whiskers’, outliers as filled circles for the break points of regression trees for riparian width (B and E), and time since disturbance (C and F). Riparian forest quality is measured over a 500 m transect and the mode of a forest quality score (0-5; (Ewers et al. 2011)) is measured, riparian width (m) is measured from satellite imagery, and averaged over 500 m, and time since disturbance (years) is measured from the time since oil-palm planting or the last round of logging within the catchment.

1591

1592 Comparisons of the lower root mean square error (Appendix 4.3.1 and 4.3.2) on the training data
 1593 showed that regression trees were a better fit to the data for species richness, functional richness
 1594 and functional diversity. Regression trees and linear models had a very similar fit for biomass,

1595 functional evenness and functional divergence. Across models, riparian forest quality was the
 1596 variable that stands out as having the greatest impact on fish communities.

1597

1598 **4.3.3. SPECIES LEVEL**

1599 Mixed models (Appendix 4.4.1) showed a significant increase in the abundances of 20 species with
 1600 increasing riparian forest quality (Figure 3; $\chi^2_{(5)} = 39.07$, $P < 0.001$). Species as a random effect
 1601 explained a considerable proportion of the variance in the model for species richness (conditional R^2
 1602 = 0.36, marginal R^2 = 0.04). Tukey's HSD test shows that forest qualities of 4 and 5 had significantly
 1603 higher abundance ($p < 0.05$) than forest qualities of 0, 2 and 3.

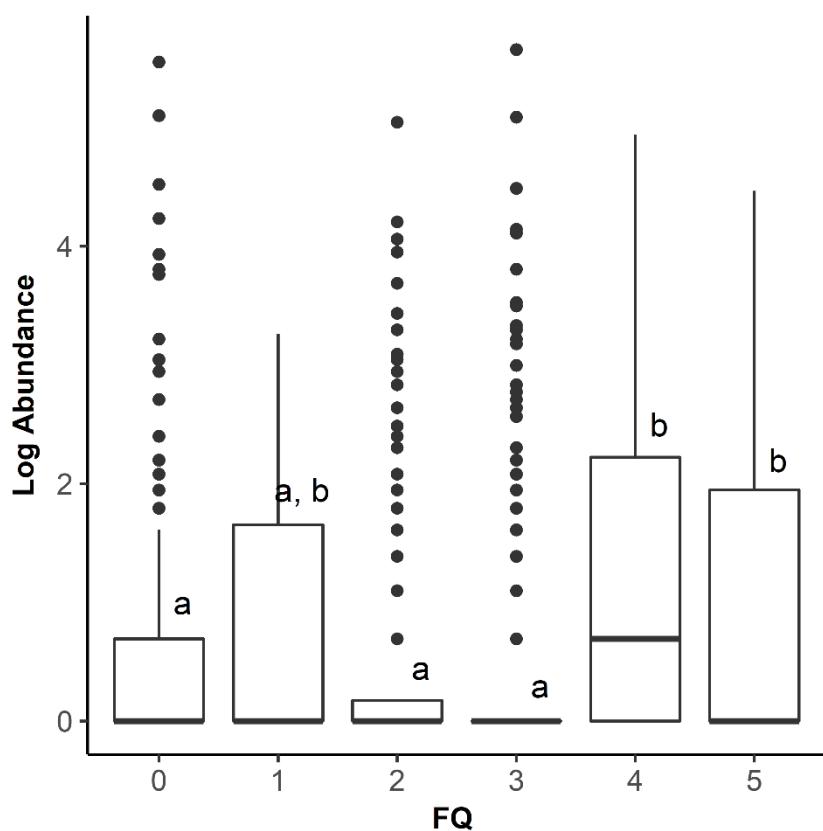


Figure 3. Box and whisker plots of the relationship between riparian forest quality and abundance of 20 species of fish. Box and whisker plots indicate the median (dark band), interquartile range (within each rectangle), and the highest and lowest values of the data, excluding outliers, in the whiskers, with outlying points as black dots.

1604

1605 Abundances of the 15 common individual species showed that, as with the community metrics, all
1606 three riparian variables were important. Riparian forest quality affected all species, but there was a
1607 complex relationship with the other variables. In generalised linear models, we found forest quality
1608 significantly explained the abundance patterns for three of the 15 species, and was retained in the
1609 models of all other species. However, each of these three species had higher abundances at
1610 different levels of forest quality: *Anguilla borneensis* ($\chi_{(28)} = 60.104$, $P < 0.001$, $R^2 = 0.39$) and
1611 *Nemacheilus olivaceus* ($\chi_{(28)} = 50.15$, $P < 0.001$, $R^2 = 0.27$) had the highest abundance in streams with
1612 high riparian forest quality, whereas *Gastromyzon ingeri* ($\chi_{(28)} = 50.15$, $P < 0.001$, $R^2 = 0.27$) had the
1613 highest abundance in streams with low quality riparian forest, typically fast flowing, logged forest or
1614 oil-palm plantation streams (Appendix 4.4.2, 4.4.3). Models of *Anguilla marmorata* and *Rasbora*
1615 *hubbsi* retained both riparian width and riparian forest quality: *Anguilla marmorata* abundance was
1616 highest in low forest quality streams but increased with width ($\chi_{(28)} = 45.61$, $P < 0.001$, $R^2 = 0.63$),
1617 whereas *Rasbora hubbsi* abundance increased in streams with increasing width and higher forest
1618 quality ($\chi_{(27)} = 154.03$, $P < 0.001$, $R^2 = 0.28$). The other 10 species all had complex models with all
1619 three variables and multiple interactions, but very different responses. For example, *Protomyzon*
1620 *griswoldi* and *Tor ticto* had higher abundances in streams with higher riparian forest quality and a
1621 longer time since disturbance, whereas the abundance of *Gastromyzon lepidogaster*, *Hemibagrus*
1622 *baramensis*, *Nematabramis everetti*, *Osteochilus ingeri* and *Rasbora cf. sumatrana* increased with
1623 increasing riparian width but decreased in time since disturbance (Appendix 4.4.2, 4.4.3).

1624 Regression trees similarly indicated that all three riparian variables were important, with all featured
1625 in the first tree split of at least one species (Fig. 2d–f). Eleven species had forest quality as the first
1626 and only node split. For five of these eleven species, the threshold was determined by high and low
1627 riparian forest quality (i.e., forest quality of 0, 1, and 2 versus 3, 4, and 5), whereas the other six
1628 species thresholds had more mixed sets of forest quality scores. Riparian width was the first node for
1629 two species (*Hemibagrus baramensis* and *Rasbora cf. sumatrana*), and featured in trees of two other

1630 species. All thresholds for riparian widths were associated with higher abundance in streams with
1631 wider reserves, and thresholds were 35–64 m (mean = 44 m) on each bank. Time since disturbance
1632 was the first node for three species (*Nemacheilus olivaceus*, *Rasbora hubbsi*, and *Tor tambra*), was
1633 present in an additional two trees, and thresholds ranged from 6–10.5 years (mean = 8.4 years) since
1634 disturbance. Comparisons of the lower root mean square error (Appendix 4.4.3) and the generalised
1635 linear models of species and regression trees, showed similar results. However, regression trees had
1636 lower error for all species that it was able to be calculated for.

1637 **4.4. DISCUSSION**

1638 Studies to date have looked at the efficacy of riparian reserves compared to primary forest or a lack
1639 of reserve (Gomi et al. 2006; de Souza et al. 2013; Giam et al. 2015), but few have determined more
1640 specifically, what riparian reserve ‘conditions’ are necessary to protect aquatic diversity. Our study
1641 shows that riparian width, forest quality and time since disturbance are all important in determining
1642 the abundance of species and metrics of fish community diversity, demonstrating the complexity of
1643 reaction to changes in stream conditions, during land-use change. Overall, riparian forest quality was
1644 the variable that most frequently exerted significant effects on multiple species and community
1645 metrics. However, across all species and metrics there was no clear threshold of forest quality above
1646 which fish species and communities improved, but we note that this variable predominantly
1647 separated the streams based on land-use (as shown in Wilkinson et al. 2018a). By contrast, we
1648 detected clear thresholds for the two other metrics of riparian quality, finding higher abundance and
1649 diversity in riparian reserves > 35 m wide and that were last disturbed more than six years ago.

1650 Our results are consistent with literature from this region and elsewhere. Results from Brazil found
1651 that forest structure and quality affected stream conditions that in turn impacted local biodiversity
1652 (de Souza, et al. 2013), a result consistent with our finding that riparian forest quality had a
1653 significant positive impact on species and functional richness and on the abundances of 15 species.
1654 Martin-Smith (1998a, b) showed that increased time since logging positively affected the abundance

1655 of common cyprinids in Borneo, which is consistent with our finding that the longer the time since
1656 disturbance the higher the functional diversity and abundance of ten species. We also found a
1657 significant increase in Simpson's diversity index and the abundances of six species with increased
1658 width of riparian reserves. Other studies have shown that to protect aquatic diversity, reserves of >
1659 30 m are necessary (Sweeney & Newbold 2014), but our data, suggest this may be an
1660 underestimate, as thresholds in the regression trees ranged from 35–64 m.

1661 Freshwater diversity and ecosystem processes are influenced at multiple scales (Luke et al. 2017a),
1662 from the entire upstream catchment to localised riparian reserves and down to the within-stream,
1663 mesohabitat scale. It is likely that other factors beyond riparian reserve quality alone may also be
1664 beneficial for freshwater fish in modified tropical landscapes, and should be included in legislation to
1665 conserve freshwater biodiversity (Leal et al. 2018). This understanding is exemplified by the
1666 Roundtable for Sustainable Palm Oil (RSPO), who developed best practice guidelines that support
1667 retaining forested riparian reserves, as well as maintaining headwater and steep-slope forest cover,
1668 and protecting forest patches within catchments to help maintain freshwater ecosystems and the
1669 services they provide after land conversion (Barclay et al. 2017). These requirements indicate that
1670 riparian reserve retention is necessary, though not necessarily sufficient, to fully maintain stream
1671 ecosystems and the goods and services they provide (Leal et al. 2018), and highlights the importance
1672 of broader scale conservation strategies being promoted by organisations such as the RSPO.

1673 There is a wide range of catchment or landscape scale issues that affect freshwater biodiversity
1674 beyond riparian reserves. Catchment scale forest cover have also been shown to influence stream
1675 conditions (Heartsill-Scalley & Aide 2003; Allan 2004; Death & Collier 2010; Luke et al. 2017a). For
1676 example, 20% catchment deforestation resulted in consistently warmer streams (Leal et al. 2016),
1677 but more research is needed in extensively deforested landscapes to determine if riparian reserves
1678 sustain functions they are retained for (Lorion & Kennedy 2009). However, at the riparian scale,
1679 reserves also need to be continuous, as reserves that have gaps cannot adequately protect

1680 freshwater ecosystems (Jones et al. 1999; Wahl et al. 2013). The majority of logged forest and oil-
1681 palm plantation streams within this study had roads crossing the streams, gaps in the riparian forest,
1682 or as with the oil-palm plantation streams, riparian reserves are often not present higher in the
1683 catchment. Therefore it seems that catchment-scale planning and careful creation and maintenance
1684 of designated reserve areas are needed for efforts to be effective. This planning should include
1685 consideration of the proximity and number of roads within plantations, due to the flux of sediment
1686 that enters freshwater systems during the creation and subsequent use of roads (Gomi et al. 2006;
1687 Walsh et al. 2011). RSPO guidelines suggest roads should be perpendicular to streams rather than
1688 run parallel to streams (Barclay et al. 2017), but roads that are parallel to streams are common
1689 within this study location (C. Wilkinson, Pers. Obs.). However, with the best plans in place, there is a
1690 trade-off between the number and density of streams that can be protected and the creation of
1691 profitable plantations. If stream density is high as it is at our study site, it is likely that many upland
1692 hill streams will remain unprotected by riparian reserves as the surrounding catchment is converted
1693 to monoculture. This can lead to altered stream conditions, with high sediment loads and
1694 potentially pollution after rainfall events (Luke et al. 2017a; de Souza et al. 2013).

1695 Regardless of all of these confounding factors influencing stream biodiversity and abiotic
1696 characteristics, riparian reserves have been shown to be valuable for water quality, aquatic
1697 biodiversity and a range of other terrestrial biodiversity (Naiman & Décamps 1997; Nagasaka &
1698 Nakamura 1999; Dudgeon 2000b; Heartsill-Scalley & Aide 2003; Lorion & Kennedy 2009; Cruz et al.
1699 2013; Gray et al. 2014; Giam et al. 2015; Luke et al. 2017b). Our results provide unambiguous
1700 evidence that the quality of riparian reserves is crucial to maintaining fish communities in tropical
1701 agricultural landscapes. Due to the continued expansion of oil-palm plantations within Southeast
1702 Asia, and in both the Neotropics (Lees & Vieira 2013) and Afrotropics (Wich et al. 2014), these
1703 results are relevant globally. We advocate not only designation of riparian reserves, but the need for

1704 strict guidelines during logging and conversion of land to maintain riparian reserves that are at least
1705 64 m wide and that have high forest quality (350 t ha^{-1}).

1706

1707

CHAPTER 5

1708 **RESILIENCE OF A TROPICAL FRESHWATER FISH SPECIES (*NEMATABRAMIS EVERETTI*) TO SEVERE,**
1709 **DROUGHT-INDUCED DISTURBANCE OVER A LAND-USE GRADIENT IN SABAH, MALAYSIA**

1711

1712 **ABSTRACT**

1713 Biodiversity-rich forests in tropical Southeast Asia are being extensively logged and converted to oil-
1714 palm monocultures. In addition, extreme climatic events such as droughts are becoming more
1715 common. Land-use change and extreme climatic events are thought to have synergistic impacts on
1716 aquatic biodiversity, but few studies have directly tested this. A severe El Niño drought in Southeast
1717 Asia in early 2016 caused 16 low-order hill streams across a land-use gradient encompassing primary
1718 forest, logged forest and oil-palm plantations in Sabah, Malaysia to dry up into a series of
1719 disconnected pools. The resulting disturbance tolerated by the fish during the drought exceeded any
1720 worst-case scenario for climate change-induced warming. We quantified the biomass, density and
1721 movement of the dominant freshwater fish species, *Nematabramis everetti* (Cyprinidae), in these
1722 streams across this land-use gradient before, during, and after the 2016 El Niño drought period.
1723 Density of *N. everetti* was significantly lower in logged forest streams than primary forest or oil-palm
1724 streams, and the biomass of individuals captured was lower during drought than prior to the
1725 drought; however, there was no change in the biomass density of individuals during drought. The
1726 distance moved by *N. everetti* was significantly lower during and after the drought compared to
1727 before the drought. We detected a significant antagonistic interaction on biomass of captured fish,
1728 with the magnitude of the drought impact reduced according to land-use. Populations of *N. everetti*
1729 were surprisingly resilient to drought and seem most affected instead by land-use. Despite this
1730 resilience, it is important to monitor how this widespread and abundant species, which provides an
1731 important ecosystem service to local human communities, is affected by future land-use and climate

1732 change, as logging, deforestation and conversion to plantation monocultures continues across

1733 Southeast Asia.

1734

1735 **5.1. INTRODUCTION**

1736 Freshwater ecosystems have been severely affected by anthropogenic impacts and are the most

1737 threatened ecosystems globally (Thomsen et al. 2012). The widespread degradation of these

1738 ecosystems threatens aquatic biodiversity at both local and regional scales (Richter et al. 1997;

1739 Vörösmarty et al. 2010). Anthropogenic land cover change, through logging or conversion to

1740 agricultural plantation, causes marked declines in biodiversity (Phalan et al. 2013). This destruction is

1741 of particular importance in the tropics, owing to the disproportionately high levels of biodiversity

1742 (Bradshaw et al. 2009; Laurance et al. 2012). Further perturbations to ecosystems due to extreme

1743 climatic events (such as El Niño-induced drought) puts additional stress on biodiversity, pushing

1744 species to their limits of survival (Castello & Macedo 2015). It is important to understand how these

1745 multiple stressors (land-use and climate change) interact and impact aquatic biodiversity.

1746 Land-use change can cause significant impacts to freshwater ecosystems. However, the extent of

1747 this impact varies on the type of land disturbance (logging, deforestation or conversion to

1748 agriculture), and if any mitigation strategies are implemented. Freshwater ecosystems are affected

1749 by land-use changes because of widespread, within-stream, habitat modifications that can result in

1750 changes in sediment load, nutrient runoff (e.g., from fertilisers), canopy cover and thus temperature,

1751 inputs of leaf litter and woody debris (Luke et al. 2017a). All of these impacts change the

1752 microhabitats that fish inhabit and can affect taxonomic or functional groups differently (e.g.,

1753 Newcombe and Macdonald, 1991; Jones et al., 1999; Sazima et al., 2006). Fish species richness has

1754 been shown to increase (Lorion & Kennedy 2009), decrease (Toham & Teugels 1999; Brook & Sodhi

1755 2003), or be unaffected (Bojsen & Barriga 2002) by tropical deforestation. Fish community

1756 composition can also show equally variable impacts (Bojsen & Barriga 2002; Giam et al. 2015),
1757 including being more strongly structured at the mesohabitat (pool, riffle or run) scale than by land-
1758 use at a catchment scale (Martin-Smith 1998a, b). Variation in the type of land-use disturbance can
1759 also lead to significantly different outcomes: for example, slash and burn agricultural techniques led
1760 to longer term degradation of streams compared to selective-logging regimes (Iwata, et al. 2003a).
1761 Mitigation, such as retention of riparian reserves and forest patches can protect freshwater diversity
1762 during conversion of forest to oil-palm monoculture (Giam et al. 2015), although a recent study in
1763 Sabah showed that any disturbance to land-use within primary forest stream catchments resulted in
1764 a significant loss of species and functional richness (Wilkinson et al. 2018a).

1765 Extreme climatic events can also cause severe disturbance to freshwater ecosystems (White et al.
1766 2016). Unlike climate change, extreme climatic events such as drought do not manifest through
1767 gradual temperature change, which could allow time for adaptation or acclimatisation. Rather, they
1768 cause acute mortality episodes that can be substantial threats to local aquatic populations (Covich et
1769 al. 1999; McHugh et al. 2015; White et al. 2016). Although populations can recover post-drought
1770 through recruitment and immigration (Oliver et al. 2013), the immediate influence of drought on
1771 populations depends heavily on survival rates during drought. Effects of extreme low flow events on
1772 stream communities can, therefore, persist for several years (Lake 2003; Fritz & Dodds 2004), and
1773 the abundance of key taxa may take several years to recover (Ledger et al. 2013; Woodward et al.
1774 2015). Prolonged low flow events can affect freshwater populations by limiting migration through
1775 the drying out of riffles and waterfalls and a reduction in pool volumes and stream connectivity
1776 (Covich et al. 2003; Covich et al. 2006). They also alter food webs and species interactions by
1777 creating narrowly constrained channels, decrease reproductive rates, and restrict flow-related
1778 chemical communication (Covich et al. 2003; Covich et al. 2006). Drought conditions can also cause
1779 significant reductions in water quality, through the concentration of organic and inorganic materials
1780 that can reduce dissolved oxygen levels during decomposition (Covich et al., 2000; Iwata et al.

1781 2003a; Pringle 2003). Furthermore, drought conditions are associated with increased water
1782 temperatures that affect fish directly through high physiological demands and stress caused by
1783 higher temperatures, and indirectly by reducing the oxygen saturation and therefore dissolved
1784 oxygen levels of water. This combination of increased metabolic demand and decreased oxygen
1785 availability can prove limiting or lethal to fully aquatic stream biodiversity (Jackson et al. 2001).

1786 Climate and land-use change often act synergistically (Castello and Macedo 2015). Deforestation can
1787 amplify the magnitude and severity of droughts in comparison to areas with full forest cover (Bagley
1788 et al. 2014). Droughts can then fuel further land-use changes or forest degradation by killing trees
1789 (Lewis et al. 2011) or by triggering wildfires (Brando et al. 2014). In our study site located in tropical
1790 Sabah, Malaysia, the climate is typically aseasonal, with a propensity for drought from February to
1791 early May in major El Niño–Southern Oscillation years (Walsh & Newbery 1999). However, evidence
1792 indicates that extreme droughts and floods are intensifying (Huntington 2006), and this predicted
1793 increase in magnitude and frequency is an often overlooked threat of global warming on aquatic
1794 biodiversity (Ledger et al. 2013; Thompson et al. 2013; Jiménez-Cisneros et al. 2014; Woodward et
1795 al. 2015). Changes in climate could increase the risk of abrupt and non-linear changes in many
1796 ecosystems, which would affect their function, biodiversity and productivity (Tockner & Stanford
1797 2002). The increasing severity of these ecosystem stressors has led to calls for future research efforts
1798 to advance understanding and management of small tropical streams in relation to drought and
1799 multiple stressor effects (Taniwaki et al. 2017). More realistic and informative experiments are
1800 needed to understand the effects of the key agricultural stressors, land-use change and climate-
1801 change effects on tropical stream communities and biodiversity loss (Taniwaki et al. 2017).

1802 This study is part of a long term project monitoring the impact of deforestation and conversion of
1803 forest to oil-palm plantations on freshwater ecosystems in Sabah, Malaysia (Ewers et al. 2011; Luke
1804 et al. 2017a, b; Nainar et al. 2017; Wilkinson et al. 2018a, b). The impact of drought and recovery of
1805 freshwater fish communities is relatively understudied, and to our knowledge has not been

1806 examined across a land-use gradient in tropical Asia despite calls to explore the impacts of extreme
1807 climatic events and land-use change (Taniwaki et al. 2017). We aimed to determine the interactive
1808 impact of land-use and a severe, El Niño induced drought that occurred January–June 2016 on the
1809 most common species of freshwater fish present at our study site (Wilkinson et al. 2018a, b). We
1810 expected to find a synergistic effect in which the impact of drought would be greater in more heavily
1811 disturbed streams, as these will likely experience greater levels of drying, increased temperatures
1812 and lower dissolved oxygen concentrations (Covich et al. 2000; Iwata et al. 2003a; Pringle 2003). We
1813 note, however, that this is the opposite of what has been shown for interacting stressors in
1814 predominantly temperate studies, where antagonistic interactions are more frequently observed
1815 (Jackson et al. 2016). Specifically, we expected the drought would exacerbate the impacts of land-
1816 use on our target fish species, hypothesising: (a) a decline in fish density during the drought,
1817 reflecting rapidly elevated mortality during the drought event, but recovery after the drought as
1818 populations stabilise; (b) a decline in total fish biomass during the drought, but showing some
1819 recovery after drought; and (c) fish movement would be reduced during the drought relative to
1820 before and after drought conditions. With continued deforestation and conversion to oil-palm
1821 plantations in Southeast Asia, our study provides crucial insight into how these ongoing land-use
1822 changes will interact with extreme climatic events to impact freshwater ecosystems.

1823 **5.2 METHODS**

1824 **5.2.1. STUDY SITE**

1825 We sampled 16 streams in Southeastern Sabah, Malaysian Borneo. The sites form part of the
1826 Stability of Altered Forest Ecosystems (SAFE) project (Ewers et al. 2011; SAFE project: 4° 38' N to 4°
1827 46' N and 116° 57' E to 117° 42' E, and Danum Valley Conservation Area: 5° 01' N and 117° 48.75' E).
1828 The landscape is drained by tributaries of the Brantian, Kalabakan and Segama Rivers, all of which
1829 flow into the Celebes Sea. Data were collected from 16 small, headwater streams (3–10 m wide, ≤
1830 1.2 m depth) across a gradient of land-use intensity (as in Wilkinson et al. 2018b): four in primary

1831 forest (three at Danum Valley Conservation Area, and one in the Brantian Virgin Jungle Reserve;
1832 average above-ground biomass (AGB) = 350 T ha⁻¹) seven in logged forest (one in twice-logged
1833 forest, last logged ~ 20 years ago, and six in salvage-logged forest, logged in 2013-2016, average AGB
1834 = 95–122 T ha⁻¹), five in oil-palm plantations (varying in age since planting from 7–12 years; average
1835 AGB = 38 T ha⁻¹) (Pfeifer et al. 2016). A 200 m transect was located in each stream, and all streams
1836 were independent tributaries to ensure spatial independence of data.

1837 **5.2.2. FISH SAMPLING**

1838 Fishes were sampled over four sampling years: April–June 2013, March–August 2015, February–July
1839 2016, and February–July 2017. Just eight streams were sampled in 2013, but all 16 streams were
1840 sampled in all other years. Seasonal rainfall variation at our study site is usually very limited (Walsh
1841 & Newbery 1999; Kumagai et al. 2005), suggesting little effect of the differences in timing of the
1842 sampling within years. Rainfall data from the SAFE project field camp during the El Niño drought
1843 period of January–June 2016 had mean monthly rainfall of 164 mm month⁻¹ and a mean of 15 dry
1844 days per month, compared to average values across years of 203 mm and nine dry days per month
1845 (R.P.D. Walsh, Unpub. Data). During the drought, many streams in the study area were reduced to a
1846 series of disconnected pools (Figure 1).

1847

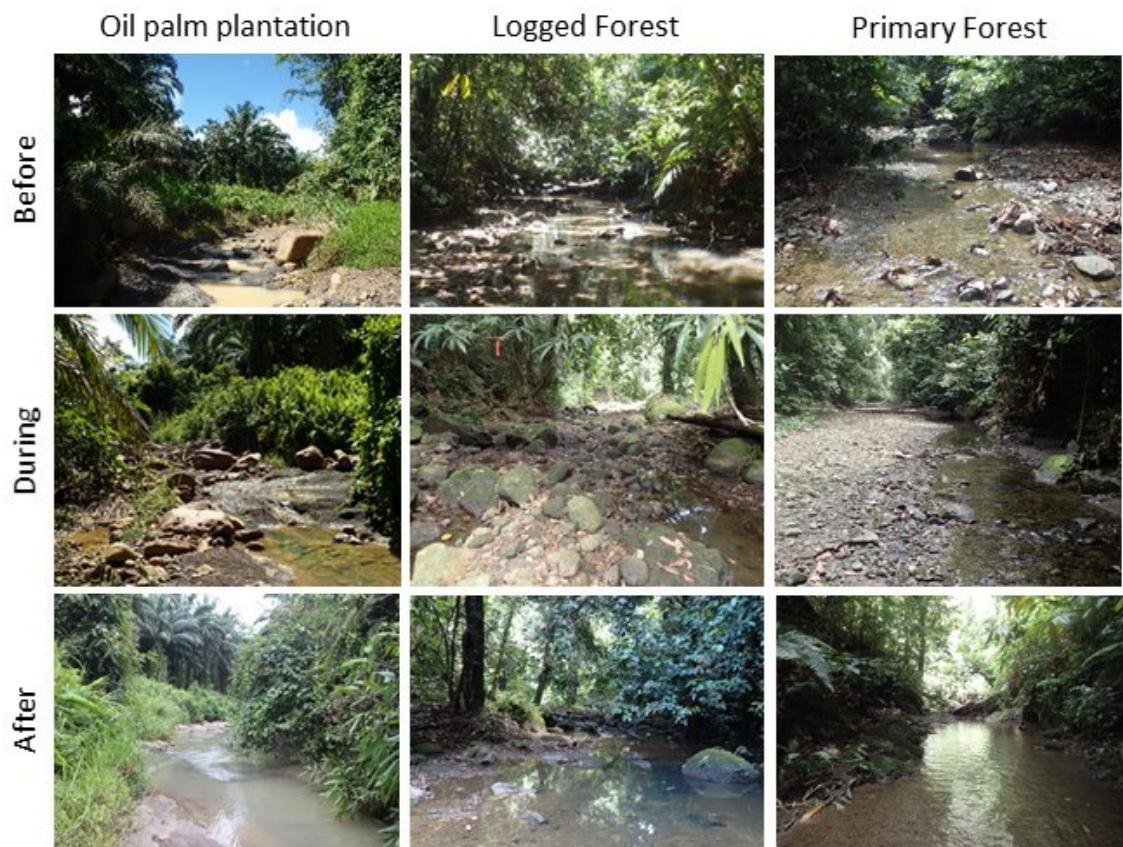


Figure 1. Streams in primary forest, logged forest and oil-palm plantation streams, before, during and after drought, illustrating the impact of the 2016 El Niño drought on stream conditions.

1848

1849 Fishes were sampled using a 2.75 m diameter cast net with 1 cm mesh and plastic, and with baited
 1850 funnel traps (1.5 L plastic water bottles with an entrance diameter of 2.6 cm), as part of a long-term
 1851 monitoring project at the SAFE project. Each stream transect was sampled for between four and six
 1852 consecutive days (mean = 4.28), with around 20 throws of the net per day (mean = 16, range = 10 to
 1853 36), and 20 funnel traps (10 baited with bread and 10 with fresh fish, placed every 10 m along the
 1854 stream). The number of throws per transect varied with the number and size of pools.

1855 Captured fishes were identified to species (Inger & Chin 2002; Kottelat 2013), measured (2013 and
 1856 2015 sampling), weighed using a portable balance (2015 sampling only), and returned to the stream
 1857 at the point of capture. Fish of over 6 cm total length were tagged with a passive integrated
 1858 transponder (PIT) tag (Biomark) to allow for unique identification of individuals upon recapture. Fish

1859 capture, handling and euthanisation protocols were reviewed and approved by the Animal Welfare
1860 and Ethical Review Body at Imperial College London.

1861 Previous studies have shown that *Nematabramis everetti* (Cyprinidae) is the most abundant fish
1862 species in the study streams, accounting for 29% of all fish captures and present in all land-uses and
1863 in the majority (88%) of streams sampled (Wilkinson et al. 2018a, b). *N. everetti* was the only species
1864 with a sufficient number of recaptures at the majority of stream transects to obtain rigorous
1865 estimates of population size and movement rates, therefore we restricted our study to focus on this
1866 single species.

1867 **5.2.3. ENVIRONMENTAL VARIABLES**

1868 To monitor the abiotic changes caused by land-use and drought, 11 stream measurements were
1869 taken every 10 m along the 200 m stream transect. Environmental data were collected in the 2015,
1870 2016 and 2017 sampling years. Temperature ($^{\circ}\text{C}$), dissolved oxygen (mg L^{-1}), conductivity ($\mu\text{S cm}^{-1}$),
1871 and pH were measured with a YSI Professional Plus multi-parameter meter, every day during
1872 sampling at the downstream end of the transect, in addition to the further 20 point measurements
1873 along the transect. Wetted width (m), depth (cm), mean surface current speed (m s^{-1} ; measured by
1874 timing a tennis ball travelling 2 m, repeated three times and converting to m s^{-1}), substrate (%; sand,
1875 gravel, pebbles, large rocks, bedrock), littoral leaf litter cover (%; measured in a 50 cm transect
1876 across the stream and recorded to the nearest 10%), sedimentation (presence or absence), canopy
1877 cover (densiometer readings oriented upstream, downstream, and to the left and right banks) were
1878 measured at the 21 points, every sampling year.

1879 **5.2.4. RESPONSE METRICS**

1880 Stream-specific density estimates (number of fish per kilometre) were calculated using spatially
1881 explicit mark-recapture models (secr) using the R package ‘seclinear’ (Efford 2014). We analysed
1882 data only from stream transects that had more than five recaptures per sampling year, resulting in

1883 five streams being omitted from the analysis (three in logged forest, one in primary forest, and one
1884 from oil-palm plantation). Populations were assumed to be closed in the short (4–6 day) time period
1885 in which they were sampled each year. Both density (D) and detection parameters (g_0 and sigma)
1886 were included in the model for each stream transect, and three models were run, with either density
1887 or density and the detection parameters varying by sampling year. Models were fitted and
1888 compared on the basis of their corrected Akaike Information Criterion (AICc), chosen over the more
1889 routinely used AIC because AICc is additionally adjusted to account for small-sample biases (Cooch &
1890 White 2006). The model with the lowest AICc was selected and density estimates extracted.

1891 Individual biomass (g) was calculated for all fish. For individuals collected in 2015 this was recorded
1892 directly using an electronic balance. For the remaining collections, biomass was estimated from
1893 individual measurements of total body length, using a regression equation previously calculated and
1894 reported at these study sites (Wilkinson et al. 2018a). Two metrics of biomass were calculated to
1895 examine biomass density and availability of fish for capture: a) total biomass captured for each
1896 stream, in each sampling year; and b) predicted density of biomass (kg km^{-1}), calculated by
1897 multiplying the density of individuals with average biomass of individuals in each stream, each
1898 sampling year. The former measure is relevant as a measure of fish biomass as an accessible
1899 resource for subsistence fishing (Wilkinson et al. 2018b), whereas the latter is a more ecologically
1900 relevant metric of population responses to disturbance. All recaptures were excluded from these
1901 population-level biomass calculations.

1902 Mark-recapture data were used to measure the movement distances of fish between captures. All
1903 movement distances were positive, ignoring the direction of travel (upstream or downstream), and
1904 each was assigned to a category depending on the time frame since the last capture (week = within
1905 the 4–6 day sampling period; month = within 2–4 months since last capture; and year = at least 10
1906 months since last capture).

1907

1908 **5.2.5. ANALYSIS**

1909 Focal fish species metrics (biomass, density and movement (individuals caught in multiple years))
1910 and environmental variables were analysed as the response variables. As predictor variables, we
1911 used the land-use gradient (categorised into primary forest, logged forest, or oil-palm) and drought
1912 disturbance (categorised into before drought, during drought and after drought), and their
1913 interaction. In addition, we analysed how the time frame (week, month or year) affected the
1914 movement of *N. everetti*, using time as the predictor variable. Biomass, density and some
1915 environmental variables were log transformed prior to analysis to ensure model assumptions would
1916 be met. Generalised linear mixed models were used (GLMMs; Bates et al. 2014), including
1917 differences in intercept between streams as an independent random effect. For the movement
1918 models a Poisson error distribution was applied, for all other models a Gaussian error distribution
1919 was applied (Zuur et al. 2009). Log-likelihood ratio tests were used to assess model significance. The
1920 relative importance of fixed and random effects was ascertained using the methods of Nakagawa
1921 and Schielzeth (2013).

1922 **5.3. RESULTS**

1923 In total, *Nematabramis everetti* accounted for 36% of all captures (3,658 of 10,160 individuals
1924 belonging to 29 species). The best secr model allowed density, g₀, and sigma to vary by sampling
1925 year (Appendix 5.1). Density of *N. everetti* ranged from 138 ± 37 to 2774 ± 1004 fish km⁻¹ (mean =
1926 1152 ± 328) across the 11 streams it was present at.

1927 **5.3.1. ENVIRONMENTAL VARIABLES**

1928 Mean stream water temperatures were significantly warmer, by 2.5°C and 5.5°C , in logged forest
1929 and oil-palm streams, respectively, in comparison to primary forest streams (Table 1), and
1930 significantly warmer in 2016 during the drought than before or after the drought (Table 2). Streams
1931 in primary forest were shown to be buffered from El Niño-induced changes in temperature, with <1

1932 °C temperature change throughout the three years sampled (2015–2017), however streams in
1933 logged forest and oil-palm plantations were 2–4 °C warmer in 2015 compared to 2017, and 4–5.5 °C
1934 in 2016 compared to 2017. In addition, dissolved oxygen was significantly lower in logged forest and
1935 oil-palm, and this was further exacerbated by the drought. Conductivity, pH, mean surface flow, and
1936 all substrate classes varied significantly during the drought, and canopy openness and leaf litter
1937 cover varied by land-use (Table 1, 2).

1938 **5.3.2. EFFECTS ON *NEMATABRAMIS EVERETTI***

1939 There was a significant effect of land-use (Figure 2a; $\chi^2_{(2)} = 7.34$, $P = 0.03$), but not drought (Figure
1940 2b; $\chi^2_{(2)} = 1.38$, $P = 0.50$), or their interaction (Figure 2c; $\chi^2_{(4)} = 7.11$, $P = 0.13$) on the population
1941 density of *N. everetti*. Density of fish was significantly higher in oil-palm than in logged forest
1942 streams. In addition, stream as a random effect explained a considerable proportion of the variance
1943 in the model ($R^2_c = 0.68$, $R^2_m = 0.32$).

1944 There was a significant effect of drought (Figure 2d; $\chi^2_{(2)} = 6.23$, $P = 0.04$), and the interaction of
1945 drought and land-use (Figure 2f; $\chi^2_{(2)} = 10.30$, $P = 0.04$), but not land-use alone (Figure 2e; $\chi^2_{(4)} =$
1946 13.80, $P = 0.15$) on the biomass captured of *N. everetti*. Captured biomass was significantly lower
1947 during the drought compared to before the drought, but that decrease was greater in oil-palm
1948 plantations than in primary forest streams, and remained unchanged in logged forest streams.
1949 Stream as a random effect explained a substantial proportion of the variance explained in the model
1950 ($R^2_c = 0.55$, $R^2_m = 0.34$). However, there was no significant effect of land-use (Figure 2g; $\chi^2_{(2)} = 4.35$,
1951 $P = 0.11$), drought (Figure 2h; $\chi^2_{(2)} = 1.11$, $P = 0.57$), or their interaction (Figure 2i; $\chi^2_{(4)} = 4.98$, $P =$
1952 0.29) on biomass density (kg km^{-1}) of *N. everetti*. Again, stream as a random effect explained a
1953 substantial proportion of the variance explained in the model ($R^2_c = 0.62$, $R^2_m = 0.22$).
1954 There was insufficient data to analyse distance moved of *N. everetti* with land-use and drought as
1955 interacting factors, so they were analysed separately. No significant effect of land-use was found on

1956 the movement of *N. everetti* (Figure 1j; $\chi^2_{(2)} = 4.81$, $P = 0.09$), but there was a significant effect of
1957 drought (Figure 1k; $\chi^2_{(3)} = 126.00$, $P < 0.01$). Fish moved further during the drought than before or
1958 after the drought. Unsurprisingly, the time since previous capture had a significant effect on
1959 movement (Figure 3; $\chi^2_{(2)} = 1460$, $P < 0.01$), with fish moving further over a longer time period. The
1960 model explained very little variation in the data ($R^2_m = 0.08$), and even over a period of one year fish
1961 moved relatively short distances (median = 10 m). Stream as a random effect explained a small
1962 proportion of the variance in the model for land-use and drought ($R^2_c = 0.08$, $R^2_m = 0.11$), and in the
1963 model for movement over time ($R^2_c = 0.04$, $R^2_m = 0.08$).

1964

1965

Table 1. Summary of stream environmental variables by year (note that 2016 was the year the drought occurred) and land-use (OP = oil-palm, LF = logged forest, and PF = primary forest). Temperature ($^{\circ}\text{C}$), dissolved oxygen (mg L^{-1}), conductivity ($\mu\text{S cm}^{-1}$), and pH, measured with a YSI Professional Plus. Wetted width (m) and depth (cm) - measured with tape measures, mean surface current speed (m s^{-1}) - measured by timing a tennis ball travelling 2 m, repeated three times), substrate (%; sand, gravel, pebbles, large rocks, bedrock), littoral leaf cover (%; measured in a 50 cm transect across the stream and recorded to the nearest 10%), and canopy cover (densiometer readings oriented upstream, downstream, and to the left and right banks) were measured visually.

Year	Mea	Wetted	Dept	Substrate				pH	Temper	Dissolv-	Conductiv	Canopy	Sedimenta-	leaf		
	n	width	h	sand	gravel	pebbles	Large	Bed-	-ature	ed	-ity	opennes	tion	litter		
	Flow	(cm)	(cm)					rocks	rock	($^{\circ}\text{C}$)	oxygen	($\mu\text{s cm}^{-1}$)	s	0=none,	cover	
(mg L ⁻¹)																
O	2015	0.09	489.45	13.85	47.92	32.66	43.19	37.93	65.00	7.81	29.70	7.07	366.15	NA	NA	4.95
P	2016	0.15	483.16	13.23	30.36	28.02	37.28	34.26	66.92	8.13	31.22	5.64	2678.86	60.56	1.00	4.76
	2017	0.50	590.76	16.00	15.62	16.19	39.71	19.71	8.38	7.33	25.62	7.48	97.14	52.83	0.80	10.00
LF	2015	0.18	649.67	21.36	40.20	39.06	44.75	52.53	86.01	7.90	25.63	7.48	283.69	NA	NA	10.07
	2016	0.17	575.94	14.87	28.59	31.04	34.14	37.11	64.13	8.30	28.26	6.70	770.17	32.30	0.69	12.27
	2017	0.78	658.05	13.85	12.76	16.96	31.25	23.83	14.79	7.92	23.87	7.89	119.31	28.52	0.14	8.51
P	2015	0.07	529.17	18.35	24.42	38.83	37.37	40.72	77.50	7.75	25.42	6.14	676.12	NA	NA	22.63
F	2016	0.07	552.68	21.54	23.19	31.18	40.17	36.89	46.88	7.52	25.76	6.89	1127.32	19.35	0	12.5
	2017	0.50	486.43	18.93	10.83	17.86	33.57	31.79	5.71	8.06	24.72	7.67	197.30	23.30	0	8.21

Table 2. Mixed model outputs of environmental variables by land-use, drought and the interaction between land-use and drought. Model outputs include: DF = degrees of freedom, χ^2 = Chi-squared, and P = p-value. Temperature ($^{\circ}\text{C}$), dissolved oxygen (mg L^{-1}), conductivity ($\mu\text{s cm}^{-1}$), and pH, measured with a YSI Professional Plus. Wetted width (m) and depth (cm) - measured with tape measures, mean surface current speed - measured by timing a tennis ball travelling 2 m, repeated three times), substrate (%; sand, gravel, pebbles, large rocks, bedrock), littoral leaf litter cover (%; measured in a 50 cm transect across the stream and recorded to the nearest 10%), and canopy cover (densiometer readings oriented upstream, downstream, and to the left and right banks) were measured visually. Results in bold illustrate significant impacts of the predictor variable on the environmental response.

Environmental variable	Land-use			Drought			Land-use: Drought interaction			R2m	R2c
	DF	χ^2	P	DF	χ^2	P	DF	χ^2	P		
(log)Temperature	2	40.4	< 0.01	2	45.90	< 0.01	4	10.5	0.03	0.67	0.67
(log) Dissolved oxygen (mg L^{-1})	2	14.4	< 0.01	2	46.9	< 0.01	4	13.2	0.01	0.61	0.61
(log) Conductivity ($\mu\text{s cm}^{-1}$)	2	5.26	0.07	2	60.38	< 0.01	4	9.18	0.06	0.60	0.61
(log) pH	2	4.72	0.09	2	13.4	< 0.01	4	7.12	0.13	0.34	0.65
(log) Mean Flow	2	5.59	0.06	2	165.09	< 0.001	4	6.72	0.15	0.65	0.85
(log) Wetted width (cm)	2	1.12	0.57	2	1.79	0.41	4	4.70	0.32	0.10	0.61
Depth (cm)	2	4.98	0.08	2	1.94	0.38	4	7.05	0.13	0.23	0.28
(log) Canopy openness	2	9.12	0.01	1	0.91	0.34	2	4.97	0.08	0.37	0.95
(log) leaf litter cover	2	6.16	0.05	2	0.95	0.62	4	10.12	0.04	0.28	0.42
Substrate: sand	2	4.31	0.12	2	58.71	< 0.01	4	6.46	0.17	0.52	0.68
Substrate: gravel	2	2.40	0.30	2	100.44	< 0.01	4	1.54	0.82	0.64	0.72
Substrate: pebbles	2	0.89	0.64	2	13.05	< 0.01	4	7.10	0.13	0.23	0.54
Substrate: large rocks	2	3.10	0.21	2	62.50	< 0.01	4	11.3	0.02	0.47	0.75
Substrate: bedrock	2	3.36	0.19	2	151.17	< 0.01	4	3.08	0.54	0.82	0.85

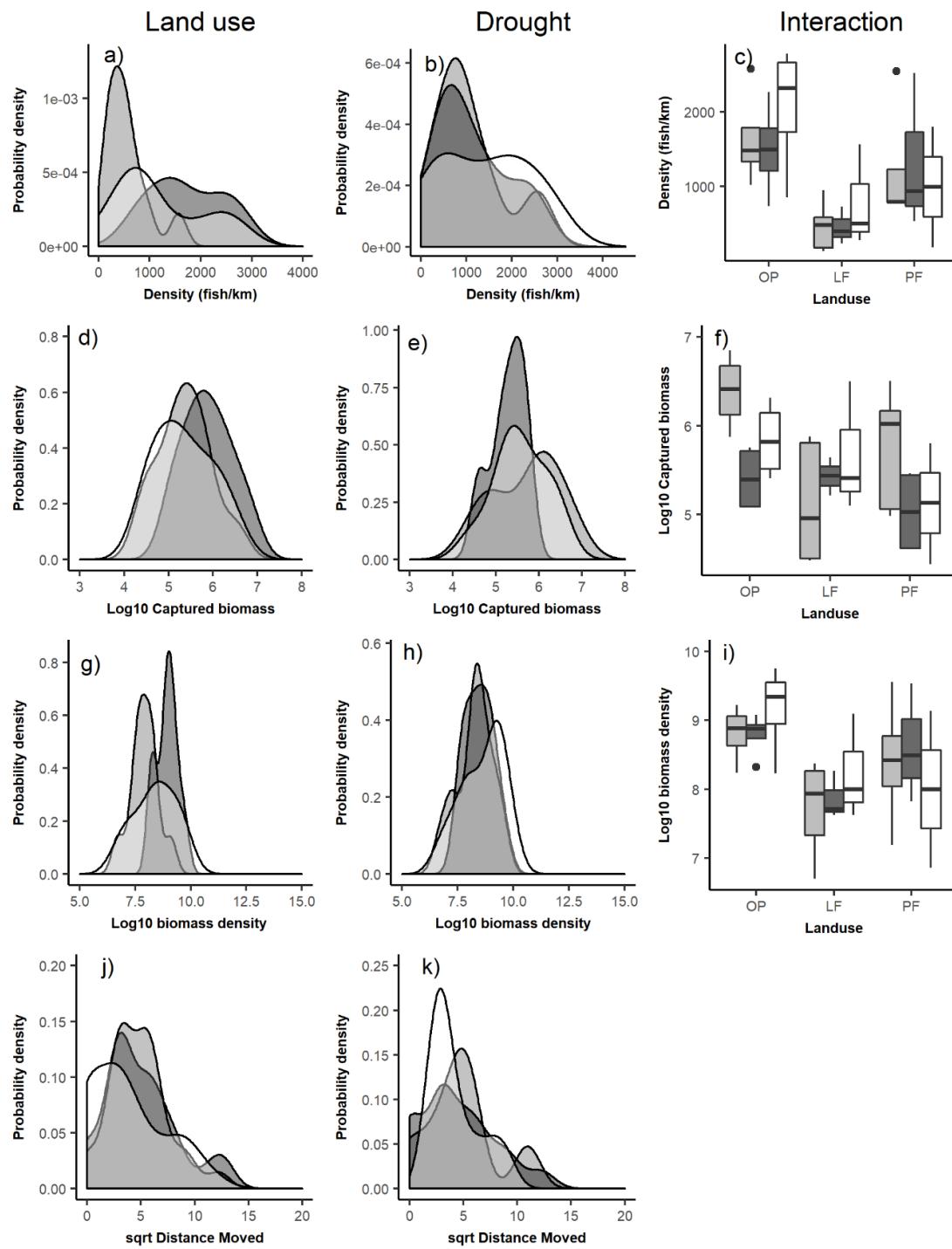


Figure 2. The impact of land-use, drought and their interaction on the density (fish km^{-1} ; a–c, respectively), \log_{10} captured biomass (d–f, respectively), \log_{10} biomass density (calculated from density estimates multiplied by the average mass of fish in each stream in each sampling year; g–i, respectively), and square root of movement between captures (j–l, respectively) of *Nematabramis everetti*. Graphs a, d, and g, show the probability density at each land-use: white = primary forest, light grey = logged forest and dark grey = oil-palm. Graphs b, e and h, show the probability density at each drought category: before = light grey, during = dark grey, and after = white. Graphs c, f, and i, show the interaction between land-use and drought, coloured by drought categories: before = light grey, during = dark grey, and after = white.

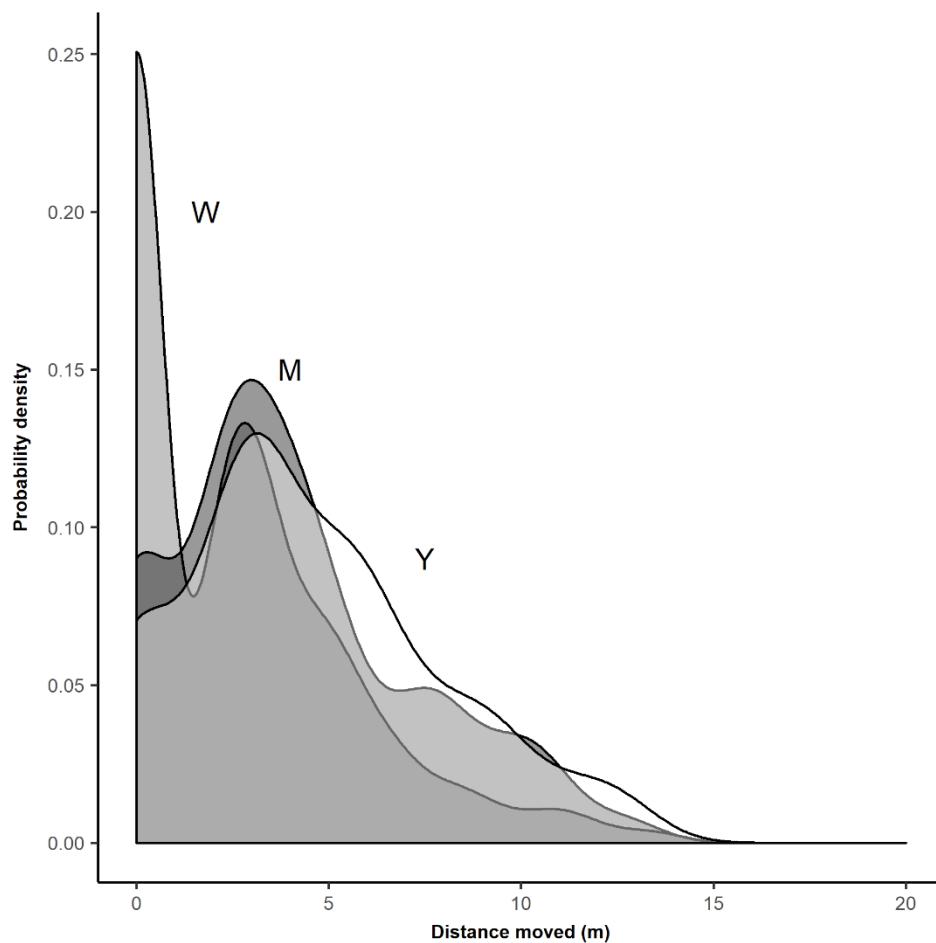


Figure 3. The impact of time since last capture (W = week, M = month, Y= Year) on the movement of *Nematabramis everetti* individuals.

1968

1969

1970

1971

1972

1973

1974 **5.4. DISCUSSION**

1975 Catchment land-use had a significant effect on the density of the most common and abundant
1976 freshwater fish species at our study site, *Nematabramis everetti*. It did not, however, impact the
1977 total captured biomass, biomass density or the distance moved of this species. In contrast, the
1978 severe, El Niño induced drought had a significant impact on the total captured biomass of *N.*
1979 *everetti*, but not on the biomass density of *N. everetti*. The drought was associated with a reduction
1980 in captured biomass during the event, and no significant recovery was seen one year after the
1981 drought during this study. Together, these results suggest that individuals of *N. everetti* became
1982 more difficult to catch during the drought, but that there is no overall reduction in the density or
1983 biomass of fish in the streams. These results indicate that *N. everetti* is highly resilient to an extreme
1984 El Niño drought, but that fishermen in rural communities that may be relying on this species as a
1985 food source may find it more difficult to capture during drought.

1986 The 2016 El Niño induced drought in Sabah was shown to have significant effects on the within-
1987 stream conditions and water quality (Table 1), with water temperatures during the drought more
1988 than 5 °C warmer in oil-palm streams in comparison to primary forest streams, and all streams had
1989 lowered dissolved oxygen levels. Martin-Smith and Laird (1998) also demonstrated the high
1990 variability of small forest streams in Danum Valley Conservation Area, Sabah, with streams drying to
1991 disconnected pools and poor water quality (lowered levels of dissolved oxygen and high levels of
1992 decaying organic material) during drought periods. We note that our environmental variables were
1993 all taken as point samples on arrival at each stream transect, as opposed to being collected
1994 continuously at permanent monitoring stations. The peaks in temperature seen during the drought
1995 may therefore not be representative of the average stream daily conditions, where a daily
1996 temperature range, or maximum value may be more appropriate to look at the possible impacts of
1997 raised temperature on the metabolism of fish.

1998 Many of the species found within hill streams in this study, and in streams sampled by Martin-Smith
1999 and Laird (1998), have adaptations to cope with low oxygen levels. *Nematobramis everetti* are
2000 surface-feeding insectivores, swim very close to the air-water interface where they probably gulp air
2001 while feeding, and can spawn all year round (Martin-Smith and Laird 1997). Despite these
2002 adaptations, this study showed a significant reduction in total captured biomass during and after the
2003 drought compared to before the drought, despite there being no difference in the biomass density
2004 of fish. Together, this indicates a change in the catchability, and therefore availability, of fish rather
2005 than a true decrease in biomass. As all experimental streams had dried up into series of
2006 disconnected pools, we had expected that we would see a decrease in biomass of fish caused by a
2007 decrease in available habitat and associated increase in competition for food, and shelter within
2008 pools, increased predation risk, and the inability to tolerate extreme changes in stream water quality
2009 (Matthews & Matthews 2003). Our results, though, suggested that *N. everetti* is remarkably resilient
2010 to perturbations caused by drought conditions, and that drought does not remove them from their
2011 status of being the most abundant and common species in these streams.

2012 Quantitative studies in Borneo show mixed effects for the impact of logging and conversions to oil-
2013 palm plantation on freshwater fish communities. Wilkinson et al. (2018a) showed that there was a
2014 reduction in species and functional richness in streams with any disturbance from primary forest,
2015 whilst others show that the impact of selective-logging is more benign to freshwater fish (Martin-
2016 Smith 1998a, c; Iwata et al. 2003b) than clear cutting and agricultural conversion (Beamish et al.
2017 2003; Giam et al. 2015), and that the impact of land conversion for oil-palm or other agricultural
2018 plantations can be mitigated by the retention of forest fragments and riparian reserves (Giam et al.
2019 2015). We had expected to see a difference across the land-use gradient, with primary forest having
2020 the greatest density and biomass, and oil-palm streams having the lowest density and biomass of *N.*
2021 *everetti*. However, it was logged forest that had the lowest density of *N. everetti*, with no difference
2022 between oil-palm and primary forest. We postulate that this is due the recent salvage-logging in six

2023 out of seven logged forest streams studied, which caused large influxes of sediment and changes in
2024 substrate (Table 1). It has been shown that streams can take more than 20 years to recover from
2025 the impacts of logging (Luke et al. 2017a), therefore the 2–4 years since the last round of logging is
2026 probably not sufficient for the freshwater community to have fully recovered and may explain why
2027 *N. everetti* populations were reduced in this habitat. A second hypothesis is that there may be a
2028 decrease in the allochthonous input (i.e., inputs of external organic material and invertebrates)
2029 ‘falling’ into logged forest streams in comparison to primary forest (Chan et al. 2008), and
2030 preliminary results from the study site suggest similar rates of invertebrates falling into oil-palm
2031 streams as primary forest streams (Cassel 2017). *Nematabramis everetti* is a surface-to midwater
2032 feeding insectivore and predominantly feeds upon such invertebrates (Inger & Kong 2002; Phipps
2033 2014). A decline in prey biomass entering the stream ecosystem may therefore translate into a
2034 reduced abundance and density of *N. everetti*.

2035 Our results and conclusions may have been influenced by the sampling methods chosen and their
2036 effectiveness in the altered stream conditions caused by the drought, with fish catchability likely to
2037 be altered during drought conditions. This is strongly indicated by our data showing a reduction in
2038 captured biomass despite no detectable reduction in fish or biomass density. We also observed an
2039 increase in the proportion of fish caught in funnel traps compared to cast netting during the drought
2040 (C. Wilkinson, Pers. Obs.). The change in captures by method are likely due to the result of drought
2041 as there is a greater difficulty in deploying the cast net in small areas, and fish are restricted to
2042 smaller, more concentrated pools leading to greater catches in funnel traps. Together, the
2043 combination of the two sampling methods and the use of spatially explicit mark recapture models
2044 helps reduce the influence of sampling variation on fish and biomass density estimates. The use of
2045 cast nets for monitoring fish communities is important, however, as it provides a metric of the
2046 availability of fish as a resource to local people in our study landscape (Wilkinson et al. 2018b). In
2047 that context, our finding that fish catchability is reduced during drought is an important one, and

2048 indicates that drought may exert a negative impact on local communities despite having little
2049 ecological effect on the species itself.

2050 Despite freshwater fish stream communities being shown to suffer large reductions in species
2051 richness during land disturbance, logging and conversion to oil-palm (Wilkinson et al. 2018a), this
2052 study highlights the resilience of at least one dominant species, *N. everetti*, to both land-use change
2053 and severe drought conditions. This ecological resilience may not, however, translate into a resilient
2054 ecosystem service of fish provisioning to local communities. This study was also able to focus on just
2055 one species, with a lack of data preventing us from examining impacts on the many rare species that
2056 may suffer the most during multiple stressor events. It is therefore essential to continue monitoring
2057 freshwater fish communities across modified landscapes and through time to continue building the
2058 data needed to fully quantify the impacts of these multiple stressors on freshwater ecosystems
2059 across Southeast Asia.

2060

CHAPTER 6

2061 **GENERAL DISCUSSION: IMPACTS OF LAND-USE CHANGE ON AQUATIC BIODIVERSITY**

2062 _____

2063 **OVERVIEW**

2064 Anthropogenic impacts through changes in land-use, agricultural expansion and intensification is
2065 currently a major driver of global biodiversity and forest loss (MEA 2005; Phalan et al. 2013). The
2066 destruction of tropical forests is of particular significance owing to the disproportionately high levels
2067 of biodiversity present in the tropics (Bradshaw et al. 2009; Laurance et al. 2012), marked declines in
2068 biodiversity when tropical forest is converted to other land-use types (Phalan et al., 2013) and the
2069 unabated levels of deforestation due to increasing human demands for food, timber and other
2070 products (Sodhi et al. 2004; Wilcove et al. 2013). Primary forests are critically important for
2071 conserving tropical biodiversity (Gibson et al., 2011) and once-logged forests in Southeast Asia have
2072 high conservation value for terrestrial taxa (Edwards et al. 2014a), but focussing on these habitats
2073 alone is not sufficient. Large areas of logged forest and agricultural plantation will be key features of
2074 future tropical landscapes as they now dominate the land area of many regions. This thesis aimed to
2075 answer questions on the spatial and temporal impacts of land-use change and climatic stressors on
2076 freshwater ecosystems in Sabah, Malaysia, and aimed to determine if and how current mitigation
2077 strategies protect freshwater ecosystems.

2078 The results of this thesis lead to three main discussion themes: (1) Primary rainforest streams are
2079 irreplaceable in terms of freshwater biodiversity; (2) Riparian reserves provide protection to
2080 freshwater biodiversity, but reserves alone are not sufficient to protect freshwater ecosystems; (3)
2081 Common freshwater fish are highly resilient to multiple perturbations or stressors. I will discuss each
2082 point in turn to understand the implications for current freshwater ecosystems, and to place them in
2083 a broader context. I then go on to discuss the future management options for industry, the
2084 limitations of this study and the possible future directions of tropical freshwater research.

2085 **6.1. PRIMARY RAINFORESTS ARE IRREPLACEABLE**

2086 The most widespread and destructive threat to aquatic ecosystems is habitat modification that
2087 results from converting natural areas to agricultural land (Allan & Flecker, 1993; Laurance et al.,
2088 2014). Land-use change results in loss of vegetation, increases in bare ground and use of fertilisers
2089 and other chemicals, and can have substantial impacts on flow rate, sediment input, organic matter,
2090 light levels, temperature, and water quality (e.g., Douglas et al. 1993; Brooks & Spencer 1997; Iwata,
2091 et al. 2003a, b; Bruijnzeel 2004; Sweeney et al. 2004; Souza et al. 2013; Fernandes et al. 2015; Luke,
2092 et al. 2017a). A growing body of research is showing that selectively-logged, salvage-logged and
2093 converted forest (to oil-palm plantation) in Southeast Asia have substantial negative impacts on
2094 terrestrial (Fitzherbert et al. 2008; Gray et al. 2014; Mercer et al. 2014; Konopik et al. 2015; Wearn et
2095 al. 2017) and aquatic (Iwata et al., 2003a, 2003b; Giam et al., 2015; Konopik et al., 2015; Luke et al.,
2096 2017b) biodiversity. For terrestrial ecosystems, high levels of biodiversity are found to persist in
2097 selectively-logged forests (Berry et al. 2010; Edwards et al. 2011; Woodcock et al. 2011; Edwards et
2098 al. 2014b; Wearn et al. 2017), but are significantly reduced in oil-palm plantations perhaps owing to
2099 the changes in climate and reduction in habitat complexity (Bruhl & Eltz 2010; Fayle et al. 2010;
2100 Luskin & Potts 2011; Edwards et al. 2013; Senior et al. 2013; Edwards et al. 2014a; Hardwick et al.
2101 2015).

2102 However for aquatic diversity, results seem more mixed. In response to deforestation, for example,
2103 fish species richness can be increased (Lorion & Kennedy 2009), decreased (Brook et al., 2003;
2104 Toham & Teugels, 1999), or remain unaffected (Bojsen & Barriga 2002), with fish community
2105 composition showing equally variable impacts (Bojsen & Barriga 2002; Giam et al. 2015) in
2106 comparison to primary forest. This variation in the impacts of land-use change on freshwater
2107 ecosystems, led to renewed calls to better understand the results of land-use change and the
2108 potential interactions of land-use change with other stressors specific to certain regions such as
2109 dams, drought or invasive species (Macedo et al. 2013; Taniwaki et al. 2017). However, the impact of

2110 conversion to oil-palm, compared to forested land, has been shown to have clear negative impacts
2111 on the diversity and community structure of fish (Giam et al. 2015), frogs (Konopik et al. 2015), and
2112 macroinvertebrates (Luke et al. 2017b) in Southeast Asia.

2113 In this thesis, I found that primary forests are irreplaceable in protecting and supporting high levels
2114 of aquatic diversity. Streams in all disturbed land-use regimes (selective-logging, salvage-logging and
2115 conversion to oil-palm plantation) suffered losses in species and functional richness relative to
2116 primary, protected forest streams (Chapter 3); riparian forest of high quality (primary forest)
2117 supported higher levels of species and functional richness, and showed greater abundance of
2118 individual species compared to lower quality forest (Chapter 4). Several endemic, fast flowing, hill
2119 stream specialist species were only found in low numbers inside protected forest catchments
2120 (Chapters 2 and 3), suggesting these range-restricted species are likely to be threatened by land-use
2121 change (Giam et al. 2011). The results of this thesis demonstrate the extensive negative results of
2122 land disturbance, since losses were recorded in all land-uses including twice-logged, three-times
2123 logged and salvage-logged forest catchments; previous studies have predominantly only considered
2124 once-selectively-logged forest catchments (e.g., Giam et al., 2015; Martin-Smith, 1998a, b, c). These
2125 disturbance effects are likely to be the most pronounced in the years immediately after conversion
2126 due to the drastic within stream abiotic changes, with varying rates of recovery to pre-conversion
2127 conditions, dependent on the severity of disturbance, possible restoration of vegetation and
2128 geographic location (Malmer & Grip 1994; Iwata et al. 2003a; Bruijnzeel 2004; Luke et al. 2017a).
2129 The results indicate that any land-use change has lasting, negative impacts on the freshwater
2130 ecosystem, and that undisturbed, protected forest areas are essential in protecting freshwater
2131 diversity, and therefore should be a priority for conservation.

2132 In addition to the declines in species richness, loss of endemic species from disturbed landscapes
2133 and changes in community composition are also a conservation issue. Changes in species
2134 assemblage, community structure and loss of species from modified aquatic habitats may have

2135 impacts on the way in which these disturbed aquatic ecosystems function and the services they
2136 provide. Although still debated, there is mounting evidence that suggests that ecosystems with
2137 lower levels of biodiversity have reduced ecosystem function and are less resilient to further
2138 perturbations (Hooper et al. 2005). Despite this, there was no change in the availability of
2139 freshwater fish as a resource available to local, rural communities in Sabah, across the land-use
2140 gradient (Chapter 2), suggesting that the provisioning ecosystem service at least is maintained.
2141 Similarly, dung removal rates are maintained across the land-use gradient (Gray et al. 2014). In
2142 contrast, other studies in the region have shown reduced levels in both ecosystem functions and
2143 supporting and regulating ecosystem services, with increased disturbance across this gradient of
2144 land-use from primary forest to oil-palm plantations e.g., reduced leaf litter decomposition (Luke
2145 2016), and increased algal growth (A. Milton Pers. Comms.; and in other locations: Benstead &
2146 Pringle 2004; England & Rosemond 2004).

2147 **6.2. EFFICACY OF RIPARIAN RESERVES AND OTHER MANAGEMENT OPTIONS**

2148 Riparian reserves, the strip of protected or forested land either side of streams or rivers, are the
2149 default conservation tool to protect aquatic biodiversity, water quality and ecosystem services in
2150 production landscapes (Naiman and & Décamps, 1997). Recent studies have shown that oil-palm
2151 plantation streams with a riparian reserve in Indonesia support 42% more fish species than streams
2152 with no reserve, through increased levels of littoral leaf cover, maintenance of coarse substrates and
2153 decreased sedimentation (Giam et al. 2015; Brejão et al. 2018). Results in this thesis further show
2154 that riparian reserves need to be of high ‘forest quality’ and adequate width (discussed below) to
2155 maintain freshwater fish communities (Chapter 4). I suggest, similarly to Giam et al. (2015), this is
2156 because of the need for maintenance of leaf litter inputs and substrate (Chapter 3). These results
2157 provide some of the first indications of how riparian reserves could be specifically applied within
2158 degraded natural habitats where logging has significant negative effects, as thus far have
2159 predominantly been considered and used only in agricultural landscapes.

2160 Riparian reserves are widely advocated to protect ecosystem services and ecological integrity in the
2161 face of catchment scale stressors (eg., Iwata et al. 2003a; Sabo et al. 2005; Gomi et al. 2006; Casatti
2162 et al. 2012; Gray et al. 2014; Giam et al. 2015; Luke et al. 2017a), but there is little empirical
2163 evidence that determines the ideal or specific riparian features and conditions (width, quality,
2164 length, and location in catchment), of these reserves. The width of riparian reserves is the most
2165 common, and often the only, specification in policy and legislation. My results indicate that not only
2166 the width of reserve but also the quality of riparian vegetation are both important factors in
2167 maintaining freshwater fish communities in Sabah (Chapter 4). I thus advocate reserves of high
2168 forest quality, and widths of more than 64 m (as a conservative figure to ensure all species are
2169 protected). This is significantly larger than the 30 m reserve width recommended by the Roundtable
2170 for Sustainable Palm Oil (RSPO) guidelines (RSPO 2013) and several other studies of aquatic diversity
2171 (Davies & Nelson 1994; Pusey & Arthington 2003; Gomi et al. 2006; Lorion & Kennedy 2009).
2172 However, my results do demonstrate that enforcing just the 30 m width currently applied in many
2173 plantations in Sabah will still benefit biodiversity and ecosystem services. In addition, restoring
2174 reserves in areas where they were not retained should be made a priority. The results also indicate
2175 that forest quality and structure of vegetation within reserves should be detailed in legislation, but
2176 this will need regulation and enforcement systems in place in order to be managed effectively. This
2177 can be achieved through limiting logging that occurs within riparian reserves (within logging
2178 concessions and oil-palm plantations) or initiating restoration programmes to plant trees to fill gaps
2179 in canopy cover within reserves. It is also important to note that although these recommendations
2180 of width and forest quality are for freshwater fish, they are also relevant to other aquatic and
2181 terrestrial taxa that rely upon and use riparian reserves. The RSPO best practice guidelines (2017),
2182 for example, illustrate that riparian widths of up to 60 m and 200 m are required for water quality
2183 and terrestrial mammals, respectively (Barclay et al. 2017).

2184 Despite the obvious benefits of riparian reserves to aquatic biodiversity and ecosystem services,
2185 there is considerable uncertainty in the tropics about whether a legislative focus on protecting
2186 riparian vegetation is sufficient to conserve stream environments and fauna (Leal et al. 2018).
2187 Previously, this focus of legislative efforts has been largely based on maintaining terrestrial forest
2188 extent and has paid little heed to the critical features of hydrological systems such as the size and
2189 distribution of river catchments (Castello & Macedo 2015). In addition, the impacts of riparian
2190 reserves are scale dependent, and influenced by other environmental stressors such as pollution,
2191 climate, and invasive species. My results clearly show , as in the majority of mixed effects models,
2192 that 'stream identity' explained a considerable amount of variation (Chapter 2 and 5). This highlights
2193 the need to better understand how each stream is influenced by the wider catchment and
2194 determine how manipulations of the wider catchment can protect freshwater ecosystems.
2195 Therefore, to safeguard species-rich freshwater diversity in streams across the tropics, conservation
2196 needs to move towards managing whole catchments as part of integrated river management.

2197 In addition, we strongly recommend that industry follows further legislation with regards to
2198 freshwater ecosystems, for example the oil-palm plantation best practice guidelines (Barclay et al.
2199 2017). As well as riparian reserves, it details other necessary conditions to limit pollution and
2200 sediment inputs to freshwater ecosystems. For example, through the restriction of converting forest
2201 in steep areas and how to design road networks to minimise erosion and maintain bank stability. The
2202 main focus of these efforts is currently on agricultural landscapes, however we show that logging
2203 can have as severe negative impacts as conversion to plantation, and advocate that similar
2204 guidelines be developed for forestry and logging concessions. This could be implemented through
2205 reduced impact logging practices that regulate the number and species of trees, and how the trees
2206 are extracted.

2207 As already suggested, we need to conserve primary forest areas and retain forested riparian
2208 reserves for freshwater ecosystems as well as additional management within industry. This study, as

2209 well as that by Giam et al. (2015), suggests that a land sharing, biodiversity-friendly approach to
2210 conservation following the definition of Phalan et al., (2011) is effective in the conservation of
2211 freshwater ecosystems in oil-palm plantations. Streams with higher quality, forested riparian
2212 reserves support more fish species, higher biomass and functional diversity than those that lack
2213 reserves. Despite this, there is increasing evidence for terrestrial species in the humid tropics, that a
2214 general strategy of land sparing will retain higher levels of biodiversity for a given crop yield in a
2215 defined area since many species are highly sensitive to any increase in yield (Phalan et al. 2011;
2216 Edwards et al. 2013). It is essential that landscape level conservation planning incorporates the
2217 requirements of all taxa and ecosystem services to protect the environment as these industries
2218 intensify and expand.

2219

2220 **6.3. RESILIENCE OF FRESHWATER FISH TO MULTIPLE STRESSORS**

2221 Converting land for agriculture is a key human activity that interacts with many other stressors (e.g.,
2222 climate change—flood, drought, and invasive species) to biodiversity. Tropical regions have the
2223 difficulty of trying to increase their food and crop production, whilst also trying to mitigate the
2224 effects of climate change (Defries & Rosenzweig 2010). Agricultural activities cause hydrological
2225 modifications through abstraction of water, construction of dams, and create opportunities for
2226 invasive species (Dudgeon et al. 2006). The impacts of land-use change are discussed above, but the
2227 interacting effects of land-use and climate change have received little research to date, and
2228 predominantly are in temperate regions. A recent meta-analysis of freshwater ecosystems to paired
2229 stressors revealed more antagonistic responses than synergistic or additive ones, possibly due to the
2230 environmental variability of streams that enable the potential for acclimatisation and co-adaptation
2231 to multiple stressors (Jackson et al. 2016). Disentangling the complicated mechanisms behind these
2232 relationships remains a challenge (Piggott et al. 2015; Côté et al. 2016).

2233 This thesis examined the interacting effects of land-use change and an El Niño induced drought on a
2234 common cyprinid (Chapter 5). Land-use has a larger impact on fish density, whereas only catchability
2235 of the species decreased during drought as fish were restricted to small, disconnected pools
2236 (Chapter 6). The results followed those of Jackson et al. (2016), showing a significant antagonistic
2237 interaction on biomass of captured fish, with the magnitude of the drought impact reduced
2238 according to land-use. Populations of *N. everetti*, were surprisingly resilient to drought and seem
2239 most affected instead by land-use.

2240 In addition to drought and land-use change impacts, two introduced species were captured in oil-
2241 palm streams without riparian reserves (Chapter 3). Mozambique tilapia (*Oreochromis*
2242 *mossambicus*) and common or striped snakehead (*Channa striata*) are both common food fish that
2243 are routinely introduced to tropical streams (Diana 2009; Gozlan et al. 2010). Despite the fact that
2244 fish may be being introduced for a food resource, we demonstrated that when using local fishing
2245 techniques to capture freshwater fish, there was no change across the land-use gradient in biomass
2246 available as a provisioning ecosystem service (Chapter 2). Although it is important to continue
2247 monitoring the impact of local fishing, and potential spread or interaction of introduced species in
2248 native habitats, currently fish communities in these streams are a resilient source of food or
2249 supplementary income for rural communities in Sabah.

2250

2251 **6.4. RECOMMENDATIONS FOR FUTURE MANAGEMENT**

2252 Land within fertile tropical regions such as Southeast Asia is subject to trade-offs between industry
2253 and conservation as growing populations increase demand for resource extraction and food
2254 production, whilst still conserving the natural environment. In Malaysia, forestry and agriculture
2255 (palm-oil) are the two largest industries, and create substantial revenue, jobs and social benefits, to
2256 what is still a developing country with relatively poor communities in rural areas (McMorrow & Talip

2257 2001; Wilcove et al. 2013). A clear evidence base is critical to the effective management of natural
2258 resources (Sutherland et al. 2004), and mitigation strategies should find a balance between
2259 development of agriculture and industry whilst providing protection for the environment. Based on
2260 the findings from this thesis, several recommendations can be made about how the trade-offs
2261 between sustainable management of forestry or oil-palm plantations can remain profitable, whilst
2262 potential harm to related freshwater ecosystems is reduced. Recommendations for management:

- 2263 - Malaysian timber is among the most profitable in the world, reflected by the highest rates of
2264 logging and timber prices (profits from a hectare of forest can be between US\$9,000–
2265 13,000; Fisher et al., 2011; Wilcove et al., 2013). However, logging (selective and salvage)
2266 has a clear, significant, negative impact on freshwater diversity. Streams in disturbed
2267 landscapes had lower canopy cover, littoral leaf litter cover, higher percentages of sand and
2268 sediment substrate, but lower bedrock and gravel, and higher temperatures, all of which
2269 have an impact on aquatic biodiversity. We need improvements to be made on this process
2270 to limit the impact on freshwater ecosystems. Mitigation needs to start with the initial
2271 impact of logging, through measures of reduced-impact logging, that pay particular
2272 attention to road planning and positioning to reduce sediment inputs. Logging practices
2273 should also include habitat restoration practices to facilitate recovery after logging, to
2274 minimise the continued impact of the disturbance through time.
- 2275 - Malaysia is now the second largest exporter of oil-palm, and the extent of oil-palm
2276 plantations has increased considerably as the income from an area of land can be nearly
2277 doubled by converting degraded forest to oil-palm plantation giving profits of US\$11,000
2278 ha⁻¹ over a 25-year plantation lifetime (FAO 2010; Fisher et al. 2011; Gunarso et al. 2013).
- 2279 - Oil-palm plantation streams are shown to be more severely affected in some studies than
2280 forested streams. Whilst the spatial scale over which land-use change affects freshwater
2281 ecosystems (riparian versus catchment) will remain to be debated, it has been shown that

2282 riparian reserves are effective in maintaining ‘forest-like conditions’. Riparian reserves
2283 should be maintained where possible and restored, in areas where they have been lost, to
2284 the appropriate standard (width and forest quality). Roads are a point of weakness, creating
2285 fragments in riparian reserves, and sources of sediment influx to streams, so should be
2286 carefully planned to minimise crossing points. In addition, fertiliser application and creation
2287 and planting of new plantations needs to be monitored, following the RSPO best practice
2288 guidelines recommended in all plantations.

2289 - Existing legislation to protect biodiversity and ecosystem services predominantly focuses on
2290 retention of riparian reserves. This is an important start, but there needs to be a shift in
2291 freshwater conservation efforts towards integrated river basin management, and
2292 management of river basins as a whole, in addition to the agricultural practices already in
2293 place.

2294 - Biotic indices should be developed for taxa that are sensitive and vulnerable to stream
2295 disturbance and land-use change. Abundance and richness of endemic ‘sucker’ fish (Family
2296 Gastromyzontidae), as well as tolerant taxa have the potential to be developed as an index
2297 in these streams, and benefit from being easily sampled and are identifiable in the field.
2298 Water quality assessments in Malaysia, are predominantly based on chemical tests (the
2299 Malaysian Water Quality Index (WQI)) and often do not consider biotic measures, which
2300 have the potential to inform about the systems water quality and health. Ghani et al. (2018)
2301 demonstrated the use of biotic indices (e.g., Biomonitoring Working Party (BMWWP-Thai or –
2302 Viet, Singapore Biotic Index (SingScore), and Average Score per Taxon (ASPT) were more
2303 sensitive to pollution events and should be implemented in Malaysia in addition to the WQI.

2304

2305

2306

2307 **6.5. LIMITATIONS & FUTURE RESEARCH**

2308 This thesis is limited in its application as I only focussed on freshwater fish and a single provisioning
2309 ecosystem service (resource availability). However, the benefit of conducting research at a large,
2310 integrated project site is that many other researchers are studying different taxa or ecosystem
2311 functions and processes within the same locations. For example, freshwater macroinvertebrates
2312 (e.g., effects on dragonflies; Luke et al. 2017b), frogs (Konopik et al. 2015), hydrology (including
2313 levels of suspended sediment, discharge, chemical levels, temperature and storm surges; Nainar et
2314 al. 2016, 2017; Luke et al., 2017a), leaf litter breakdown and algal growth have all been quantified at
2315 the same study site where I collected my data. This research needs to be collated and synthesised
2316 into a review or meta-analysis of the impacts of logging on freshwater ecosystems in Southeast Asia,
2317 as it is one of the first projects to contain a data set of this breadth.

2318 Understanding the impacts and resultant change to ecosystems as they undergo conversion to oil-
2319 palm is equally important. It is essential to continue monitoring these streams and populations as
2320 the logged forest streams are converted to oil-palm plantation at the SAFE project experiment area
2321 (site of study), enabling us to determine the impact of conversion to oil-palm on freshwater
2322 biodiversity and ecosystem services. The major benefit of this study over others, is the before-after-
2323 control-impact (BACI) design, which allows for understanding the temporal as well as spatial
2324 gradients. We have been able to monitor the impacts of a severe, El Nino induced drought and
2325 salvage-logging. However, we may not have seen the full effects of the disturbances so far, due to
2326 lag effects that may only become apparent over longer time frames, if monitoring continues.

2327 In addition, this continued monitoring should examine the extent to which within stream conditions
2328 change as an indirect interaction with broader-scale human pressures and land-use change, such as
2329 decreases in forest cover. It is highly probable that the human alterations at riparian and catchment
2330 scales play indirect roles in influencing fish assemblages by, for example, regulating channel
2331 morphology, bed substrate composition, wood and leaf litter inputs, shade and water quality

2332 (Kaufmann and Hughes 2006; Leal et al. 2016; Leitão et al. 2017). Metrics of forest cover that are
2333 currently addressed in existing legislation, are therefore more likely to be able to be used to
2334 implement changes to management. This continued research will be able to further inform
2335 management of logging concessions and oil-palm plantations across the tropics.

2336 **6.6. CONCLUSIONS**

2337 This thesis answers calls from other researchers for further knowledge on temporal and spatial
2338 impacts of land-use change, how land-use change interacts with climatic stressors (drought), and
2339 adds to existing knowledge about the efficacy of riparian reserves in Southeast Asia. The key
2340 findings reported in this thesis suggest that freshwater fish and streams within Borneo are
2341 surprisingly resilient to the effects of land-use change and climate change, although some
2342 stenotopic, specialist taxa are likely to be lost, under existing approaches to logging and oil-palm
2343 agriculture. Despite this, informed, evidence based management decisions have potential to
2344 mitigate some of these harmful effects, and thus strike a balance between human resource needs
2345 and conservation of natural habitats.

BIBLIOGRAPHY

- Achard, F., Eva, H. D., Stibig, H. J., Mayaux, P., Gallego, J., Richards, T., & Malingreau, J. P., 2014. Determination of deforestation rates of the world's humid tropical forests. *Science* (New York, N.Y.), 297(5583), pp.999–1002.
- Adams, A.J., Wolfe, R.K., Pine, W.E. & Thornton, B.L., 2006. Efficacy of PIT tags and an autonomous antenna system to study the juvenile life stage of an estuarine-dependent fish. *Estuaries and Coasts*, 29(2), pp.311–317.
- Allan, J. D., 2004. Landscapes and Riverscapes: The Influence of Land Use on Stream Ecosystems. *Annual Review of Ecology and Systematics*, 35, pp.257–284.
- Allan, D. J. & Castillo, M. M., 2007. *Stream Ecology - Structure and function of running waters*, Springer Science & Business Media.
- Allan, J. D. & Flecker, A. S., 1993. Biodiversity Conservation in Running Waters. *BioScience*, 43(1), pp.32–43.
- Arthington, A. H., Dulvy, N. K., Gladstone, W., & Winfield, I. J., 2016. Fish conservation in freshwater and marine realms: status, threats and management. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 26(5), pp.838–857.
- Arthur, R. I., Lorenzen, K., Homekingkeo, P., Sidavong, K., Sengvilaikham, B., & Garaway, C. J., 2010. Assessing impacts of introduced aquaculture species on native fish communities: Nile tilapia and major carps in SE Asian freshwaters. *Aquaculture*, 299(1-4), pp.81–88.
- Bagley, J.E., Desai, A.R., Harding, K.J., Snyder, P.K. & Foley, J.A., 2014. Drought and deforestation: Has land cover change influenced recent precipitation extremes in the Amazon? *Journal of Climate*, 27(1), pp.345–361.
- Baker, M. E. & King, R. S., 2010. A new method for detecting and interpreting biodiversity and ecological community thresholds. *Methods in Ecology and Evolution*, 1(1), pp.25–37.
- Balian, E.V., Lévéque, C., Segers, H. and Martens, K. eds., 2008. *Freshwater animal diversity assessment* (Vol. 198). Springer Science & Business Media.
- Banks-Leite, A. C., Ewers, R. M., & Metzger, J. P., 2012. Unraveling the drivers of community dissimilarity and species extinction in fragmented landscapes. *Ecology*, 93(12), pp.2560–2569.
- Barclay, H., Gray, C. L., Luke, S. H., Nainar, A., Snaddon, J. L., & Turner, E. C., 2017. RSPO Manual on Best Management Practices (BMPs) for the Management and Rehabilitation of Riparian Reserves. Available at: <http://www.rspo.org/key-documents/supplementary-materials>.
- Basiron, Y., 2007. Palm oil production through sustainable plantations. *European Journal of Lipid Science and Technology*, 109(4), pp.289–295.
- Bates, D., Maechler, M., Bolker, B. M., & Walker, S., 2014. Fitting linear mixed-effects models using lme4. Available at: <http://arxiv.org/abs/1406.5823>.
- Beamish, F., Beamish, R., & Lim, S., 2003. Fish assemblages and habitat in a Malaysian blackwater peat swamp. *Environmental Biology of Fishes*, 68(1), pp.1–13.
- Benstead, J., Douglas, M. & Pringle, C., 2003. Relationships of stream invertebrate communities to deforestation in eastern Madagascar. *Ecological Applications*, 13(5), pp.1473–1490.

Bibliography

- Berry, N.J., Phillips, O.L., Lewis, S.L., Hill, J.K., Edwards, D.P., Tawatao, N.B., Ahmad, N., Magintan, D., Khen, C.V., Maryati, M. & Ong, R.C., 2010. The high value of logged tropical forests: lessons from northern Borneo. *Biodiversity and Conservation*, 19(4), pp.985–997.
- Bilio, M., 2007. Controlled reproduction and domestication in aquaculture. *Aquaculture Europe*, 32(1), pp.5-14.
- Bojsen, B. H., & Barriga, R., 2002. Effects of deforestation on fish community structure in Ecuadorian Amazon streams. *Freshwater Biology*, 47(11), pp.2246–2260.
- Boyce, M.S., Vernier, P.R., Nielsen, S.E. & Schmiegelow, F.K., 2002. Evaluating resource selection functions. *Ecological modelling*, 157(2-3), pp.281-300.
- Bradshaw, C. J., Sodhi, N. S. & Brook, B. W., 2009. Tropical turmoil: a biodiversity tragedy in progress. *Frontiers in Ecology and the Environment*, 7(2), pp.79–87.
- Brando, P.M., Balch, J.K., Nepstad, D.C., Morton, D.C., Putz, F.E., Coe, M.T., Silvério, D., Macedo, M.N., Davidson, E.A., Nóbrega, C.C. & Alencar, A., 2014. Abrupt increases in Amazonian tree mortality due to drought-fire interactions. *Proceedings of the National Academy of Sciences*, 111(17), pp.6347–6352.
- Brashares, S. J., Arcese, P., Sam, M. K., Coppolillo, P. B., Sinclair, A. R. E., & Balmford, A., 2004. Bushmeat hunting, Wildlife declines, and fish supply in West Africa. *Science*, 306(5699), pp.1180–1183.
- Brejão, G.L., Hoeinghaus, D.J., Pérez-Mayorga, M.A., Ferraz, S.F. & Casatti, L., 2017. Threshold responses of Amazonian stream fishes to timing and extent of deforestation. *Conservation Biology*. <https://doi.org/10.1111/cobi.13061>
- Broadmeadow, S. & Nisbet, T.R., 2004. The effects of riparian forest management on the freshwater environment: a literature review of best management practice. *Hydrology and Earth System Sciences Discussions, Copernicus Publications*, 8(3), pp.286–305.
- Brook, B. W., & Sodhi, N. S., 2003. Catastrophic extinctions follow deforestation in Singapore deforestation. *Nature*, 424(6947), pp.420–421.
- Brooks, S.M. & Spencer, T., 1997. Changing Soil Hydrology Due to Rain Forest Logging : an Example from Sabah Malaysia. *Journal of Environmental Management*, 49(3), pp.297–310.
- Brooks, T.M., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A., Rylands, A.B., Konstant, W.R., Flick, P., Pilgrim, J., Oldfield, S., Magin, G. & Hilton-Taylor, C., 2002. Habitat loss and extinction in the hotspots of biodiversity. *Conservation biology*, 16(4), pp.909-923.
- Bruhl, C.A. & Eltz, T., 2010. Fuelling the biodiversity crisis: species loss of ground-dwelling forest ants in oil palm plantations in Sabah, Malaysia (Borneo). *Biodiversitas*, 19(2), pp.519–529.
- Bruijnzeel, L.A., 2004. Hydrological functions of tropical forests: not seeing the soil for the trees? *Agriculture Ecosystems & Environment*, 104(1), pp.185–228.
- Burcher, C.L., McTammany, M.E., Benfield, E.F. & Helfman, G.S., 2008. Fish assemblage responses to forest cover. *Environmental Management*, 41(3), pp.336-346.
- Campos-silva, J.V. & Peres, C.A., 2016. Community-based management induces rapid recovery of a high-value tropical freshwater fishery. *Scientific reports*, 6, pp.1–13.
- Canonico, G. C., Arthington, A., McCrary, J. K., & Thieme, M. L., 2005. The effects of introduced tilapias on native biodiversity. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 15(5), pp.463–483.

Bibliography

- Casatti, L., Teresa, F.B., Gonçalves-Souza, T., Bessa, E., Manzotti, A.R., Gonçalves, C.D.S., Zeni, J.D.O., 2012. From forests to cattail: How does the riparian zone influence stream fish? *Neotropical Ichthyology*, 10(1), pp.205–214.
- Cassell, C., 2017. A preliminary study of the allochthonous inputs into tropical streams across a land use gradient in Sabah, Malaysia. *Zenodo*, 10.5281/zenodo.1198557.
- Castello, L. & Macedo, M.N., 2015. Large-scale degradation of Amazonian freshwater ecosystems. *Global Change Biology*, 22(3), pp.990–1007.
- Chan, E.K.W., Zhang, Y. & Dudgeon, D., 2008. Arthropod “rain” into tropical streams: The importance of intact riparian forest and influences on fish diets. *Marine and Freshwater Research*, 59(8), pp.653–660.
- Chan, K.M.A., Satter, T. & Goldstein, J., 2012. Rethinking ecosystem services to better address and navigate cultural values. *Ecological Economics*, 74, pp.8–18.
- Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K. & Ellison, A.M., 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs*, 84(1), pp.45-67.
- Chazdon, R.L., Peres, C.A., Dent, D., Sheil, D., Lugo, A.E., Lamb, D., Stork, N.E. & Miller, S.E., 2009. The Potential for Species Conservation in Tropical Secondary Forests. *Conservation Biology*, 23(6), pp.1406–1417.
- Cheng, L., Lek, S., Lek-Ang, S. & Li, Z., 2012. Predicting fish assemblages and diversity in shallow lakes in the Yangtze River basin. *Limnologica-Ecology and Management of Inland Waters*, 42(2), pp.127-136.
- Chong, V.C., Lee, P.K.Y. & Lau, C.M., 2010. Diversity, extinction risk and conservation of Malaysian fishes. *Journal of fish biology*, 76(9), pp.2009-2066.
- Chovanec, A., Hofer, R. & Schiemer, F., 2003. Fish as bioindicators. In *Trace metals and other contaminants in the environment* (Vol. 6, pp. 639-676). Elsevier.
- Clapcott, J.E., Collier, K.J., Death, R.G., Goodwin, E.O., Harding, J.S., Kelly, D., Leathwick, J.R. & Young, R.G., 2012. Quantifying relationships between land-use gradients and structural and functional indicators of stream ecological integrity. *Freshwater Biology*, 57(1), pp.74-90.
- Closs, G.P., Angermeier, P.L., Darwall, W.R. & Balcombe, S.R., 2015. Why are freshwater fish so threatened. *Conservation of Freshwater Fishes*; Closs, GP, Krkosek, M., Olden, J., Eds, pp.37-75.
- Collen, B., McRae, L., Kothari, G., Mellor, R., Daniel, O., Greenwood, A., Amin, R., Holbrook, S. & Baillie, J., 2008. Living Planet Index. *2010 and beyond: rising to the biodiversity challenge*. WWF, Gland, Suisse.
- Cooch, E. & White, G., 2006. Program MARK: a gentle introduction, Available at:
<http://scholar.google.com/scholar?hl=en&btnG=Search&q=intitle:Program+MARK:+A+gentle+introduction#0>
- Côté, I.M., Darling, E.S. & Brown, C.J., 2016. Interactions among ecosystem stressors and their importance in conservation. *Proceedings of the Royal Society B: Biological Sciences*, 283(1824), p.20152592.
- Covich, A.P., Crowl, T. & Heartsill-Scalley, T., 2006. Effects of drought and hurricane disturbances on headwater distributions of palaemonid river shrimp (*Macrobrachium* spp.) in the Luquillo Mountains, Puerto Rico. *Journal of the North American Benthological Society*, 25(1), pp.99–107.
- Covich, A.P., Crowl, T.A. & Scatena, F.N., 2003. Effects of extreme low flows on freshwater shrimps in a perennial tropical stream. *Freshwater Biology*, 48(7), pp.1199–1206.

Bibliography

- Covich, A.P., Crowl, T.A. & Scatena, F.N., 2000. Linking habitat stability to floods and droughts: effects on shrimp in montane streams, Puerto Rico. *SIL Proceedings, 1922–2010*, 27(4), pp.2430–2434.
- Covich, A.P., Palmer, M.A. & Crowl, T.A., 1999. The role of benthic invertebrate species in freshwater ecosystems: zoobenthic species influence energy flows and nutrient cycling. *BioScience*, 49(2), pp.119-127.
- Cramb, R. & Curry, G.N., 2012. Oil palm and rural livelihoods in the Asia–Pacific region: An overview. *Asia Pacific Viewpoint*, 53(3), pp.223-239.
- Cruz, B.B., Miranda, L.E. & Cetra, M., 2013. Links between riparian landcover, instream environment and fish assemblages in headwater streams of south-eastern Brazil. *Ecology of Freshwater Fish*, 22(4), pp.607-616.
- Cunjak, R., Roussel, J.-M. & Gray, M., 2005. Using stable isotope analysis with telemetry or mark-recapture data to identify fish movement and foraging. *Oecologia*, 144(4), pp.636–46.
- Cushman, S.A., Macdonald, E.A., Landguth, E.L., Malhi, Y. & Macdonald, D.W., 2017. Multiple-scale prediction of forest loss risk across Borneo. *Landscape Ecology*, 32(8), pp.1581-1598.
- Darwall, W.R.T. & Freyhof, J., 2016. *Lost fishes, who is counting? The extent of the threat to freshwater fish biodiversity*. Conservati. G. P. Closs, M. Krkosek, & J. D. Olden, eds., Cambridge: Cambridge University Press.
- Davies, P.E. & Nelson, M., 1994. Relationships between Riparian Buffer Widths and the Effects of Logging on Stream Habitat , Invertebrate Community Composition and Fish Abundance. *Australian Journal of Marine & Freshwater Research*, 45, pp.1289–305.
- Dayang Norwana, A.A.B., Kanjappan, R., Chin, M., Schoneveld, G.C., Potter, L. & Andriani, R., 2011. The local impacts of oil palm expansion in Malaysia; An assessment based on a case study in Sabah State. *Center for International Forestry Research (CIFOR) working paper*, 78, pp.1-17.
- Death, R.G. & Collier, K.J., 2010. Measuring stream macroinvertebrate responses to gradients of vegetation cover: when is enough enough? *Freshwater Biology*, 55(7), pp.1447-1464.
- Defries, R. & Rosenzweig, C., 2010. Toward a whole-landscape approach for sustainable land use in the tropics. *Proceedings of the National Academy of Sciences*, 107(46), pp.19627–19632.
- Detenbeck, N.E., DeVore, P.W., Niemi, G.J. & Lima, A., 1992. Recovery of temperate-stream fish communities from disturbance: a review of case studies and synthesis of theory. *Environmental Management*, 16(1), p.33.
- Dewi, S., van Noordwijk, M., Ekadinata, A. & Pfund, J.L., 2013. Protected areas within multifunctional landscapes: Squeezing out intermediate land use intensities in the tropics? *Land Use Policy*, 30(1), pp.38-56.
- Diana, J.S., 2009. Aquaculture Production and Biodiversity Conservation. *Bioscience* 59(1), 27–38.
- Diana, M., Allan, J.D. & Infante, D., 2006. The influence of physical habitat and land use on stream fish assemblages in southeastern Michigan. *American Fisheries Society Symposium*, 48(8), pp.359–374.
- Douglas, I., Greer, T., Bidin, K. & Spilsbury, M., 1993. Impacts of rainforest logging on river systems and communities in Malaysia and Kalimantan. *Global Ecology and Biogeography Letters*, 3(4), pp.245-252.

Bibliography

- Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.I., Knowler, D.J., Lévéque, C., Naiman, R.J., Prieur-Richard, A.H., Soto, D., Stiassny, M.L. & Sullivan, C.A., 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological reviews*, 81(2), pp.163-182.
- Dudgeon, D., 2000a. Large-Scale Hydrological Changes in Tropical Asia: Prospects for Riverine Biodiversity. *American Institute of Biological Sciences*, 50(9), pp.793–806.
- Dudgeon, D., (2000b). The ecology of tropical Asian rivers and streams in relation to biodiversity conservation. *Annual Review of Ecology and Systematics*, 31(1), 239–63.
- Duncan, J.R. & Lockwood, J.L., 2001. Extinction in a field of bullets: a search for causes in the decline of the world's freshwater fishes. *Biological conservation*, 102(1), pp.97-105.
- ECD, 2002. *Environmental Impact Assessment (EIA) Guidelines Oil Palm Plantation Development*. Available at: http://www.sabah.gov.my/jpas/assessment/eia/handbook/handbook_oil_palm.pdf [Accessed November 5, 2014].
- Edwards, F.A., Edwards, D.P., Larsen, T.H., Hsu, W.W., Benedick, S., Chung, A., Vun Khen, C., Wilcove, D.S. & Hamer, K.C., 2014. Does logging and forest conversion to oil palm agriculture alter functional diversity in a biodiversity hotspot? *Animal conservation*, 17(2), pp.163-173.
- Edwards, D.P., Tobias, J.A., Sheil, D., Meijaard, E. & Laurance, W.F., 2014. Maintaining ecosystem function and services in logged tropical forests. *Trends in ecology & evolution*, 29(9), pp.511-520.
- Edwards, F.A., Edwards, D.P., Hamer, K.C. & Davies, R.G., 2013. Impacts of logging and conversion of rainforest to oil palm on the functional diversity of birds in Sundaland. *Ibis*, 155(2), pp.313-326.
- Edwards, D.P., Larsen, T.H., Docherty, T.D., Ansell, F.A., Hsu, W.W., Derhé, M.A., Hamer, K.C. & Wilcove, D.S., 2011. Degraded lands worth protecting : the biological importance of Southeast Asia ' s repeatedly logged forests. *Proceedings of the Royal Society B: Biological Sciences*, 278(1702), pp.82–90.
- Efford, M., 2014. Seclinear - Spatially Explicit Capture – Recapture for Linear Habitats. pp.1–21. Available at: https://scholar.google.co.uk/scholar?hl=en&as_sdt=0%2C5&q=Spatially+Explicit+Capture+%E2%80%93+Recapture+for+Linear+Habitats&btnG=
- Eisner, R., Seabrook, L.M. & McAlpine, C.A., 2016. Are changes in global oil production influencing the rate of deforestation and biodiversity loss? *Biological Conservation*, 196, pp.147–155.
- England, L.E. & Rosemond, A.D., 2004. Small reductions in forest cover weaken terrestrial- aquatic linkages in headwater streams. *Freshwater Biology*, 49(6), pp.721–734.
- Ewers, R.M., Didham, R.K., Fahrig, L., Ferraz, G., Hector, A., Holt, R.D., Kapos, V., Reynolds, G., Sinun, W., Snaddon, J.L. & Turner, E.C., (2011). A large-scale forest fragmentation experiment: the Stability of Altered Forest Ecosystems Project. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1582), 3292–302.
- Fahrig, L., 2003. Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 34(1), pp.487–515.
- FAO, Food and Agricultural Organisation., 2010. Global Forest Resources Assessment 2010. *FAO Forestry paper 163*, pp.1-333.

Bibliography

- Fayle, T.M., Turner, E.C., Snaddon, J.L., Chey, V.K., Chung, A.Y., Eggleton, P. & Foster, W.A., 2010. Oil palm expansion into rain forest greatly reduces ant biodiversity in canopy, epiphytes and leaf-litter. *Basic and Applied Ecology*, 11(4), pp.337-345.
- Fernandes, I., Penha, J. & Zuanon, J., 2015. Size-dependent response of tropical wetland fish communities to changes in vegetation cover and habitat connectivity. *Landscape Ecology*, 30(8), pp.1421–1434.
- Ferreira, M.C., Begot, T.O., da Silveira Prudente, B., Juen, L. & de Assis Montag, L.F., 2018. Effects of oil palm plantations on habitat structure and fish assemblages in Amazon streams. *Environmental Biology of Fishes*, 101(4), pp.547-562.
- Fisher, B., Edwards, D. P., Giam, X. & Wilcove, D. S., 2011. The high costs of conserving Southeast Asia's lowland rainforests. *Frontiers in Ecology and the Environment*, 9(6), 329-334.
- Fitzherbert, E.B., Struebig, M.J., Morel, A., Danielsen, F., Brühl, C.A., Donald, P.F. & Phalan, B., 2008. How will oil palm expansion affect biodiversity? *Trends in ecology & evolution*, 23(10), pp.538–45.
- Fitzmaurice, A., 2014. The Direct and Indirect Impacts of Logging on Mammals in Sabah, Borneo. *Masters dissertation*. Imperial College London, UK.
- Flecker, A.S., 1992. Fish Trophic Guilds and the Structure of a Tropical Stream: Weak Direct vs. Strong Indirect Effects. *Ecology*, 73(3), p.927.
- Foley, J.A., Ramankutty, N., Brauman, K.A., Cassidy, E.S., Gerber, J.S., Johnston, M., Mueller, N.D., O'Connell, C., Ray, D.K., West, P.C. & Balzer, C., 2011. Solutions for a cultivated planet. *Nature*, 478(7369), p.337.
- Fritz, K.M. & Dodds, W.K., 2004. Resistance and resilience of macroinvertebrate assemblages to drying and flood in a tallgrass prairie stream system. *Environmental Protection*, 527(1), pp.99–112.
- Fugère, V., Nyboer, E. A., Bleecker, J. C., & Chapman, L. J., 2016. Impacts of forest loss on inland waters: Identifying critical research zones based on deforestation rates, aquatic ecosystem services, and past research effort. *Biological Conservation*, 201, pp.277–283.
- Gardner, T. A., Barlow, J., Chazdon, R., Ewers, R. M., Harvey, C. A., Peres, C. A., & Sodhi, N. S., 2009. Prospects for tropical forest biodiversity in a human-modified world. *Ecology letters*, 12(6), pp.561-582.
- Gaveau, D.L., Sloan, S., Molidena, E., Yaen, H., Sheil, D., Abram, N.K., Ancrenaz, M., Nasi, R., Quinones, M., Wieland, N. & Meijaard, E., 2014. Four decades of forest persistence, clearance and logging on Borneo. *PloS one*, 9(7), pp.1-11.
- Ghani, W. M. H. W. A., Kutty, A. A., Mahazar, M. A., Al-Shami, S. A., & Ab Hamid, S., 2018. Performance of biotic indices in comparison to chemical-based Water Quality Index (WQI) in evaluating the water quality of urban river. *Environmental monitoring and assessment*, 190(5), p.297.
- Giam, X., Ng, T.H., Lok, A.F. & Ng, H.H., 2011. Local geographic range predicts freshwater fish extinctions in Singapore. *Journal of Applied Ecology*, 48(2), pp.356-363.
- Giam, X., Hadiaty, R. K., Tan, H. H., Parenti, L. R., Wowor, D., Sauri, S., Chong, K. Y., Yeo, D.C., & Wilcove, D. S. (2015). Mitigating the impact of oil-palm monoculture on freshwater fishes in Southeast Asia. *Conservation Biology*, 29(5), pp.1357–1367.
- Gibbs, H.K., Ruesch, A.S., Achard, F., Clayton, M.K., Holmgren, P., Ramankutty, N. & Foley, J.A., 2010. Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. *Proceedings of the National Academy of Sciences*, 107(38), pp.16732-16737.

Bibliography

- Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A., Bradshaw, C.J., Laurance, W.F., Lovejoy, T.E. & Sodhi, N.S., 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*, 478(7369), p.378.
- Gomi, T., Sidle, R. C., Noguchi, S., Negishi, J. N., Nik, A. R. & Sasaki, S., 2006. Sediment and wood accumulations in humid tropical headwater streams: Effects of logging and riparian buffers. *Forest Ecology and Management*, 224(1-2), pp.166–175.
- Government of Malaysia, 1965. National Land Code (65 of 1965), Available at:
<http://www.kptg.gov.my/sites/default/files/article/NLC1956DIGITAL-VER1.pdf> [Accessed January 28, 2015].
- Gozlan, R.E., Britton, J.R., Cowx, I., Copp, G.H., 2010. Current knowledge on non-native freshwater fish introductions. *Journal of fish biology*, 76(4), pp.751-786.
- Gray, C. L., Slade, E. M., Mann, D. J. & Lewis, O. T., 2014. Do riparian reserves support dung beetle biodiversity and ecosystem services in oil-palm-dominated tropical landscapes? *Ecology and evolution*, 4(7), pp.1049–60.
- Gregory, S.V., Swanson, F.J., McKee, W.A. & Cummins, K.W., 1991. An Ecosystem Perspective of Riparian Zones. *BioScience*, 41(8), pp.540–551.
- Gunarso, P., Hartoyo, M.E., Agus, F. & Killeen, T.J., 2013. Oil palm and land use change in Indonesia, Malaysia and Papua New Guinea. *Reports from the Technical Panels of the 2nd greenhouse gas working Group of the Roundtable on Sustainable Palm Oil (RSPO)*, pp.29-64.
- Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D. & Cook, W.M., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, 1(2), p.e1500052.
- Hagen, E. M., McTammany, M. E., Webster, J. R., & Benfield, E. F., 2010. Shifts in allochthonous input and autochthonous production in streams along an agricultural land-use gradient. *Hydrobiologia*, 655(1), pp.61–77.
- Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R. & Kommareddy, A., 2013. High-resolution global maps of 21st-century forest cover change. *Science*, 342(6160), pp.850-853.
- Hansen, M. C., Stehman, S. V. & Potapov, P. V., 2010a. Quantification of global gross forest cover loss. *Proceedings of the National Academy of Sciences of the United States of America*, 107(19), pp.8650–8655.
- Hansen, B., Reich, P., Lake, P.S. & Cavagnaro, T., 2010b. Minimum width requirements for riparian zones to protect flowing waters and to conserve biodiversity: a review and recommendations. *Report to the Office of Water, Victorian Department of Sustainability and Environment. Monash University.*, p.150pp.
- Harding, J.S., Benfield, E.F., Bolstad, P.V., Helfman, G.S. & Jones, E.B.D., 1998. Stream biodiversity: the ghost of land use past. *Proceedings of the national academy of sciences*, 95(25), pp.14843-14847.
- Hardwick, S.R., Toumi, R., Pfeifer, M., Turner, E.C., Nilus, R. & Ewers, R.M., 2015. The relationship between leaf area index and microclimate in tropical forest and oil palm plantation: Forest disturbance drives changes in microclimate. *Agricultural and Forest Meteorology*, 201, pp.187–195.

Bibliography

- Harris, N.L., Brown, S., Hagen, S.C., Saatchi, S.S., Petrova, S., Salas, W., Hansen, M.C., Potapov, P.V. & Lotsch, A., 2012. Baseline Map of Carbon Emissions from Deforestation in Tropical Regions. *Science*, 336(6088), pp.1573–1576.
- Harris, J.H., 1995. The use of fish in ecological assessments. *Austral Ecology*, 20(1), pp.65–80.
- Heartsill-Scalley, T. & Aide, T. M., 2003. Riparian vegetation and stream condition in a tropical agriculture–secondary forest mosaic. *Ecological Applications*, 13(1), pp.225–234.
- Hermoso, V., Abell, R., Linke, S., & Boon, P., 2016. The role of protected areas for freshwater biodiversity conservation: challenges and opportunities in a rapidly changing world. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 26(S1), pp.3–11.
- Hoeinghaus, D.J., Winemiller, K.O. & Birnbaum, J.S., 2007. Local and regional determinants of stream fish assemblage structure : inferences based on taxonomic vs . functional groups. *Journal of Biogeography*, 34(2), pp.324–338.
- Holmlund, C.M. & Hammer, M., 1999. Ecosystem services generated by sh populations. *Ecological Economics*, 29(2), pp.253–268.
- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S. & Schmid, B., 2005. Effects of Biodiversity on Ecosystem Functioning : A Consensus of Current Knowledge. *Ecological Monographs*, 75(1), pp.3–35.
- Hsieh, T. C., Ma, K. H., & Chao, A., 2014. iNEXT: iNterpolation and EXTrapolation for species diversity. R package version 2.0. URL: <http://chao.stat.nthu.edu.tw/blog/software-download>.
- Huntington, T.G., 2006. Evidence for intensification of the global water cycle: Review and synthesis. *Journal of Hydrology*, 319(1–4), pp.83–95.
- Ibarra, A.A., Gevrey, M., Park, Y.S., Lim, P. & Lek, S., 2003. Modelling the factors that influence fish guilds composition using a back-propagation network: assessment of metrics for indices of biotic integrity. *Ecological Modelling*, 160(3), pp.281–290.
- Inger, R. F. & Chin, P. K., 2002. *Freshwater fishes of northern Borneo*. Fieldiana: Zoology, 45, 1–268. Second reprint (2002) of Inger & Chin (1962), with a revised supplementary chapter, Natural History Publications (Borneo), Kota Kinabalu.
- Iñiguez-Armijos, C., Leiva, A., Frede, H. G., Hampel, H., & Breuer, L., 2014. Deforestation and benthic indicators: How much vegetation cover is needed to sustain healthy Andean streams? *PLoS ONE*, 9(8), pp.1–10.
- Inogwabini, B. I., 2014. Bushmeat, over-fishing and covariates explaining fish abundance declines in the Central Congo Basin. *Environmental Biology of Fishes*, 97(7), pp.787–796.
- Inoue, M. & Nakano, S., 1998. Effects of woody debris on the habitat of juvenile masu salmon (*Oncorhynchus manou*) in nothern Japanese streams. *Freshwater Biology*, 40(1), pp.1–16.
- Inoue, M., & Nunokawa, M., 2005. Spatial variation in density of stream benthic fishes in northern Hokkaido, Japan: does riparian vegetation affect fish density via food availability? *Limnology*, 6(1), pp.7–14.
- IUCN, 2009. The IUCN Red List of Threatened Species. *International Union for the Conservation of Nature*. Available at: <http://www.iucnredlist.org/> [Accessed February 26, 2015].
- Iwata, T., Nakano, S., & Inoue, M., 2003a. Impacts of past riparian deforestation on stream communities in a tropical rain forest in Borneo. *Ecological Applications*, 13(2), pp.461–473.

Bibliography

- Iwata, T., Inoue, M., Nakano, S., Miyasaka, H., Doi, A. & Covich, A.P., 2003b. Shrimp abundance and habitat relationships in tropical rain-forest streams, Sarawak, Borneo. *Journal of Tropical Ecology*, 19(4), pp.387–395.
- Jackson, D., Peres-Neto, P.R. & Olden, J.D., 2001. What controls who is where in freshwater fish communities: the roles of biotic, abiotic, and spatial factors. *Canadian Journal of Fisheries and Aquatic Sciences*, 58(1), pp.157–170.
- Jackson, M. C., Loewen, C. J. G., Vinebrooke, R. D. & Chimimba. C. T., 2016. Net effects of multiple stressors in freshwater ecosystems: a meta-analysis. *Global Change Biology* 22(1), pp.180–189.
- Jacoby, D. & Gollock, M., 2014. *Anguilla marmorata*. The IUCN Red List of Threatened Species 2014: e.T166189A45832585. <http://dx.doi.org/10.2305>
- Jarvis, A., Reuter, H. I., Nelson, A., & Guevara, E., 2008. Hole-filled SRTM for the globe Version 4, available from the CGIAR-CSI SRTM 90m Database (<http://srtm.csi.cgiar.org>).
- Jiménez-Cisneros, B.E., Oki, T., Arnell, N.W., Benito, G., Cogley, J.G., Döll, P., Jiang, T. & Mwakalila, S.S., 2014. Freshwater resources in climate change 2014: Impacts, adaptation, and vulnerability. Part a: global and sectoral aspects. *Contribution of working group II to the fifth assessment report of the intergovernmental panel on climate change*, eds. Field, CB, VR Barros, DJ Dokken, KJ Mach, MD Mastrandrea, TE Bilir, M. Chatterjee, KL Ebi, YO Estrada, RC Genova, B. Girma, ES Kissel, AN Levy, S. MacCracken, PR Mastrandrea, and LL White, p.1132.
- Jones, E. B. D., Helfman, G. S., Harper, J. O., Bolstad, P. V., 1999. Effects of Riparian Forest Removal on Fish Assemblages in Southern Appalachian Streams. *Conservation Biology*, 13(6), pp.1454–1465.
- Jones, R. I., Grey, J., Sleep, D., & Quarmby, C., 1998. An assessment, using stable isotopes, of the importance of allochthonous organic carbon sources to the pelagic food web in Loch Ness. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 265(1391), pp.105–111.
- Juen, L., Cunha, E.J., Carvalho, F.G., Ferreira, M.C., Begot, T.O., Andrade, A.L., Shimano, Y., Leao, H., Pompeu, P.S., Montag, L.F.A., 2016. Effects of oil palm plantations on the habitat structure and biota of streams in Eastern amazon. *River Research and Applications*, 32(10), pp.2081–2094.
- Kaufmann, P.R. & Hughes, R.M., 2006. Geomorphic and Anthropogenic Influences on Fish and Amphibians in Pacific Northwest Coastal Streams. In *In R. M. Hughes, L. Wang, & P. W. Seelbach (Eds.), Landscape influences on stream habitats and biological assemblages* (pp. 429–455). Bethesda, MD: American Fisheries Society. pp. 429–455.
- Kendall, M. G., 1938. A New Measure of Rank Correlation. *Biometrika*, 30(1/2), pp.81.
- Kennard, M. J., Pusey, B. J., Harch, B. D., Dore, E. & Arthington, A. H., 2006. Estimating local stream fish assemblage attributes: sampling effort and efficiency at two spatial scales. *Marine and Freshwater Research*, 57(6), pp.635-653.
- Kleiber, C., Zeileis, A. & Zeileis, M.A., 2017. Package ‘AER’. R package version 1.2, p.4.
- Koh, L. P. & Wilcove, D. S., 2007. Cashing in palm oil for conservation. *Nature*, 448(7157), pp.993–994.
- Kominoski, J.S., Marczak, L.B., Richardson, J.S., Kominoski, S., Marczak, B., Richardson, S., 2011. Riparian forest composition affects stream litter decomposition despite similar microbial and invertebrate communities. *Ecology*, 92(1), pp.151-159.
- Kominoski, J.S., Pringle, C.M., 2009. Resource-consumer diversity: Testing the effects of leaf litter species diversity on stream macroinvertebrate communities. *Freshwater Biology*, 54(7), pp.1461-1473.

Bibliography

- Konopik, O., Steffan-Dewenter, I. & Gafe, T.U., 2015. Effects of Logging and Oil Palm Expansion on Stream Frog Communities on Borneo, Southeast Asia. *Biotropica*, 47(5), pp.636–643.
- Kottelat, M., 2012. *Tor tambda*. The IUCN Red List of Threatened Species 2012: e.T188012A1845199. <http://dx.doi.org/10.2305/IUCN.UK.2012-1.RLTS.T188012A1845199.en>.
- Kottelat, M., 2013. The fishes of the inland waters of Southeast Asia: A catalogue and core bibliography of the fishes known to occur in freshwaters, mangroves and estuaries, *Raffles Bulletin of Zoology, supplement* 27, 1-663.
- Kottelat, M. & Tan, H.H., 2008. Kottelatlimia hipporhynchos, a new species of loach from southern Borneo (Teleostei: Cobitidae). *Zootaxa*, 1967, pp.63-72.
- Kottelat, M. & Tan, H.H., 2011. Crossocheilus elegans, a new species of fish from northern Borneo (Teleostei: Cyprinidae). *The Raffles Bulletin of Zoology*, 59(2), pp.195-99.
- Kottelat, M., & Whitten, T., 1996. *Freshwater Biodiversity in Asia: With Special Reference to Fish* (Volume 343). World Bank Publications.
- Kottelat, M., Whitten, A., Kartikasari, S., & Wirjoatmodjo, S., 1993. *Freshwater fishes of Western Indonesia and Sulawesi*. Periplus Editions, Hong Kong.
- Kumagai, T.O., Saitoh, T.M., Sato, Y., Takahashi, H., Manfroi, O.J., Morooka, T., Kuraji, K., Suzuki, M., Yasunari, T. & Komatsu, H., 2005. Annual water balance and seasonality of evapotranspiration in a Bornean tropical rainforest. *Agricultural and Forest Meteorology*, 128(1-2), pp.81-92.
- Kwik, J. T. B., & Yeo, D. C. J., 2015. Differences in fish assemblages in protected and non-protected freshwater streams in a tropical urbanized country. *Hydrobiologia*, 762(1), pp.143–156.
- Lajuin, J., 2013. Enforce law on oil-palm plantation encroachment – Masidi. *Borneo Post Online*. Available at: <http://www.theborneopost.com/2013/11/12/enforce-law-on-oil-palm-plantation-encroachment-masidi/> [Accessed February 3, 2015].
- Lake, P.S., 2003. Ecological effects of perturbation by drought in flowing waters. *Freshwater Biology*, 48(7), pp.1161–1172.
- Laliberté, E., Legendre, P., Shipley, B. & Laliberté, M.E., 2014. Package ‘FD’. Measuring functional diversity from multiple traits, and other tools for functional ecology.
- Laliberté, E., & Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91(1), pp.299–305.
- Laurance, W., Sayer, J., & Cassman, K., 2014. Agricultural expansion and its impacts on tropical nature. *Trends in Ecology & Evolution*, 29(2), pp.107–116.
- Laurance, W.F., Useche, D.C., Rendeiro, J., Kalka, M., Bradshaw, C.J., Sloan, S.P., Laurance, S.G., Campbell, M., Abernethy, K., Alvarez, P. & Arroyo-Rodriguez, V., 2012. Averting biodiversity collapse in tropical forest protected areas. *Nature*, 489(7415), p.290.
- Lawton, J.H., & Brown, V.K., 1994. Redundancy in ecosystems. In *Biodiversity and ecosystem function* (pp. 255-270). Springer, Berlin, Heidelberg.
- Leal, C.G., Barlow, J., Gardner, T.A., Hughes, R.M., Leitão, R.P., Mac Nally, R., Kaufmann, P.R., Ferraz, S.F., Zuanon, J., de Paula, F.R. & Ferreira, J., 2018. Is environmental legislation conserving tropical stream faunas? A large-scale assessment of local, riparian and catchment-scale influences on Amazonian fish. *Journal of Applied Ecology*, 55(3), pp.1312-1326.

Bibliography

- Leal, C.G., Pompeu, P.S., Gardner, T.A., Leitão, R.P., Hughes, R.M., Kaufmann, P.R., Zuanon, J., de Paula, F.R., Ferraz, S.F., Thomson, J.R. & Mac Nally, R., 2016. Multi-scale assessment of human-induced changes to Amazonian instream habitats. *Landscape Ecology*, 31(8), pp.1725–1745.
- Ledger, M.E., Brown, L.E., Edwards, F.K., Milner, A.M. & Woodward, G., 2013. Drought alters the structure and functioning of complex food webs. *Nature Climate Change*, 3(3), pp.223–227.
- Lee, P., Smyth, C. & Boutin, S., 2004. Quantitative review of riparian buffer width guidelines from Canada and the United States. *Journal of Environmental Management*, 70(2), pp.165–180.
- Lees, A.C. & Peres, C. A., 2008. Conservation value of remnant riparian forest corridors of varying quality for Amazonian birds and mammals. *Conservation biology*, 22(2), pp.439–49.
- Lees, A.C. & Vieira, I.C., 2013. Forests: Oil-palm concerns in Brazilian Amazon. *Nature*, 497(7448), p.188.
- Leitão, R.P., Zuanon, J., Mouillot, D., Leal, C.G., Hughes, R.M., Kaufmann, P.R., Villéger, S., Pompeu, P.S., Kasper, D., de Paula, F.R. & Ferraz, S.F., 2018. Disentangling the pathways of land use impacts on the functional structure of fish assemblages in Amazon streams. *Ecography*, 41(1), pp.219–232.
- Leprieur, F., Beauchard, O., Blanchet, S., Oberdorff, T. & Brosse, S., 2008. Fish invasions in the world's river systems: when natural processes are blurred by human activities. *PLoS biology*, 6(2), p.e28.
- Lepš, J., & Šmilauer, P., 2003. *Multivariate analysis of ecological data using CANOCO*. Cambridge University Press.
- Leroy, C.J. & Marks, J.C., 2006. Litter quality, stream characteristics and litter diversity influence decomposition rates and macroinvertebrates. *Freshwater biology*, 51(4), pp.605–617.
- Lévêque, C., Oberdorff, T., Paugy, D., Stiassny, M.L.J. & Tedesco, P.A., 2007. Global diversity of fish (Pisces) in freshwater. *Hydrobiologia*, 595(1), pp.545–567.
- Lévêque, C., 1995. Role and consequences of fish diversity in the functioning of African freshwater ecosystems: a review. *Aquatic Living Resources*, 8(1), pp.59–78.
- Lewis, S.L., Edwards, D.P. & Galbraith, D., 2015. Increasing human dominance of tropical forests. *Science*, 349(6250), pp.827–832.
- Lewis, S.L., Brando, P.M., Phillips, O.L., van der Heijden, G.M. & Nepstad, D., 2011. The 2010 Amazon drought. *Science*, 331(6017), p.554.
- Liew, J.I.A.H., Tan, H.H. & Yeo, D.C.J., 2016. Dammed rivers : impoundments facilitate fish invasions. *Freshwater Biology*, 61(9), pp.1421–1429.
- Liew, J. H., Tan, H. H., & Yeo, D. C. J., 2012. Some cichlid fishes recorded in Singapore. *Nature in Singapore*, 5, pp.229–236.
- Ligtermoet, E., Chambers, J.M., Kobryn, H.T. & Davis, J., 2009. Determining the extent and condition of riparian zones in drinking water supply catchments in Sarawak, Malaysia. *Water Science & Technology*, 9(5), pp.517–533.
- Lim, K. K. P. & Wong, A., 1994. Fishes of the Kinabatangan basin. Sandakan district, Sabah, East Malaysia. *Sabah Museum Journal*, 1, pp.39–71.
- Livengood, E. J., & Chapman, F. A., 2007. The Ornamental Fish Trade: An Introduction with Perspectives for Responsible Aquarium Fish Ownership. *University of Florida IFAS Extension*, pp.1–8.
- Lorion, C. M. & Kennedy, B. P., 2009. Riparian forest buffers mitigate the effects of deforestation on fish assemblages in tropical headwater streams. *Ecological Applications*, 19(2), pp.468–479.

Bibliography

- LPR, 2014. *Living Planet Report 2010/2012*, Available at:
http://assets.wwf.org.uk/downloads/lpr2014_low_res_embargo.pdf.
- Luke, S.H., Barclay, H., Bidin, K., Chey, V.K., Ewers, R.M., Foster, W.A., Nainar, A., Pfeifer, M., Reynolds, G., Turner, E.C. & Walsh, R.P., 2017a. The effects of catchment and riparian forest quality on stream environmental conditions across a tropical rainforest and oil-palm landscape in Malaysian Borneo. *Ecohydrology*, 10(4), pp.1–14.
- Luke, S.H., Dow, R.A., Butler, S., Vun Khen, C., Aldridge, D.C., Foster, W.A. and Turner, E.C., 2017b. The impacts of habitat disturbance on adult and larval dragonflies (Odonata) in rainforest streams in Sabah, Malaysian Borneo. *Freshwater Biology*, 62(3), pp.491–506.
- Luke, S. H., 2016. The impacts of land-use on environmental conditions, invertebrate biodiversity, and ecosystem function of freshwater streams in Sabah, Malaysia. *PhD thesis*, University of Cambridge, UK.
- Luskin, M.S., Christina, E.D., Kelley, L.C. & Potts, M.D., 2014. Modern hunting practices and wild meat trade in the oil palm plantation-dominated landscapes of Sumatra, Indonesia. *Human Ecology*, 42(1), pp.35–45.
- Luskin, M.S. & Potts, M.D., 2011. Microclimate and habitat heterogeneity through the oil palm lifecycle Oil palm. *Basic and Applied Ecology*, 12(6), pp.540–551.
- Lutz, W. & Samir, K.C., 2010. Dimensions of global population projections: what do we know about future population trends and structures? *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1554), pp.2779–2791.
- Macedo, M. N., Coe, M. T., DeFries, R., Uriarte, M., Brando, P. M., Neill, C., & Walker, W. S., 2013. Land-use-driven stream warming in southeastern Amazonia. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 368(1619), p.20120153.
- MacKinnon, K., Hatta, G., Mangalik, A. & Halim, H., 1996. *The ecology of Kalimantan* (Vol. 3). Oxford University Press.
- Malmer, A. & Grip, H., 1994. Converting tropical rainforest to forest plantation in sabah, malaysia. Part II. Effects on nutrient dynamics and net losses in streamwater. *Hydrological Processes*, 8(3), pp.195–209.
- Marczak, L.B., Sakamaki, T., Turvey, S.L., Deguisse, I., Wood, S.L. & Richardson, J.S., 2010. Are forested buffers an effective conservation strategy for riparian fauna? An assessment using meta-analysis. *Ecological Applications*, 20(1), pp.126–134.
- Martin-Smith, K.M., 1996. Length/weight relationships of fishes in a diverse tropical freshwater community, Sabah, Malaysia. *Journal of Fish Biology*, 49(4), pp.731–734.
- Martin-Smith, K.M., 1998a. Effects of disturbance caused by selective timber extraction on fish communities in Sabah, Malaysia. *Environmental Biology of Fishes*, 53(2), pp.155–167.
- Martin-Smith, K.M., 1998b. Relationships between fishes and habitat in rainforest streams in Sabah, Malaysia. *Journal of Fish Biology*, 52(3), pp.458–482.
- Martin-Smith, K.M., 1998c. Biodiversity patterns of tropical freshwater fish following selective timber extraction : A case study from Sabah, Malaysia. *Italian Journal of Zoology*, 65(S1), pp.363–368.
- Martin-Smith, K. M., 2004. Aquatic habitats in forest ecosystems. *Encyclopaedia of Forest Sciences*, 1(1), pp.96–102.

Bibliography

- Martin-Smith, K.M. & Laird, L., 1997. Reproductive patterns in some Cypriniformes from Borneo. *Proceedings of the 5th Indo-Pacific Fish Conference, Noumea*, pp.493–504.
- Martin-Smith, K.M. & Laird, L., 1998. Depauperate freshwater fish communities in Sabah: the role of barriers to movement and habitat quality. *Journal of Fish Biology*, 53(sA), pp.331–344.
- Martin-Smith, K.M. & Tan, H.H., 1998. Diversity of freshwater fishes from Eastern Sabah: Annotated checklist for Danum Valley and a consideration of inter- and intra-catchment variability. *The Raffles Bulletin of Zoology*, 46(2), pp.573–604.
- Matthews, W.J. & Marsh-Matthews, E., 2003. Effects of drought on fish across axes of space, time and ecological complexity. *Freshwater Biology*, 48(7), pp.1232–1253.
- McHugh, P.A., Thompson, R.M., Greig, H.S., Warburton, H.J. & McIntosh, A.R., 2015. Habitat size influences food web structure in drying streams. *Ecography*, 38(7), pp.700–712.
- McIntosh, P., & Laffan, M., 2005. Soil erodibility and erosion hazard: Extending these cornerstone soil conservation concepts to headwater streams in the forestry estate in Tasmania. *Forest Ecology and Management*, 220(1-3), pp.128-139.
- McMorrow, J. & Talip, M.A., 2001. Decline of forest area in Sabah, Malaysia: relationship to state policies, land code and land capability. *Global Environmental Change*, 11(3), pp.217-230.
- MEA, (Millenium Ecosystem Assessment), 2005. Ecosystems and Human Well-being Synthesis: Millennium Ecosystem Assessment Series. *World Resources Institute*, Washington, DC, p.155.
- Meijaard, E. & Sheil, D., 2013. Oil-palm plantations in the context of biodiversity conservation. In *Encyclopedia of biodiversity*. Elsevier Science Publishers, Netherlands.
- Mercer, E.V., Mercer, T.G. & Sayok, A.K., 2014. Effects of forest conversions to oil palm plantations on freshwater macroinvertebrates: a case study from Sarawak, Malaysia. *Journal of Land Use Science*, 9(3), pp.260-277.
- Ministry of Natural Resources and Environment Malaysia, 2014. Water Quality Standards for Malaysia—Annex, National Water Quality Standards for Malaysia—Annex.
- Moraes, A.B., Wilhelm, A.E., Boelter, T., Stenert, C., Schulz, U.H. & Maltchik, L., 2014. Reduced riparian zone width compromises aquatic macroinvertebrate communities in streams of southern Brazil. *Environmental Monitoring & Assessment*, 186(11), pp.7063–7074.
- Myers, N. & Mittermeier, R., 2000. Biodiversity hotspots for conservation priorities. *Nature*, 403(6772), pp.853–858.
- Mysinchew. (2010). Empurau, the most expensive fish. Retrieved August 1, 2017, from <http://www.mysinchew.com/node/36931>
- Naeem, S., 1998. Species Redundancy and Ecosystem Reliability. *Conservation biology*, 12(1), 39–45.
- Nagasaka, A. & Nakamura, F., 1999. The influences of land-use changes on hydrology and riparian environment in a northern Japanese landscape. *Landscape ecology*, 14(6), pp.543-556.
- Naiman, R.J., Bilby, R.E. & Bisson, P.A., 2000. Riparian Ecology and Management in the Pacific Coastal Rain Forest. *BioScience*, 50(11), p.996.
- Naiman R. J. & Décamps, H., 1997. The ecology of interfaces: Riparian Zones. *Annual Review of Ecology and Systematics*, 28(1), pp.621–658.

Bibliography

- Nainar, A., Bidin, K., Walsh, R.P., Ewers, R.M. & Reynolds, G., 2017. Effects of different land-use on suspended sediment dynamics in Sabah (Malaysian Borneo)—a view at the event and annual timescales. *Hydrological Research Letters*, 11(1), pp.79–84.
- Nainar, A., Bidin, K., Walsh, R.P. & Annammala, K.V., 2016. Turbidity and conductivity changes during storm events in repeat-selectively-logged and old regrowth lightly logged rainforests catchments in Sabah. In SAFE Workshop—Science@SAFE.
- Nakagawa, S. & Schielzeth, H., 2013. A general and simple method for obtaining R² from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4(2), pp.133–142.
- Nesadurai, H.E., 2013. Food security, the palm oil–land conflict nexus, and sustainability: a governance role for a private multi-stakeholder regime like the RSPO? *The Pacific Review*, 26(5), pp.505–529.
- Newcombe, C.P., & Macdonald, D.D., 1991. Effects of Suspended Sediments on Aquatic Ecosystems. *North American journal of fisheries management*, 11(1), pp.72–82.
- Ng, P.K.L., & Tan, H.H., 1997. Freshwater fishes of Southeast Asia: potential for the aquarium fish trade and conservation issues. *Aquarium Sciences and Conservation*, 1(2), pp.79–90.
- Ng, H.H. & Tan, H.H., 1999. The fishes of the Endau drainage, Peninsular Malaysia with descriptions of two new species of catfishes (Teleostei: Akysidae, Bagridae). *Zoological Studies Taipei*, 38(3), pp.350–366.
- Nilsson, C. & Berggren, K., 2000. Alterations of Riparian Ecosystems Caused by River Regulation. *BioScience*, 50(9), pp.783.
- Nilsson, C., Reidy, C.A., Dynesius, M. & Revenga, C., 2005. Fragmentation and flow regulation of the world's large river systems. *Science*, 308(5720), pp.405–8.
- Northcote, T.G. & Hartman, G.F., 2008. *Fishes and Forestry: Worldwide Watershed Interactions and Management*. John Wiley & Sons.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H. & Oksanen, M.J., 2013. Package ‘vegan’. Community ecology package, version, 2(9).
- Olden, J.D., Kennard, M.J., Leprieur, F., Tedesco, P.A., Winemiller, K.O. & García-Berthou, E., 2010. Conservation biogeography of freshwater fishes: recent progress and future challenges. *Diversity and Distributions*, 16(3), pp.496–513.
- Oliver, T.H., Brereton, T. & Roy, D.B., 2013. Population resilience to an extreme drought is influenced by habitat area and fragmentation in the local landscape. *Ecography*, 36(5), pp.579–586.
- Olson, D.H., Anderson, P.D., Frissell, C.A., Welsh Jr, H.H. & Bradford, D.F., 2007. Biodiversity management approaches for stream–riparian areas: Perspectives for Pacific Northwest headwater forests, microclimates, and amphibians. *Forest Ecology and Management*, 246(1), pp.81–107.
- Osborne, L.L. & Kovacic, D.A., 1993. Riparian vegetated buffer strips in water-quality restoration and stream management. *Freshwater Biology*, 29(2), pp.243–258.
- de Paula, F.R., Gerhard, P., Wenger, S.J., Ferreira, A., Vettorazzi, C.A. & de Barros Ferraz, S.F., 2013. Influence of forest cover on in-stream large wood in an agricultural landscape of southeastern Brazil: A multi-scale analysis. *Landscape Ecology*, 28(1), pp.13–27.
- Payne, J., Nais, J., & Ambu, L., 2007. Application of IUCN categories for protected Areas in Sabah, Malaysia. *Kota Kinabalu, Sabah Biodiversity Centre. BBEC I Technical Report*.

Bibliography

- Pereira, H.M., Leadley, P.W., Proen  a, V., Alkemade, R., Scharlemann, J.P., Fernandez-Manjarr  s, J.F., Ara  o, M.B., Balvanera, P., Biggs, R., Cheung, W.W. & Chini, L., 2010. Scenarios for global biodiversity in the 21st century. *Science*, 330(6010), pp.1496-1501.
- Perry, L.G., Andersen, D.C., Reynolds, L.V., Nelson, S.M. & Shafrroth, P.B., 2012. Vulnerability of riparian ecosystems to elevated CO₂ and climate change in arid and semiarid western North America. *Global Change Biology*, 18(3), pp.821-842.
- Petchey, O.L. & Gaston, K.J., 2006. Functional diversity: back to basics and looking forward. *Ecology letters*, 9(6), pp.741-758.
- Petchey, O.L., 2004. On the statistical significance of functional diversity effects. *Functional Ecology*, 18(3), pp.297-303.
- Pfeifer, M., Lefebvre, V., Turner, E., Cusack, J., Khoo, M., Chey, V. K., Peni, M. & Ewers, R .M., 2015. Deadwood biomass: An underestimated carbon stock in degraded tropical forests? *Environmental Research Letters*, 10(4), 044019.
- Pfeifer, M., Kor, L., Nilus, R., Turner, E., Cusack, J., Lysenko, I., Khoo, M., Chey, V.K., Chung, A.C. & Ewers, R.M., 2016. Mapping the structure of Borneo's tropical forests across a degradation gradient. *Remote Sensing of Environment*, 176, pp.84-97.
- Phalan, B., Bertzky, M., Butchart, S.H.M., Donald, P.F., Scharlemann, J.P.W., Stattersfield, A.J., Balmford, A., 2013. Crop expansion and conservation priorities in tropical countries. *PLoS One*, 8(1), e51759.
- Phalan, B., Onial, M., Balmford, A. & Green, R.E., 2011. Reconciling food production and biodiversity conservation: land sharing and land sparing compared. *Science*, 333(6047), pp.1289-1291.
- Phipps, C.D., 2014. Investigating the effects of riparian timber extraction on trophic interactions of three Cyprinid Species from the the Kalabakan Basin, Northern Borneo, Using DNA Metabarcoding. *MSc thesis*, Imperial College London.
- Piggott, J.J., Townsend, C.R. & Matthaei, C.D., 2015. Climate warming and agricultural stressors interact to determine stream macroinvertebrate community dynamics. *Global Change Biology*, 21(5), pp.1887–1906.
- Pine, W.E., Pollock, K.H., Hightower, J.E., Kwak, T.J. & Rice, J.A., 2003. A review of tagging methods for estimating fish population size and components of mortality. *Fisheries*, 28(10), pp.10-23.
- Pool, T.K., Grenouillet, G. & Vill  ger, S., 2014. Species contribute differently to the taxonomic, functional, and phylogenetic alpha and beta diversity of freshwater fish communities. *Diversity and Distributions*, 20(11), pp.1235–1244.
- Poos, M., Lawrie, D., Tu, C., Jackson, D.A. & Mandrak, N.E., 2012. Estimating local and regional population sizes for an endangered minnow, redside dace (*Clinostomus elongatus*), in Canada. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 22(1), pp.47–57.
- Pringle, C., 2003. What is hydrologic connectivity and why is it ecologically important? *Hydrological Processes*, 17(13), pp.2685–2689.
- Pringle, C.M., Naiman, R.J., Bretschko, G., Karr, J.R., Oswood, M.W., Webster, J.R., Welcomme, R.L., & Winterbourn, M.J., 1988. Patch Dynamics in Lotic Systems: The Stream as a Mosaic. *Journal of the North American Bentholological Society*, 7(4), pp.503-524.
- Pusey, B. & Arthington, A., 2003. Importance of the riparian zone to the conservation and management of freshwater fish: a review. *Marine and Freshwater Research*, 54(1), pp.1–16.

Bibliography

- Pye, O., Radjawali, I. & Julia, 2017. Land grabs and the river: eco-social transformations along the Kapuas, Indonesia. *Canadian Journal of Development Studies/Revue canadienne d'études du développement*, 38(3), pp.378-394.
- R Core Development Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Rabeni, C.F. & Smale, M.A., 1995. Effects of siltation on stream fishes and the potential mitigating role of the buffering riparian zone. *Hydrobiologia*, 303(1–3), pp.211–219.
- Rachmatika, I., Nasi, R., Sheil, D., & Wan, M., 2005. A First Look at the Fish Species of the Middle Malinau A First Look at the Fish Species of the Middle Malinau. *Center for International Forestry Research (CIFOR)*, pp.1-35.
- Rahim, K., Long, S. & Abang, F., 2002. A survey of freshwater fish fauna in the upper rivers of Crocker Range National Park Sabah Malaysia. *ASEAN Review of Biodiversity and Environmental Conservation (ARBEC)*, pp.1–9.
- Ramírez, A., Pringle, C.M. & Wantzen, K.M., 2008. Tropical stream conservation. In *Tropical stream ecology* (pp. 285-304).
- Rani, P., Immanuel, S., & Kumar, N. R., 2014. Ornamental Fish Exports from India: Performance, Competitiveness and Determinants. *International Journal of Fisheries and Aquatic Studies*, 1(4), pp.85–92.
- Rashleigh, B., 2004. Relation of environmental characteristics to fish assemblages in the upper French Broad River basin, North Carolina. *Environmental monitoring and assessment*, 93(1–3), pp.139–56.
- Republic of Indonesia., 1990. Keputusan Presiden No. 32 Tahun 1990 Tentang: Pengelolaan Kawasan Lindung.
- Richardson, J.S., Naiman, R.J., Swanson, F.J. & Hibbs, D.E., 2005. Riparian communities associated with Pacific Northwest headwater streams: assemblages, processes, and uniqueness. *Journal of the American Water Resources Association*, 41(4), pp.935-947.
- Richter, B. D., Braun, D. P., Mendelson, M. A., & Master, L. L., 1997. Threats to Imperiled Freshwater Fauna. *Conservation Biology*, 11(5), pp.1081–1093.
- Ripley, B., 2016. tree: Classification and Regression Trees. R package, version 1.0-37.
- Roberts, T. R., 1989. The freshwater fishes of western Borneo (Kalimantan, Barat, Indonesia). *Memoirs of the California Academy of Sciences, San Francisco*, 14, pp.1–210.
- Rodrigues, M. E., de Oliveira Roque, F., Quintero, J. M. O., de Castro Pena, J. C., de Sousa, D. C. & Junior, P. D. M., 2016. Nonlinear responses in damselfly community along a gradient of habitat loss in a savanna landscape. *Biological Conservation*, 194, pp.113–120.
- Rood, S.B., Pan, J., Gill, K.M., Franks, C.G., Samuelson, G.M. & Shepherd, A., 2008. Declining summer flows of Rocky Mountain rivers: Changing seasonal hydrology and probable impacts on floodplain forests. *Journal of Hydrology*, 349(3–4), pp.397–410.
- Rowe, D.K., Smith, J., Quinn, J. & Boothroyd, I., 2002. Effects of logging with and without riparian strips on fish species abundance, mean size, and the structure of native fish assemblages in Coromandel, New Zealand, streams. *New Zealand Journal of Marine and Freshwater Research*, 36(1), pp.67-79.

Bibliography

- RSPO, 2013. Roundtable on Sustainable Palm Oil: Principles and Criteria for the Production of Sustainable Palm Oil. Available at:
<https://www.rspo.org/file/RSPO%20Principles%20&%20Criteria%20Document.pdf>
- Ryan, D.K. & Kelly-Quinn, M., 2015. Effects of riparian canopy cover on salmonid diet and prey selectivity in low nutrient streams. *Journal of fish biology*, 86(1), pp.16–31.
- Rykken, J.J., Moldenke, A.R. & Olson, D.H., 2007. Headwater riparian forest floor invertebrate communities associated with alternative management practices. *Ecological Applications*, 17(4), pp.1168–1183.
- Sabah Water Resources Enactment, 1998. State of Sabah. Available at: <http://sabah.gov.my/phb/wp-content/uploads/2011/05/SabahWaterResourcesEnactment1998.pdf> [Accessed November 5, 2014].
- Sabo, J.L., Sponseller, R., Dixon, M., Gade, K., Harms, T., Heffernan, J., Jani, A., Katz, G., Soykan, C., Watts, J. & Welter, J., 2005. Riparian zones increase regional species richness by harboring different, not more, species. *Ecology*, 86(1), pp.56–62.
- Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A. & Leemans, R., 2000. Global Biodiversity Scenarios for the Year 2100. *Science*, 287(5459), pp.1770–1774.
- Salemi, L.F., Groppo, J.D., Trevisan, R., de Moraes, J.M., de Paula Lima, W. & Martinelli, L.A., 2012. Riparian vegetation and water yield: A synthesis. *Journal of Hydrology*, 454, pp.195–202.
- Sazima, I., Carvalho, L.N., Mendonça, F.P., Zuanon, J., 2006. Fallen leaves on the water-bed: Diurnal camouflage of three night active fish species in an Amazonian streamlet. *Neotropical Ichthyology* 4(1), 119–122.
- Schoneveld, G.C., 2014. The politics of the forest frontier: Negotiating between conservation, development, and indigenous rights in Cross River State, Nigeria. *Land Use Policy*, 38, pp.147–162.
- Scott, M.C. & Helfman, G.S., 2001. Native invasions, homogenization, and the mismeasure of integrity of fish assemblages. *Fisheries*, 26(11), pp.6–15.
- Senior, M.J., Hamer, K.C., Bottrell, S., Edwards, D.P., Fayle, T.M., Lucey, J.M., Mayhew, P.J., Newton, R., Peh, K.S.H., Sheldon, F.H. & Stewart, C., 2013. Trait-dependent declines of species following conversion of rain forest to oil palm plantations. *Biodiversity and Conservation*, 22(1), pp.253–268.
- Shea, K., Roxburgh, S.H. & Rauschert, E.S.J., 2004. Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. *Ecology Letters*, 7(6), pp.491–508.
- Sheil, D., Casson, A., Meijaard, E., Van Noordwijk, M., Gaskell, J., Sunderland-Groves, J., Wertz, K. & Kanninen, M., 2009. *The impacts and opportunities of oil palm in Southeast Asia: What do we know and what do we need to know?* (Vol. 51). Bogor, Indonesia: Center for International Forestry Research (CIFOR).
- Simpson, E.H., 1949. Measurement of diversity. *Nature*, 163(4148), p.688.
- Sloan, S., Jenkins, C.N., Joppa, L.N., Gaveau, D.L. & Laurance, W.F., 2014. Remaining natural vegetation in the global biodiversity hotspots. *Biological Conservation*, 177, pp.12–24.
- Small, G.E., Pringle, C.M., Pyron, M. & Duff, J.H., 2011. Role of the fish *Astyanax aeneus* (Characidae) as a keystone nutrient recycler in low-nutrient Neotropical streams. *Ecology*, 92(2), pp.386–397.
- Smucker, N. J., Detenbeck, N. E. & Morrison, A. C., 2013. Diatom responses to watershed development and potential moderating effects of near-stream forest and wetland cover. *Freshwater Science*, 32(1), pp.230–249.

Bibliography

- Sodhi, N.S., Koh, L.P., Brook, B.W. & Ng, P.K., 2004. Southeast Asian biodiversity: an impending disaster. *Trends in ecology & evolution*, 19(12), pp.654-660.
- de Souza, A. L., Fonseca, D. G., Libório, R. A. & Tanaka, M. O., 2013. Influence of riparian vegetation and forest structure on the water quality of rural low-order streams in SE Brazil. *Forest Ecology and Management*, 298, pp.12–18.
- Stibig, H.J., Achard, F., Carboni, S., Rasi, R. & Miettinen, J., 2014. Change in tropical forest cover of Southeast Asia from 1990 to 2010. *Biogeosciences*, 11(2), p.247.
- Strayer, D. L., & Dudgeon, D., 2010. Freshwater biodiversity conservation: recent progress and future challenges. *Journal of the North American Benthological Society*, 29(1), 344-358.
- Susanti, A., & Burgers, P., 2013. Oil Palm Expansion: Competing Claim of Lands for Food, Biofuels, and Conservation. In *Sustainable Food Security in the Era of Local and Global Environmental Change* (pp. 301–320). Dordrecht: Springer Netherlands.
- Sutherland, W.J., Pullin, A.S., Dolman, P.M. & Knight, T.M., 2004. The need for evidence-based conservation. *Trends in Ecology and Evolution*, 19(6), pp.305–308.
- Sweeney, B.W., Bott, T.L., Jackson, J.K., Kaplan, L.A., Newbold, J.D., Standley, L.J., Hession, W.C. & Horwitz, R.J., 2004. Riparian deforestation, stream narrowing, and loss of stream ecosystem services. *Proceedings of the National Academy of Sciences of the United States of America*, 101(39), pp.14132–7.
- Sweeney, B.W. & Newbold, J.D., 2014. Streamside forest buffer width needed to protect stream water quality, habitat, and organisms: A literature review. *Journal of the American Water Resources Association*, 50(3), pp.560–584.
- Syvitski, J.P., Vörösmarty, C.J., Kettner, A.J. & Green, P., 2005. Impact of humans on the flux of terrestrial sediment to the global coastal ocean. *Science*, 308(5720), pp.376-380.
- Tabacchi, E., Correll, D.L., Hauer, R., Pinay, G., Planty-Tabacchi, A.M. & Wissmar, R.C., 1998. Development, maintenance and role of riparian vegetation in the river landscape. *Freshwater biology*, 40(3), pp.497-516.
- Tan, H. & Sulaiman, Z., 2006. Three new species of *Gastromyzon* (Teleostei: Balitoridae) from the Temburong River basin, Brunei Darussalam, Borneo. *Zootaxa*, 19, pp.1–19.
- Tan, H.H. & Leh, C.U.M., 2006. Three new species of *Gastromyzon* (Teleostei: Balitoridae) from southern Sarawak. *Zootaxa*, 1126(1), pp.1-19.
- Taniwaki, R.H., Piggott, J.J., Ferraz, S.F. & Matthaei, C.D., 2017. Climate change and multiple stressors in small tropical streams. *Hydrobiologia*, 793(1), pp.41-53.
- Taubert, F., Fischer, R., Groeneveld, J., Lehmann, S., Müller, M.S., Rödig, E., Wiegand, T. & Huth, A., 2018. Global patterns of tropical forest fragmentation. *Nature*, 554(7693), pp.519–522.
- Thompson, R.M., Beardall, J., Beringer, J., Grace, M. & Sardina, P., 2013. Means and extremes: building variability into community-level climate change experiments. *Ecology letters*, 16(6), pp.799-806.
- Thomsen, P., Kielgast, J.O.S., Iversen, L.L., Wiuf, C., Rasmussen, M., Gilbert, M.T.P., Orlando, L. & Willerslev, E., 2012. Monitoring endangered freshwater biodiversity using environmental DNA. *Molecular Ecology*, 21(11), pp.2565–73.
- Tockner, K. & Stanford, J.A., 2002. Review of: Riverine Flood Plains: Present State and Future Trends. *Environmental conservation*, 29(3), pp.308–330.

Bibliography

- Toham, A.K. & Teugels, G.G., 1999. First data on an index of biotic integrity (IBI) based on fish assemblages for the assessment of the impact of deforestation in a tropical West African river system. *Hydrobiologia*, 397, pp.29-38.
- Turner, E. C., Snaddon, J. L., Fayle, T. M. & Foster, W. A., 2008. Oil-palm research in context: Identifying the need for biodiversity assessment. *PLoS ONE*, 3(2), pp.2–5.
- Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R. & Cushing, C.E., 1980. The River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Sciences*, 37(1), pp.130–137.
- Venter, O., Sanderson, E.W., Magrach, A., Allan, J.R., Beher, J., Jones, K.R., Possingham, H.P., Laurance, W.F., Wood, P., Fekete, B.M. & Levy, M.A., 2016. Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nature Communications*, 7, p.12558.
- Viegas, G., Stenert, C., Schulz, U.H. & Maltchik, L., 2014. Dung beetle communities as biological indicators of riparian forest widths in southern Brazil. *Ecological Indicators*, 36, pp.703–710.
- Villéger, S., Ramos Miranda, J., Flores Hernández, D., Mouillot, D., 2010. Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. *Ecological Applications*, 20(6), 1512–1522.
- Villéger, S., Mason, N. W. & Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, 89(8), pp.2290–2301.
- Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional! *Oikos* 116(5), 882–892.
- Vörösmarty, C.J., McIntyre, P.B., Gessner, M.O., Dudgeon, D., Prusevich, A., Green, P., Glidden, S., Bunn, S.E., Sullivan, C.A., Liermann, C.R. & Davies, P.M., 2010. Global threats to human water security and river biodiversity. *Nature*, 467(7315), p.555.
- Wahl, C. M., Neils, A. & Hooper, D., 2013. Impacts of land use at the catchment scale constrain the habitat benefits of stream riparian buffers. *Freshwater Biology*, 58(11), pp.2310–2324.
- Wallace, J.B., Eggert, S.L., Meyer, J.L., Webster, J.R., 1997. Multiple Trophic Levels of a Forest Stream Linked to Terrestrial Litter Inputs. *Science* 277(5322), pp.102–104.
- Walsh, R.P.D. & Newbery, D.M., 1999. The ecoclimatology of Danum, Sabah, in the context of the world's rainforest regions, with particular reference to dry periods and their impact. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 354(1391), pp.1869-1883.
- Walsh, R. P. D., Bidin, K., Blake, W. H., Chappell, N. A., Clarke, M. A., Douglas, I., Ghazali, R., ... Annammala, K. V., 2011. Long-term responses of rainforest erosional systems at different spatial scales to selective logging and climatic change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1582), pp.3340–3353.
- Wantzen, K. & Mol, J., 2013. Soil Erosion from Agriculture and Mining: A Threat to Tropical Stream Ecosystems. *Agriculture*, 3(4), pp.660–683.
- Watson, J.E., Shanahan, D.F., Di Marco, M., Allan, J., Laurance, W.F., Sanderson, E.W., Mackey, B. & Venter, O., 2016. Catastrophic Declines in Wilderness Areas Undermine Global Environment Targets. *Current Biology*, 26(21), pp.2929–2934.
- Wearn, O.R., Rowcliffe, J.M., Carbone, C., Pfeifer, M., Bernard, H. & Ewers, R.M., 2017. Mammalian species abundance across a gradient of tropical land-use intensity: A hierarchical multi-species modelling approach. *Biological Conservation*, 212, pp.162-171.

Bibliography

- White, R.S.A., McHugh, P.A. & McIntosh, A.R., 2016. Drought-survival is a threshold function of habitat size and population density in a fish metapopulation. *Global Change Biology*, 22(10), pp.3341–3348.
- Wich, S. A., Garcia-Ulloa, J., Kühl, H. S., Humle, T., Lee, J. S. & Koh, L. P., 2014. Will oil-palm's homecoming spell doom for Africa's great apes? *Current Biology*, 24(14), pp.1659–63.
- Wilcove, D. S., Giam, X., Edwards, D. P., Fisher, B. & Koh, L. P., 2013. Navjot's nightmare revisited: logging, agriculture, and biodiversity in Southeast Asia. *Trends in ecology & evolution*, 28(9), pp.531-540.
- Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A. & Losos, E., 1998. Quantifying threats to imperiled species in the United States. *BioScience*, 48(8), pp.607-615.
- Wilkie, D.S. & Carpenter, J.F., 1999. Bushmeat hunting in the Congo Basin: an assessment of impacts and options for mitigation. *Biodiversity & Conservation*, 8(7), pp.927-955.
- Wilkinson, C. L., Yeo, D. C. J., Tan, H. H., Hadi Fikir, A. & Ewers, R. M., 2018a. Land-use change is associated with a significant loss of freshwater fish species and functional richness in Sabah, Malaysia. *Biological Conservation*, 222, pp.164-171.
- Wilkinson, C. L., Yeo, D. C. J., Tan, H. H., Hadi Fikir, A. & Ewers, R. M., 2018b. Freshwater fish resource availability is maintained across a land use gradient in Sabah, Borneo. *Aquatic Conservation: Marine & Freshwater*.
- Woodcock, P., Edwards, D.P., Fayle, T.M., Newton, R.J., Khen, C.V., Bottrell, S.H. & Hamer, K.C., 2011. The conservation value of South East Asia's highly degraded forests: evidence from leaf-litter ants. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 366(1582), pp.3256-3264.
- Woodward, G., Bonada, N., Feeley, H.B. & Giller, P.S., 2015. Resilience of a stream community to extreme climatic events and long-term recovery from a catastrophic flood. *Freshwater Biology*, 60(12), pp.2497–2510.
- Woodward, G., Gessner, M.O., Giller, P.S., Gulis, V., Hladyz, S., Lecerf, A., Malmqvist, B., McKie, B.G., Tiegs, S.D., Cariss, H. & Dobson, M., 2012. Continental-Scale Effects of Nutrient Pollution on Stream Ecosystem Functioning. *Science*, 336(6087), pp.1438–1440.
- Yule, C.M., Leong, M.Y., Liew, K.C., Ratnarajah, L., Schmidt, K., Wong, H.M., Pearson, R.G. & Boyero, L., 2009. Shredders in Malaysia: abundance and richness are higher in cool upland tropical streams. *Journal of the North American Benthological Society*, 28(2), pp.404-415.
- Zeni, J.O., Hoeinghaus, D.J. & Casatti, L., 2017. Effects of pasture conversion to sugarcane for biofuel production on stream fish assemblages in tropical agroecosystems. *Freshwater Biology*, 62(12), pp.2026–2038.
- Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M., 2009. *Mixed effects models and extensions in ecology* with R. New York, NY: Springer New York.

APPENDIX

1 **APPENDIX 1 – FISHES OF THE BRANTIAN DRAINAGE, SABAH, MALAYSIA WITH DESCRIPTION OF A**
2 **NEW RASBORA SPECIES (TELEOSTEI: CYPRINIDAE)**

3 **In review: Raffles Bulletin of Zoology**

4 Clare L Wilkinson^{1, 2}, & Tan Heok Hui^{3*}

5 ¹Department of Life Sciences, Imperial College London, UK

6 ² Department of Biological Sciences, National University of Singapore, Singapore

7 ³Lee Kong Chian Natural History Museum, National University of Singapore, Singapore

8 *Corresponding author: heokhui@nus.edu.sg

9

10 **ABSTRACT**

11 Fish surveys were conducted between 2011 and 2017 in the Brantian drainage, Sabah, Malaysia. The fish fauna
12 of the drainage includes a total of 34 species in 14 families, of which 23 species appear to be the first records for
13 the Brantian drainage. All recorded species except one (*Oreochromis mossambicus*) are native, and 25 species
14 are endemic to Borneo. *Rasbora pycnopeza*, new species, is described herein, specimens were earlier identified
15 as *R. sumatrana*. *Rasbora pycnopeza* is distinguished from its congeners in Southeast Asia by a combination of
16 characters: slender body and distinctive caudal-fin colour pattern consisting of a thick distal black margin
17 (covering $\frac{1}{3}$ to $\frac{1}{2}$ of upper and lower caudal fin lobes); a thin black lateral stripe and a black supraanal stripe.

18

19 **Keywords:** Biodiversity, Checklist, Freshwater fishes, Borneo, *Cyprinidae*, *Rasbora*

20 **Running title:** Fishes of Brantian (Sabah) with new *Rasbora* species

21

22 Introduction

23 The freshwater ichthyofauna of the island of Borneo is relatively well studied compared to other islands in
24 Southeast Asia beginning with the pioneering work of Inger & Chin (1962). More recent studies are those on the
25 Kapuas River, West Kalimantan (Roberts, 1989), Sabah (Ng et al., 2017), Sentarum lakes (Kottelat & Winarti,
26 2005), Rejang River (Parenti & Lim, 2005), Belait River (Parenti & Meissner, 2005), Temburong River (Choy
27 & Chin, 1994), Segama River (Martin-Smith & Tan, 1998), Kinabatangan River (Lim & Wong, 1994), Tawau
28 Hills (Nyanti et al, 1995), Bintulu region, Sarawak (Tan & Lim, 2007), Crocker Range (Rahim, Long, & Abang,
29 2002), and Rayu basin (Doi et al. 2001). Despite these studies, the ichthyofauna of the Brantian drainage near
30 Kalabakan, has not previously been documented.

31 The Brantian drainage is a medium sized drainage in Sabah, East Malaysia, unlike the larger drainages of the
32 Segama and the Kinabatangan which were the focus of earlier studies of the faunal diversity of freshwater
33 ecosystems (Martin-Smith & Tan, 1998). Seasonal changes in the lowland dipterocarp forests of Borneo are
34 very limited, resulting in no contrasting seasons (Kumagai et al., 2005; Walsh & Newbery, 1999), other than
35 occasional droughts. The Brantian drainage is at low elevation, with sites ranging up to around 400 m above sea
36 level.

37 Headwater streams dominate the sampling locations in this study and may harbour endemic species (e.g. loaches
38 in the Family Gastromyzontidae) which are specialised for fast flowing, highly oxygenated waters (Roberts
39 1989). In addition, horizontal variation in fish communities occurs over short geographic distances in this region
40 (Martin-Smith & Tan, 1998), and is important in determining the overall biodiversity, especially if species
41 composition differs between drainages (Kottelat & Whitten 1996). Some difference is thus expected between
42 these communities and the Brantian drainage.

43 The Brantian river and tributaries, predominantly in the Kalabakan Forest Reserve drains a landscape that is a
44 mosaic of twice-logged lowland dipterocarp rainforest, oil palm plantations (planted between 1998 and 2011;
45 with and without riparian buffers), and primary rainforest (Brantian Tantulit Virgin Jungle Reserve). We
46 sampled sites across this land use gradient, as fish communities were thought to be influenced by different land
47 uses.

48 New species are regularly discovered from Sabah, and more widely across Borneo, demonstrating that our
49 knowledge of freshwater fish in the region is incomplete. A series of field collections from across the drainage

50 were conducted from 2011 to 2017 by both authors. We present here a list of the species known from the
51 Brantian drainage, and describe a new species of *Rasbora* herein (see Appendix 1).

52

53 Material and methods

54 Qualitative and quantitative samples were taken of fish from 39 streams across the Upper Brantian catchment in
55 the SAFE project (Ewers et al., 2011) (Fig. 1) in varying land uses during the period October 2011–June 2017
56 (Figs. 2a-d).

57 For quantitative sampling, two methodologies were applied to collect fishes. (1) Fish were sampled every year
58 from 2011 to 2017 (excluding 2012 and 2014) from 200 m transects at 11 different head streams across the land
59 use gradient using cast netting (2.75 m diameter of net and 1 cm mesh size; as done by Wilkinson et al., 2018a,
60 2018b) and baited funnel traps (1.5 L plastic water bottles with an entrance diameter of 2.6 cm). Streams were
61 sampled for four to six consecutive days, with up to 20 throws of the cast net and 20 traps (10 baited with bread
62 and 10 with fresh fish, placed every 10 m along the stream). This long term experiment was set up to monitor
63 the impact of salvage logging and conversion of land to oil palm plantation in six stream catchments in a before-
64 after-control-impact design, as part of the Stability of Altered Forest Ecosystems (SAFE) project. (2) Exhaustive
65 sampling on clear-weather days using three capture methods, performed in the following order at each site: (a)
66 multiple pass electrofishing (EFGI 650), (b) cast net (2.75 m diameter of net and 1 cm mesh size), and (c) push
67 net (60 cm by 40 cm, mesh size 2mm, double net layer) was used in 100 m transects in the 11 catchments
68 described, and 16 additional oil palm streams with varying widths of riparian reserves and two additional logged
69 forest streams, February-June 2017 (Wilkinson et al., 2018a, 2018b).

70 Qualitative samples in the Lower Brantian River and tributaries were taken opportunistically based on access to
71 streams and rivers. Ten sites were sampled between February-June 2017 using cast net, push net and
72 electrofishing. Details of these locations and the methods used are given in Appendix 2. The species observed or
73 recorded in the Brantian drainage are listed in Table 1.

74 All measurements for the new species description are taken from point-to-point on the left side (whenever
75 possible) of fish with dial callipers. The method for taking counts and measurement follow Kottelat (2001) &
76 Kottelat & Freyhoff (2007). Trunk length is measured from tip of posterior-most margin of opercle to base of
77 caudal fin. The last two branched dorsal and anal rays articulating on a single pterygiophore are counted as “1

78 $\frac{1}{2}$ ". Unless otherwise noted, fish identifications follow Kottelat (2013). Abbreviations used: SL – standard
79 length; TL – total length.

80 Unless otherwise stated, our material will be eventually deposited in the Borneensis Collection, Sabah, Malaysia
81 and the Zoological Reference Collection (ZRC) of Lee Kong Chian Natural History Museum, National
82 University of Singapore.

83

84 **Results**

85 A total of 34 fish species in 14 families are recorded from present surveys. Twenty-five fish species (73.5 %) are
86 endemic to Borneo, of which *Gastromyzon ingeri* appears to be restricted to Sabah (see Table 1). One family
87 and one species (Cichlidae - *Oreochromis mossambicus*) is non-native to Sabah and the region.

88

89 **Family Anguillidae**

90 *Anguilla borneensis* Popita, 1924

91 **Remarks.** Commonly found in small hill streams and larger rivers in all land use types.

92

93 *Anguilla marmorata* Quoy & Gaimard, 1824

94 **Remarks.** Commonly found in the majority of sites and all land use types.

95

96 **Family Megalopidae**

97 *Megalops cyprinoides* (Broussonet, 1782)

98 **Remarks.** One single sub-adult specimen was collected in the Brantian River mainstream with a cast net. The
99 presence of both Megalopidae and Anguillidae indicate that the Brantian drainage still has direct passage to the
100 sea, as these two taxa require a marine phase in their life cycles.

101

102 **Family Cyprinidae**

103 *Barbodes sealei* (Herre, 1933)

104 *Puntius sealei* - Inger & Chin 1962: 73, Fig. 30C.

105 **Remarks.** Most common fish in both forested and oil palm estate catchments. Species seems highly plastic,
106 with slight variations in body depth and coloration, dependent upon stream features (e.g. rate of water flow;
107 pers. obs., Martin-Smith & Tan, 1998).

108

109 *Barbonymus balleroides* (Valenciennes, in Cuvier & Valenciennes, 1842)

110 *Puntius bramoides* - Inger & Chin 1962: 75, Fig. 33.

111 **Remarks.** Present but not abundant in any streams in this study, in comparison to being described as common
112 in Danum Valley (Martin-Smith & Tan, 1998).

113

114 *Cyclocheilichthys apogon* (Valenciennes, in Cuvier & Valenciennes, 1842)

115 **Remarks.** This appears to be a new record for the Brantian drainage.

116

117 *Cyclocheilichthys repasson* (Bleeker, 1853)

118 *Cyclocheilichthys repasson* – Inger & Chin, 1962: 67.

119 **Remarks.** Common in larger rivers, but rare in fast flowing water, forested stream catchments.

120

121 *Hampala sabana* Inger & Chin, 1962

122 *Hampala macrolepidota sabana x bimaculata* - Inger & Chin 1962: 82, Fig, 37.

123 **Remarks.** Common in forested stream catchments but never abundant (present study; Martin-Smith & Tan,
124 1998). Rare in oil palm estate catchments. Individuals have been found eating or having just eaten other fishes.

125

126 *Leptobarbus melanotaenia* Boulenger, 1894

127 **Remarks.** Found predominantly in pools of forested stream catchments. It is common but not abundant.

128

129 *Nematobramis everetti* Boulenger, 1894

130 *Nematabramis everetti* – Inger & Chin, 1962: 49.

131 **Remarks.** Ubiquitous and highly abundant in forested streams. Abundance is lower in highly disturbed or oil palm estate streams.

133

134 *Osteochilus chini* Karnasuta, 1993

135 **Remarks.** Ubiquitous but not very abundant in smaller streams, feeding on detritus and algae.

136

137 *Osteochilus ingeri* Karnasuta, 1993

138 **Remarks.** Less abundant, but often sympatric with *O. chini*. It differs from *O. chini* in the number of scale rows above lateral line (4-4 ½ for *O. ingeri* vs 5-5½ for *O. chini*), and colour of fins - yellowish for *O. Ingeri*, and reddish for *O. chini*.

141

142 *Parachela ingerkongi* (Banarescu, 1969)

143 **Remarks.** Rare, present in fast flowing, forested streams and large rivers.

144

145 *Rasbora elegans* Voltz, 1903

146 *Rasbora elegans* – Inger & Chin, 1962: 54.

147 **Remarks.** Only found at one logged forest site (R70B) at the eastern edge to of the Brantian catchment.

148

149 *Rasbora hubbsi* Brittan, 1954

150 *Rasbora hubbsi* – Inger & Chin, 1962: 60.

151 **Remarks.** A small species, TL up to 43.9 mm, considerably smaller than *R. pycnopeza*. Found in fast flowing
152 streams in forested streams and rivers, but rare in oil palm estate streams.

153

154 *Rasbora pycnopeza*, new species

155 (Figs. 3, 4 and 5)

156 See Appendix 1 for Description and Table 2 for morphometric data.

157

158 *Rasbora rutteni* Weber & de Beaufort, 1916

159 **Remarks.** Present in one steep, boulder strewn primary forest stream; and one still water pool adjacent to the
160 Brantian River.

161

162 *Tor tambda* (Valenciennes, in Cuvier & Valenciennes, 1842)

163 **Remarks.** We herein treat *Tor tambda* as one species. *Tor tambda* is the valid name if *Tor tambda* and *Tor*
164 *tambroides* are assumed to be synonyms (following Kottelat, 2013). Juveniles are common in small fast flowing
165 streams and while larger individuals were found in larger streams and Brantian river. Both morphotypes of *Tor*
166 (*tambda* with a short mental lobe, and *tambroides* with a long mental lobe) are present in this region (see Fig. 6).

167

168 **Family Cobitidae**

169 *Pangio mariarum* (Inger & Chin, 1962)

170 **Remarks.** A single specimen was found inhabiting a submerged root mat in Sungai Menggaris (a low gradient
171 river).

172

173 **Family Gastromyzontidae**

174 *Gastromyzon ingeri* Tan, 2006

175 **Remarks.** A common species of *Gastromyzon* found in riffles of forested streams and rivers. The live
176 colouration of this species has not been documented previously (see Tan, 2006). Living fish having a brownish-
177 yellow body colouration, turquoise sheen over body dorsum, with gold highlights on every dorsal and lateral
178 body scale; eye with a thin gold iris; dorsal fin hyaline with 2-3 rows of black spots; pectoral and pelvic fins
179 brownish-yellow; anal fin hyaline; base of caudal peduncle and fin is grey, caudal fin is light-blue with up to 5
180 rows of black spots (Fig. 7).

181

182 *Gastromyzon lepidogaster* Roberts, 1982

183 **Remarks.** The most common and abundant *Gastromyzon* in the headwaters of the Brantian stream, found in all
184 land uses. As with other studies, it is the largest *Gastromyzon* (up to 94 mm SL, vide Tan, 2006), can be variable
185 in colour and is often found in small groups.

186

187 *Parhomaloptera microstoma* (Boulenger, 1899)

188 **Remarks.** This is an uncommon species, but abundant when found in fast flowing riffles of forested streams.

189

190 *Protomyzon aphelocheilus* Inger & Chin, 1962

191 **Remarks.** This species had been located in one fast flowing hill stream thus far, but can be expected to occur in
192 other similar habitats in the Brantian drainage.

193

194 *Protomyzon borneensis* Hora & Jayaram, 1952

195 **Remarks.** Uncommon species, but always sympatric with *P. griswoldi*.

196

197 *Protomyzon griswoldi* (Hora & Jayaram, 1952)

198 **Remarks.** A highly ubiquitous species found in small groups. It can easily be observed feeding whilst
199 snorkelling in streams. Abundant in both forested and oil palm estate streams.

200

201 **Family Nemacheilidae**

202 *Nemacheilus olivaceus* Boulenger, 1894

203 **Remarks.** Ubiquitous species, also commonly found in groups in both forested and oil palm estate streams.

204

205 **Family Bagridae**

206 *Hemibagrus baramensis* (Regan, 1906)

207 **Remarks.** Ubiquitous species, but common in oil palm estate streams. Predominantly caught in baited traps or
208 electrofishing.

209

210 *Hemibagrus fortis* (Popa, 1904)

211 **Remarks.** Less common than *H. baramensis*, but also predominantly found in oil palm estate streams.

212

213 **Family Clariidae**

214 *Clarias anfractus* Ng, 1999

215 **Remarks.** Uncommon species, only found in low gradient oil palm estate streams with riparian reserves.

216

217 **Family Sisoridae**

218 *Glyptothorax major* (Boulenger, 1894)

219 **Remarks.** This species inhabits riffles and other fast flowing sections of streams. Specimens from Sabah have
220 all been identified as *G. major* (vide Ng & Kottelat, 2016).

221

222 **Family Cichlidae**

223 *Oreochromis mossambicus* (Peters, 1852)

224 **Remarks.** This is an introduced species thus far obtained from one oil palm estate stream, but its presence is
225 expected to be wider in distribution.

226

227 **Family Gobiidae**

228 *Stenogobius gymnopomus* (Bleeker, 1853)

229 *Stenogobius gymnopomus* – Inger & Chin, 1962: 179.

230 **Remarks.** This species was not obtained from the present surveys, as the lower reaches of the Brantian River
231 were not thoroughly sampled.

232

233 **Family Osphronemidae**

234 *Betta ocellata* de Beaufort, 1933

235 *Betta unimaculata* - Inger & Chin 1962: 158.

236 **Remarks.** Present in some forested streams, but rare in comparison to its abundance in other catchments (e.g.
237 Segama, Danum Valley; pers. obs.).

238

239 **Family Channidae**

240 *Channa striata* (Bloch, 1793)

241 **Remarks.** Uncommon species in this catchment. Several specimens collected from oil palm estate streams.

242

243 **Family Mastacembelidae**

244 *Mastacembelus unicolor* Valenciennes, in Cuvier & Valenciennes, 1832

245 **Remarks.** This species of spiny eel is uncommon, but present in all land use habitats. Only several individuals
246 were encountered.

247

248 **Discussion**

249 The total number of fish species collected from the Brantian catchment in the Kalabakan Forest Reserve and
250 surrounding area now stands at 34. This is lower than nearby catchments of the Upper Segama (47 species) and
251 Kuamat (36 species; Martin-Smith & Tan, 1998). The Brantian drainage is smaller than the Segama and
252 Kuamat drainages, and has been subjected to more severe logging regimes and conversion of land to palm oil
253 plantations, so this lower number was expected. However the surveys of this catchment are restricted to foothills
254 and the upper reaches. It is expected that this list could be extended, as in the adjacent Kalabakan basin an
255 additional 20 species were recorded by Inger and Chin (1962; with taxonomic updates herein), predominantly
256 present in the lower reaches or tidal areas. These include: *Anguilla bicolor* (Anguillidae), *Nemacheilus*
257 *elegantissimus* (Nemacheilidae), *Ompok sabanus* (Siluridae), *Leiocassis collina* (Bagridae), *Arius*
258 *microcephalus* (Ariidae), *Dermogenys bispina* (Zenarchopteridae), *Osphronemus goramy* (Osphronemidae),
259 *Johnius semiluctuosus* (Sciaenidae), *Prionobutis dasyrhynchus*, *Eleotris fusca*, *E. melanosoma* (Eleotridae),
260 *Periophthalmodon septemradiatus*, *Awaous stamoneus*, *Glossogobius giuris*, *Pseudogobiopsis javanicus*, *P.*
261 *oligactis*, *Redigobius isognathus* (Gobiidae), *Taenioides cirratus* (Taenioidae) and *Pao leiurus*
262 (Tetraodontidae). Therefore, the Brantian drainage can be considered to have a moderately rich fish fauna for its
263 size.

264 As expected, species composition varies by land use and stream order. Some species are absent or abundance is
265 drastically reduced in oil palm estate streams (all Gastromyzontidae), but many were also only found within oil
266 palm estate streams (e.g. *Clarias anfractus*, *Oreochromis mossambicus* and *Pangio mariarum*, present study).
267 Many species are specific to particular stream orders. Gastromyzontidae are restricted to fast, flowing low order
268 streams, whereas many families (Megalopidae, Siluridae) were only found in higher order rivers, and we expect
269 that species in the families of Ariidae, Zenarchopteridae, Sciaenidae, Eleotridae, Gobiidae, Taenioididae,

270 Tetraodontidae, would be restricted to the lower reaches with some restricted in brackish waters (Inger & Chin,
271 1962).

272 A current total of 166 species has been recorded in Sabah (Ng et al., 2017), however more species are being
273 described, including one in this study, so it is estimated that more species will continue to be discovered.
274 Despite extensive logging or land conversion in the Brantian drainage, relatively high levels of species richness
275 are observed. We urge others to continue to survey widely across Sabah, to document species diversity and to
276 determine how land use change is affecting freshwater ecosystems and thus diversity.

277

278 Acknowledgements

279 CLW would like to thank the following: Sabah Biodiversity Council, Yayasan Sabah, Danum Valley
280 Conservation Area Management Committee and SEARRP for providing research permission (Licence No:
281 JKM/MBS.1000-2/2 JLD.3 (90)) for field work in Sabah; the SAFE project coordinator, Ryan Gray, and the
282 SAFE project field staff provided logistical support and helped with data collection; Robert Ewers, the Royal
283 Geographic Society, UK IBG grant and Sime Darby Foundation for funding and support; and Kelvin Lim, for
284 access to the collection at the Lee Kong Chian Natural History Museum. THH would like to acknowledge the
285 source of funding from SAFE, Lee Kong Chian Natural History Museum and National University of Singapore.

286

287 References

- 288 Brittan MR (1954) A revision of the Indo-Malayan fresh-water fish genus *Rasbora*. Monographs of the Institute
289 of Science and Technology, Manila, 3: 1–224, 3 pls.
- 290 Chin PK (2002) The Fresh-water Fishes of North Borneo, supplementary chapter. 78 pp., 65 figs. In: reprint
291 (2002) of Inger & Chin (1962) by the Natural History Publications (Borneo), Kota Kinabalu.
- 292 Choy S & Chin PK (1994) Freshwater fishes from the headwaters of the Belalong-Temburong river system,
293 Brunei, Darussalam, Borneo. Raffles Bulletin of Zoology, 42(4): 757–774.
- 294 Doi A, Iwata T, Inoue M, Miyasaka H, Sabki MS & Nakano S (2001) A collection of freshwater fishes from the
295 Rayu basin of western Sarawak, Malaysia. Raffles Bulletin of Zoology, 49: 13–17.

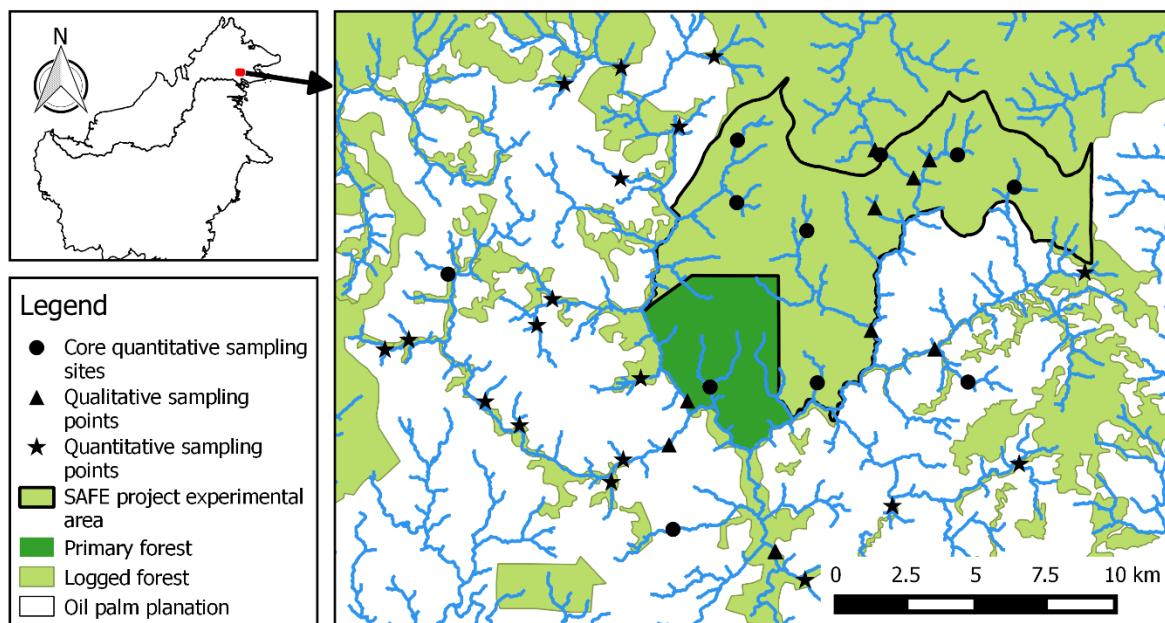
Appendix

- 296 Ewers RM, Didham RK, Fahrig L, Ferraz G, Hector A, Holt RD, Kapos V, Reynolds G, Sinun W, Snaddon JL
297 & Turner EC (2011) A large-scale forest fragmentation speriment: the Stability of Altered Forest
298 Ecosystems Project. Philosophical Transactions of the Royal Society B (2011) 366, 3292-3302.
- 299 Inger RF & Chin PK (1962) The fresh-water fishes of north Borneo. Fieldiana, Zoology, 45: 1-268.
- 300 Kottelat M (2001) Fishes of Laos. Wildlife Heritage Trust Publications. 198 pp.
- 301 Kottelat M (2005) *Rasbora notura*, a new species of cyprinid fish from the Malay Peninsula (Teleostei:
302 Cyprinidae). Ichthyological Exploration of Freshwaters, 16(3): 265-270.
- 303 Kottelat M (2013) The fishes of the inland waters of Southeast Asia: A catalogue and core bibliography of the
304 fishes known to occur in freshwaters, mangroves and estuaries. Raffles Bulletin of Zoology, supplement
305 27: 1-663.
- 306 Kottelat M & Freyhoff J (2007) Handbook of European Freshwater Fishes. Kottelat, Cornol & Freyhof, Berlin,
307 xiv + 646 pp.
- 308 Kottelat M, Whitten AJ, Kartikasari SN & Wirjoatmodjo S (1993) Freshwater Fishes of Western Indonesia and
309 Sulawesi. Periplus Editions, Hong Kong. 221 pp. + 84 pl.
- 310 Kumagai T, Saitoh TM, Sato Y, Takahashi H, Manfroi OJ, Morooka T, & Komatsu H (2005) Annual water
311 balance and seasonality of evapotranspiration in a Bornean tropical rainforest. Agricultural and Forest
312 Meteorology, 128(1-2), 81–92. <http://doi.org/10.1016/j.agrformet.2004.08.006>
- 313 Lim KKP & Wong A (1994) Fishes of the Kinabatangan basin, Sandakan District, Sabah, East Malaysia. Sabah
314 Museum Journal, 1(2): 39-71.
- 315 Martin-Smith KM & Tan HH (1998) Diversity of freshwater fishes from eastern Sabah: annotated checklist for
316 Danum Valley and a consideration of inter- and intra-catchment variability. Raffles Bulletin of Zoology,
317 46(2): 573-604.
- 318 Ng HH & Kottelat M (2016) The *Glyptothorax* of Sundaland: a revisionary study (Teleostei: Sisoridae).
319 Zootaxa 4188 (1): 1-92.

- 320 Ng CKC, Abdullah F, Biun H, Ibrahim MK, Mustapha S & Sade A (2017) Review: A working checklist of the
321 freshwater fish diversity for habitat management and conservation work in Sabah, Malaysia, North
322 Borneo. *Biodiversitas* 18 (2): 560-574.
- 323 Nyanti L, Ghaffar MA & Samad A (1995) An ichthyological survey of Tawau Hills Park, Sabah; p. 173-189. In:
324 A Scientific Journey Through Borneo. Tawau Hills Park, Sabah. Ismail G, Omar S & Laily bin Din (Eds.).
325 Universiti Malaysia Sarawak, Pelanduk Publications, 213 pp.
- 326 Parenti LR & Lim KKP (2005) Fishes of the Rajang basin, Sarawak, Malaysia. *Raffles Bulletin of Zoology*
327 supplement 13: 175–208.
- 328 Parenti LR & Downing Meisner AL (2003) Fishes of the Belait River. *Brunei Museum Journal* 10[1995]:17-54.
- 329 Rahim KAA, Long SM and Abang F (2001) A survey of freshwater fish fauna in the upper rivers of Crocker
330 Range National Park Sabah, Malaysia. In: Ismail G & Ali L 9eds.). A Scientific Journey through Borneo.
331 Crocker Range National Park Sabah. Volume 1. Natural ecosystem and species components. ASEAN
332 Academic Press, London, pp. 119-130.
- 333 Roberts TR (1989) The freshwater fishes of western Borneo (Kalimantan Barat, Indonesia). *Memoirs of the*
334 *California Academy of Sciences*, 14: 1–210.
- 335 Tan HH (2006) The Borneo Suckers. Revision of the Torrent Loaches of Borneo (Balitoridae: *Gastromyzon*,
336 *Neogastromyzon*). Natural History Publications (Borneo), Kota Kinabalu, 245 pp.
- 337 Tan HH (2013) SAFE Project – Sabah: Kalabakan. Freshwater fish list with pictures (based on October 2011
338 survey). 8 page PDF, 3 March 2013. <http://www.safeproject.net/wp-content/uploads/2011/10/SAFE-Project-FW-fish-list-w-PIC-Tan-Heok-Hui.pdf>
- 340 Tan HH & Kottelat M (2009) The fishes of the Batang Hari drainage, Sumatra, with description of six new
341 species. *Ichthyological Exploration of Freshwaters*, 20(1), 13–69.
- 342 Tan HH & Lim KKP (2007) The fishes of Binyo-Penylam and Bukit Sarang conservation areas Bintulu
343 Division, Sarawak. Proceedings of the Regional Conference: Biodiversity Conservation in Tropical
344 Planted Forests Southeast Asia, 15-18 January 2007, Eds. Stuebing RB, Unggang J, Ferner J, Gimant B &
345 Kee KP. Forest Department, Sarawak Forestry Corporation & G, (i-ix), 232 pp.

Appendix

- 346 Walsh RPD & Newbery DM (1999) The ecoclimatology of Danum, Sabah, in the context of the world's
347 rainforest regions, with particular reference to dry periods and their impact. Philosophical Transactions of
348 the Royal Society B-Biological Sciences, 354(1391), 1869–1883.
- 349 Wilkinson CL, Yeo DCJ, Tan HH, AH Fikri & Ewers RM (2018a) The availability of freshwater fish resources
350 is maintained across a land-use gradient in Sabah, Borneo. Aquatic Conservation: Marine and Freshwater
351 Ecosystems, 2018: 1-11.
- 352 Wilkinson CL, Yeo DCJ, Tan HH, AH Fikri & Ewers RM (2018b) Land-use change is associated with a
353 significant loss of freshwater fish species and functional richness in Sabah, Malaysia. Biological
354 Conservation 222 (2018): 164-171.

355 **FIGURES**

356

357 **Fig. 1.** Map of all core quantitative (circles), other quantitative (stars), and qualitative (triangles) sampling
358 locations in the Brantian catchment.



359

360 **Fig. 2.** Examples of streams in across the land use gradient in the Brantian catchment. A) Primary forest stream
361 within the Tantulit Virgin Jungle Reserve (2015); B) Logged forest river (Brantian River, 2017); C) Oil palm

Appendix

362 estate river with a riparian reserve (Menggaris River, 2017); and D) Oil palm estate stream with no riparian
363 reserve (RR16, 2017).

364

365



366

367 **Fig. 3.** *Rasbora pycnopeza*, new species, live specimen from Tawau, not preserved (photographed by THH in
368 2008).



369

370 **Fig. 4.** *Rasbora pycnopeza*, new species, freshly dead specimen from Kalabakan Forest Reserve (photographed
371 by THH in 2011).



372

373 **Fig. 5.** *Rasbora pycnopeza*, new species, ZRC56719, holotype, 87.8 mm SL (top with black background, bottom
374 with white background), from SAFE 120m stream in Kalabakan Forest Reserve.

375



377 **Fig. 6.** *Tor tambra*, uncatalogued specimens showing two morphotypes – left specimen 100.0 mm SL with short
378 lower lip mentum, right specimen 107.5 mm SL with long lower lip mentum; both collected from same location
379 on the same day.

380



381

382 **Fig. 7.** *Gastromyzon ingeri*, ca. 40 mm SL, not preserved; Kalabakan Forest Reserve (THH, photographed in
383 2011).

384

385

Table 1. Fishes in Brantian drainage (* endemic to Borneo).

Family Anguillidae	Family Sisoridae
<i>Anguilla marmorata</i>	<i>Glyptothorax major</i> *
<i>Anguilla borneensis</i> *	
	Family Bagridae
Family Megalopidae	<i>Hemibagrus baramensis</i> *
<i>Megalops cyprinoides</i>	<i>Hemibagrus fortis</i> *
Family Cyprinidae	Family Clariidae
<i>Barbodes sealei</i> *	<i>Clarias anfractus</i> *
<i>Barbonymus balleroides</i> *	
<i>Cyclocheilichthys apogon</i>	Family Gastromyzontidae
<i>Cyclocheilichthys repasson</i>	<i>Gastromyzon ingeri</i> *
<i>Hampala sabana</i> *	<i>Gastromyzon lepidogaster</i> *
<i>Leptobarbus melanotaenia</i> *	<i>Parhomaloptera microstoma</i> *
<i>Nematabramis everetti</i> *	<i>Protomyzon aphelocheilus</i> *
<i>Osteochilus chini</i> *	<i>Protomyzon borneensis</i> *
<i>Osteochilus ingeri</i> *	<i>Protomyzon griswoldi</i> *
<i>Parachela ingerkongi</i> *	
<i>Rasbora elegans</i>	Family Osphronemidae
<i>Rasbora pycnopeza</i> *	<i>Betta ocellata</i> *
<i>Rasbora hubbsi</i> *	
<i>Rasbora rutteni</i> *	Family Channidae
<i>Tor ticta</i>	<i>Channa striata</i>
	Family Mastacembelidae
Family Cobitidae	<i>Mastacembelus unicolor</i>
<i>Pangio mariarum</i> *	
	NON-NATIVE
Family Nemacheilidae	Family Cichlidae
<i>Nemachilus olivaceus</i> *	<i>Oreochromis mossambicus</i>

386

387

388 **Table 2.** Morphometric data of holotype and 20 paratypes of *Rasbora pycnopeza*, new species.

	Holotype	Paratypes (data below includes holotype)		
catalogue no.	ZRC56719	ZRC56720, 56721, 56722, 56723, 56724, 56725, 56726, 56727, 56728, 56729, 56730, 56731		
Standard length (mm)	87.8	67.1-104.1		
% standard length				
Total length	130.3	range	mean	±SD
Body length	78.4	74.1-78.8	76.1	1.4
Predorsal length	53.4	49.6-54.6	52.1	1.1
Preanal length	68.7	63.3-69.7	67.1	1.7
Prepelvic length	47.7	42.6-50.1	47.4	1.8
Head length	23.0	22.5-26.7	25.0	1.0
Body depth at dorsal-fin origin	25.6	22.1-25.9	23.9	1.0
Body depth at anus	20.8	18.2-22.3	19.8	0.9
Caudal peduncle depth	13.4	11.9-13.7	12.7	0.5
Caudal peduncle length	21.5	21.2-25.7	23.2	1.3
Dorsal-fin base length	12.0	10.1-13.8	11.9	1.0
Anal-fin base length	10.9	9.5-11.5	10.5	0.4
Pelvic-fin length	20.7	16.7-21.1	18.8	1.1
Pectoral-fin length	22.9	18.1-22.9	20.9	1.1
Upper caudal-fin lobe length	31.8	29.4-35.1	31.8	1.7
Median caudal-fin length	19.0	16.3-20.9	18.1	1.3
Lower caudal-fin lobe length	34.1	31.1-37.2	33.6	1.7
% head length				
Head width	52.0	48.9-57.3	52.7	2.4
Snout length	33.7	28.3-34.2	31.3	1.7
Orbital diameter	25.2	26.5-31.2	28.5	1.3
Interorbital width	44.6	39.4-53.1	46.2	3.6

389

390

391 **Appendix 1. Description of *Rasbora pycnopeza*, new species**

392 *Rasbora pycnopeza*, new species

393 (Figs. 3, 4 and 5)

394 *Rasbora sumatrana* (non-Bleeker) – Brittan, 1954: 56 (part), fig. 7; Inger & Chin, 1962: 56, fig. 23;

395 Kottelat et al., 1993: 65 (part); Martin-Smith & Tan, 1998: 584; Chin, 2002: S-12, fig. S7.

396 *Rasbora cf. sumatrana* - Tan, 2013: no. 9.

397

398 Material examined:

399 **Holotype.** ZRC56719, 87.8 mm SL; Malaysia: Sabah: Brantian drainage near Kalabakan, 120 m stream (SAFE
400 project experimental area); Wilkinson CL, July 2015.

401 **Paratypes.** ZRC56720, 1 ex., 74.2 mm SL; same locality data as holotype. - ZRC56722, 2 ex., 90.0-104.1 mm
402 SL; Malaysia: Sabah: Brantian drainage near Kalabakan, 30 m buffer stream (SAFE project experimental area);
403 Wilkinson CL, 21 June 2016. - ZRC56721, 3 ex., 70.3-80.4 mm SL; Malaysia: Sabah: Brantian drainage near
404 Kalabakan, 30 m stream (SAFE project experimental area); Wilkinson CL, 23 April 2016. - ZRC56730, 3 ex.,
405 74.2-88.1 mm SL; Malaysia: Sabah: Brantian drainage near Kalabakan, 30 m buffer stream (SAFE project
406 experimental area); Wilkinson CL et al., 23 April 2017. - ZRC56723, 1 ex., 78.3 mm SL, Malaysia: Sabah:
407 Brantian drainage near Kalabakan, Virgin Jungle Reserve stream (SAFE project experimental area); Wilkinson
408 CL et al., 23 June 2016. - ZRC56724, 3 ex., 80.7-100.4 mm SL; Malaysia: Sabah: Brantian drainage near
409 Kalabakan, 0 m buffer stream (SAFE project experimental area); Wilkinson CL, July 2015. - ZRC56725, 2 ex.,
410 88.3-102.7 mm SL; Malaysia: Sabah: Brantian drainage near Kalabakan, 0 m buffer stream (SAFE project
411 experimental area); Wilkinson CL, July 2015. - ZRC56728, 6 ex., 63.0-75.5 mm SL; Malaysia: Sabah: Brantian
412 drainage near Kalabakan, Logged Forest Edge stream (SAFE project experimental area); Wilkinson CL, 4 May
413 2015. - ZRC56731, 1 ex., 77.8 mm SL; ZRC56730, 3 ex., 74.2-88.1 mm SL; Malaysia: Sabah: Brantian
414 drainage near Kalabakan, Logged Forest Edge stream (SAFE project experimental area); Wilkinson CL et al.,
415 24 April 2017. - ZRC56729, 2 ex., 64.8-71.0 mm SL; Malaysia: Sabah: Brantian drainage near Kalabakan,
416 Virgin Forest Reserve stream (SAFE project experimental area); Wilkinson CL, 7 May 2015. - ZRC56726, 1
417 ex., 73.3 mm SL; Malaysia: Sabah: Segama drainage near Danum Valley field centre, West Stream; Wilkinson

418 CL, 1 March 2016. – ZRC56727, 2 ex., 65.5-65.8 mm SL; Malaysia: Sabah: Segama drainage near Danum

419 Valley field centre, Tembaling Stream; Wilkinson CL, 10 March 2016.

420

421 **Diagnosis.** *Rasbora pycnopeza* is distinguished from its congeners in Southeast Asia by the following
422 combination of characters: size up to at least 104mm (SL) and its distinctive caudal-fin colour pattern consisting
423 of a thick distal black margin, covering $\frac{1}{3}$ to $\frac{1}{2}$ of upper and lower fin lobes; a distinct thin black lateral stripe
424 starting 5-6 scales posterior to opercle edge to base of caudal-fin; and a black stripe at supraanal region covering
425 entire anal-fin base. When live or freshly preserved, dorsal fin is orange, pectoral, pelvic and anal fins are
426 yellow, and the caudal fin is faintly yellow with a distinct black margin, the upper and lower caudal-fin lobes
427 with up to a third or half black.

428 **Description.** General appearance in Figs. 3, 4 and 5; morphometric data of holotype and 20 paratypes in Table
429 s3. Streamlined, slender body, deepest at dorsal-fin origin, tapering towards the caudal peduncle. Snout pointed,
430 symphysal knob present. Dorsal fin with 1 simple and 7½ branched rays; origin above lateral line scale 10-13.
431 Pectoral fin slightly falcate, with 15 rays, not reaching pelvic-fin origin. Pelvic fin slightly pointed, with 9 rays,
432 reaching about anus; axillary scale present. Anal fin with 1 simple and 5½ branched rays. Caudal peduncle 1.6-
433 2.0 times longer than deep, and caudal fin length appears large (TL – SL) is 210.1- 279.5 % caudal peduncle
434 depth, with 8-9 + 10 principle rays, 7-8 + 9 branched; deeply forked. Lateral line complete, perforating 28-33 +
435 1 scales (29 + 1 modally) along lateral line, 10-12 predorsal scales (12 modally), $\frac{1}{4}$ /1½ scales in transverse,
436 $\frac{1}{3}$ /1½ scales in transverse on caudal peduncle, 1 scale between lateral line and pelvic-fin origin. Vertebral
437 count consist of 15-16 abdominal + 16-17 caudal, total of 31-33 (mode 33, n = 21).

438 **Colouration.** See figure of preserved specimen (Fig. 5). Body dark brown on the dorsum, fading to yellowish
439 brown on the lateral and cream on the ventrum. Dorsum has a fine reticulated pattern due to diffused
440 melanophores along posterior edge of body scales, darker and more defined dorsally and paler ventrally only
441 extending below midlateral stripe anteriorly. A black midlateral stripe originating 5-6 lateral scales posterior to
442 opercle edge to caudal-fin base. Black lateral stripe most defined in central to posterior half (up to half a scale
443 deep), and ends in a widened but faint elongated triangular blotch at caudal-fin base, not continuing on median
444 caudal rays. A conspicuous black, elongated supra-anal streak, extending the length of the anal-fin base wider
445 anterior of anal fin. Rest of fins hyaline, without black margins; except the caudal fin which has a distinct black
446 posterior margin covering $\frac{1}{3}$ to $\frac{1}{2}$ of the fin.

- 447 In life (Figs. 3 and 4; Martin-Smith & Tan, 1998: 584): Body silvery, lateral line dark blue; supra-anal streak
448 black, conspicuous; orange dorsal fin; yellow pectoral, pelvic and anal fins; yellow caudal fin with a distinct
449 black posterior margin covering $\frac{1}{3}$ to $\frac{1}{2}$ of the fin.
- 450 **Distribution.** *Rasbora pycnopeza* is currently recorded from Kinabatangan (plus the Kuamut sub-basin draining
451 from Danum Valley), Segama, Tawau Hills and Kalabakan basins in western Sabah. Inger & Chin (1962: 57)
452 also lists the following locations (but material from these locations have not been examined except marked with
453 *): Jesselton District – Menggatal; Kinbatangan District – Sungai Gaja, Sungai Kretam Kechil, Deramakot;
454 Sandakan District – Sungai Gum Gum, Sungai Kabili*, Sandakan, Sungai Sapagaya, Sepilok Forest Reserve*;
455 Semporna District – Sungai Mapat; Tawau District – Selimpopon River, Sungai Tawau*, Sungai Balung,
456 Sungai Kinabutan, Sungai Tawan, Sungai Magam, Sungai Brantian; Tuaran District – Kiulu. Chin (2002: SC-
457 12) includes Ranau District – Ranau, Sungai Liwagu*. It is expected to occur in the majority of these drainages
458 in Sabah, as well as in the northernmost part of Kalimantan Timur (for example in Sembakung drainage, which
459 originates in Sabah).
- 460 **Etymology.** From the conjugation of the Greek *pyknos*, meaning thick, dense; and Greek *peza*, meaning border,
461 edge; in allusion to the thick black border of the caudal fin. Used as a noun in apposition.
- 462 **Remarks.** *Rasbora pycnopeza* belongs to the *Rasbora sumatrana-elegans* complex described by Brittan (1954:
463 53), which then included the following valid species on Borneo: *R. sumatrana*, *R. volzii* and *R. elegans*. Brittan
464 diagnosed this complex by a combination of the following: 12 rows of scales around the caudal peduncle, a
465 complete lateral line, the dorsal-fin origin above or behind the posterior extremity of the pelvic-fin base, the
466 presence of a poorly contrasted mid-lateral stripe (sometimes missing), the axial streak ending in a precaudal
467 spot in some species, or with a conspicuous dark blotch in the middle of the side in some species. These
468 complexes were constructed by Brittan based on the similarity of general appearance, but are now outdated by
469 the description of numerous additional species since 1954 and species being re-described. These complexes are
470 nevertheless a convenient tool to ease comparison of species.
- 471 Among the species originally included in the *R. sumatrana-elegans* complex, the status of *R. sumatrana* has
472 been discussed by Tan & Kottelat (2009) and Kottelat (2005). As recognised by Brittan (1954), *R. sumatrana*
473 was distinguished by having a black midlateral stripe ending in a diamond shaped blotch at the base of the
474 caudal fin. *Rasbora sumatrana* sensu stricto is restricted to the highlands of western Sumatra (Tan & Kottelat,
475 2009). Its whole geographic range is not yet known precisely; there is also a likelihood that several species are

Appendix

476 presently confused under that name. The fishes earlier identified as *R. sumatrana* from Borneo by Brittan (1954)
477 are now re-identified as *R. hosii* and *R. calliura* (fide Tan & Kottelat, 2009). In Borneo, there are several
478 described taxa which we feel maybe confused with *R. pycnopeza*. These are *R. atranus*, *R. cryptica*, *R. hubbsi*,
479 *R. tornieri* and *R. rheophila*.

480 *Rasbora pycnopeza* is distinguished from *R. rheophila* by snout shape (pointed vs. rounded); snout length (28.3-
481 34.2 % HL, vs. 26.3 %); shortened and conspicuous lateral stripe starting midway between pectoral and pelvic
482 fins (vs. continuous stripe); fewer circumpeduncular scales (12, vs. 14); fewer lateral scales (28-33 +1 vs. 31 +
483 2); more anterior placement of dorsal-fin origin (position in relation to lateral scales 10-13 vs. 15); wider extent
484 of pigments along the posterior margin of the caudal-fin lobes ($\frac{1}{3}$ to $\frac{1}{2}$ of the fin covered, vs. extreme outer
485 margin of upper caudal-fin lobe); and longer head length (22.5-26.7 % SL, vs. 22.9).

486 Tan & Kottelat (2009), concluded that *R. hosii* is the valid name of the Sarawak *R. 'sumatrana'* from the type
487 locality in the Baram River. *Rasbora pycnopeza* differs from *R. hosii* by a larger size (total length up to 104 mm,
488 vs. 61-73); shorter predorsal length (49.6-54.6 % SL, vs. 55.4-57.3); less body depth at dorsal-fin origin (22.1-
489 25.9 % SL, vs. 26.4-27.9) giving *R. pycnopeza* a slimmer appearance; more distinct black streak along whole
490 anal-fin base (vs. a diffused appearance); midlateral black stripe is distinct and sharply contrasted (vs. indistinct
491 and gradually narrowing on the caudal peduncle); extent of pigments along the posterior margin of the caudal-
492 fin lobes ($\frac{1}{3}$ to $\frac{1}{2}$ of the fin covered, vs. extreme outer margin).

493 *Rasbora pycnopeza* is distinguished from *R. atranus* by a longer body (trunk length 74.1-78.8 % SL, vs. 68.5-
494 74.9); shorter head length (22.5-26.7 % SL, vs. 27.1-30.3); shape of the supraanal stripe (a longitudinal streak
495 along whole anal-fin base, vs. an elliptical to triangular blotch); presence of a conspicuous blackish posterior
496 margin on the caudal-fin lobes (vs. absence); midlateral black stripe clearly marked and gradually narrowing
497 (vs. less sharply contrasted or indistinct and markedly narrowing on the caudal peduncle).

498 Several other species of *Rasbora* are present in hill stream habitats in Borneo and these include *R. cryptica*, *R.*
499 *hubbsi*, *R. tornieri*, *R. vaillanti* and *R. volzii*. These taxa are also compared with *R. pycnopeza*.

500 *Rasbora pycnopeza* is distinguished from *R. cryptica* by a longer body (trunk length 74.1-78.8 % SL, vs. 72.0-
501 75.1); shorter predorsal length (49.6-54.6 % SL, vs. 54.0-56.2); different caudal fin pattern (thick black margin,
502 covering $\frac{1}{3}$ to $\frac{1}{2}$ of caudal-fin lobes, vs. none); a distinct thin black lateral stripe 3-5 scales posterior to opercle

- 503 edge till base of caudal-fin, vs. a thin diffused stripe with a mid-body black blotch and an elongate triangular
504 black blotch at caudal peduncle.
- 505 *Rasbora pycnopeza* lives sympatrically with *R. hubbsi* in the Kalabakan and Segama drainages. *R. pycnopeza* is
506 distinguished from *R. hubbsi* by maximum standard length (up to 104 mm vs. 41.4-43.9), less body depth at
507 dorsal (22.1-25.9 % SL, vs. 26.8-29.2), longer median caudal length (16.3-20.9 % SL, vs. 13.3-16.4), having 12
508 vs. 14 circumpeduncular scales rows, 1 vs. 2 scale rows between the lateral line and the origin of the pelvic fin,
509 and an distinct midlateral black stripe with an equal intensity along whole length (vs. thick stripe, more intense
510 posteriorly, with an abrupt transition to the much diffused anterior portion).
- 511 *Rasbora pycnopeza* differs from *R. tornieri* by having 12 vs. 14 circumpeduncular scales rows; a different
512 lateral head profile (slightly concave vs. straight); caudal-fin pattern consisting of a thick black margin, covering
513 $\frac{1}{3}$ to $\frac{1}{2}$ of caudal-fin lobes, vs. a black margin $\frac{1}{4}$ to $\frac{1}{5}$ of caudal fin; distinct thin black lateral stripe starting 5-6
514 scales posterior to opercle edge to base of caudal-fin, vs. presence of a broad, dark, sharply defined midlateral
515 stripe, extending from opercle to caudal-fin base and separated from the dark dorsum by a highly contrasting
516 cream longitudinal area; distinct black stripe at supraanal region covering entire anal-fin base, vs. none or a faint
517 black streak at supraanl region.
- 518 *Rasbora pycnopeza* differs from *R. vaillanti* in having a shorter predorsal length (49.6-54.6 % SL, vs. 55.2-
519 58.8); less body depth at dorsal-fin origin (22.1-25.9 % SL, vs. 27.4-32.7), body depth at anus (18.2-22.3 % SL,
520 vs. 21.8-24.2), and caudal peduncular depth (11.9-13.7 % SL, vs. 13.0-13.8); a conspicuous black streak along
521 anal-fin base, thicker at the anterior end, vs. a less distinct and thinner streak, not extending along the whole
522 length of the anal fin base; caudal fin with thicker black margin ($\frac{1}{3}$ to $\frac{1}{2}$ of caudal-fin lobes, vs. extreme outer
523 margin).
- 524 *Rasbora pycnopeza* is distinguished from *R. volzii* by the shape of the black mark above the anal-fin origin (a
525 conspicuous thickened black streak, vs. thin black streak along whole anal-fin base); pointed snout (vs.
526 rounded); the colour of the fins in life (orange/yellow, vs. hyaline); presence of a black distal margin on caudal-
527 fin lobes (vs. absence).
- 528 *Rasbora pycnopeza* can be distinguished from *R. calliura* by shape of the black mark above the anal-fin origin
529 (a conspicuous thickened black streak, vs. thin and diffused black streak along whole anal-fin base); longer
530 snout (vs. shorter); distinct mid-lateral stripe (vs. indistinct, present on posterior half of body); the colour of the

531 fins in life (orange/yellow, vs. reddish-orange); caudal fin with black margin (black margin thickened on $\frac{1}{3}$ to $\frac{1}{2}$
532 of caudal-fin lobes, vs. $\frac{1}{4}$ of caudal fin lobes).

533

534 **Comparative material.** *Rasbora atranu*s: ZRC-51186, 5 ex., 65.3-80.8 mm SL; Borneo: Kalimantan,
535 Mahakam drainage: Barito Utara. – *Rasbora calliura*: ZRC 56406, 5 ex., 46.7-76.3 mm SL; Borneo: Sarawak:
536 Upper Sarawak basin, Kiri River, Kan River. - *Rasbora cryptica*: ZRC-52463, 1 ex., ZRC-52462, 4 ex., 44.3-
537 70.8 mm SL; Borneo: Sarawak: Penrissen foothills near Serian. - *Rasbora hosii*: ZRC 42725, 5, 61.1-77.3 mm
538 SL; Borneo: Brunei. - *Rasbora hubbsi*: ZRC, 2 ex., 41.4-43.9 mm SL; Borneo: Sabah: Brantian drainage. -
539 *Rasbora rheophila*: ZRC47505, 1 ex., paratype, 68.1 mm SL; Borneo: Sabah: Kota Marudu. - *Rasbora*
540 *sumatrana*: ZRC 42289, 5 ex., 42.1-59.5 mm SL; Indonesia: Sumatra: Danau Lingkat. - *Rasbora tornieri*: ZRC
541 46077, 2 ex., ZRC 42726, 3 ex., 84.8-111.7 mm SL; Borneo: Sarawak: Miri, & Brunei. - *Rasbora vaillanti*:
542 ZRC, 5 ex., 54.6-62.4 mm SL; Borneo: Kalimantan: Mahakam drainage: Kota Bungan. - *Rasbora volzii*: ZRC
543 47024, 5 ex., ZRC 45627, 1 ex., 59.9-109.8 mm SL; Borneo: Kalimantan: Kayan drainage.

544

545

546 **Appendix 2. Sampling locations in the Brantian drainage.**

547 **Core quantitative sampling using electrofishing, cast netting, tray netting and funnel traps.**

548 S1 - 0m: small, logged forest stream, within the SAFE project experimental area (N 04° 41.991' E 117° 34.379'),
549 steep rapids and deep pools, substrate sandy and rocky.

550 S2 – 5m: small, logged forest stream, within the SAFE project experimental area (N 04° 42.452' E 117°
551 33.059'), steep rapids and deep pools, substrate sandy and rocky.

552 S3 – 15m: small, logged forest stream, within the SAFE project experimental area (N 04° 39.051' E 117°
553 34.568'), relatively shallow with some deep pools, substrate gravel and rocky.

554 S4 – 30m: small, logged forest stream, within the SAFE project experimental area (N 04° 43.520' E 117°
555 37.338'), a large flood in 2011 stripped the bank side vegetation and the stream is recovering.

556 S5 – 60m: small, logged forest stream, within the SAFE project experimental area (N 04° 43.699' E 117°
557 33.031'), steep rapids and deep pools, substrate large boulders and stones/pebbles.

558 S6 – 120m: small, logged forest stream, within the SAFE project experimental area (N 04° 42.902' E 117°
559 38.413'), steep rapids and deep pools, substrate gravel to medium-large rocks.

560 S7 – VJR: small, primary forest stream, within the Brantian Tantulit Virgin Jungle Reserve (N 04° 39.008' E
561 117° 32.498'), moderate gradient, substrate sand/gravel with some rocky boulders.

562 S8 – LFE: small, logged forest stream, adjacent to the SAFE project experimental area (N 04° 43.484' E 117°
563 35.900'), moderate gradient, but deeper than previous streams, substrate coarse sand, bedrock and rocky.

564 S9 – Binuang estate: small, oil palm stream with no riparian reserve, close to the SAFE project experimental
565 area (N 04° 41.156' E 117° 27.379'), high turbidity and sedimentation levels, substrate sand, gravel and silt.

566 S10 – Merbau: small, oil palm stream with ~30 m riparian reserve, close to the SAFE project experimental area
567 (N 04° 39.073' E 117° 37.481'), substrate sand, small-medium rocks.

568 S11 – Gaharu: small, oil palm stream with ~60 m riparian reserve, close to the SAFE project experimental area
569 (N 04° 36.147' E 117° 31.844'), substrate sand, small-medium rocks.

570 **Other quantitative sampling locations**

571 S12 – RR1A: small, logged forest stream, adjacent to the SAFE project experimental area (N 04° 45.382' E 117°
572 32.623'), moderate gradient, but deeper than previous streams, substrate sand, small-medium rocks.

573 S13 – RR2: small, oil palm stream with narrow riparian reserve, close to the SAFE project experimental area (N
574 04° 42.989' E 117° 30.749'), substrate sand, small-medium rocks.

575 S14 – RR3A: small, oil palm stream with riparian reserve, close to the SAFE project experimental area (N 04°
576 40.632' E 117° 29.380'), substrate sand, small-large rocks.

577 S15 – RR3B: small, steep, oil palm stream with riparian reserve, close to the SAFE project experimental area (N
578 04° 40.188' E 117° 29.122'), substrate sand, small-large rocks.

579 S16 – RR4: medium sized, oil palm stream with riparian reserve, close to the SAFE project experimental area
580 (N 04° 39.731' E 117° 26.190'), substrate sand, small-medium rocks.

581 S17 – RR4A: small, oil palm stream with riparian reserve, close to the SAFE project experimental area (N 04°
582 49.855' E 117° 26.644'), substrate sand, small-medium rocks.

583 S18 – RR8A: small, oil palm stream with riparian reserve, close to the SAFE project experimental area (N 04°
584 35.226' E 117° 34.339'), substrate sand, small-medium rocks.

585 S19 - RR11: small, oil palm stream with narrow riparian reserve, close to the SAFE project experimental area
586 (N 04° 44.058' E 117° 31.928'), substrate sand, small-large rocks.

- 587 S20 – RR13: small, oil palm stream with narrow riparian reserve, close to the SAFE project experimental area
588 (N 04° 36.642' E 117° 36.052'), substrate sand and gravel.
- 589 S21 – RR14: small, oil palm stream with no riparian reserve, close to the SAFE project experimental area (N
590 04° 37.471' E 117° 38.459'), substrate sand, small-medium rocks.
- 591 S22 – RR16: small, oil palm stream with no riparian reserve, close to the SAFE project experimental area (N
592 04° 38.672' E 117° 28.148'), substrate sand, small-medium rocks.
- 593 S23 – R16A: small, oil palm stream with narrow riparian reserve, close to the SAFE project experimental area
594 (N 04° 38.245' E 117° 28.798'), substrate sand, small-large rocks.
- 595 S24 – R19A: small, steep, oil palm stream with narrow riparian reserve, close to the SAFE project experimental
596 area (N 04° 39.150' E 117° 31.153'), substrate sand, small-large rocks.
- 597 S25 – RR20: small, steep, oil palm stream with riparian reserve, close to the SAFE project experimental area (N
598 04° 38.000' E 117° 26.647'), substrate sand, small-large rocks.
- 599 S26 – R21A: small, steep, oil palm stream with riparian reserve, close to the SAFE project experimental area (N
600 04° 37.563' E 117° 30.804'), substrate sand, small-large rocks.
- 601 S27 – R21B: small, oil palm stream with riparian reserve, close to the SAFE project experimental area (N 04°
602 37.166' E 117° 30.566'), substrate sand, small-large rocks.
- 603 S28 – RR30: small, oil palm stream with riparian reserve, close to the SAFE project experimental area (N 04°
604 44.486' E 117° 29.675'), substrate sand, small-large rocks.
- 605 S29 – R70B: small, logged forest stream, close to the SAFE project experimental area (N 04° 41.194' E 117°
606 39.733'), substrate sand, bedrock and small rocks.

607 Qualitative sampling locations

- 608 S30 – Sungai Brantian: Medium sized river in logged forest, within the SAFE project experimental area (N 04°
609 40.132' E 117° 35.649'), substrate silt, sand and bedrock.
- 610 S31 – Sungai VJR/Brantian: Medium sized river in logged forest, adjacent to the Brantian Tantulit Virgin
611 Jungle Reserve (N 04° 38.729' E 117° 32.030'), substrate sand and rocks, turbid from rain.
- 612 S32 – Sungai Rob: Small, steep stream in logged forest, within the SAFE project experimental area (N 04°
613 41.842' E 117° 35.340'), substrate sand, rocks and bedrock.
- 614 S32 – Sungai Gaharu (RR10): Medium sized, fast flowing river in oil palm plantation, close to the SAFE project
615 experimental area (N 04° 37.827' E 117° 31.677'), substrate sand and rocks.
- 616 S33 – Sungai Brantian (Seraya estate): Large river in oil palm plantation, close to the SAFE project
617 experimental area (N 04° 36.651' E 117° 33.542'), substrate sand and rocks.
- 618 S34 – Pool next to Sungai Brantian: Stagnant pool next to Brantian river (N 04° 36.651' E 117° 33.542'), water
619 almost clear.
- 620 S35 – 30m (downstream): Small, fast flowing stream in logged forest, within the SAFE project experimental
621 area (N 04° 43.368' E 117° 36.748'), substrate sand, rocks and bedrock.
- 622 S36 – LFE (~1km downstream of quantitative transect): Medium sized, fast flowing stream in logged forest,
623 within the SAFE project experimental area (N 04° 43.046' E 117° 36.448'), substrate sand, rocks and bedrock.
- 624 S37 – Sungai Menggaris: Medium sized, fast flowing river in oil palm plantation, close to the SAFE project
625 experimental area (N 04° 39.727' E 117° 36.879'), substrate sand and rocks
- 626 S38 – LFE(~300m upstream of quantitative transect): Small, fast flowing stream in logged forest, within the
627 SAFE project experimental area (N 04° 43.475' E 117° 35.791'), substrate sand, rocks and bedrock.

628

629

Appendix

630

631 APPENDIX 2 – FOR CHAPTER 2

APPENDIX 2.1 – STREAMS SAMPLED IN EACH YEAR

Stream code and associated name at the SAFE project	Transect Co-ordinates	2011	2013	2015
OG1 – West	N4° 57.678' E117° 47.658'			X
OG2 – Rhinopool	N4° 56.970' E117° 47.788'			X
OG3 - Tembaling	N4° 56.758' E117° 48.320'			X
OG4 – VJR	N 04° 39.008' E 117° 32.498'	X	X	X
LF1 – 0m	N 04° 41.991' E 117° 34.379'	X	X	
LF2 – 5m	N 04° 42.452' E 117° 33.059'	X	X	
LF3 – 15m	N 04° 39.051' E 117° 34.568'	X		
LF4 – 30m	N 04° 43.520' E 117° 37.338'	X	X	
LF5 – 60m	N 04° 43.699' E 117° 33.031'	X		
LF6 – 120m	N 04° 42.902' E 117° 38.413'	X	X	
LF7 – LFE	N 04° 43.484' E 117° 35.900'	X	X	X
OP1 – Binuang	N 04° 41.156' E 117° 27.379'			X
OP2 – Selangan batu/ OP1	N4° 37.927' E117° 27.375'	X	X	X
OP3 – Gaharu	N 04° 36.147' E 117° 31.844'			X
OP4 – Keruing	N4° 34.618' E117° 37.320'			X
OP5 – Merbau	N 04° 39.073' E 117° 37.481'		X	X
Total		9	8	10

APPENDIX 2.2 – BIOMASS REGRESSION EQUATIONS

Table A2. Biomass regression equations were calculated for each species. Equations were calculated where more than 30 sampled individuals of each species had total length and mass measurements. If not enough individuals from a species had length and mass measurements, generic equations were used and calculated for two groups of fish: heavy bodied and flattened (based on Martin-Smith (1996)). Regression equations take the form $\log W = a \log L + b$.

Species	N	Slope of regression (a)	Intercept of regression (b)	Notes
Heavy bodied				
<i>Barbodes sealei</i>	428	2.9377	-1.8819	
<i>Hampala sabana</i>	57	3.0611	-2.1401	†
<i>Hemibagrus baramensis</i>	24	2.8276	-1.9478	All <i>Hemibagrus</i> species
<i>Hemibagrus fortis</i>	7	2.8276	-1.9478	were grouped together for calculations
Flattened				
<i>Leptobarbus melanotaenia</i>	-	2.8587	-1.8928	†
<i>Lobocheilus erinaceus</i>	32	3.1776	-2.331	
<i>Osteochilus chini</i>	209	2.5345	-1.5802	2
<i>Osteochilus ingeri</i>	48	2.8931	-1.955	
<i>Pseudomystus armatus</i>	-	2.8587	-1.8928	†
<i>Tor tambra</i>	233	2.8886	-1.9095	
Flattened				
<i>Barbonymus balleroides</i>	124	2.6274	-1.6398	Both <i>Barbonymus</i> species were grouped together.
<i>Barbonymus collingwoodi</i>	-	2.6274	-1.6398	
<i>Betta unimaculata</i>	-	2.8137	-1.9468	†
<i>Crossocheilus elegans</i>	77	2.9223	-2.0954	
<i>Garra borneensis</i>	-	2.8137	-1.9468	†
<i>Gastromyzon ingeri</i>	8	2.9924	-1.8204	All <i>Gastromyzon</i> species
<i>Gastromyzon lepidogaster</i>	155	2.9924	-1.8204	were grouped together for calculations
<i>Gastromyzon umbrus</i>	4	2.9924	-1.8204	
<i>Luciosoma pelligrini</i>	-	2.8137	-1.9468	†
<i>Nematobramis borneensis</i>	-	2.8059	-1.9745	Both <i>Nematobramis</i> species were grouped together.
<i>Nematobramis everetti</i>	1613	2.8059	-1.9745	
<i>Nemacheilus olivaceus</i>	-	2.8137	-1.9468	†
<i>Parhomaloptera microstoma</i>	-	2.8137	-1.9468	†
<i>Protomyzon griswoldi</i>	83	2.927	-1.9539	83
<i>Rasbora cf. sumatrana</i>	605	2.795	-1.9508	All <i>Rasbora</i> species were grouped together for calculations
<i>Rasbora einthovenii</i>	-	2.795	-1.9508	
<i>Rasbora hubbsi</i>	7	2.795	-1.9508	

†calculated from standard group equation as not enough individuals

633 APPENDIX FOR CHAPTER 3

634 APPENDIX 3.1 – FISH FUNCTIONAL TRAITS

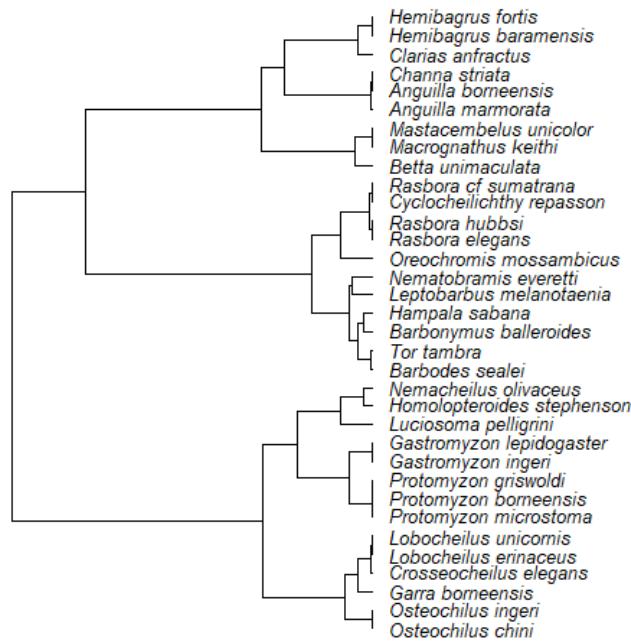


Figure A3.1.1. Dendrogram of freshwater fish caught during this study, clustered using the ward.D methodology through functional diversity analysis.

635

636

Table A3.1.2. The nine species traits used to characterize functional diversity and their functional relevance

Trait	Function	Variable type and levels
Total length	Length is used as a proxy for size. Length can correlate with different life history strategies, and also determines the rate of energy flows in the ecosystem and the type of prey the fish can consume.	Continuous (in mm)
Air-breathing capability	Can enable species to move between water bodies to expand range, escape predators or survive in low oxygen environments e.g., during low water flows or dry seasons.	Binary (0 or 1)
Gregariousness	Gregarious or schooling behaviour. Groups may be better able to find and exploit patchy food resources, habitat and avoid predators.	Binary (0 or 1)
Mouth position	Reflects feeding strata or trophic group.	Factorial (Terminal, Inferior, Superior)
Body shape	To indicate mode of locomotion and preferred habitat.	Factorial (Laterally compressed, Dorsal-ventrally depressed or flattened, Cylindrical).
Presence of barbels	Barbels help fishes in sensing the environment and finding prey.	Binary (0 or 1)
Vertical position	Indicates habitat use within the water column.	Factorial (Benthic, Benthopelagic, Pelagic, Surface)
Presence of oral jaw teeth	Determines the mode of feeding and the type of prey that can be captured and consumed by the fish.	Binary (0 or 1)
Trophic group	Feeding strategy. The trophic ecology of the species affects energy flow in the system, depending on which resources are available and in what abundance.	Factorial (Herbivore, Invertivore, Omnivore, Carnivore)

637

638

Appendix

Table A3.1.3. Functional traits of each species present in this study. TL = mean total length (N = number of specimens, SD = standard deviation).

	TL in cm (N, SD)	Body shape	Trophic position	Mouth position	Jaw teeth (0=absent; 1=present)	Gregariousness (0=absent; 1=present)	Barbels (0=absent; 1=present)	Position in water column	Air-breathing (0=absent; 1=present)
<i>Anguilla borneensis</i>	24.14 (50, 9.93)	Cylindrical	Carnivore	Terminal	1	0	1	Benthopelagic	1
<i>Anguilla marmorata</i>	30.56 (47, 8.58)	Cylindrical	Carnivore	Terminal	1	0	1	Benthopelagic	1
<i>Barbodes sealei</i>	8.51 (869, 3.62)	Compressed	Omnivore	Terminal	0	1	1	Pelagic	0
<i>Barbodus balleroides</i>	11.36 (20, 1.36)	Compressed	Invertivore	Terminal	0	1	1	Pelagic	0
<i>Betta unimaculata</i>	7.59 (9, 1.22)	Compressed	Invertivore	Terminal	1	0	0	Benthopelagic	1
<i>Channa striata</i>	-	Cylindrical	Carnivore	Terminal	1	0	1	Benthopelagic	1
<i>Clarias anfractus</i>	19.77 (3, 3.30)	Compressed	Carnivore	Terminal	0	0	1	Benthopelagic	0
<i>Crossocheilus elegans</i>	9.27 (37, 0.85)	Cylindrical	Herbivore	Inferior	0	1	1	Benthopelagic	0
<i>Cyclocheilichthys repasson</i>	11.93 (9, 1.60)	Compressed	Invertivore	Terminal	0	1	0	Pelagic	0
<i>Garra borneensis</i>	8.44 (37, 0.58)	Cylindrical	Herbivore	Inferior	0	1	1	Benthic	0
<i>Gastromyzon ingeri</i>	4.28 (35, 0.82)	Depressed	Herbivore	Inferior	0	0	1	Benthic	0
<i>Gastromyzon lepidogaster</i>	5.75 (127, 1.65)	Depressed	Herbivore	Inferior	0	0	1	Benthic	0
<i>Hampala sabana</i>	11.94 (123, 3.27)	Compressed	Carnivore	Terminal	0	1	1	Pelagic	0

Appendix

<i>Hemibagrus baramensis</i>	14.55 (62, 3.03)	Depressed	Carnivore	Terminal	0	0	1	Benthopelagic	0
<i>Hemibagrus fortis</i>	13.39 (19, 4.96)	Depressed	Carnivore	Terminal	0	0	1	Benthopelagic	0
<i>Homolopteroides stephensonii</i>	5.67 (6, 0.81)	Depressed	Invertivore	Inferior	0	0	1	Benthic	0
<i>Leptobarbus melanotaenia</i>	12.15 (2, 1.06)	Compressed	Invertivore	Terminal	0	0	1	Pelagic	0
<i>Lobocheilos erinaceus</i>	12.33 (3, 0.55)	Cylindrical	Herbivore	Inferior	0	1	1	Benthopelagic	0
<i>Lobocheilos unicornis</i>	12.50 (6, 1.20)	Cylindrical	Herbivore	Inferior	0	1	1	Benthopelagic	0
<i>Luciosoma pelligrinii</i>	15.30 (1, NA)	Cylindrical	Invertivore	Superior	0	0	1	Surface	0
<i>Macrognathus keithi</i>	17.50 (1, NA)	Compressed	Invertivore	Terminal	1	0	0	Benthopelagic	0
<i>Mastacembelus unicolor</i>	17.35 (3, 5.86)	Compressed	Invertivore	Terminal	1	0	0	Benthopelagic	0
<i>Nemacheilus olivaceus</i>	6.80 (31, 0.93)	Cylindrical	Invertivore	Inferior	0	0	1	Benthic	0
<i>Nematobramis everetti</i>	8.53 (1441, 4.04)	Compressed	Invertivore	Superior	0	1	1	Pelagic	0
<i>Oreochromis mossambicus</i>	11.20 (3, 1.01)	Compressed	Omnivore	Terminal	1	1	0	Pelagic	0
<i>Osteochilus chini</i>	10.58 (158, 2.10)	Compressed	Herbivore	Inferior	0	1	1	Benthopelagic	0
<i>Osteochilus ingeri</i>	10.71 (76, 2.25)	Compressed	Herbivore	Inferior	0	1	1	Benthopelagic	0
<i>Protomyzon borneensis</i>	4.05 (2, 0.35)	Depressed	Herbivore	Inferior	0	1	1	Benthic	0

Appendix

<i>Protomyzon griswoldi</i>	4.26 (87, 1.15)	Depressed	Herbivore	Inferior	0	1	1	Benthic	0
<i>Parhomaloptera microstoma</i>	4.91 (24, 1.41)	Depressed	Herbivore	Inferior	0	1	1	Benthic	0
<i>Rasbora cf. sumatrana</i>	8.79 (607, 3.39)	Compressed	Invertivore	Terminal	0	1	0	Pelagic	0
<i>Rasbora elegans</i>	5.77 (10, 1.25)	Compressed	Invertivore	Terminal	0	1	0	Pelagic	0
<i>Rasbora hubbsi</i>	5.45 (73, 0.87)	Compressed	Invertivore	Terminal	0	1	0	Pelagic	0
<i>Tor tambra</i>	12.36 (327, 3.78)	Compressed	Omnivore	Terminal	0	1	1	Pelagic	0

639

640

APPENDIX 3.2 – BIOMASS REGRESSION EQUATIONS

Table A3.2.1. Biomass regression equations were calculated for each species. Equations were calculated where more than 30 sampled individuals of each species had total length and mass measurements. If not enough individuals from a species had length and mass measurements, generic equations were used and calculated for two groups of fish: heavy bodied and flattened (as done by Martin-Smith (1996)). Regression equations take the form $\log W = a \log L + b$.

Species	N	Slope of regression (x)	Intercept of regression (y)	Notes
Heavy bodied				
<i>Barbodes sealei</i>	428	2.9377	-1.8819	
<i>Channa striata</i>	-	2.8587	-1.8928	*
<i>Clarias anfractus</i>	-	2.8587	-1.8928	*
<i>Cyclocheilichthys repasson</i>	-	2.6984	-1.6815	*
<i>Hampala sabana</i>	57	3.0611	-2.1401	*
<i>Hemibagrus baramensis</i>	24	2.8276	-1.9478	All <i>Hemibagrus</i> species were grouped together for calculations
<i>Hemibagrus fortis</i>	7	2.8276	-1.9478	
<i>Leptobarbus melanotaenia</i>	-	2.8587	-1.8928	*
<i>Lobocheilos erinaceus</i>	32	3.1776	-2.331	
<i>Lobocheilos unicornis</i>	66	2.9272	-2.0808	
<i>Oreochromis mossambicus</i>	-	2.8587	-1.8928	*
<i>Osteochilus chini</i>	209	2.5345	-1.5802	
<i>Osteochilus ingeri</i>	48	2.8931	-1.955	
<i>Tor tambra</i>	233	2.8886	-1.9095	
Flattened				
<i>Barbomyrus balleroides</i>	124	2.6274	-1.6398	
<i>Betta unimaculata</i>	-	2.8137	-1.9468	*
<i>Crossocheilus elegans</i>	77	2.9223	-2.0954	
<i>Garra borneensis</i>	-	2.8137	-1.9468	*
<i>Gastromyzon ingeri</i>	8	2.9924	-1.8204	All <i>Gastromyzon</i> species were grouped together for calculations
<i>Gastromyzon lepidogaster</i>	155	2.9924	-1.8204	
<i>Gastromyzon umbrus</i>	4	2.9924	-1.8204	
<i>Homolopteroides stephensi</i>	-	2.8137	-1.9468	*
<i>Luciosoma pelligrinii</i>	-	2.8137	-1.9468	*
<i>Nematobramis everetti</i>	1613	2.8059	-1.9745	
<i>Nemacheilus olivaceus</i>	-	2.8137	-1.9468	*
<i>Parhomaloptera microstoma</i>	-	2.8137	-1.9468	*
<i>Protomyzon borneensis</i>	-	2.927	-1.9539	All <i>Protomyzon</i> species were grouped together for calculations
<i>Protomyzon griswoldi</i>	83	2.927	-1.9539	
<i>Protomyzon microstoma</i>	2	2.927	-1.9539	
<i>Rasbora cf. sumatrana</i>	605	2.795	-1.9508	Both <i>Rasbora</i> species were grouped together for calculations
<i>Rasbora elegans</i>	-	2.795	-1.9508	
<i>Rasbora hubbsi</i>	7	2.795	-1.9508	

*calculated from standard group equation as not enough individuals

APPENDIX 3.3 – ENVIRONMENTAL PREDICTORS OF SPECIES RICHNESS

Table A3.3.1. Results of univariate generalised linear models determining what environmental variables best predict species richness, and if they change significantly by land-use. P values are adjusted using Bonferroni correction, due to the multiple tests on each data set. Variables in bold are significant after p value correction.

Species Richness (Poisson or Quasipoisson *)				Land-use			
	P	Corrected P	Chisq	P	Corrected P	Chisq	
Instream							
Littoral leaf litter cover	<0.001	0.003	14.565	***	0.305	1	4.832
Turbidity*	0.335	1	0.913		0.287	1	5.005
Mean surface current speed*	0.177	1	1.821		0.110	1	7.529
Wetted width*	0.753	1	0.099		0.370	1	4.277
Mean depth*	0.125	1	2.375		0.416	1	3.925
% sand*	0.517	1	0.421		0.165	1	6.495
% gravel	<0.001	0.011	11.966	***	0.380	1	4.197
% pebbles*	0.128	1	2.312		0.552	1	3.034
% large rocks*	0.972	1	0.001		0.022	0.456	11.474
% bedrock*	0.099	1	2.716		0.583	1	2.8514
pH *	0.118	1	2.436		0.131	1	7.087
Temperature*	0.956	1	0.003		< 0.001	< 0.001	33.223
O2*	0.892	1	0.009		0.4780	1	3.487
Conductivity*	0.336	1	0.926		0.480	1	3.487
Canopy cover*	0.311	1	1.025		<0.001	< 0.001	21.338
Sedimentation	0.054	1	3.718		<0.001	< 0.001	50.87
Riparian							
Canopy cover*	0.334	1	0.935		< 0.001	< 0.001	20.488
% vines*	0.645	1	0.212		< 0.001	< 0.001	27.777
Density of trees	0.007	0.154	7.188	**	< 0.001	< 0.001	35.784
Forest quality*	0.065	1	3.398		< 0.001	< 0.001	181.07
Elevation	>0.001	>0.001	21.019	***	0.256	1	5.3161

APPENDIX 3.4 – SPECIES LIST & PRESENCE IN EACH CATCHMENT

Table A3.4.1. Full species list with the appropriate authority of 34 species found within this study.

Family Anguillidae

Anguilla borneensis Popta, 1924

Anguilla marmorata Quoy & Gaimard, 1824

Family Cyprinidae

Barbodes sealei Herre, 1933

Barbonymus balleroides (Valenciennes, in Cuvier & Valenciennes, 1842)

Crossocheilus elegans Kottelat & Tan 2011

Cyclocheilichthys repasson (Bleeker, 1853)

Garra borneensis (Vaillant, 1902)

Hampala sabana Inger & Chin, 1962

Leptobarbus melanotaenia Boulenger, 1894

Lobocheilos erinaceus Kottelat & Tan 2008

Lobocheilos unicornis Kottelat & Tan 2008

Luciosoma pelligrinii Popta 1904

Nematobramis everetti Boulenger, 1894

Osteochilus chini Karnasuta, 1993

Osteochilus ingeri Karnasuta, 1993

Rasbora cf. *sumatrana* - Tan, 2013

Rasbora elegans Voltz, 1903

Rasbora hubbsi Brittan, 1954

Tor tmbra (Valenciennes, in Cuvier & Valenciennes, 1842)

Family Nemacheilidae

Nemacheilus olivaceus Boulenger, 1894

Family Bagridae

Hemibagrus baramensis (Regan, 1906)

Hemibagrus fortis (Popta, 1904)

Family Bagridae

Clarias anfractus Ng, 1999

Family Gastromyzontidae

Gastromyzon ingeri Tan, 2006

Gastromyzon lepidogaster Roberts, 1982

Parhomaloptera microstoma (Boulenger, 1899)

Protomyzon borneensis Hora & Jayaram, 1952

Protomyzon griswoldi (Hora & Jayaram, 1952)

Family Osphronemidae

Betta ocellata de Beaufort, 1933

Family Channidae

Channa striata (Bloch, 1793)

Family Mastacembelidae

Macrognathus keithi (Herre, 1940)

Mastacembelus unicolor Cuvier, in Cuvier & Valenciennes, 1832

Family Balitoridae

Homolopteroides stephensonii (Hora, 1932)

NON-NATIVE

Family Cichlidae

Oreochromis mossambicus (Peters, 1852)

APPENDIX

Table A3.4.2. Presence of each species in each stream and land-use within this study. OP = oil-palm plantation without riparian buffer, OPB = oil-palm plantation with riparian buffer, LF3 = salvage-logged forest after the third round of logging, LF2 = twice-logged forest, and PF = protected forest catchments. Catchments are: B = Brantian, K = Kalabakan, S = Segama.

Stream	LF E	RR1 a	R70 B	30 0m	120 m	60 5m	15 m	RR1 4	S. batu	RR1 Bin	RR1 6	Mer	RR2 A	RR8 A	R16 A	RR3 B	Tem	Rhi	W es	S. Kal	VJ		
Catchment	B	B	B	B	B	B	B	B	K	B	B	B	B	B	B	B	S	S	S	S	B		
	LF2			LF3					OP					OPB					PF				
Family Anguillidae																							
<i>Anguilla borneensis</i>	0	0	0	0	0	1	1	0	1	1	0	0	1	0	0	0	0	1	1	1	1	1	0
<i>Anguilla marmorata</i>	0	1	0	1	0	1	1	0	1	1	0	0	1	1	0	0	1	0	0	0	0	1	
Family Cyprinidae																							
<i>Barbodes sealei</i>	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Barbonymus balleroides</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
<i>Cyclocheilichthys repasson</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	
<i>Crossocheilus elegans</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Garra borneensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	
<i>Hampala sabana</i>	0	1	0	1	0	1	0	0	1	0	0	0	0	0	1	0	1	1	1	1	1	1	0
<i>Leptobarbus melanotaenia</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0
<i>Lobocheilos erinaceus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
<i>Lobocheilos unicornis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0
<i>Luciosoma pelligrinii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0

APPENDIX

	LF E	RR 1a	R7 OB	30 0m	120 m	5m	60 m	15 m	RR 14	S. batu	Bin	RR 16	Mer	RR 2	RR 8A	R1 6A	RR 3B	Tem	Rhi	W es	S. Kal	V J	
	LF2			LF3					OP				OPB				PF						
<i>Nematobramis everetti</i>	0	1	1	1	0	1	0	0	1	0	1	1	1	0	1	0	0	1	1	1	1	1	1
<i>Osteochilus chini</i>	0	0	1	0	0	1	0	0	1	0	0	1	1	0	0	1	0	1	1	0	0	1	0
<i>Osteochilus ingeri</i>	0	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	1	0
<i>Rasbora cf. sumatrana</i>	1	0	1	1	1	1	0	0	1	0	0	1	0	1	1	0	0	1	1	1	1	1	0
<i>Rasbora elegans</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Rasbora hubbsi</i>	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	1	0	0	1	1
<i>Tor ticto</i>	0	1	0	0	0	1	1	0	1	0	0	1	1	1	0	0	1	1	1	1	1	1	1
Family Nemacheilidae																							
<i>Nemacheilus olivaceus</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	1	1
Family Bagridae																							
<i>Hemibagrus baramensis</i>	0	0	1	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1
<i>Hemibagrus fortis</i>	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	1	1	1	1	0
Family Bagridae																							
<i>Clarias anfractus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Family Gastromyzontidae																							
<i>Gastromyzon ingeri</i>	0	0	0	0	0	1	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	0
<i>Gastromyzon lepidogaster</i>	1	0	1	1	0	1	1	1	0	1	1	0	1	1	1	0	1	1	1	1	0	1	1

APPENDIX

	LF E	RR 1a	R7 OB	30 0m	120 m	60 5m	15 m	RR 14	S. batu	RR 16	Mer	RR 2	RR 8A	R1 6A	RR 3B	Tem	Rhi	W es	S. Kal	V J
	LF2			LF3					OP			OPB				PF				
<i>Parhomalopter a microstoma</i>	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Protomyzon borneensis</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Protomyzon griswoldi</i>	1	0	0	0	0	1	1	1	1	0	1	0	1	0	0	0	0	0	0	0
Family Osphronemidae																				
<i>Betta ocellata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
Family Channidae																				
<i>Channa striata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Family Mastacembelidae																				
<i>Macrognathus keithi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>Mastacembelus unicolor</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Family Balitoridae																				
<i>Homolopteroide s stephensonii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
NON-NATIVE																				
Family Cichlidae																				
<i>Oreochromis mossambicus</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0

APPENDIX 4 – CHAPTER 4**APPENDIX 4.1 – BIOMASS REGRESSION EQUATIONS**

Table 4.1.1. Biomass regression equations were calculated for each species. Equations were calculated where more than 30 sampled individuals of each species had total length and mass measurements. If not enough individuals from a species had length and mass measurements, generic equations were used and calculated for two groups of fish: heavy bodied and flattened (as done by Martin-Smith (1996)). Regression equations take the form $\log W = a \log L + b$.

Species	N	Slope of regression (x)	Intercept of regression (y)	Notes
Heavy bodied				
<i>Barbodes sealei</i>	428	2.9377	-1.8819	
<i>Channa striata</i>	-	2.8587	-1.8928	*
<i>Clarias anfractus</i>	-	2.8587	-1.8928	*
<i>Cyclocheilichthys repasson</i>	-	2.6984	-1.6815	*
<i>Hampala sabana</i>	57	3.0611	-2.1401	*
<i>Hemibagrus baramensis</i>	24	2.8276	-1.9478	All <i>Hemibagrus</i> species were grouped together for calculations
<i>Hemibagrus fortis</i>	7	2.8276	-1.9478	
<i>Leptobarbus melanotaenia</i>	-	2.8587	-1.8928	*
<i>Lobocheilos erinaceus</i>	32	3.1776	-2.331	
<i>Lobocheilos unicornis</i>	66	2.9272	-2.0808	
<i>Oreochromis mossambicus</i>	-	2.8587	-1.8928	*
<i>Osteochilus chini</i>	209	2.5345	-1.5802	
<i>Osteochilus ingeri</i>	48	2.8931	-1.955	
<i>Tor ticta</i>	233	2.8886	-1.9095	
Flattened				
<i>Barbomyrus balleroides</i>	124	2.6274	-1.6398	
<i>Betta ocellata</i>	-	2.8137	-1.9468	*
<i>Crossocheilus elegans</i>	77	2.9223	-2.0954	
<i>Garra borneensis</i>	-	2.8137	-1.9468	*
<i>Gastromyzon ingeri</i>	8	2.9924	-1.8204	All <i>Gastromyzon</i> species were grouped together for calculations
<i>Gastromyzon lepidogaster</i>	155	2.9924	-1.8204	
<i>Gastromyzon umbrus</i>	4	2.9924	-1.8204	
<i>Homalopteroides stephensoni</i>	-	2.8137	-1.9468	*
<i>Luciosoma pelligrini</i>	-	2.8137	-1.9468	*
<i>Nematabramis everetti</i>	1613	2.8059	-1.9745	
<i>Nemacheilus olivaceus</i>	-	2.8137	-1.9468	*
<i>Parhomaloptera microstoma</i>	-	2.8137	-1.9468	*
<i>Protomyzon borneensis</i>	-	2.927	-1.9539	
<i>Protomyzon griswoldi</i>	83	2.927	-1.9539	

Appendix

<i>Parhomaloptera microstoma</i>	2	2.927	-1.9539	All <i>Protomyzon</i> species were grouped together for calculations
<i>Rasbora cf. sumatrana</i>	605	2.795	-1.9508	Both <i>Rasbora</i> species were grouped together for calculations
<i>Rasbora elegans</i>	-	2.795	-1.9508	
<i>Rasbora hubbsi</i>	7	2.795	-1.9508	

*calculated from standard group equation as not enough individuals

APPENDIX 4.2 – SPECIES LIST AND PRESENCE IN EACH LAND-USE**Table 4.2.1.** Species list of the 34 species observed during this study, & presence in each land-use.

	PF	LF2	LF3	OPB	OP
Family Anguillidae					
<i>Anguilla borneensis</i> Popta, 1924	X		X	X	X
<i>Anguilla marmorata</i> Quoy & Gaimard, 1824	X	X	X	X	X
Family Cyprinidae					
<i>Barbodes sealei</i> (Herre, 1933)	X	X	X	X	X
<i>Barbonymus balleroides</i> (Valenciennes, in Cuvier & Valenciennes, 1842)					X
<i>Cyclocheilichthys repasson</i> (Bleeker, 1853) *					X
<i>Crossocheilus elegans</i> Kottelat & Tan 2011	X				
<i>Garra borneensis</i> (Vaillant, 1902)	X				
<i>Hampala sabana</i> Inger & Chin, 1962	X	X	X	X	
<i>Leptobarbus melanotaenia</i> Boulenger, 1894 *	X				X
<i>Lobocheilos erinaceus</i> Kottelat & Tan 2008 *	X				
<i>Lobocheilos unicornis</i> Kottelat & Tan 2008 *	X				
<i>Luciosoma pelligrini</i> Popta 1904 *	X				
<i>Nematabramis everetti</i> Boulenger, 1894	X	X	X	X	X
<i>Osteochilus chini</i> Karnasuta, 1993	X	X	X	X	X
<i>Osteochilus ingeri</i> Karnasuta, 1993	X	X	X	X	X
<i>Rasbora cf. sumatrana</i> (Bleeker, 1852)	X	X	X	X	X
<i>Rasbora elegans</i> Voltz, 1903		X			
<i>Rasbora hubbsi</i> Brittan, 1954	X	X	X	X	
<i>Tor ticta</i> (Valenciennes, in Cuvier & Valenciennes, 1842)	X	X	X	X	X
Family Nemacheilidae					
<i>Nemachilus olivaceus</i> Boulenger, 1894	X			X	X
Family Bagridae					
<i>Hemibagrus baramensis</i> (Regan, 1906)	X	X	X	X	X
<i>Hemibagrus fortis</i> (Popta, 1904)	X		X	X	X
Family Bagridae					
<i>Clarias anfractus</i> Ng, 1999 *					X
Family Gastromyzontidae					
<i>Gastromyzon ingeri</i> Tan, 2006	X		X	X	X
<i>Gastromyzon lepidogaster</i> Roberts, 1982	X	X	X	X	X
<i>Parhomaloptera microstoma</i> (Boulenger, 1899)			X	X	
<i>Protomyzon borneensis</i> Inger & Chin 1962 *			X	X	
<i>Protomyzon griswoldi</i> (Hora & Jayaram, 1952)	X	X	X	X	X
Family Osphronemidae					
<i>Betta ocellata</i> de Beaufort, 1933 *		X			
Family Channidae					
<i>Channa striata</i> (Bloch, 1793) *					X
Family Mastacembelidae					
<i>Macrognathus keithi</i> (Herre, 1940) *			X		
<i>Mastacembelus unicolor</i> Valenciennes, in Cuvier & Valenciennes, 1832 *	X				X
Family Balitoridae					
<i>Homalopteroides stephensi</i> (Hora, 1932) *			X		
NON-NATIVE					
Family Cichlidae					
<i>Oreochromis mossambicus</i> (Peters, 1852) *					X

* Rare species, < 10 individuals captured.

APPENDIX 4.3 – COMMUNITY LEVEL ANALYSESE MODEL OUTPUTS

Model	Chi-sq*	DF	AIC	P-value*	Pseudo R-sq	RMSE* (training data only (n=17))
<i>Species richness (poisson)</i>						
width + FQmode2 + TimeSinceDisturbance + width * FQmode2 + FQmode2 *		18	191.7			
TimeSinceDisturbance + width * TimeSinceDisturbance + width * TimeSinceDisturbance						
width + FQmode + TimeSinceDisturbance + width * FQmode + FQmode * TimeSinceDisturbance		19	189.71			
width * FQmode + TimeSinceDisturbance		22	192.81			
width * FQmode		23	191.12			
width + FQmode		27	188.39			
FQmode	35.768	28	186.42	< 0.001	0.496	8.310
<i>Biomass</i>						
width + FQmode2 + TimeSinceDisturbance + width * FQmode2 + FQmode2 *		18	562.81			
TimeSinceDisturbance + width * TimeSinceDisturbance						
width + FQmode + TimeSinceDisturbance + width * FQmode + FQmode * TimeSinceDisturbance		19	563.52			
width * FQmode + TimeSinceDisturbance		22	560.34			
width * FQmode		23	558.35			
width + FQmode		27	551.34			
FQmode		28	549.78			
1 (null)	NA	33	548.71	NA	NA	797.732
<i>Fric</i>						
width + FQmode2 + TimeSinceDisturbance + width * FQmode2 + FQmode2 *		18	3.1419			
TimeSinceDisturbance + width * TimeSinceDisturbance						

Appendix

width + FQmode + TimeSinceDisturbance + width * FQmode + FQmode * TimeSinceDisturbance		19	1.258			
width * FQmode + TimeSinceDisturbance		22	4.092			
width * FQmode		23	2.476			
FQmode + width		27	-4.822			
FQmode	20.521	28	-5.397	<0.001	0.423	0.240
<i>Feve</i>						
width + FQmode2 + TimeSinceDisturbance + width * FQmode2 + FQmode2 * TimeSinceDisturbance + width * TimeSinceDisturbance		18	-15.495			
width + FQmode + TimeSinceDisturbance + width * FQmode + FQmode * TimeSinceDisturbance		19	-12.380			
width * FQmode + TimeSinceDisturbance		22	-11.792			
width * FQmode		26	-13.654			
FQmode + width		27	-19.832			
Width	3.484	32	-27.085	0.062	0.098	0.178
<i>Fdiv</i>						
width + FQmode2 + TimeSinceDisturbance + width * FQmode2 + FQmode2 * TimeSinceDisturbance + width * TimeSinceDisturbance		18	-27.63			
width + FQmode + TimeSinceDisturbance + width * FQmode + FQmode * TimeSinceDisturbance		19	-29.139			
width * FQmode + TimeSinceDisturbance		22	-31.506			
width + FQmode + TimeSinceDisturbance		23	-38.339			
FQmode + TimeSinceDisturbance		27	-39.4			
TimeSinceDisturbance	4.8117	32	-47.604	0.028	0.131	0.192
<i>Simpson's diversity index</i>						
width + FQmode2 + TimeSinceDisturbance + width * FQmode2 + FQmode2 * TimeSinceDisturbance + width * TimeSinceDisturbance		18	-7.849			

Appendix

width + FQmode + TimeSinceDisturbance + width * FQmode + FQmode * TimeSinceDisturbance		19	-9.849			
width * FQmode + TimeSinceDisturbance		22	-4.952			
width * FQmode		23	-6.717			
width + FQmode		27	-11.367			
width	6.005	32	-14.671	0.014	0.158	0.185

*Values only included for the model of best fit for each response variable.

Table 3-2. Community regression tree model outputs and the root mean square error (RMSE) for community level fish analysis. Presence in the first node or tree split and within the tree are presented for each model parameter: average riparian width (Width), riparian forest quality (FQ) measured using the SAFE project forest quality score (Ewers et al., 2011), and time since disturbance (time) within the catchment. Root mean square error is recorded for the training and test datasets (randomly split, n=17 for each), and compared to the generalised linear models in Appendix 1-2.

	Presence in first node (1 st split)			Presence in tree			RMSE		
	Width (m)	FQ (score)	Time (years)	Width	FQ	Time	Training data	Test data	Comparison to lm
SR		X (2&3 v. 0,1,4,5)			X		3.339	4.308	Lower
Biomass		X (2,3,5 v.0,1,4)			X		582.151	914.732	Training is lower, test higher
fric		X (0,2,3 v.1,4,5)			X		0.178	0.205	Lower
feve		X (0,2,4 v.1,3,5)			X		0.110	0.194	Training is lower, test higher
fdiv			X (10.5)	X (35)		X	0.071	0.143	Lower
Simpson's Diversity Index	X (37)			X			0.156	0.204	Training is lower, test higher

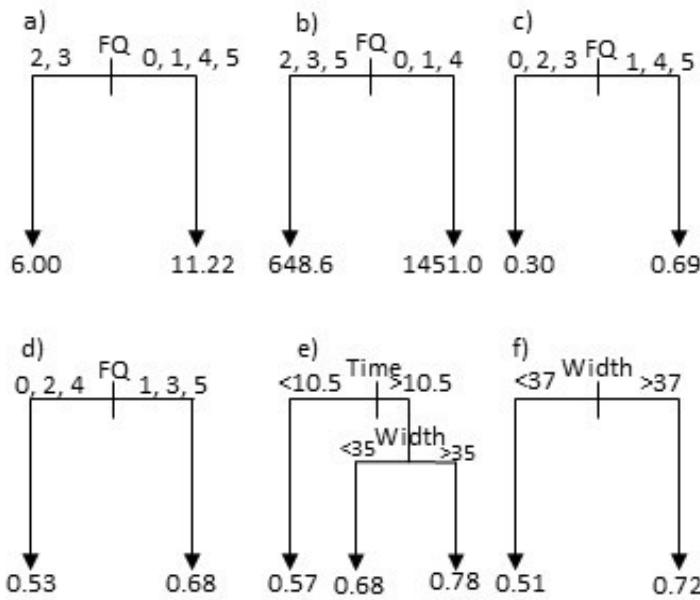


Figure 3.3. Regression trees of each freshwater fish community metric and the three riparian variables: a) species richness, b) biomass, c) functional richness, d) functional evenness, e) functional divergence, and f) Simpson's diversity index. Riparian forest quality is measured over a 500 m transect and the mode of a forest quality score (0-5; (Ewers et al. 2011)) is measured, riparian width (m) is measured from satellite imagery, and averaged over 500 m, and time since disturbance (years) is measured from the time since oil-palm planting or the last round of logging within the catchment.

APPENDIX 4.4 – SPECIES LEVEL ANALYSES MODEL OUTPUTS

Table 4.4.1. Linear mixed model outputs for fish species abundance relationship with the three riparian variables: forest quality (FQ), width and time since disturbance (time). Model degrees of freedom (DF), R-squared (R-sq), and AIC are given for all models, model chi-squared (Chi-sq), and p value only given for the most parsimonious model.

Model	Chi-sq	DF	R2m & R2c	P-value	AIC
width + FQmode2 + TimeSinceDisturbance + width * FQmode2 + FQmode2 * TimeSinceDisturbance + width * TimeSinceDisturbance + (1 Species)	NA	NA	NA	NA	NA
width + FQmode + TimeSinceDisturbance + width * FQmode + FQmode * TimeSinceDisturbance + (1 Species)	NA	NA	NA	NA	NA
Labund ~ FQmode2 * width + Time + (1 Species)	NA	14	0.04 0.36	NA	1976.1
Labund ~ FQmode2 * width + (1 Species)	NA	13	0.04 0.36	NA	1974.7
Labund ~ FQmode2 + width + (1 Species)	NA	9	0.04 0.36	NA	1970.6
Labund ~ FQmode2 + (1 Species)	39.07	5	0.04 0.36	< 0.001	1969.1

Table 4.4.2. Generalised linear model outputs for each fish species with sufficient data to be modelled. Degrees of freedom (DF), and Akaike information criterion (AIC) values are given for all models, but the Deviance or Chi-squared value (Chi-sq), pseudo R-squared (R-sq), and p values are only given for the model with the lowest AIC. The p-value and Chi-squared values are calculated using a likelihood ratio test comparing to the null model.

Model	Chi-sq/ deviance*	DF	AIC	P- value*	Pseudo R-sq
<i>Anguilla borneensis</i>					
width + FQmode2 + TimeSinceDisturbance + width * FQmode2 + FQmode2 * TimeSinceDisturbance + width * TimeSinceDisturbance		18	NA		
width + FQmode + TimeSinceDisturbance + width * FQmode + FQmode * TimeSinceDisturbance		19	NA		
width * FQmode + TimeSinceDisturbance		22	NA		
width * FQmode		23	NA		
width + FQmode		27	109.91		
FQmode	60.104	28	121.56	<0.001	0.39
1		33	171.66		
<i>Anguilla marmorata</i>					
width + FQmode2 + TimeSinceDisturbance + width * FQmode2 + FQmode2 * TimeSinceDisturbance + width * TimeSinceDisturbance		18	113.5		
width + FQmode + TimeSinceDisturbance + width * FQmode + FQmode * TimeSinceDisturbance		19	111.52		
width * FQmode + TimeSinceDisturbance		22	110		
width * FQmode	45.613	23	110.87	<0.001	0.625
width + FQmode		27	114.7		
FQmode		28	112.72		
1		33	140.71		
<i>Barbodes sealei</i>					

width + FQmode2 + TimeSinceDisturbance + width * FQmode2 + FQmode2 * TimeSinceDisturbance + width * TimeSinceDisturbance	777.79	18	953.42	<0.001	0.267
width + FQmode + TimeSinceDisturbance + width * FQmode + FQmode * TimeSinceDisturbance		19	1053.6		
width * FQmode + TimeSinceDisturbance		22	1163.4		
width * FQmode		23	1167.6		
width + FQmode		27	1224.9		
Width		28	1224.4		
1		33	1495.5		
<i>Gastromyzon ingeri</i>					
width + FQmode2 + TimeSinceDisturbance + width * FQmode2 + FQmode2 * TimeSinceDisturbance + width * TimeSinceDisturbance		18	NA		
width + FQmode + TimeSinceDisturbance + width * FQmode + FQmode * TimeSinceDisturbance		19	NA		
width * FQmode + TimeSinceDisturbance		22	115.42		
width + FQmode + TimeSinceDisturbance		23	108.8		
FQmode + TimeSinceDisturbance		27	107.53		
FQmode	50.15	28	105.55	<0.001	0.269
1		33	145.7		
<i>Gastromyzon lepidogaster</i>					
width + FQmode2 + TimeSinceDisturbance + width * FQmode2 + FQmode2 * TimeSinceDisturbance + width * TimeSinceDisturbance		18	184.07		
width + FQmode + TimeSinceDisturbance +	73.202	19	182.44	<0.001	0.714

width * FQmode + FQmode * TimeSinceDisturbance					
width * FQmode + TimeSinceDisturbance		22	202.35		
width + FQmode + TimeSinceDisturbance		23	220.69		
FQmode + width		27	220.38		
FQmode		28	219.36		
1		33	237.41		
<i>Hampala sabana</i>					
width + FQmode2 + TimeSinceDisturbance + width * FQmode2 + FQmode2 * TimeSinceDisturbance + width * TimeSinceDisturbance	130.74	18	216.96	0.001	0.553
width + FQmode + TimeSinceDisturbance + width * FQmode + FQmode * TimeSinceDisturbance		19	225.31		
width * FQmode + TimeSinceDisturbance		22	221.24		
width * FQmode		23	219.75		
FQmode + width		27	292.22		
FQmode		28	293.21		
1		33	367.46		
<i>Hemibagrus baramensis</i>					
width + FQmode2 + TimeSinceDisturbance + width * FQmode2 + FQmode2 * TimeSinceDisturbance + width * TimeSinceDisturbance		18	NA		
width + FQmode + TimeSinceDisturbance + width * FQmode + FQmode * TimeSinceDisturbance	104.75	19	169.79	<0.001	0.226
width * FQmode + TimeSinceDisturbance		22	171.75		
width * FQmode		23	178.25		
Width + FQmode		27	185.34		
FQmode		28	188.83		
1		33	218.69		
<i>Nemacheilus olivaceus</i>					

width + FQmode2 + TimeSinceDisturbance + width * FQmode2 + FQmode2 * TimeSinceDisturbance + width * TimeSinceDisturbance		18	NA		
width + FQmode + TimeSinceDisturbance + width * FQmode + FQmode * TimeSinceDisturbance		19	NA		
width * FQmode + TimeSinceDisturbance		22	96.702		
width + FQmode + TimeSinceDisturbance		23	97.494		
FQmode + TimeSinceDisturbance		27	95.541		
FQmode	76.038	28	93.848	<0.001	0.322
1		33	159.89		
<i>Nematabramis everetti</i>					
width + FQmode2 + TimeSinceDisturbance + width * FQmode2 + FQmode2 * TimeSinceDisturbance + width * TimeSinceDisturbance	1210.3	18	1210.3	<0.001	0.510
width + FQmode + TimeSinceDisturbance + width * FQmode + FQmode * TimeSinceDisturbance		19	1236.3		
width * FQmode + TimeSinceDisturbance		22	1506.1		
width + FQmode + TimeSinceDisturbance		23	1605.1		
FQmode + TimeSinceDisturbance		27	1716.7		
FQmode		28	1794.8		
1		33	2104.8		
<i>Osteochilus chini</i>					
width + FQmode2 + TimeSinceDisturbance + width * FQmode2 + FQmode2 * TimeSinceDisturbance + width * TimeSinceDisturbance		18	NA		
width + FQmode + TimeSinceDisturbance + width * FQmode + FQmode * TimeSinceDisturbance	64.707	19	154.98	<0.001	0.959

Appendix

width * FQmode + TimeSinceDisturbance		22	174.41		
width * FQmode		23	315.6		
FQmode + width		27	337.99		
FQmode		28	368		
1		33	477.39		
<i>Osteochilus ingeri</i>					
width + FQmode2 + TimeSinceDisturbance + width * FQmode2 + FQmode2 * TimeSinceDisturbance + width * TimeSinceDisturbance		18	NA		
width + FQmode + TimeSinceDisturbance + width * FQmode + FQmode * TimeSinceDisturbance	103.36	19	167.3	<0.001	0.420
width * FQmode + TimeSinceDisturbance		22	184.84		
width + FQmode + TimeSinceDisturbance		23	182.96		
Width + FQmode		27	180.97		
FQmode		280	187.29		
<i>Protomyzon griswoldi</i>					
width + FQmode2 + TimeSinceDisturbance + width * FQmode2 + FQmode2 * TimeSinceDisturbance + width * TimeSinceDisturbance		18	179.27		
width + FQmode + TimeSinceDisturbance + width * FQmode + FQmode * TimeSinceDisturbance	103.00	19	177.27	<0.001	0.485
width * FQmode + TimeSinceDisturbance		22	212.49		
width + FQmode + TimeSinceDisturbance		23	222.4		
FQmode + TimeSinceDisturbance		27	226.25		
FQmode		28	227.01		
1		33	268.99		
<i>Rasbora cf. sumatrana</i>					
width + FQmode2 + TimeSinceDisturbance + width * FQmode2 +		18	804.83		

Appendix

FQmode2 *					
TimeSinceDisturbance + width *					
TimeSinceDisturbance					
width + FQmode +	757.34	19	868.16	<0.001	0.443
TimeSinceDisturbance +					
width * FQmode +					
FQmode * TimeSinceDisturbance					
width * FQmode +		22	903.77		
TimeSinceDisturbance					
width + FQmode +		23	1048.1		
TimeSinceDisturbance					
FQmode + TimeSinceDisturbance		27	1067.8		
<i>Rasbora hubbsi</i>					
width + FQmode2 +		18	NA		
TimeSinceDisturbance + width *					
FQmode2 +					
FQmode2 *					
TimeSinceDisturbance + width *					
TimeSinceDisturbance					
width + FQmode +		19	NA		
TimeSinceDisturbance +					
width * FQmode +					
FQmode * TimeSinceDisturbance					
width * FQmode +		22	NA		
TimeSinceDisturbance					
width + FQmode +		23	203.49		
TimeSinceDisturbance					
width + FQmode	154.03	27	201.7	<0.001	0.276
Width		28	274.35		
1		33	282.62		
<i>Tor tambra</i>					
width + FQmode2 +		18	390.62		width + FQmode2 +
TimeSinceDisturbance + width *					TimeSinceDisturbance + width * FQmode2 +
FQmode2 +					FQmode2 *
FQmode2 *					TimeSinceDisturbance + width *
TimeSinceDisturbance + width *					TimeSinceDisturbance
TimeSinceDisturbance					
width + FQmode +	272.51	19	390.72	<0.001	width + FQmode +
TimeSinceDisturbance + width *					TimeSinceDisturbance + width * FQmode +
FQmode +					FQmode *
FQmode * TimeSinceDisturbance					TimeSinceDisturbance
width * FQmode +		22	446.36		width * FQmode +
TimeSinceDisturbance					TimeSinceDisturbance
width * FQmode		23	446.1		width * FQmode

Appendix

FQmode + width		27	541.63		FQmode + width
Width		32	584.81		Width
1		33	648.63		1

*Values only included for the model of best fit for each response variable.

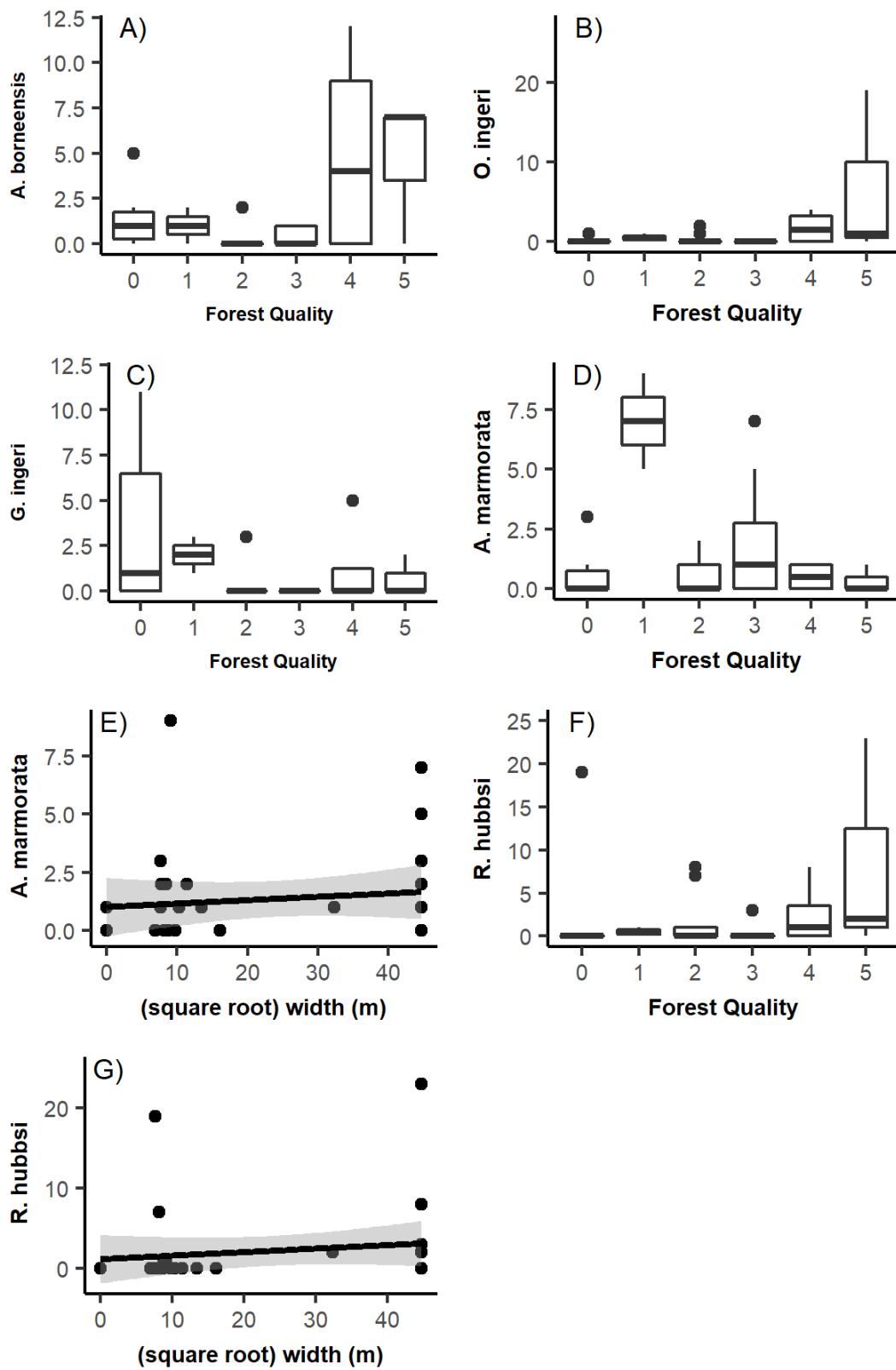


Figure 4.4.3. Relationship between *Anguilla borneensis* (A), *Osteochilus ingeri* (B), *Gastromyzon ingeri* (C), *Anguilla marmorata* (D), and *Rasbora hubbsi* (F) with riparian forest quality; *Anguilla marmorata* (E) and *Rasbora hubbsi* (G) with riparian width. Lines and 95% confidence intervals show results of linear models.

Table 4.4.4. Species regression tree model outputs and the root mean square error (RMSE) for community level fish analysis. Presence in the first node or tree split and within the tree are presented for each model parameter: average riparian width (Width), riparian forest quality (FQ) measured using the SAFE project forest quality score (Ewers et al., 2011), and time since disturbance (time) within the catchment. Root mean square error is recorded for the training and test datasets (randomly split, n=17 for each), and compared to the generalised linear models in Appendix 4-2. ** Comparison GLM cannot converge with only training data.

	Presence in first node (1 st split)			Presence in tree			RMSE		
	Width (m)	FQ (score)	Time (years)	Width	FQ	Time	Training data	Test data	Comparison to glm (glm RMSE)
<i>Anguilla borneensis</i>		X (1,2,3 v. 0,4,5)			X		2.787	2.087	Lower (12.406)
<i>Anguilla marmorata</i>		X (2,3,4,5 V. 0,1)			X		1.912	2.534	Lower (16.211)
<i>Barbodes sealei</i>		X (0,1,2 v. 3,4,5)		X (35)	X		11.920	63.827	Lower (124.11)
<i>Gastromyzon ingeri</i>		X (2,3,4,5 V. 0,1)			X		2.394	2.107	Lower (15.298)
<i>Gastromyzon lepidogaster</i>		X (2,3,4,5 V. 0,1)			X	X (7.5)	4.148	4.350	NA
<i>Hampala sabana</i>		X (0,1,3,5 v. 2,4)			X		7.014	6.463	NA
<i>Hemibagrus baramensis</i>	X (37)			X		X (9.5)	2.959	4.349	NA
<i>Nemacheilus olivaceus</i>			X (10.5)			X	0.818	4.521	Lower (13.279)
<i>Nematabramis everetti</i>		X (0,4 v. 1,2,3,5)		X (40)	X		46.408	48.869	Lower (4505.688)
<i>Osteochilus chini</i>		X (0,3,5 v. 1,2,4)			X		3.123	14.426	NA
<i>Osteochilus ingeri</i>		X (1,2,3,5 v. 0,4)			X		2.475	7.513	Lower (188.339)
<i>Protomyzon griswoldi</i>		X (1,2,4,5 v. 0,3)			X		3.759	5.167	NA
<i>Rasbora cf. sumatrana</i>	X (64)			X			11.742	68.780	NA
<i>Rasbora hubbsi</i>			X (8.5)			X	4.626	5.194	Lower (13.239)
<i>Tor tmbra</i>			X (6)		X	X	9.178	16.560	NA

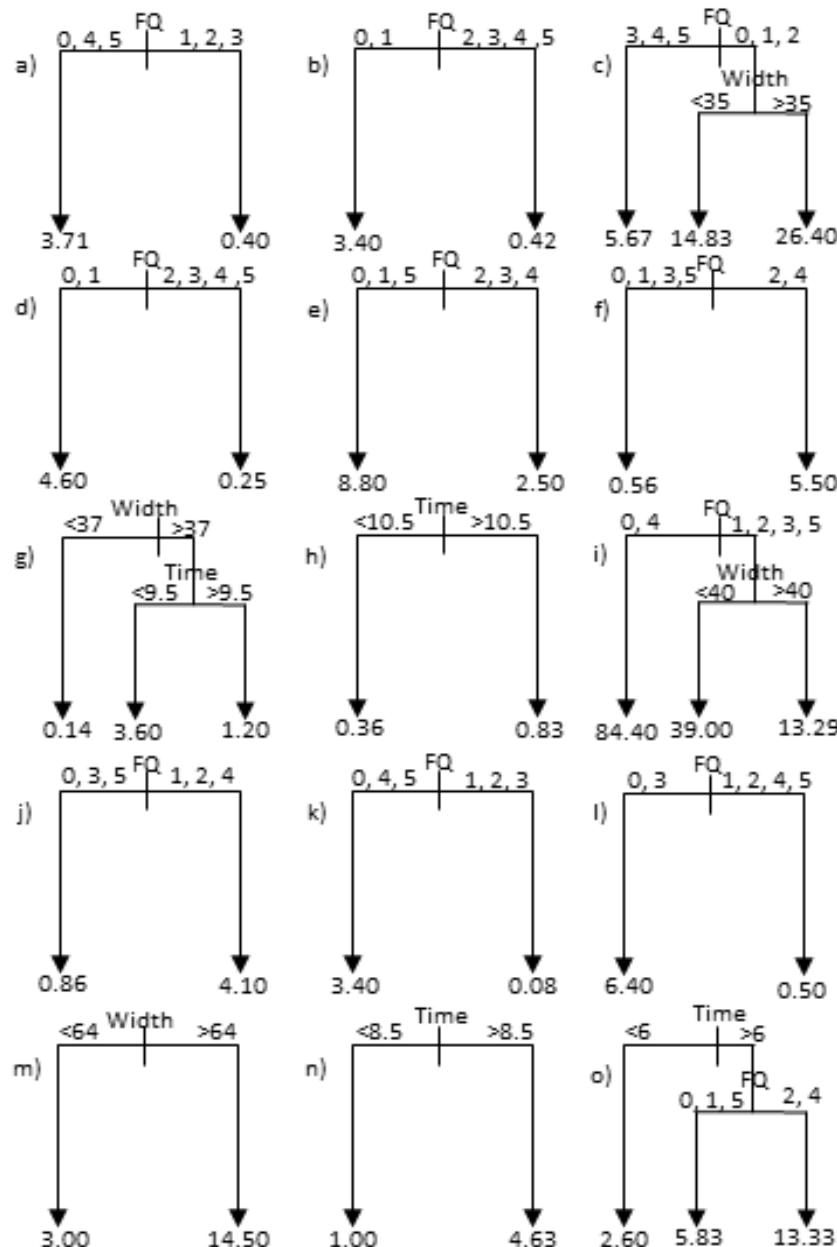


Figure 4.4.5. Regression trees of each species and the three riparian variables, each tree shows the splits relevant to each species: a) *Anguilla borneensis*, b) *Anguilla marmorata*, c) *Barbodes sealei*, d) *Gastromyzon ingeri*, e) *Gastromyzon lepidogaster*, f) *Hampala sabana*, g) *Hemibagrus baramensis*, h) *Nemacheilus olivaceus*, i) *Nematabramis everetti*, j) *Osteochilus chini*, k) *Osteochilus ingeri*, l) *Protomyzon griswoldi*, m) *Rasbora cf. sumatrana*, n) *Rasbora hubbsi*, and o) *Tor tambra*. Riparian forest quality is measured over a 500 m transect and the mode of a forest quality score (0-5; (Ewers et al. 2011)) is measured, riparian width (m) is measured from satellite imagery, and averaged over 500 m, and time since disturbance (years) is measured from the time since oil-palm planting or the last round of logging within the catchment.

APPENDIX 5 – CHAPTER 5**APPENDIX 5.1 – SECR MODEL COMPARISONS AND DENSITY ESTIMATES**

Table 5.1. Comparison of AIC values for all the SECRlinear models run on each stream in our data. The specification of each model, stream and which sampling years it was sampled is displayed. The raw AIC values, corrected AIC values (AICc), the difference of each value from the lowest in the comparison (dAIC) and the within-comparison weighting (AIC Wt) are displayed, as are the models which we selected. Horizontal lines separate each streams AIC comparisons.

Stream	Years sample d	Model	npar	AIC	AICc	dAICc	AICweight	Used ?
Binuang	2015-2017	D~year, g0~1, sigma~1	5	2017	2217	5.344	0.0471	N
Binuang	2015-2017	D~year, g0~year, sigma~1	7	2013	2213	1.843	0.2712	N
Binuang	2015-2017	D~year, g0~year, sigma~year	9	2011	2212	0	0.6816	Y
5m	2013-2017	D~year, g0~1, sigma~1	6	1216	1216	9	0.5757	Y
5m	2013-2017	D~year, g0~year, sigma~1	9	1216	1218	1.336	0.2952	N
5m	2013-2017	D~year, g0~year, sigma~year	12	1217	1219	2.989	0.1292	N
Gaharu	2016-2017	D~year, g0~1, sigma~1	4	982.6	983	6.271	0.0411	N
Gaharu	2016-2017	D~year, g0~year, sigma~1	5	984.6	985.1	8.440	0.0139	N
Gaharu	2016-2017	D~year, g0~year, sigma~year	6	975.9	976.7	0	0.945	Y
0m	2013-2017	D~year, g0~1, sigma~1	6	1188	1189	0	0.7469	Y
0m	2013-2017	D~year, g0~year, sigma~1	9	1191	1193	4.569	0.1772	N
0m	2013-2017	D~year, g0~year, sigma~year	12	1188	1192	2.877	0.0760	N
120m	2013-2017	D~year, g0~1, sigma~1	6	2498	2498	0	0.3967	Y
120m	2013-2017	D~year, g0~year, sigma~1	9	2498	2499	0.093	0.3787	N
120m	2013-2017	D~year, g0~year, sigma~year	12	2498	2500	1.138	0.2246	N
Merbau	2013-2017	D~year, g0~1, sigma~1	6	5466	5466	86.94	0	N
Merbau	2013-2017	D~year, g0~year, sigma~1	9	5417	5418	38.50	0	N
Merbau	2013-2017	D~year, g0~year, sigma~year	12	5379	5379	0	1	Y
VJR	2013-2017	D~year, g0~1, sigma~1	6	3363	3363	8.075	0.0173	N
VJR	2013-2017	D~year, g0~year, sigma~1	9	4935	4936	1580.28	0	N
VJR	2013-2017	D~year, g0~year, sigma~year	12	3354	3355	0	0.9827	Y

Appendix

Rhinopool	2015-2017	D~year, g0~1, sigma~1	5	2144	2144	17.80	0	N
Rhinopool	2015-2017	D~year, g0~year, sigma~1	7	2145	2145	18.62	0	N
Rhinopool	2015-2017	D~year, g0~year, sigma~year	9	2126	2126	0	1	Y
Tembalin	2015-g 2017	D~year, g0~1, sigma~1	4	1831	1831	29.53	0	N
Tembalin	2015-g 2017	D~year, g0~year, sigma~1	5	1801	1801	0	0.6559	Y
Tembalin	2015-g 2017	D~year, g0~year, sigma~year	6	1802	1803	1.29	0.3441	N
Keruing	2015-2017	D~year, g0~1, sigma~1	5	1745	1746	3.646	0.1076	N
Keruing	2015-2017	D~year, g0~year, sigma~1	7	1744	1744	2.162	0.2261	N
Keruing	2015-2017	D~year, g0~year, sigma~year	9	1741	1742	0	0.6663	Y
15m	2015-2017	D~year, g0~1, sigma~1	5	2273	2273	39.09	0	N
15m	2015-2017	D~year, g0~year, sigma~1	7	2270	2270	36.36	0	N
15m	2015-2017	D~year, g0~year, sigma~year	9	2233	2234	0	1	Y

Table 5.2. Density and standard error estimates of *N. everetti* in each sampling year at each stream from the selected SECR model. Horizontal lines separate each streams density estimates.

Stream	Year	Logging	Drought	Landuse	Density	SE
0m	2013	0	Before	LF	137.5	36.6
0m	2015	1	Before	LF	182.4	46.2
0m	2016	1	During	LF	243.2	55.2
0m	2017	1	After	LF	287.4	66.5
120m	2013	0	Before	LF	588.6	87.5
120m	2015	1	Before	LF	485.9	77.7
120m	2016	1	During	LF	728.8	100.4
120m	2017	1	After	LF	504.9	91.9
15m	2015	1	Before	LF	953.4	126.6
15m	2016	1	During	LF	401.8	192.5
15m	2017	1	After	LF	1564	614.84
5m	2013	0	Before	LF	1211	382.3
5m	2015	1	Before	LF	1048	336.3
5m	2016	1	During	LF	349.3	136.7
5m	2017	1	After	LF	1140	390.3
Binuang	2015	0	Before	OP	1526	287.7
Binuang	2016	0	During	OP	737	375.5
Binuang	2017	0	After	OP	2774	1004
Gaharu	2016	0	1	OP	1365	695.5
Gaharu	2017	0	0	OP	2020	972.8
Keruing	2015	0	Before	OP	1438	306.3
Keruing	2016	0	During	OP	1619	501.8
Keruing	2017	0	After	OP	2617	317.7
Merbau	2013	0	Before	OP	2576	286.4
Merbau	2015	0	Before	OP	1020	100.9
Merbau	2016	0	During	OP	2265	553.1
Merbau	2017	0	After	OP	853	233.7
Rhinopool	2015	0	Before	PF	2543	605.4
Rhinopool	2016	0	During	PF	2518	1465
Rhinopool	2017	0	After	PF	1798	472.6
Tembaling	2015	0	0	PF	771.8	99.7
Tembaling	2016	0	1	PF	937.5	244.6
VJR	2013	0	Before	PF	793.3	97.3
VJR	2015	0	Before	PF	796	116.6
VJR	2016	0	During	PF	539	284.3
VJR	2017	0	After	PF	191.5	38.1

