Resilience of tropical, freshwater fish (*Nematabramis everetti*) populations to severe drought over a land-use gradient in Borneo

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Keywords: El Niño drought, freshwater fish, oil palm, logged forest, antagonistic interaction, mark-recapture, SECR

Abstract

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

Introduction

Freshwater ecosystems have been severely affected by anthropogenic impacts and are the most threatened ecosystems globally (Thomsen et al 2012). The widespread degradation of these ecosystems threatens aquatic biodiversity at both local and regional scales (Richter et al 1997, Vörösmarty et al 2010). Anthropogenic land cover change, through logging or conversion to agricultural plantation, causes marked declines in biodiversity (Phalan et al 2013). Further perturbations to ecosystems due to extreme climatic events (e.g. El Niño-induced drought) puts additional stress on biodiversity, pushing species to their limits of survival (Castello and Macedo 2015). It is important to understand how these multiple stressors (land-use and climate change) interact and impact aquatic biodiversity.

Land-use change can significantly impact freshwater ecosystems. However, the extent of this impact varies on the type of land disturbance, and if any mitigation strategies are implemented. Land-use changes can affect freshwater ecosystems through changes in...
sediment load, nutrient runoff, canopy cover and thus temperature, and leaf litter and woody debris inputs (Luke et al. 2017a). These impacts change the microhabitats that fish inhabit and can affect taxonomic or functional groups differently (e.g. Newcombe and Macdonald 1991, Jones et al 1999, Sazima et al 2006). Extreme climatic events can cause severe disturbance to freshwater ecosystems (White et al. 2016). Unlike climate change, extreme climatic events such as drought do not manifest through gradual temperature change, which could allow time for adaptation or acclimatisation. Rather, they cause acute mortality episodes that can be substantial threats to local aquatic populations (McHugh et al. 2015, White et al. 2016). Effects of extreme low flow events on stream communities can persist for several years (Lake 2003, Fritz and Dodds 2004), and the abundance of key taxa may take several years to recover (Ledger et al. 2013, Woodward et al. 2015). Prolonged low flow events or drought conditions can cause: (a) alterations to food webs and species interactions by creating narrowly constrained channels, decreasing reproductive rates, limiting migration and restricting flow-related chemical communication through the drying out of ripples and waterfalls and reduction in pool volumes and stream connectivity (Covich et al. 2003, 2006); (b) significant reductions in water quality, through the concentration of organic and inorganic materials that can reduce dissolved oxygen levels during decomposition (Covich et al. 2000, Iwata et al. 2003, Pringle 2003); and (c) increased water temperatures that affect fish directly through high physiological demands and stress, and indirectly by reducing the oxygen saturation levels of water. This combination of increased metabolic demand and decreased oxygen availability can prove limiting or lethal to fully aquatic stream biodiversity (Jackson et al. 2001).

Climate and land-use change often act synergistically (Castello and Macedo 2015). Deforestation can amplify the magnitude and severity of droughts in comparison to areas with full forest cover (Bagley et al. 2014). Droughts can then fuel further land-use changes or forest degradation by killing trees (Lewis et al. 2011) or by triggering wildfires (Brando et al. 2014). In our study site located in Sabah, Malaysia, the tropical climate is typically aseasonal, with a propensity for drought from February to early May in major El Nino Southern Oscillation years (Walsh and Newbery 1999). However, extreme droughts and floods are intensifying in magnitude and frequency (Huntington 2006). The increasing severity of these ecosystem stressors has led to calls for future research efforts to advance understanding and management of small tropical streams in relation to drought and multiple stressor effects (Taniwaki et al. 2017).

The impact of drought and recovery of freshwater fish communities is relatively understudied, and to our knowledge has not been examined across a land-use gradient in tropical Asia. We aimed to determine the interactive impact of land-use and a severe, El Niño-induced drought that occurred during January–June 2016 on the most common species of freshwater fish, Nematabramis everetti, present at our study site (Wilkinson et al. 2018a). We expected to find a synergistic effect in which the impact of drought would be greater in more heavily disturbed streams, as these will likely experience greater levels of drying, increased temperatures and lower dissolved oxygen concentrations (Covich et al. 2000, Iwata et al. 2003, Pringle 2003). We note, however, that this is the opposite of what has been shown for interacting stressors in predominantly temperate studies where antagonistic interactions are more frequently observed (Jackson et al. 2016). Specifically, we expected the drought would exacerbate the impacts of land-use on our target fish species, hypothesising: (a) a decline in fish density during the drought, reflecting elevated mortality during the drought event, but subsequent recovery to pre-drought levels; (b) a decline in total fish biomass during the drought, but biomass will recover slower than density levels after drought, due to the mortality of large individuals and recruitment of small individuals; and (c) fish movement would be reduced during the drought relative to before and after drought conditions. With continued deforestation and conversion to oil palm plantations in Southeast Asia, our study provides crucial insight into how these land-use changes will interact with extreme climatic events to impact freshwater ecosystems.

Methods

Study site

We sampled 16 streams in Southeastern Sabah, Malaysian Borneo. The sites form part of the Stability of Altered Forest Ecosystems (SAFE) project (Ewers et al. 2011; 4° 38’ N to 4° 46’ N and 116° 57’ E to 117° 42’ E) and Danum Valley Conservation Area (5° 01’ N and 117° 48.75’ E). Tributaries of the Brantan, Kalabakan and Segama Rivers drain the landscape, all of which flow into the Celebes Sea. Data were collected from 16 small, headwater streams (3–10 m wide, ≤1.2 m depth) across a gradient of land-use intensity (see Wilkinson et al. 2018b): four in primary forest (three at Danum Valley Conservation Area, and one in the Brantan Virgin Jungle Reserve; average aboveground biomass (AGB) = 350 T ha⁻¹) seven in logged forest (one in twice-logged forest, last logged ~20 years ago, and six in salvage-logged forest, logged in 2013–2016, average AGB = 95–122 T ha⁻¹), five in oil palm plantations (varying in age since planting from 7 to 12 years; average AGB = 38 T ha⁻¹; Pfeifer et al. 2016). A 200 m transect was located in each stream. All streams were independent tributaries to ensure spatial independence of data.
Fish sampling

Fishes were sampled over four years: April–June 2013, March–August 2015, February–July 2016, and February–July 2017. Only eight streams were sampled in 2013, but all 16 streams were sampled in all other sampling years. Seasonal rainfall variation at our study site is usually very limited (Walsh and Newbery 1999, Kumagai et al. 2005), suggesting little effect of the differences in timing of the sampling within years. Rainfall data from the SAFE project field camp during the El Niño drought period of January–June 2016 showed a lowered mean monthly rainfall of 164 mm month$^{-1}$ and a mean of 15 dry days month$^{-1}$, compared to average values across all years (2011–2018) of 203 mm and nine dry days month$^{-1}$ (R.P.D. Walsh, unpub. data). During the drought, many streams in the study area were reduced to disconnected pools (figure 1).

Fish samples were taken using a 2.75 m diameter cast net with 1 cm mesh, and with baited funnel traps (entrance diameter of 2.6 cm). Each stream transect was sampled for between four and six consecutive days (mean = 4.28), with around 20 throws of the net per day (mean = 16, range = 10–36), and 20 funnel traps (10 baited with bread and 10 with fresh fish, placed every 10 m along the stream). The number of throws per transect varied with the number and size of pools.

Captured fishes were identified to species (Inger and Chin 2002, Kottelat 2013), measured, weighed (2015 sampling only), and returned to the stream at the point of capture. To allow for unique identification of individuals, cyprinids of over 6 cm total length were tagged with a passive integrated transponder tag (Biomark). The Animal Welfare and Ethical Review Body at Imperial College London reviewed and approved the fish capture, handling and euthanisation protocols.

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

Environmental variables

To monitor the abiotic changes (within streams) caused by land-use and drought, 21 stream measurements were taken every 10 m along the 200 m stream transect. Environmental data were collected in 2015–2017. Temperature (°C), dissolved oxygen (mg l$^{-1}$), conductivity (μS cm$^{-1}$), and pH were measured with a YSI Professional Plus multi-parameter meter, every day.
during sampling at the downstream end of the transect, in addition to the further 21 point measurements along the transect. Wetted width (m), depth (cm), mean surface current speed (m s⁻¹; measured by timing a tennis ball travelling 2 m, repeated three times and converting to m s⁻¹), 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%), sedimentation (presence or absence), canopy cover (densiometer readings oriented upstream, downstream, and to the left and right banks) were measured at the 21 points, every sampling year.

Response metrics
Stream-specific density estimates (number of fish km⁻¹) were calculated using spatially explicit mark-recapture models (secr) in the R package ‘secrlinear’ (Efford 2014). For inclusion in the analysis, stream transects had to have more than five recaptures per sampling year, resulting in five streams being omitted from the analysis (three in logged forest, one in primary forest, and one from oil palm plantation). Populations were assumed to be closed in the short (4–6 d) time period in which they were sampled each year. Density (D) and detection parameters (g0 and sigma) were included in the models, and three models were run, with either density or density and the detection parameters varying by sampling year for each stream transect. Models were fitted and compared on the basis of their corrected Akaike Information Criterion (AICc), which accounts for small-sample biases (Cooch and White 2006). The model with the lowest AICc was selected and density estimates extracted.

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

Mark-recapture data were used to measure the distance moved by fish between captures between sampling seasons (at least 10 months since last capture).

All movement distances were positive, ignoring the direction of travel (upstream or downstream).

Analysis
Focal fish species metrics (biomass, density and movement) and environmental variables were analysed as the response variables. As predictor variables, we used the land-use gradient (categorised into primary forest, logged forest, or oil palm) and drought disturbance (categorised into before, during and after drought), and their interaction. Biomass, density and some environmental variables were log transformed prior to analysis to ensure model assumptions would be met. Generalised linear mixed models were used (Bates et al 2014), including differences in intercept between streams as an independent random effect. For the movement models a Poisson error distribution was applied, for all other models a Gaussian error distribution was applied (Zuur et al 2009). Log-likelihood ratio tests were used to assess model significance. The relative importance of fixed (marginal R-squared) and random effects (conditional R-squared) was ascertained using the methods of Nakagawa and Schielzeth (2013).

Results
In total, Nematalbramis everetti accounted for 36% of all captures (3658 of 10 160 individuals belonging to 29 species). The best secr model allowed density, g0, and sigma to vary by sampling year (Appendix 1 of the supplementary materials, available online at stacks.iop.org/ERL/14/045008/mmedia). Density of N. everetti ranged from 138 ± 37 to 2774 ± 1004 fish km⁻¹ (mean = 1152 ± 328) across the 11 streams in which it occurred.

Environmental variables
Mean stream water temperatures were significantly higher, by 2.5 °C and 5.5 °C, in logged forest and oil palm streams, respectively, compared to primary forest streams (table 1), and significantly warmer during the drought than before or after the drought (table 2). Streams in primary forest were buffered from El Niño-induced changes in temperature, with <1 °C temperature change throughout the three years sampled (2015–2017); however streams in logged forest and oil palm plantations were 2 °C–4 °C warmer in 2015 compared to 2017, and 4 °C–5.5 °C in 2016 compared to 2017. In addition, dissolved oxygen was significantly lower in logged forest and oil palm, and this was further exacerbated by the drought. Conductivity, pH, mean surface current speed, and all substrate classes varied significantly during the drought, whilst canopy openness and leaf litter cover varied by land-use (tables 1, 2).
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 (°C), dissolved oxygen (mg l⁻¹), conductivity (μS 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 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.

| Year | Mean surface current speed | Wetted width (cm) | Depth (cm) | Sand | Gravel | Pebbles | Large rocks | Bedrock | pH | Temperature (°C) | Dissolved oxygen (mg l⁻¹) | Canopy openness | Conductivity (μS cm⁻¹) | Sedimentation | Leaf litter cover |
|------|---------------------------|-------------------|-----------|------|--------|---------|-------------|---------|----|----------------|-------------------|----------------|-------------------|---------------|-----------------|
| OP   |                           |                   |           |      |        |         |             |         |    |                 |                   |                |                   |               |                 |
| 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            |
| 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   | 32.53       | 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| 16.36  | 31.25   | 23.83       | 14.79   | 7.92| 23.87          | 7.89              | 119.31         | 28.52             | 0.14          | 8.51            |
| PF   |                           |                   |           |      |        |         |             |         |    |                 |                   |                |                   |               |                 |
| 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           |
| 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, $\chi^2 = $ Chi-squared, and $P = p$-value. Temperature ($^\circ$C), dissolved oxygen (mg l$^{-1}$), conductivity ($\mu$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 (dendrometer 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 |
|------------------------|----------|---------|--------------------------------|
|                        | $\chi^2$ | $P$     | $\chi^2$ | $P$ | $\chi^2$ | $P$ | $\chi^2$ | $P$ | R2m | R2c |
| (log)Temperature        | 2        | 40.4    | <0.01   | 2   | 45.90    | <0.01 | 4   | 10.5 | 0.03 | 0.67 | 0.67 |
| (log)Dissolved oxygen   | 2        | 14.4    | <0.01   | 2   | 46.9     | <0.01 | 4   | 13.2 | 0.01 | 0.61 | 0.61 |
| (mg l$^{-1}$)           | 2        | 1.21    | 0.57    | 2   | 1.79     | 0.41  | 4   | 4.70 | 0.32 | 0.10 | 0.61 |
| (log)Mean surface current speed | 2 | 5.59 | 0.06 | 2 | 165.09 | <0.01 | 4 | 6.72 | 0.15 | 0.65 | 0.85 |
| (log)Wetted width (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)Substrate: sand    | 2        | 6.16    | 0.05    | 2   | 0.95     | 0.62  | 4   | 10.12| 0.04 | 0.28 | 0.42 |
| (log)Substrate: gravel  | 2        | 4.31    | 0.12    | 2   | 58.71    | <0.01 | 4   | 6.46 | 0.17 | 0.52 | 0.68 |
| (log)Substrate: pebbles | 2        | 2.40    | 0.30    | 2   | 100.44   | <0.01 | 4   | 1.54 | 0.82 | 0.64 | 0.72 |
| (log)Substrate: large rocks | 2 | 0.89   | 0.64    | 2   | 13.05    | <0.01 | 4   | 7.10 | 0.13 | 0.23 | 0.54 |
| (log)Substrate: bedrock | 2        | 3.10    | 0.21    | 2   | 62.50    | <0.01 | 4   | 11.3 | 0.02 | 0.47 | 0.75 |
|                        | 2        | 3.36    | 0.19    | 2   | 151.17   | <0.01 | 4   | 3.08 | 0.54 | 0.82 | 0.85 |

**Effects on Nematabramis everetti**

There was a significant effect of land-use (figure 2(a); $\chi^2 = 7.34$, $P = 0.03$), but not drought (figure 2(b); $\chi^2 = 1.38$, $P = 0.50$), or their interaction (figure 2(c); $\chi^4 = 7.11$, $P = 0.13$) on the population density of *N. everetti*. Density of fish was significantly higher in oil palm than in logged forest streams. In addition, stream as a random effect explained a considerable proportion of the variance in the model (R2c = 0.68, R2m = 0.32).

There was a significant effect of drought (figure 2(d); $\chi^2 = 6.23$, $P = 0.04$), and the interaction of drought and land-use (figure 2(f); $\chi^2 = 10.30$, $P = 0.04$), but not land-use alone (figure 2(e); $\chi^2 = 13.80$, $P = 0.15$) on the biomass captured of *N. everetti*. Captured biomass was significantly lower during the drought compared to before the drought, but that decrease was greater in oil palm plantations than in primary forest streams, and remained unchanged in logged forest streams. Stream as a random effect explained a substantial proportion of the variance explained in the model (R2c = 0.55, R2m = 0.34). However, there was no significant effect of land-use (figure 2(g); $\chi^2 = 4.35$, $P = 0.11$), drought (figure 2(h); $\chi^2 = 1.11$, $P = 0.57$), or their interaction (figure 2(i); $\chi^4 = 4.98$, $P = 0.29$) on biomass density (kg km$^{-1}$) of *N. everetti*. Again, stream as a random effect explained a substantial proportion of the variance explained in the model (R2c = 0.62, R2m = 0.22).

There was insufficient data to analyse distance moved of *N. everetti* with land-use and drought as interacting factors, so they were analysed separately. No significant effect of land-use was found on the movement of *N. everetti* (figure 2(j); $\chi^2 = 4.81$, $P = 0.09$), but there was a significant effect of drought (figure 2(k); $\chi^2 = 126.00$, $P < 0.01$). Fish moved further during the drought than before or after the drought. Stream as a random effect explained a small proportion of the variance in the model for land-use and drought (R2c = 0.08, R2m = 0.11).

**Discussion**

Catchment land-use had a significant effect on the density of the most common and abundant freshwater fish species at our study site, *Nematabramis everetti*. Land-use did not, however, impact the total captured biomass, biomass density or the distance moved of this species. In contrast, the severe, El Niño-induced drought had a significant impact on the total captured biomass of *N. everetti*, but not on the biomass density of *N. everetti*. Together, these results suggest that individuals of *N. everetti* became more difficult to catch during the drought, but that there is no overall reduction in the density or biomass of fish in the streams. These results indicate that *N. everetti* is highly resilient to an extreme El Niño drought, but that fishermen in rural communities that may be relying on this species as a food source may find it more difficult to capture during drought.

The most frequent impacts of droughts are population declines and changes in the community assemblage that arise from habitat loss, negative changes in water quality, movement within catchments, and crowding of fish in reduced microhabitats (Matthews and Marsh-Matthews 2003). The 2016 El Niño-induced drought in Sabah was shown to have significant effects on the within-stream conditions and...
water quality (table 1), with water temperatures during the drought >5 °C warmer in oil palm streams in comparison to primary forest streams, and all streams had lowered depth and dissolved oxygen levels (as also shown in many drought studies e.g. Lake 2003, Magoullick and Kobza 2003). Martin-Smith and Laird (1998) also demonstrated the high variability of small forest streams in Danum Valley Conservation Area, Sabah, with streams drying to unconnected pools and poor water quality (lowered levels of dissolved oxygen and high levels of decaying organic material) during drought periods.

Many of the species found within hill streams in this study, and in streams sampled by Martin-Smith...
and Laird (1998), have adaptations to cope with low oxygen levels. *Nematabramis everetti* are surface-feeding insectivores, which swim very close to the air-water interface where they probably gulp air while feeding, and can spawn all year round (Martin-Smith and Laird 1997). Despite these adaptations, this study showed a significant reduction in total captured biomass during and after the drought compared to before the drought, despite there being no difference in the biomass density of fish. Together, this indicates a change in the catchability, and therefore availability, of fish rather than a true decrease in biomass. Although other studies show no difference in catch rates between wet and dry seasons (e.g. Olopade et al. 2017), or suffer reduced catches with 'El Niño'-induced droughts (Swales et al. 1999), we expected an increase in catchability of fishes as they were restricted to pools. We believe the decline in fish captures was due to increased escapes from the cast net, which was more frequently entangled in vegetation and exposed rocks in and around the smaller, shallower pools in drought conditions (C.Wilkinson, pers. obs.).

In addition, the drought caused all experimental streams to dry into series of disconnected pools, which is known to lead to a decrease in available habitat and associated increase in competition for food, decreased shelter within pools, increased predation risk, and extreme changes in stream water quality (Matthews and Marsh-Matthews 2003). We had expected that we would see impacts on the density and biomass of fish caused by alterations in size/age structure of fish communities (Lake 2003, Fabré et al. 2017). Over time, fish species diversity would be reduced, with the most tolerant taxa being favoured (Matthews 1998). Our results suggested that *N. everetti* is remarkably resilient and tolerant to perturbations caused by drought conditions, and that drought does not remove them from their status of being the most abundant and common species in these streams.

Quantitative studies in Borneo show mixed effects for the impact of logging and conversions to oil palm plantation on freshwater fish communities (Martin-Smith 1998a, 1998b, 1998c, Beamish et al. 2003, Iwata et al. 2003, Giam et al. 2015, Wilkinson et al. 2018a). We had expected that primary forest would have the greatest density and biomass, and oil palm streams the lowest density and biomass of *N. everetti*. However, it was logged forest that had the lowest density of *N. everetti*, with no difference between oil palm and primary forest. We postulate that this is due to the recent salvage-logging in six out of seven logged forest streams studied, which caused large influxes of sediment and changes in substrate (table 1). It has been shown that streams can take more than 20 years to recover from the impacts of logging (Luke et al. 2017), therefore the 2–4 years since the last round of logging is probably not sufficient for the freshwater community to have fully recovered and may explain why *N. everetti* populations were reduced in this habitat. A second hypothesis is that there may be a decrease in the allochthonous input (i.e. inputs of external organic material and invertebrates) ‘falling’ into logged forest streams in comparison to primary forest and oil palm streams (Chan et al. 2008, Cassell 2017). *Nematabramis everetti* is a surface-to midwater-feeding insectivore and predominantly feeds upon such invertebrates (Inger and Chin 2002, Phipps 2014). A decline in prey biomass entering the stream ecosystem may therefore translate into a reduced abundance and density of *N. everetti*.

Our results and conclusions may have been influenced by the sampling methods chosen and their effectiveness in the altered stream conditions caused by the drought. Together, the combination of the two sampling methods and the use of secr models helps reduce the influence of sampling variation on fish and biomass density estimates. The use of cast nets for monitoring fish communities is important, however, as it provides a metric of the availability of fish as a resource to local people in our study landscape (Wilkinson et al. 2018b). In that context, our finding that fish catchability is reduced during drought is an important one, and indicates that drought may exert a negative impact on local communities despite having little ecological effect on the species itself.

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

Acknowledgments

We thank the Sabah Biodiversity Council, Yayasan Sabah, Danum Valley Conservation Area Management Committee and SEARRP for providing research permission (Licence No: JKM/MBS.1000–2/2JLD.3 (90)) for field work in Sabah. The SAFE Project coordinator, Ryan Gray, and SAFE project field staff provided logistical support and helped with data collection. This study was supported by Sime Darby Foundation funding to the SAFE Project. CLW was supported by an ICL-NUS PhD Scholarship from Imperial College London. This paper represents a
contribution to Imperial College’s Grand Challenges in Ecosystems and the Environment Initiative.

Data archive
Data available from the SAFE project database (https://doi.org/10.5281/zenodo.1478526).

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