

1 **The effects of catchment and riparian forest quality on stream environmental conditions**
2 **across a tropical rainforest and oil palm landscape in Malaysian Borneo**

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27 **Keywords**

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29 Freshwater; habitat disturbance; oil palm; rainforest; riparian buffer; selective logging; Southeast
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37 **Abstract**

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39 Freshwaters provide valuable habitat and important ecosystem services, but are threatened
40 worldwide by habitat loss and degradation. In Southeast Asia, rainforest streams are particularly
41 threatened by logging and conversion to oil palm, but we lack information on the impacts of this
42 on freshwater environmental conditions, and the relative importance of catchment versus
43 riparian-scale disturbance. We studied sixteen streams in Sabah, Borneo, including old growth
44 forest, logged forest, and oil palm sites. We assessed forest quality in riparian zones and across
45 the whole catchment, and compared it with stream environmental conditions including water
46 quality, structural complexity and organic inputs. We found that streams with the highest riparian
47 forest quality were nearly 4 °C cooler, over 20 cm deeper, had over 40% less sand, greater
48 canopy cover, more stored leaf litter and wider channels than oil palm streams with the lowest
49 riparian forest quality. Other variables were significantly related to catchment-scale forest
50 quality, with streams in the highest quality forest catchments having 40% more bedrock and 20
51 times more dead wood, along with higher phosphorus, and lower nitrate-N levels compared to
52 streams with the lowest catchment-scale forest quality. Although riparian buffer strips went some
53 way to protecting waterways, they did not maintain fully forest-like stream conditions. In
54 addition, logged forest streams still showed signs of disturbance 10-15 years after selective
55 logging. Our results suggest that maintenance and restoration of buffer strips can help to protect
56 healthy freshwater ecosystems, but logging practices and catchment-scale forest management
57 also need to be considered.

58 **Introduction**

59

60 Freshwater ecosystems are intricately linked with their surrounding terrestrial habitats. In the
61 case of stream systems, all inputs of water, sediment, organic matter and sunlight are strongly
62 influenced by properties of the stream catchment and riparian zone, which in turn shape the
63 structure, nutrient availability and ecology of the stream habitat (Allan, 2004). Any changes in
64 land use therefore have the potential to affect freshwater ecosystems fundamentally. Globally it
65 has been estimated that 65% of river habitats are under moderate to high threat from land-use
66 change (Vörösmarty et al., 2010). Freshwater ecosystems provide essential services for people,
67 including water for drinking, homes, agriculture and industry, as well as food resources such as
68 fish and crustaceans. They also provide habitat for 6% of the world's species (Dudgeon et al.,
69 2006), of which it is estimated that 10,000-20,000 are currently at risk of extinction (Vörösmarty
70 et al., 2010). If the ecosystems and services provided by freshwaters are to be maintained and
71 managed effectively, it is essential that the impacts of land-use change and degradation on
72 waterways are understood.

73 Southeast Asia, particularly the Sundaland region which includes Borneo, has some of the
74 highest rates of land-use change in the world (Sodhi et al., 2004) and had lost nearly 70% of its
75 lowland forests by 2010 (Wilcove et al., 2013). By 2009, just 25% of land in Sabah, Malaysian
76 Borneo, was covered by intact forest, whilst 31% was degraded or severely degraded forest,
77 much of which had been logged multiple times (Bryan et al., 2013). Increasingly, these logged
78 forests are also being converted to timber, rubber and, particularly, oil palm plantations (Wilcove
79 et al., 2013). By 2010, 20% of Sabah's land area was being used to grow oil palm (*Elaeis*
80 *guineensis*) and it is estimated that 62% of all plantations in Sabah have been established on land

81 directly converted from forests (Gunarso et al., 2013). Although selective logging only removes
82 the largest trees of commercial species (mainly of the family Dipterocarpaceae), it is estimated
83 that many more die, with 41% of remaining trees being uprooted and crushed and another 18%
84 suffering damage to their crowns or bark (Pinard and Putz, 1996). In addition, bulldozers directly
85 affect approximately 30-40% of any area being logged (Bryan et al., 2013). Skid trails, log
86 landing areas and logging roads, along with full-scale conversion for agriculture, create large
87 areas of exposed and compacted soil that are vulnerable to increased runoff and high rates of soil
88 erosion (Brooks and Spencer, 1997; Douglas, 1999).

89 It is likely that logging and oil palm agriculture are having substantial impacts on freshwater
90 systems in the region. A broad literature on the impacts of catchment-scale and riparian land use
91 exists for temperate freshwaters (e.g. reviewed by Allan, 2004; Tabacchi et al., 2000). But those
92 impacts are less clear for tropical freshwater systems, which differ substantially from temperate
93 ones in terms of rainfall and flooding regime, nutrient loads, biotic interactions and normal levels
94 of sediment and organic matter (Boulton et al., 2008; Dudgeon, 1999; Payne, 1986). In addition,
95 the type and extent of land-use changes being experienced in the tropics often differ from those
96 in temperate regions. Temperate or tropical land-use changes that result in larger areas of bare
97 soil increase surface runoff, gully formation, potential for flash floods and may cause
98 permanently higher streamflow (Brooks and Spencer, 1997; Bruijnzeel, 2004; Douglas, 1999).
99 This can increase sediment flow into streams, loss of nutrients from soils (Douglas, 1999;
100 Malmer, 1996; Malmer and Grip, 1994) and streamwater nutrient and mineral concentrations
101 (Douglas, 1999). Loss of vegetation decreases water interception by canopy and leaf litter, and
102 reduces removal rates of water by transpiration, whilst soil disturbance and compaction reduces
103 water infiltration (Bruijnzeel, 2004; Douglas, 1999). Loss or degradation of forest in the riparian

104 zone may alter channel cross-sectional size and shape, reduce inputs of woody debris, reduce
105 shading and promote algal growth, change water chemistry, and remove the final barrier to
106 sediment and nutrient inputs into streams (de Souza et al., 2013; Dosskey et al., 2010; Fernandes
107 et al., 2013; Sweeney et al., 2004). It is uncertain how long it takes for freshwater ecosystems to
108 recover from disturbance caused by land-use change, with studies showing mixed results.

109 Recovery to pre-disturbance sediment levels has been reported only two years after oil palm
110 plantation establishment in Malaysia (DID, 1986, in Douglas, 1999). In contrast, studies in Kuala
111 Lumpur (Lai 1992 and 1993, in Douglas et al., 1999) found that it took 8-20 years for erosion
112 levels to return to normal, and streamflow had still not returned to normal 7 years after logging at
113 another site in Peninsular Malaysia (Rahim and Zulkifli, 1994, in Bruijnzeel, 2004).

114 Several mitigation strategies have been proposed to reduce the impacts of land-use change on
115 freshwaters and aid recovery after disturbance. Reduced impact logging using practices such as
116 stock mapping, skid trail planning, liana cutting, and avoiding slopes steeper than 25° (Pinard and
117 Putz, 1996; Putz et al., 2008; Putz and Pinard, 1993), minimises damage to remaining forest and
118 therefore nearby freshwaters compared to traditional mechanised approaches (Bruijnzeel, 2004;
119 Chappell et al., 2008; Douglas, 1999; Walsh et al., 2011). Terracing of slopes, planting of cover
120 crops, and appropriate road construction are also recommended for reducing erosion in oil palm
121 plantations (RSPO, 2013). Retaining riparian vegetation and forest fragments in agricultural
122 areas has been found to substantially reduce impacts on freshwater systems in a range of tropical
123 regions (e.g. de Souza et al., 2013; Fernandes et al., 2013; Heartsill-Scalley and Aide, 2003;
124 Suga and Tanaka, 2012). Riparian buffer strips (protected zones of natural habitat left beside
125 waterways) have been widely adopted as a mitigation strategy for reducing impacts of land-use
126 change on freshwaters and they are one of the certification criteria for sustainable palm oil

127 production under the Roundtable on Sustainable Palm Oil (RSPO, 2013). In Sabah, 20 m wide
128 riparian buffers are required along all rivers measuring 3 m or more in width in order to maintain
129 water volume and flow, prevent degradation of water quality and damage to the aquatic
130 environment (State of Sabah, 1998) although these regulations are often poorly enforced and
131 many rivers currently lack adequate, or indeed any, riparian buffers. In tropical ecosystems in
132 particular, a consensus has not yet been reached on the most appropriate width for riparian
133 buffers or the extent of forest cover across the wider catchment that needs to be retained in order
134 to minimise limnological change. Furthermore, few studies have considered effects on a range of
135 stream conditions simultaneously, or the effects of forest disturbance over multiple spatial scales
136 (Allan, 2004). There have been calls for a greater consideration of potential changes to
137 freshwaters in logged forest landscapes (Bruijnzeel, 2004), and research into the impacts of oil
138 palm on freshwaters is very limited.

139 This study assesses how stream conditions, including sediment characteristics, water quality,
140 channel structure and organic inputs, change along a gradient of forest disturbance, comprising
141 old growth forest, logged forest of varying quality, oil palm with riparian buffer strips of
142 differing widths, and oil palm with no buffer strips in Sabah, Malaysian Borneo. We consider
143 how stream environmental conditions vary in relation to quality of forest at the catchment scale
144 and in the riparian zone, the effects of riparian buffer strips, and the rate at which streams
145 recover after forest disturbance.

146 **Methods**147 **Stream sites**

148 We conducted survey work in Sabah, Malaysian Borneo (Figure 1). The region has an equatorial
149 climate with high annual rainfall and little seasonality, but with a tendency for drought from
150 February to early May in major ENSO years (Walsh and Newbery, 1999). Mean annual rainfall
151 at Danum Valley Field Centre 1985-2012 was 2883 mm (Walsh et al., 2013), and 2455 mm at
152 the “Stability of Altered Forest Ecosystems” (SAFE) Project site near Tawau, 2012-2015 (Rory
153 P.D. Walsh, unpublished data). The geology is similar across stream sites and comprises a
154 mixture of sedimentary rocks including sandstones, mudstones and tuff, and orthic Acrisols are
155 the dominant soil type (see Nainar et al., 2015 for more information). The natural vegetation is
156 lowland dipterocarp rainforest (Marsh and Greer, 1992).

157 We surveyed sixteen streams (Figure 1) that were located at a mean altitude of 236 m asl \pm SE
158 26 m, and were matched according to slope (mean slope across the whole catchment of $18.24^\circ \pm$
159 SE 0.81°). In each stream we started our survey work at matched points that had an upstream
160 catchment size of $3.16 \text{ km}^2 \pm$ SE 0.31 km^2 , and approximately 2 km of headwater flow. We will
161 henceforth refer to these points as the ‘0 m point’ of each stream. Stream catchments were
162 located across three research areas: the Danum Valley Conservation Area ($117^\circ 48.75' \text{ E}$ and 5°
163 $01' \text{ N}$), the Maliau Basin Conservation Area ($116^\circ 54' \text{ E}$, $4^\circ 49' \text{ N}$) and the “Stability of Altered
164 Forest Ecosystems” (SAFE) Project site in an area of the Kalabakan Forest Reserve ($116^\circ 57'$ to
165 $117^\circ 42' \text{ E}$, $4^\circ 38' \text{ N}$ to $4^\circ 46' \text{ N}$) (Figure 1). The SAFE Project is a large-scale, long term
166 research project that is making use of government-planned forest clearance and conversion to oil
167 palm to investigate the impacts of land-use change and forest fragmentation on ecosystems (see
168 Ewers et al., 2011 for more information). We chose catchments in areas that had undergone

169 different levels of habitat disturbance and conversion which are typical of the major types of
170 habitat change found in this region (Reynolds et al., 2011).

171 i) Four streams in old growth lowland dipterocarp rainforest (old growth, OG). Old growth forest
172 sites were within the Danum Valley Conservation Area, the Maliau Basin Conservation Area and
173 a Virgin Jungle Reserve (VJR) at the SAFE Project site (Figure 1). The two Danum Valley sites
174 (OG-West and OG-Rhinopool) had never been logged. The Maliau Basin site (OG-Maliau) had
175 been very lightly logged (to provide timber for adjacent field centre buildings) and the VJR (OG-
176 VJR) had suffered minimal illegal felling (Ewers et al., 2011), but neither the VJR or Maliau had
177 experienced the extent of commercial selective logging characteristic of the wider region, and
178 tree cover at the Maliau site remained similar to that at undisturbed sites (Hamzah Tangki,
179 unpublished data from Maliau for PhD dissertation, University of Zurich, 2014).

180 ii) Seven streams in forests that had been selectively logged to different extents (logged forest,
181 LF). Logged forest sites were located at the SAFE Project (Figure 1). At the time of the study the
182 ‘SAFE experimental area’ was continuous forest that had undergone a round of selective logging
183 during the 1970s that removed approximately 113 m^3 of hardwood timber per hectare, and
184 multiple rounds from the late 1990s-2000s that removed a further $66 \text{ m}^3 \text{ ha}^{-1}$ (LF-1, LF-2, LF-3,
185 LF-4, LF-5 and LF-6), although in the case of LF-7 this second round was only a single harvest
186 of $37 \text{ m}^3 \text{ ha}^{-1}$ (Fisher et al., 2011; Pfeifer et al., 2015; Struebig et al., 2013). Although logging
187 had been completed at the same time across the landscape, the logged forest sites were very
188 heterogeneous with patches of forest with closed canopy interspersed with early re-growth, gaps
189 and roads.

190 iii) Three streams in oil palm plantations with forested riparian buffer strips remaining beside the
191 streams (oil palm with buffer, OPB). Oil palm sites were located in areas of mature oil palm
192 (planted between 1999 and 2009) near the SAFE Project experimental area (Figure 1). Oil palms
193 are usually planted 9 m apart, with a cover crop (often leguminous) grown between to help
194 decrease soil erosion and nutrient loss (Corley and Tinker, 2003). The palms had not yet grown
195 sufficiently to give a closed canopy (Luskin and Potts, 2011). All oil palm stream catchments
196 were predominantly planted with oil palm, but varied in the amount of forest cover and riparian
197 buffer strip remaining in the catchment. OPB-Gaharu had a wide riparian buffer strip (mean
198 ~331 m, minimum ~75 m) on each side of the stream. OPB-Keruing had a medium width
199 riparian buffer strip (mean ~68 m, minimum ~33 m) on each side of the stream. OPB-Merbau
200 had a narrow riparian buffer strip (mean ~26 m, minimum ~2 m) on each side of the stream.

201 iv) Two streams in oil palm plantations with no buffer strips (oil palm no buffer, OP). These
202 were located in the same regions as detailed (in iii) above.

203 We sampled more streams in logged forest than in old growth forest and oil palm because logged
204 forest sites were expected to show greater habitat heterogeneity, and it was important to ensure
205 that the sites chosen covered a range of forest qualities. Forest quality varies continuously within
206 our broad habitat categories (old growth forest, OG/logged forest, LF/oil palm with buffers,
207 OPB/oil palm no buffers, OP) and some categories encompass more variation than others. We
208 therefore conducted analyses using continuous measures of forest quality rather than these
209 simplified categories.

210 Sites were surveyed before forest clearance and conversion to oil palm occurred at the SAFE
211 Project, and so they therefore form a valuable baseline data set for later comparison with post-

212 conversion data. Supplementary Materials Table S1 gives details of how each stream will be
213 affected by proposed future logging at the SAFE Project.

214 **Forest quality**

215 We assessed riparian forest quality in each of the sixteen streams at 50 m intervals, for 500 m
216 upstream of the '0 m point'. At each survey point measurements were taken 10 m into the
217 forest/oil palm on both sides of the stream. Canopy openness was measured using a spherical
218 densiometer (with measurements directed upstream, downstream, towards and away from the
219 stream, and then averaged) (Lemmon, 1956). Tree density was measured using a hand-held
220 relascope (Bitterlich, 1984), which is based on the angle-count sampling method. To allow for
221 lower tree numbers where the stream flowed, trees were counted in a 180° turn from upstream, to
222 away from the stream, to downstream; the resulting count was then doubled to represent a full
223 turn. Values were converted to an estimate of basal area ($\text{m}^2 \text{ha}^{-1}$) by doubling the value again.
224 Forest quality and percentage cover of vines in the canopy within 10 m around the survey point
225 were assessed visually. Forest quality was scored using the SAFE Project forest quality scale: 0
226 = oil palm; 1 = very poor- no trees, open canopy with ginger/vines or low scrub; 2 = poor- open
227 with occasional small trees over ginger/vine layer; 3 = OK- small trees fairly abundant/canopy at
228 least partially closed; 4 = good- lots of trees, some large, canopy closed; 5 = very good- closed
229 canopy with large trees, no evidence of logging (Ewers et al., 2011; Pfeifer et al., 2015).
230 Measurements were made once at each site in June-December 2011-2013, and repeated at all
231 sites except OG-West and OG-Rhinopool in May-August 2014. Measurements were averaged to
232 give a single value of each variable for each stream.

233 To quantify forest quality across the whole stream catchment we used forest stand structure maps
234 developed by Pfeifer et al., (2016). Maps showed mean above-ground living biomass (AGB,

235 t/ha), leaf area index (LAI, defined as leaf area per ground area) and percentage forest cover
236 (FCover) values within a 25 m² pixel. They were produced by modelling the relationship
237 between on-the-ground measurements from forest quality plots ($n = 193$, taken in 2010 and
238 2011) and the corresponding spectral intensity, spectral vegetation indices and texture data from
239 RapidEyeTM satellite images (taken during 2012 and 2013), and upscaling the relationship for
240 each pixel across the extent of the study area (for full details please refer to Pfeifer et al. (2016)).
241 To assess forest quality within each stream catchment, we first calculated catchment areas using
242 ArcMap Hydrology toolbox (Environmental Systems Research Institute (ESRI), 2014)) with an
243 ASTER Digital Elevation Model (DEM) (ASTER GDEM is a product of METI and NASA) and
244 the start point of the catchment (snapping point) set to the '0 m point' in our catchments. These
245 methods use topography information to calculate the likely path of flow and accumulation of
246 water over the landscape, and therefore delineate streams and catchments. Once catchment areas
247 had been mapped, we used the library 'raster' (Hijmans, 2014) in R statistical software (R Core
248 Team, 2014) to clip the AGB, LAI and FCover maps to each of the catchment areas and compute
249 mean forest quality values (meanAGB, meanLAI, meanFCover) for each one. In the case of OG-
250 West and OG-Rhinopool, the stream catchments were obscured by cloud, making it impossible
251 to calculate forest quality values for these catchments. Instead we used forest quality values for
252 the entire Danum Valley Conservation Area. As the Danum Valley area is continuous forest that
253 has never been logged or disturbed, it is very homogenous in cover and structure and is likely to
254 offer a good approximation for the OG-West and OG-Rhinopool catchments.

255 **Stream environmental variables**

256 Measurements of a wide range of stream environmental variables were made once at each stream
257 in April-August 2012, November-December 2012 or April-June 2013, in non-flood conditions

258 along 200 m transects starting at the '0 m point' and going upstream. Water chemistry variables,
259 including temperature, pH, conductivity (Hanna Combo pH and EC Meter) and dissolved oxygen
260 (Hach-Lange HQ40 digital DO meter), were measured at five points in each stream (0 m, 50 m,
261 100 m, 150 m, and 200 m upstream of the '0 m point'). Stream structural variables including
262 canopy openness over the stream, wetted width, total channel width, maximum depth, maximum
263 velocity, sediment cover and leaf litter were measured every 10 m. Canopy openness was
264 measured from the middle of the stream in four directions (upstream, downstream, left and right
265 at each point) using a spherical densiometer. Channel width and wetted width of the stream were
266 measured using a tape measure, and maximum depth was measured using a ruler. We measured
267 maximum velocity at the fastest flowing part of the stream at each measurement point using a 2
268 m string, tennis ball and stopwatch. The time taken for the ball to travel 2 m was recorded three
269 times and then averaged. We assessed sediment size in a 50 cm wide band across the wetted
270 width of the stream using percentage cover within five different size categories: bedrock, large
271 rocks (heavy, need two hands to move), small rocks (could pick up in one hand), pebbles, and
272 sand. To assess the amount of leaf material retained within the stream (e.g. caught between
273 rocks), we collected leaves from a 20 cm wide band across the wetted width of the stream at each
274 10 m point. Leaves were oven-dried to a constant weight, which was then recorded.

275 In addition to point measurements every 10 m, we characterised the entire stream channel section
276 between successive 10 m points in terms of percentage cover of dead tree trunks (henceforth
277 shortened to dead wood), rapids, riffles and pools. If water was still or near-still with no ripples,
278 we defined the area as a pool; if water was moving and the surface was rippled, it was defined as
279 a riffle; if water was moving fast enough to give white water, we defined it as a rapid. For

280 analysis, we calculated the percentage contributions of rapids, riffles and pools to this water
281 total.

282 Water samples (~500 ml in a plastic bottle) were taken at the '0 m point' during non-flood
283 conditions. Samples were taken approximately monthly for a subset of streams (LF-1, LF-2, LF-
284 3, LF-4, LF-5, LF-6, LF-7, OG-VJR, OP-Selangan Batu) between 2011 and 2014 (giving a total
285 of between 13 and 29 samples from each stream), and on a single occasion for another subset of
286 streams (OP-Gaharu, OP-Keruing, OP-Merbau, OG-West) in 2014 (giving one sample for each
287 stream). Samples were kept frozen and later analysed for nitrate-N and phosphorus content using
288 HACH nitrate and phosphate pocket colorimeters. We analysed Nitrate-N using the cadmium
289 reduction method (APHA, 2005), whilst reactive-P was analysed using the acidic molybdenum-
290 blue method (APHA, 2005). Unfiltered samples were used unless they were very turbid.

291 We calculated mean values for each variable from all the measurements taken in each stream,
292 and then used these values in subsequent analyses.

293 **Statistical methods**

294 All statistical analyses were conducted using the R statistical package (R Core Team, 2014). As
295 forest quality variables were non-independent we used Principal Component Analysis (PCA) on
296 the mean values for each variable to summarise the major axes of variation in forest quality. We
297 ran separate PCAs for the riparian and catchment forest quality variables to produce summary
298 riparian and catchment forest quality variables. Riparian PC1 and Catchment PC1 were used as
299 forest quality variables in subsequent analyses.

300 We used linear mixed effects models (library 'lme4', Bates et al., 2014) with random intercepts
301 to assess individual relationships between riparian and catchment forest quality and each

302 instream environmental variable measured. In each model, we treated the specific in-stream
303 environmental condition as the response variable and either riparian (Riparian PC1) or catchment
304 forest quality (Catchment PC1) as the fixed effect, and stream identity as a random effect to take
305 account of non-independence of multiple measurements within a stream. Model residuals were
306 checked for homoscedasticity and normality, and transformations were used where necessary to
307 ensure that model assumptions were met. All percentage cover data were normalised using an
308 arcsine square root transformation prior to analysis. For full details of statistical tests refer to
309 Table 2. We used log-likelihood ratio tests to generate p-values to assess model significance.
310 Original data, fitted models and 95% confidence intervals (CI) of the model were plotted using
311 library ‘ggplot2’ (Wickham, 2009, with reference to Chang, 2013).

312

313 **Results**

314 **Riparian and catchment forest quality**

315 Principal Component Analysis (PCA) produced summary scores for catchment and riparian
316 forest quality. In the riparian PCA, the first Principal Component (Riparian PC1) explained
317 77.6% of the variation in measurements of riparian forest quality. Riparian PC1 scores were
318 multiplied by -1 to make the scale more readily interpretable from low to high forest quality. In
319 the catchment PCA, the first Principal Component explained 92.1% of the variation in AGB,
320 LAI and FCover measurements across catchments. Loadings of each of the original forest quality
321 measurements on each principal component are shown in Supplementary Materials Table S2.
322 Catchment PC1 and Riparian PC1 scores were correlated (Pearson’s $r = 0.57$, $t=2.60$, $df=14$,

323 $p=0.0211$). Despite this, there were substantial differences in Riparian PC1 and Catchment PC1
324 scores for some streams, particularly the oil palm and oil palm buffer streams (Supplementary
325 Materials Figure S1), indicating that the riparian and catchment scales should be considered
326 separately in analyses.

327 **Responses of stream variables to riparian forest quality**

328 Streams with high riparian forest quality (high Riparian PC1 scores) had significantly higher
329 canopy cover at the centre of the stream, more leaf litter found lodged within the stream, and
330 lower water temperatures than streams that had lower riparian forest quality (Figure 2a-c, Table
331 2). The model results suggest that streams with the highest riparian forest quality had over ten
332 times as much trapped instream leaf matter and were nearly 4 °C cooler than oil palm streams
333 with the lowest riparian forest quality (Figure 2b, 2c). Water temperature and canopy openness
334 also decreased with rising catchment forest quality (Catchment PC1), but the effect was less
335 significant (Table 2). In terms of differences between broad habitat types (OG, LF, OPB, OP),
336 the results suggest that logged forest and old growth streams were similar in water temperature
337 and instream canopy openness, whereas oil palm buffer streams were warmer, with a more open
338 canopy, but less so than the non-buffered oil palm streams (Figure 2a-c, Table 1). Oil palm
339 buffer streams and logged forest streams were the most similar in their stocks of submerged
340 leaves, whilst oil palm streams without buffers had substantially fewer leaves and old growth
341 forest streams had substantially more (Table 1).

342 Streams with high riparian forest quality also had lower percentage cover of sand on the stream
343 bed and a greater maximum depth and total channel width than streams with lower riparian forest
344 quality (Figures 2d-f, Table 2). High quality forest streams had approximately 2% sand on the

345 stream bed, compared to a modelled result of 45% in the lowest quality oil palm streams,
346 although there was substantial variation between streams. Across broad habitat types, only
347 logged forest streams were similar to old growth forest streams in terms of sand cover, whilst
348 sand cover was higher in the oil palm streams, even in oil palm streams with riparian buffers
349 (Figure 2d, Table 1). Streams with the highest quality riparian vegetation had a maximum depth
350 over 20 cm deeper than that modelled for streams with the lowest riparian forest quality. These
351 results correspond to a progressively increasing maximum depth across the habitat types from oil
352 palm through to old growth forest (Figure 2e, Table 1). Model results suggest that the highest
353 forest quality streams were double the total width, from bank to bank, than the lowest forest
354 quality streams, but that there was no significant difference in wetted width between high and
355 low quality streams (Figure 2f, Table 2). This means that there were more dry areas in the
356 channel of higher forest quality streams and that percentage cover of the channel by water was
357 significantly related to forest quality. Oil palm streams without riparian buffers were only just
358 over half as wide as streams in old growth forest, logged forest and oil palm streams with
359 buffers, all of which had similar channel widths. However, while old growth forest and logged
360 forest streams had similar percentage cover of water within the channel, oil palm streams had
361 higher percentage water cover (fewer dry areas) than the forested streams and this difference was
362 found in oil palm streams with and without riparian buffers (Figures 2g, Table 1).

363 **Responses of stream variables to catchment forest quality**

364 Other instream environmental variables showed significant relationships with catchment-scale
365 forest quality rather than riparian forest quality. Modelled results indicate that streams with the
366 highest catchment forest quality had 46% bedrock cover compared to only 6% in the lowest
367 quality catchment streams, and had over 20 times more dead wood than lowest forest quality oil

368 palm streams (Figures 2h-i). Considering broad differences between major habitat types, logged
369 forest and old growth forest streams had similarly high levels of exposed bedrock, with lower
370 levels in oil palm streams. Levels of dead wood in the streams declined steadily from old growth
371 through to logged forest, then oil palm, with the lowest levels in the oil palm streams with
372 buffers (Table 1).

373 Nitrate-N levels were significantly lower in higher quality catchment streams with models
374 suggesting that nitrate values were about 12 times lower in the highest quality streams than in the
375 lowest quality oil palm streams (Figure 2j, Table 2). Phosphorus showed the opposite trend, with
376 levels being three times higher in streams with high catchment forest quality scores than those in
377 the lowest quality oil palm catchment (Figure 2k, Table 2), although the difference was only
378 approximately 0.1 mg/l. Across the broad habitat types, logged forest and old growth appear
379 most similar in terms of nitrate-N and phosphorus levels, with oil palm streams showing higher
380 nitrate-N and lower phosphorus levels, with the highest values recorded at oil palm sites with
381 riparian buffers (Table 1). All nitrate and phosphorus values, however, are well below pollution
382 threshold levels.

383 We found no significant differences in other aspects of water quality (dissolved oxygen, pH,
384 conductivity) in relation to either riparian or catchment quality, nor in a range of other water
385 flow and sediment conditions (velocity; wetted width; percentage cover of rapids or pools;
386 percentage cover of large rocks, small rocks or pebbles) (Table 2).

387

388 **Discussion**

389

390 Our study is the first to demonstrate how riparian and catchment forest quality affect stream
391 environmental variables across a habitat degradation landscape in Southeast Asia. We show that
392 forest quality at both the riparian and catchment scales are significantly related to stream
393 environmental conditions, and that different conditions are affected by habitat quality across
394 different scales. In accordance with other studies in the region, our results indicate that the
395 impacts of selective logging are still evident in stream environmental conditions over 10 years
396 after logging, because logged forest streams showed differences in conditions to the old-growth
397 forest streams. In turn, oil palm streams with riparian buffers retained more natural stream
398 conditions than oil palm streams without buffers, illustrating the importance of retaining or
399 restoring riparian buffers for freshwater management in these systems. However, they still
400 differed from forested streams in many of their channel characteristics and some of their
401 chemical conditions, suggesting that riparian buffer strips alone are not sufficient to protect
402 streams fully from the impacts of oil palm agriculture.

403 Specifically we found that streams with higher quality riparian forest had significantly lower
404 canopy openness over the stream, lower water temperatures and higher levels of leaf material in
405 the water. They also had lower percentage cover of sand, greater maximum depth and greater
406 channel widths compared to streams with lower quality riparian habitat. Other variables showed
407 stronger trends with forest quality across the catchment-scale. Percentage cover of bedrock, dead

408 wood and phosphorus levels were significantly higher in streams with higher catchment forest
409 quality, whilst water cover within the stream channel, and nitrate-N levels were lower.

410 **Responses of stream variables to riparian forest quality**

411 Loss of tree cover in the riparian zone through selective logging or complete clearance for oil
412 palm reduces the canopy cover above the stream, leading to higher canopy openness scores over
413 the centre of the stream, and lower availability of leaves to fall into the water. As well as
414 increasing light levels and reducing leaf input, lower riparian forest cover reduces shading and
415 consequently results in higher water temperatures (e.g. Kiffney et al., 2003; Moore et al., 2005).
416 In our study, light exposure almost doubled and water temperature was approximately 4 °C
417 higher in streams with lowest riparian forest quality compared to those of the highest quality.
418 Water temperature was also significantly correlated with catchment-scale forest quality, and
419 other studies have found that upstream forest cover, for at least a few hundred metres, is
420 important for stabilising downstream water temperatures (Scarsbrook and Halliday, 1999; Storey
421 and Cowley, 1997). This may be because temperature of runoff water into streams is affected by
422 temperatures across the catchment. Air temperatures have been found to increase by up to 6.5 °C
423 when forest is converted to oil palm (Hardwick et al., 2015) and with the average surface
424 temperature in Borneo predicted to increase by up to 3-4 °C by 2081–2100 relative to 1986–
425 2005, as a result of climate change (Intergovernmental Panel on Climate Change (IPCC), 2014),
426 higher water temperatures are likely to become increasingly common.

427 Streams with lower riparian forest quality had narrower channels, lower maximum depths and
428 higher percentage cover of sand on the streambed. Narrow channels were a feature of the oil
429 palm streams without buffer strips, perhaps because reduced riparian shading may allow

430 increased growth of understory vegetation on the stream edge which hold the banks together and
431 reduce erosion (Sweeney et al., 2004). The maximum depth of oil palm streams was almost half
432 that of streams in old growth forest. Despite allowing growth of bank-stabilising plants near the
433 stream edge, reduced vegetation cover in the wider riparian landscape increases the likelihood of
434 there being areas of bare ground from which soil can be eroded, and fewer leaves, roots and less
435 leaf litter to act as a barrier to its transport directly into the stream (Bruijnzeel, 2004). It is well-
436 established that increased terrestrial disturbance can lead to increased sediment levels in streams.
437 Sediment loadings up to fifty times higher than normal levels have been recorded in disturbed
438 sites in Malaysia (Douglas et al., 1993), whilst high sediment yields were found in streams
439 draining both newly planted and mature (>10 years old) oil palm plantations in Indonesia
440 (Carlson et al., 2014). In addition, clear-felling forest and replacing it with cocoa and oil palm
441 increased sediment loads by nearly fifteen times (from a mean of 28 t/km² to 414 t/km² in one of
442 the streams) (DID, 1986; DID, 1989, in Douglas, 1999) relative to pre-logging conditions. Such
443 increases in stream sediment loads probably contributes to high levels of sand and silt settlement
444 on the streambed, resulting in a shallower average depth, infilling of the deepest pools and
445 overall simplification of the stream bed habitat (Allan, 2004).

446 **Responses of stream variables to catchment forest quality**

447 Several stream variables showed significant relationships with catchment-scale forest quality
448 rather than riparian forest quality. Percentage cover of bedrock, dead wood, and levels of
449 phosphorus in the water were significantly higher in streams with higher catchment forest
450 quality, whilst levels of nitrate-N were lower. Nitrates are readily leached from tropical soils
451 (Payne, 1986), particularly when land is disturbed by clearance (Malmer and Grip, 1994), and so
452 levels in stream water may be high until vegetation re-growth removes more nitrogen from soil

453 water (Malmer and Grip, 1994). The elevated nitrate levels in oil palm streams most likely
454 resulted from runoff of fertilisers that are added to oil palm plantations (Yusoff and Hansen,
455 2007). However, local guidelines stipulate that fertiliser application should be monitored
456 carefully to maximise benefits and minimise losses (Wahid et al., 2010), and fertiliser application
457 at our sites appeared to be targeted through use of slow-release fertilisers from semi-permeable
458 bags (personal observation). It is also noteworthy that although we detected significant
459 differences between sites, nitrate levels were low. Levels were generally lower than those found
460 in a study of oil palm and forested control streams in Sarawak (mean nitrate-N in oil palm 2.70
461 mg/l *cf.* 1.71 mg/l in our study, and mean nitrate in forest of 1.92 mg/l *cf.* 0.60 mg/l in our study,
462 Mercer et al. 2013), and (apart from one outlier) our results are still within recommended limits
463 for sensitive aquatic species based on Malaysian National Water Quality Standards (Ministry of
464 Natural Resources and Environment Malaysia, 2014). They are also substantially lower than
465 values recorded in agricultural catchments in eastern England over recent decades, which have
466 often exceeded the maximum 50 mg/l level required for drinking water (Skinner et al., 1997).

467 Phosphorus levels showed the opposite trend to nitrate-N levels, with highest phosphorus values
468 in the logged and old growth forest sites, and lower levels in oil palm, despite fertilisers being
469 added to plantations. This may be because phosphorus is needed in large quantities by rapidly
470 growing plants (de Souza et al., 2013; Dosskey et al., 2010) which would include oil palm, scrub
471 and forest re-growth in the low quality forest streams. However, less is taken up by slow-
472 growing, mature vegetation, perhaps resulting in the higher levels observed in the old growth and
473 less disturbed logged forest sites. In addition, high throughflow and runoff rates in more
474 disturbed catchments (Bruijnzeel, 2004; Douglas, 1999) may dilute the phosphorus released from
475 weathering of underlying rocks and organic matter breakdown. However the numerical

476 difference was small and therefore unlikely to have substantial impacts on the stream system.

477 Inputs of tree trunks into streams depends entirely on supply of dead trees from the surrounding

478 forest and, because wood is often carried a long way downstream, particularly in flood events, it

479 makes sense that higher levels of forest at the catchment-scale gave higher levels of wood in both

480 our study and in others (Cadot and Wohl, 2010; Heartsill-Scalley and Aide, 2003).

481 **Other factors affecting stream conditions**

482 Although many of the patterns in environmental variables in our stream are likely to be directly

483 and causatively linked with forest quality at the riparian and catchment-scale, it is important to

484 recognise that some patterns might be correlative and simply the result of human choices about

485 which areas to develop. For example, in Sabah and other areas of the tropics, logging and

486 development is limited to the lowlands by feasibility and regulations; slopes above 25 ° are

487 considered unworkable and are generally not released for logging, apart from by helicopter

488 logging (Reynolds et al., 2011), and inaccessible areas are generally avoided. This may mean

489 that catchments and streams selected for oil palm cultivation may already have a suite of

490 characteristics that are different from those that remain forested, rather than differences caused

491 by the clearance itself. High levels of bedrock in higher quality forest catchments may be an

492 example of this, as rocky areas may be less likely to be chosen for oil palm development.

493 However, given that these policies are so widely followed, it may be that some features are still

494 generalizable to high quality forest streams, although caused by human selection of which sites

495 to log and convert to oil palm rather than any hydrological or ecological process brought about

496 by forest quality.

497 Consequences for freshwater ecosystems

498 Our findings of elevated light levels, temperatures, sand and nitrate-N found in disturbed
499 streams, along with lower levels of habitat heterogeneity in terms of leaf and woody matter,
500 rockiness, channel width and depth, are likely to have substantial impacts on stream ecosystems
501 and the services that streams provide. Temperature increases caused by habitat conversion,
502 particularly in combination with rising temperatures predicted with climate change, are likely to
503 have substantial impacts on freshwater biodiversity and ecosystem functions (Boyero et al.,
504 2011; Hogg and Williams, 1996). Tropical insects in particular have been shown to be vulnerable
505 because they are sensitive to temperature change and are currently living near their optimal
506 temperature (Deutsch et al., 2008). Increases in light levels, nitrate-N, and decreases in leaf
507 inputs could contribute to a shift to a community dominated by algal growth (Benstead and
508 Pringle, 2004; England and Rosemond, 2004) and substantial changes in stream food webs
509 (Boyero et al., 2011; Covich et al., 1999; Yule et al., 2009). Decreases in channel width, depth,
510 rockiness, and occurrence of dead wood, along with increases in levels of sand in disturbed
511 streams are likely to reduce habitat complexity and suitable habitat for many benthic
512 invertebrates (Burdon et al., 2013). Simplified benthic habitats are also less able to trap and
513 retain leaf litter, therefore reducing levels of terrestrial organic matter further. These changes in
514 environmental conditions and biota could substantially reduce water clarity, quality and fish
515 production, with adverse consequences for local people. Furthermore, lower channel width,
516 depth, and high sedimentation in disturbed streams could contribute to increased downstream
517 flood risk.

518 Management implications

519 Reduced impact logging has been suggested as a method to decrease damage to remaining
520 forests and soil during timber extraction, through approaches such as skid trail planning, cutting
521 lianas, using culverts in waterways, positioning roads along ridges and avoiding logging on
522 slopes over 25° (Putz and Pinard 1993; Pinard and Putz 1996; Putz et al. 2008; Walsh et al.
523 2011), all of which could help to minimise negative impacts of logging on freshwaters. Our
524 results indicate that environmental conditions in logged forest streams were often different from
525 old growth sites, suggesting that two rounds of conventional selective logging over 10 years
526 earlier were still affecting stream conditions. Although recovery to pre-logging levels of water
527 quality has been reported after just a few years in some cases, and for some conditions (e.g.
528 Malmer and Grip, 1994), several other studies found that it took up to 20 years to return to pre-
529 disturbance levels following logging (Bruijnzeel, 2004; Douglas et al., 1999; Iwata et al., 2003).
530 A study in Sabah found that whilst erosion rates were substantially lower 21 years after selective
531 logging than they had been during and in a secondary peak 6-10 years after logging, they had not
532 fully returned to normal (Walsh et al., 2011). Our data do not allow for the effects of reduced
533 impact logging compared to conventional logging on freshwaters to be explicitly tested, and no
534 other studies have yet done this. However, given the legacy of logging impacts we have shown,
535 it seems likely that practices that reduce the initial impact of logging on remaining forest would
536 benefit freshwaters.

537 Retaining forested riparian buffer strips, maintaining headwater and steep-slope forest cover, and
538 protecting forest patches within catchments have been proposed as ways to help maintain
539 freshwater ecosystems and the services they provide after land conversion (RSPO, 2013).
540 Legislation in Sabah currently stipulates that 20 m buffers should be maintained on all streams

541 over 3 m wide (Environment Protection Department (EPD), 2011; State of Sabah, 1998)
542 Roundtable on Sustainable Palm Oil (RSPO) guidelines also state that in addition to buffer strips
543 (minimum 5 m wide), there should not be forest clearing or oil palm planting on steep slopes and
544 that soil conservation methods, such as terracing, should be used on 9-25° slopes (RSPO, 2013).
545 Our results indicate that forest quality at both the riparian and catchment-scale have significant
546 impacts on stream environmental conditions, and that the ability of riparian buffer strips to
547 maintain forest-like stream conditions in oil palm streams depends on the environmental measure
548 being considered. This shows that riparian buffer protection is highly advantageous, but
549 apparently not sufficient to maintain stream ecosystems and services fully, and highlights the
550 importance of broader scale conservation strategies, such as protection of forest fragments and
551 terracing on steep slopes, being promoted by organisations such as the RSPO. Other studies also
552 suggest that maintaining catchment-scale forest cover in addition to the maintenance of riparian
553 buffer strips is important for determining stream conditions (e.g. Allan, 2004; Allan et al., 1997;
554 Death and Collier, 2009; Heartsill-Scalley and Aide, 2003; Sponseller et al., 2001; Suga and
555 Tanaka, 2012) and that forest structure and quality have an effect as well as area of forest cover
556 (de Souza et al., 2013). It has also been shown that riparian buffers that have gaps are not enough
557 to offer protection to freshwater ecosystems (Wahl et al., 2013). Thus it seems that catchment-
558 scale planning and careful protection of designated buffer areas are needed for efforts to be
559 effective.

560 **Conclusions**

561 We show that rainforest logging and oil palm agriculture affects a wide range of stream
562 environmental conditions, that both riparian and catchment-scale forest quality are important in
563 moderating these impacts, and that different stream conditions are affected by disturbance at

564 different scales. Our study also shows that impacts of selective logging upon stream limnology
565 can still be evident over 10 years after habitat disturbance. We consider that maintenance of
566 riparian buffer strips is essential for retaining some forest-like conditions in streams including
567 aspects of structure, water quality and organic inputs, but our data suggest that this alone is
568 unlikely to be sufficient to maintain fully forest-like conditions. We suggest that any logging in
569 the riparian zone should be prevented and that riparian buffer strips alongside streams should be
570 strictly protected. In areas where there is development in the wider catchment, Reduced Impact
571 Logging protocols should be used along with added catchment-scale protection of forest
572 fragments to help maintain freshwater ecosystems and the services that they provide.

573

574

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576

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828 **Figure legends**

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830 **Figure 1-** Schematic and map showing the location of the sixteen stream sites used in our study
831 within Sabah, Malaysian Borneo. The Borneo inset map was drawn using library ‘maps’ in R
832 statistical package (Brownrigg, 2016; R Core Team, 2014). All other maps were drawn using
833 ArcMap 10.2.1 GIS software (Environmental Systems Research Institute (ESRI), 2014)) using
834 map layers developed from Landsat imagery (Ewers et al., 2011), local maps and information
835 from maps in Douglas et al. (1992) and Hansen et al. (2013).

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837 **Figure 2-** Relationship between riparian forest quality PC1 (a-f) and catchment forest quality
838 PC1 (g-k) and stream environmental conditions. Points (jittered to aid viewing and coloured
839 according to habitat type) show original repeat measures within each stream, whilst lines and
840 95% confidence intervals show results of mixed effects models (see Table 2).

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847 **Tables**

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849 **Table 1** – Riparian forest quality, catchment forest quality and stream environmental variables850 for the sixteen streams used in this study. Values show the mean \pm standard deviation for all the

851 streams within each of four broad habitat categories: oil palm no buffer (OP), oil palm with

852 buffer strips (OPB), logged forest (LF) and old growth forest (OG). Riparian PC1 and Catchment

853 PC1 values are calculated from Principal Component Analysis (PCA) of riparian and catchment

854 forest quality variables respectively (see Statistical Methods for more detail). The designation of

855 streams into the four habitat types is shown in Figure 1. The number of streams (n) used to

856 calculate each value is the number shown in parentheses in the heading, unless otherwise stated

857 within the body of the table. Multiple values were taken in each stream (as described in

858 methods), unless specifically listed as single measurements in the body of the table.

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		Streams			
		Low forest quality	—————→		High forest quality
		Oil palm no buffer, OP (n=2)	Oil palm with buffer, OPB (n=3)	Logged forest, LF (n=7)	Old growth forest, OG (n=4)
Riparian forest quality	SAFE forest quality scale (score 0-5)	0.03 \pm 0.05	2.47 \pm 0.47	2.72 \pm 0.27	3.35 \pm 0.62
	Vines (% cover)	0.34 \pm 0.48	46.05 \pm 2.20	45.71 \pm 8.74	38.00 \pm 15.53
	Tree basal area (m ² /ha)	0	18.26 \pm 7.39	17.66 \pm 3.46	28.00 \pm 8.70
	Canopy openness (score 0-96)	51.07 \pm 25.1	16.74 \pm 6.80	12.44 \pm 3.34	7.77 \pm 2.38
	Riparian PC1	-4.20\pm0.90	0.15\pm0.84	0.39\pm0.24	1.30\pm0.54
Catchment forest quality	Above ground biomass (AGB)	2.49 \pm 0.58	1.47 \pm 0.34	5.16 \pm 0.70	18.68 \pm 6.30

	(t/ha)				
	Leaf area index (LAI)	2.44±0.05	2.22±0.19	3.74±0.32	4.50±0.29
	Forest cover (%)	55.11±0.25	48.47±1.75	69.00±2.81	81.26±5.98
	Catchment PC1	-1.58±0.06	-2.12±0.19	0.11±0.39	2.19±0.92
Stream environmental conditions	Water temperature (°C)	28.22±0.07	26.86±0.36	25.02±0.93 (n=6)	24.99±0.67
	Dissolved oxygen (mg/l)	8.10±0.09	7.98 (n=1)	8.06±0.25 (n=5)	8.04 (n=1)
	pH	7.75±0.16	7.89±0.34	8.15±0.28 (n=6)	7.87±0.46
	Conductivity (µS)	90.00±7.07	58.67±17.89	118.19±64.94 (n=6)	113.86±38.29
	Nitrate-N (mg/l)	0.74 (n=1, with multiple measures per site)	2.69±2.63 (n=3, with a single measure per site)	0.64±0.63 (n=7, with multiple measures per site)	0.56±0.31 (n=2, one with multiple measures per site, one with a single measure)
	Reactive-P (mg/l)	0.059 (n=1, with multiple measures per site)	0.010±0.0068 (n=3, a single measure per site)	0.108±0.108 (n=7, with multiple measures per site)	0.098±0.05 (n=2, one with multiple measures per site, one with a single measure)
	Time taken for ball to move 2 m (s)	5.35±1.79	6.65±0.41	4.33±3.28	9.76±7.87
	Channel width (m)	6.77±1.15	10.50±1.64	12.18±2.95	10.88±3.43
	Wetted width (m)	4.18±1.32	5.93±0.23	5.61±1.54	5.85±1.86
	Maximum depth (cm)	23.24±14.19	28.16±7.14	33.99±8.19	41.01±12.37
	Submerged leaves dry weight (g)	1.73±0.26	14.6±6.67	12.48±6.19	22.48±20.43
	Instream canopy openness (score 0-96)	73.43±15.31	49.60±8.87	30.39±13.04	28.20±5.72
	Water within channel (% cover)	60.17±4.49	63.83±15.79	45.75±8.91	46.00±8.78

Forest quality and stream conditions

Rapids (% cover)	1.96±2.77	0.36±0.32	17.52±13.16	6.09±5.38
Riffles (% cover)	42.29±3.66	47.25±20.85	46.06±18.45	27.72±10.92
Pools (% cover)	55.75±6.43	52.39±21.16	36.43±2.80	66.19±10.96
Dead wood (% cover)	2.75±3.89	0.33±0.38	3.5±1.55	4.94±3.38
Bedrock (% cover)	24.88±36.06	7.90±7.14	33.16±11.51	37.50±12.90
Large rocks (% cover)	6.22±8.67	6.21±4.90	8.16±4.03	13.93±7.10
Small rocks (% cover)	1146±6.95	23.39±11.61	18.23±8.41	15.24±2.30
Pebbles (% cover)	16.83±1.49	39.52±22.51	29.86±7.45	24.29±13.71
Sand (% cover)	40.37±49.86	22.98±6.35	10.69±3.49	9.05±2.97

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871 **Table 2** – Model equation and details of variables (including transformations) used in mixed
 872 effects models, along with results of log-likelihood ratio test comparisons of mixed model results
 873 with null models to assess significance of relationships between catchment and riparian forest
 874 quality and stream environmental variables. $n=16$ streams (unless stated otherwise in Table 1),
 875 with multiple repeat measures in each stream (see methods). Significant results are denoted by: *
 876 $p<0.05$, ** $p<0.01$, and *** $p<0.001$.

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For mixed effects models of the form:			
<i>lmer(transformed response variable~ forest quality explanatory variable +(1/Stream))</i>			
Transformed response variable	Forest quality explanatory variable	Results of log-likelihood ratio test	
		χ^2	<i>p</i>
Water temperature	Catchment PC1	9.3494	0.0022 **
	Riparian PC1	11.183	0.0008 ***
Dissolved oxygen	Catchment PC1	0.3929	0.5308
	Riparian PC1	0.0038	0.9595
pH	Catchment PC1	0.0002	0.9885
	Riparian PC1	0.3929	0.5308
Conductivity	Catchment PC1	2.4513	0.1174
	Riparian PC1	0.1647	0.6849
-1/(Nitrate-N+1)	Catchment PC1	22.188	<0.0001 ***
	Riparian PC1	0.9095	0.3402
Reactive-P	Catchment PC1	5.0749	0.0243 *
	Riparian PC1	1.789	0.1811
-1/(flow time) ^{0.5} (time for a ball to move 2 m)	Catchment PC1	0.413	0.5205
	Riparian PC1	0.0005	0.9823
Log10(total channel width)	Catchment PC1	0.7631	0.3824
	Riparian PC1	8.3182	0.0039 **
Log10(wetted width)	Catchment PC1	0.0004	0.9845
	Riparian PC1	2.7478	0.0974
Maximum depth	Catchment PC1	3.5281	0.0603
	Riparian PC1	4.5558	0.0328 *
Log10(submerged leaves weight+1)	Catchment PC1	3.6944	0.0546
	Riparian PC1	13.424	0.0002 ***
Instream canopy openness	Catchment PC1	8.9976	0.0027 **

Forest quality and stream conditions

	Riparian PC1	16.176	<0.0001 ***
Arcsin square root (% cover water stream channel)	Catchment PC1	5.1588	0.0231 *
	Riparian PC1	3.1049	0.0781
Arcsin square root (% cover of rapids)	Catchment PC1	0.6447	0.4220
	Riparian PC1	0.9061	0.3411
Arcsin square root (% cover of riffles)	Catchment PC1	2.7009	0.1003
	Riparian PC1	0.9683	0.3251
Arcsin square root (% cover of pools)	Catchment PC1	0.8109	0.3679
	Riparian PC1	0.0787	0.7790
Arcsin square root (% cover of dead wood)	Catchment PC1	7.7975	0.0052 **
	Riparian PC1	0.3899	0.5323
Arcsin square root (% cover of bedrock)	Catchment PC1	7.1287	0.0076 **
	Riparian PC1	1.4152	0.2342
Arcsin square root (% cover of large rocks)	Catchment PC1	3.1435	0.0762
	Riparian PC1	2.2871	0.1305
Arcsin square root (% cover of small rocks)	Catchment PC1	0.682	0.4089
	Riparian PC1	1.7454	0.1865
Arcsin square root (% cover of pebbles)	Catchment PC1	0.8835	0.3473
	Riparian PC1	1.1906	0.2752
Arcsin square root (% cover of sand)	Catchment PC1	4.0783	0.0434 *
	Riparian PC1	8.1223	0.0044 **

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