

Forest loss in tropical catchments has mixed impacts on stream food webs

Jia Huan Liew¹, Kenny WJ Chua², Clare Wilkinson³, Heok Hui Tan², Keith Martin-Smith⁴, Ahmad Amirudin⁵, David Dudgeon¹, and Darren Yeo²

¹University of Hong Kong

²National University of Singapore

³Imperial College London

⁴Hutchins School

⁵Universiti Malaysia Terengganu

May 5, 2020

Abstract

Forest loss is a major environmental threat in the Anthropocene. Repercussions are rarely localised and often impacts adjacent ecosystems. For example, forest loss is generally detrimental to freshwater biodiversity. There are however, some uncertainties about its effects on food webs and ecosystem functioning. We tracked changes in the food webs of four tropical stream catchments (two time points separated by a ~20-year interval) affected by varying degrees of forest loss. Our data show that the proportion of assimilated terrestrial organic matter (allochthony) remained largely invariant, but changes in food chain lengths inferred from the trophic positions of apex predators (TP) differed between catchments. Here, we found that higher rates of forest loss resulted in more significant reductions in TP. We speculate that the mechanisms involved are unrelated to diminished terrestrial subsidies as allochthony values were low (~7%) and did not shift in response to forest loss.

Introduction

Forest loss is one of the most critical threats to the biosphere in the Anthropocene (Ruddiman, 2013; Malhi et al., 2014). Impacts of forest loss are extensive and far-reaching (Morris, 2010)—driving species extinctions (Brook et al. 2003; Giam, 2017), climate change (Ramankutty et al., 2006; Lawrence & Vandecar, 2015), and threatening the health of local human communities (Myers et al., 2013). The consequences of forest loss are relatively well-documented (Gibson et al., 2011; Barlow et al., 2016) so our understanding of its impacts on terrestrial ecosystems and biodiversity is fairly robust. However, these repercussions are rarely localised to the immediate (terrestrial) area (Lawton et al., 2001; MacKenzie, 2008) and often affects adjacent ecosystems (Maina et al., 2013). Forest streams, for example, are impacted by a reduction in terrestrial inputs (e.g., leaf litter, woody debris) which are important for the creation and maintenance of microhabitats (Giam et al., 2015; Naman et al., 2018). This results in simplified systems which lack niche diversity, and are hence less speciose (Loke & Todd, 2016). Unsurprisingly, forest loss is generally detrimental to freshwater biodiversity and commonly results in the extirpation of sensitive species (Liew et al., 2018a, Wilkinson et al., 2018).

In addition, allochthonous terrestrial inputs have, until recently, been thought of as constituting an important resource subsidy for low-order forest streams (Lau et al., 2013). This seemed logical given the expected abundance of such inputs (e.g., high standing stocks of leaf litter), and lower internal (aquatic) primary productivity resulting from light attenuation under dense canopy cover. As such, it was generally assumed that forest loss in catchments would result in resource limitations, thus impacting stream food webs from a bottom-up (resource-driven) direction (Liew et al., 2018). Recent data appear to confound these expectations,

however. Stream consumers grow at a significantly lower rate on diets comprising exclusively of leaf litter (Lau et al., 2013; Guo et al., 2016), suggesting that terrestrial resource subsidies may play a more peripheral role in stream food webs than previously supposed (Lau et al., 2009; Brett et al., 2017).

Current uncertainties about the role of allochthonous terrestrial subsidies in stream food webs complicate predictions about the effects of forest loss and its underlying mechanisms. It is perhaps for this reason that studies investigating changes in aquatic food webs in response to anthropogenic impacts sometimes report conflicting findings. For example, Takimoto et al. (2008) observed no significant links between disturbance and food webs—or more specifically, food chain length—while McHugh et al. (2010) found disturbance to be one of the primary predictors of food chain length. The lack of a clear consensus is critical from a conservation perspective. Disrupted food webs are thought to impair ecosystem functions, especially those related to energy flow (Holt & Loreau, 2001). Moreover, communities associated with functionally-impacted ecosystems are also often more vulnerable to further species loss (Chua et al., 2019).

In this paper, we aim to clarify the relationship between forest loss and freshwater food webs using a longitudinal (i.e., before and after) study design to help minimise potential confounders (e.g., baseline differences in the communities surveyed). We do this by measuring changes in forest cover and food web structure at two time points approximately two decades apart in tropical Southeast Asia, a region presently undergoing significant forest loss (Miettinen et al. 2012). We used a combination of state-of-the-art ecological tracers—i.e., amino acid-specific Carbon-13 (Liew et al., 2019) and Nitrogen-15 (Chikaraishi et al., 2009) stable isotopes—and high-resolution remote-sensing, as both methods are currently the most precise tools for measuring food web indices and catchment forest cover in a longitudinal design.

At each time point, we measure two food web indices, namely, the proportion of consumer tissue comprising assimilated terrestrial organic carbon (which we interpret as the extent of *allochthony*) and trophic position (*TP*) of representative apex predators (Choy et al. 1996). Together, *allochthony* and *TP* provide information about the role of terrestrial subsidies as a basal resource (Liew et al., 2019) and the vertical complexity of food webs (Takimoto & Post, 2013; Digel et al., 2014). Conversely, we measured catchment forest cover at both time points by generating raster data of cloud-free USGS Landsat mosaic images using machine-learning algorithms. With this, we asked: (1) how have freshwater food webs changed over time?; and (2) can these changes be predicted by the extent of forest loss in the respective catchments?

Methods

Survey sites

We surveyed four river catchments: i) Danum Valley (5°N, 118°E); ii) Endau (2°N, 103°E); iii) North Selangor peat swamp forest (NSPSF) (4°N, 101°E); and iv) Nee Soon (1°N, 103°E) (Fig. 1). Each catchment was sampled twice, once between 1990–1996 (*before*) and once between 2015–2018 (*after*).

Sampling protocol

Samples from the *before* time point were obtained from the archives of preserved fish specimens (usually in 10% formalin) deposited in the Lee Kong Chian Natural History Museum of the National University of Singapore. We filtered specimens by locality and taxonomy, selecting individuals from genera of predatory fishes we encountered at the respective catchments in the *after* time point. Fin tissue was excised from suitable specimens for subsequent laboratory analyses. We also measured the standard length of individuals sample. We collected a total of 57 specimens from the *before* time point, comprising 13 individuals (one species) from Danum, 10 individuals (six species in three genera) from Endau, 12 individuals (four species in two genera) from Nee Soon, and 22 individuals (four species in three genera) from NSPSF (Supplementary Table 1).

Samples from the *after* time point were collected during field excursions to each of the four river catchments between 2015 and 2018. We used a combination of backpack electrofishing (Bretschneider Spezialelektronik EFGI-650), cast nets (2.75 m diameter; 1 cm mesh) and rigid-frame push nets (60 × 45 cm; 2 mm mesh) to maximise our catch-rate. Fin tissue was excised from all predatory fish taxa encountered and kept in 70%

ethanol or 10% formalin (= 3.7% formaldehyde) solutions for subsequent laboratory analyses. Fish specimens were also measured to determine their standard length. We collected a total of 39 specimens, comprising three individuals (one species) from Danum, 18 individuals (four species in three genera) from Endau, seven individuals (three species in two genera) from Nee Soon, and 11 individuals (five species in three genera) from NSPSF (Supplementary Table 1).

Measuring food web indices

We measured *allochthony* using amino acid specific Carbon-13 profiles ($\delta^{13}\text{C}$) (Liew et al., 2019) while *TP* was measured using amino acid specific Nitrogen-15 profiles ($\delta^{15}\text{N}$) (Chikaraishi et al., 2009). Importantly for our study, amino-acid $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ profiles are both unaffected by ethanol or formalin preservation (Hetherington et al., 2019, Chua et al., 2020). Fin clip samples from all 96 suitable specimens (57 from the *before* period and 39 from the *after* period) were rinsed in distilled water, dried over 48 hours at 70 °C, homogenised, and packed in 12 mL borosilicate tubes for laboratory analyses at the Stable Isotope Facility at the University of California, Davis. There, amino acid $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ profiles were measured using established protocols (Walsh et al., 2014).

We estimated *allochthony* using the methods described in Liew et al. (2019). Briefly, essential amino acid (i.e., isoleucine, leucine, phenylalanine, and valine) $\delta^{13}\text{C}$ profiles of our specimens were compared against a global dataset of carbon source amino acid $\delta^{13}\text{C}$ values reported in the study (Liew et al., 2019). Given that the essential amino acid $\delta^{13}\text{C}$ profiles of aquatic and terrestrial carbon sources (Liew et al., 2019) are distinct, we estimated their relative contributions to consumer tissue using Bayesian stable isotope mixing models (Parnell et al., 2013) on the *simmr* statistical package (Parnell, 2016).

We estimated *TP* using $\delta^{15}\text{N}$ primarily, although *allochthony* (estimated with $\delta^{13}\text{C}$) were important for improving the accuracy of our calculations (Choi et al., 2017). We calculate *TP* using the following formula (after Chikaraishi et al., 2009):

$$TP = \frac{\delta^{15}\text{N}_{\Gamma\lambda\upsilon} - \delta^{15}\text{N}_{\Pi\eta\epsilon} + \beta_{\mu\xi}}{\Delta\Delta_{\Gamma\lambda\upsilon} - \Delta\Delta_{\Pi\eta\epsilon}} + 1 \dots (\text{eq. 1}),$$

where $\delta^{15}\text{N}_{\Gamma\lambda\upsilon}$ and $\delta^{15}\text{N}_{\Pi\eta\epsilon}$ represent the $\delta^{15}\text{N}$ profiles of glutamic acid and phenylalanine of the fish specimen, respectively, and $\Delta\Delta_{\Gamma\lambda\upsilon}$ and $\Delta\Delta_{\Pi\eta\epsilon}$ represent their respective trophic discrimination values, while $\beta_{\mu\xi}$ represents the difference in the $\delta^{15}\text{N}_{\Gamma\lambda\upsilon}$ and $\delta^{15}\text{N}_{\Pi\eta\epsilon}$ in carbon sources (i.e., primary producers) at the bottom of the food web. We used $\Delta\Delta_{\Gamma\lambda\upsilon}$ and $\Delta\Delta_{\Pi\eta\epsilon}$ values of +8.0 as $\beta_{\mu\xi}$ differs between aquatic (-3.4 ± 0.9) terrestrial ($+8.4 \pm 1.6$) our calculations using *allochthony* estimates on a per-individual basis (after Chua et al. (2020)).

Measuring forest loss with remote-sense data

We quantified changes in forest cover for each river catchment between the *before* and *after* by comparing year-matched (i.e., from 1 January to 31 December in the year fish specimens were collected) Landsat images on Google Earth Engine (GEE) (codes in Supplementary Material 1).

First, we downloaded all raw images available of our sites taken in the sampling year by USGS Landsat 5 (*before* time point) and USGS Landsat 8 (*after* time point). These were used to create cloud-free mosaics with the simple composite function on GEE. We delineated target river catchments using HydroSHEDS polygons (Lehner & Grill, 2013). In order to classify land-cover in the images with GEE's Random Forest machine learning algorithm, we plotted 'ground-truth' polygons comprising pixels associated with forest and non-forest land-cover types. Our 'ground-truth' polygons were plotted manually over areas which were clearly associated with any of the above land-uses (e.g., residence complexes with urban land-use). We allocated 60% of our 'ground-truth' points to the training of the GEE Random Forest algorithm (or classifier) while the remaining data points were allocated for classifier testing and validation. We included the following spectral bands for land-cover classification: 1) RGB (red, green, and blue) bands; 2) near infrared; 3) shortwave infrared 1 & 2; and 4) thermal infrared 1 & 2. Generally, trained classifiers comprise models which have been parameterised with 'ground-truth' training data which can then be used to categorise all remaining pixels in relevant satellite images into one of the three land-cover types of interest. We tested the

trained classifiers against our testing data (i.e., 40% of ‘ground-truth’ points) in a validation error matrix. Classification accuracy for all eight classifiers (two time points across four river catchments) were greater than the 95% threshold we set *a priori*. Finally, we used the trained Random Forest classifiers to produce land-cover raster layers of the catchments at both time points.

We quantified the following by comparing land-cover maps in the *before* and *after* time points:

1. Proportion of total catchment area associated with forest loss ($\Delta\Phi_{\text{total}}$).
2. Net proportion of catchment area associated with forest loss ($\Delta\Phi_{\text{net}}$).
3. Ratio of catchment area associated with forest loss versus forest gain ($\Delta\Phi_{\text{ratio}}$).

In addition to catchment-wide changes, we were also interested in quantifying change in land-use cover in a sub-section of the overall catchment area, specifically, in the area upstream of our sampling points. To this end, we delineated upstream areas by processing void-filled NASA Shuttle Radar Topographic (SRTM) Digital Elevation Models (DEMs) (Jarvis et al., 2008) using watershed hydrological tools on Whitebox GAT (Lindsay, 2016). We then quantified the following:

1. Proportion of catchment area associated with forest loss in the immediate upstream area of sampling points ($\Delta\Phi_{\text{sub}, \text{total}}$).
2. Net proportion of catchment area associated with forest loss in the immediate upstream area of sampling points ($\Delta\Phi_{\text{sub}, \text{net}}$).
3. Ratio of catchment area associated with forest loss versus forest gain in the immediate upstream area of sampling points ($\Delta\Phi_{\text{sub}, \text{ratio}}$).

Statistical analyses

We divided our analyses in two parts, each corresponding to one of our research questions. In the first part, we assessed temporal trends *allochthony* and *TP* (henceforth referred to collectively as *W*) by fitting 11 models to our data set of 96 predatory fish specimens (13 species in 6 genera) ($n=96$, Supplementary Table 1). Each model describes a competing hypothesis where *allochthony* and *TP* were tested separately against combinations of the following predictors: 1) *time* (i.e., categorical predictor with two levels (*before* or *after*) representing temporal identity); 2) *size* (i.e., continuous predictor representing the scaled standard length of fish individuals); and 3) *catchment* (i.e., categorical predictor with four levels representing river catchment identity). In addition to these predictors, we also included taxonomic information (genus) as random intercept and/or random slope terms to control for possible phylogenetic differences in *W* (*allochthony* / *TP*).

Our competing models and the hypotheses they describe are as follows (details of models in Supplementary Table 2):

1. Intercept only model, where *allochthony* / *TP* does not vary with any predictor.
2. ‘Size’ only model, where *allochthony* / *TP* is best predicted by individual size.
3. ‘Location’ only model where *allochthony* / *TP* differs between catchments but shows no appreciable change over time:
4. Univariate ‘Temporal’ model, where *allochthony* / *TP* changed significantly over time across all catchments.
5. ‘Size’ controlled ‘Temporal’ model, where changes in *allochthony* / *TP* over time is significant after controlling for differences in individual body size.
6. ‘Location’ controlled ‘Temporal’ model, where changes in *allochthony* / *TP* over time is significant after controlling for catchment identity.
7. ‘Size’ and ‘Location’ controlled ‘Temporal’ model, where changes in *allochthony* / *TP* over time is significant after controlling for location and individual body size.
8. ‘Size’ interaction model where trends in *allochthony* / *TP* change over time differs between individuals of varying body sizes.

9. ‘Location’ interaction model, where trends in *allochthony* / *TP* change over time differs across catchments.
10. ‘Location’ controlled ‘Size’ interaction model, where trends in *allochthony* / *TP* change over time differs across individuals of varying body sizes, after controlling for catchment identity.
11. ‘Size’ controlled ‘Location’ interaction model, where trends in *allochthony* / *TP* over time differs across catchments, after controlling for individual body size.

All 11 competing models were parameterised with a Bayesian approach on the *rjags* *4.6 statistical package (Plummer, 2016). For each model, we ran 100,000 iterations (burn-in=10,000) on four parallel chains (thinning=1), with vaguely informative priors for both fixed and random effects. We compared the models using the Widely Applicable Information Criterion (WAIC) and the Efficient Approximate Leave-One-Out (LOO) indices (Vehtari et al., 2017) where lower values indicate greater parsimony.

In the second part of our analyses, we assessed the role of forest loss in driving food web changes. As such, we focused on food web measures (i.e., *allochthony* and/or *TP*) reflecting different temporal trends across the catchments (i.e., if models (ix) or (xi) were best supported by the data in the first part of our analyses). This portion of our analyses required the aggregation of our individual-level response variable, W , because our forest loss metrics were measured at the catchment-basin scale. We calculated ΔW , which represents the mean pairwise difference in *allochthony* (Δ *allochthony*) and/or *TP* (Δ *TP*) between fish individuals of the same species (to control for potential phylogenetic confounders) from respective time points. We calculated ΔW ($n=4$) from a total of 141 individual-level, species-specific pairwise comparisons of W between the *before* and *after* time point ($\Delta\Omega$). Considering the significant sample size restrictions, we maximised the rigour of our community-level analyses by allocating 25% percent of the individual-level pairwise data points for model-testing (described later) before the subsequent aggregation of the remaining ‘training’ data subset. The process was randomised and catchment-specific, meaning that we allocated an equal percentage of individual-level data for model training/parameterisation (75%) and model testing (25%) for every catchment. We tested ΔW against the following forest loss metrics described earlier: $\Delta\Phi_{total}$; $\Delta\Phi_{\nu\epsilon\tau}$; $\Delta\Phi_{\rho\alpha\tau\iota\omicron}$; $\Delta\Phi_{\sigma\nu\beta.total}$; $\Delta\Phi_{\sigma\nu\beta.\nu\epsilon\tau}$; and $\Delta\Phi_{\sigma\nu\beta.\rho\alpha\tau\iota\omicron}$.

In addition to forest loss metrics, we also tested ΔW against other ‘null’ predictors unrelated to forest loss. These were: 1) A_{total} , a continuous variable representing the total area of river catchments; 2) $A_{sub.total}$, a continuous variable representing the size of the catchment area immediately upstream of our sampling points; and 3) ΔQ , a continuous variable representing the mean pairwise change in pH measurements between both time points.

We had nine community-level models in total (i.e., three ‘null’ models and six predictive models using forest-loss metrics) which can be summarised as follows:

$$\Delta W_m = \beta_0 + (\beta_1) X_m \dots (\text{eq. 2}),$$

where β_1 represents the fixed-slope term describing the relationship between ΔW and the predictor variables which we collectively annotate here as X (i.e., $\Delta Q, A_{total}, A_{sub.total}, \Delta\Phi_{total}, \Delta\Phi_{\nu\epsilon\tau}, \Delta\Phi_{\rho\alpha\tau\iota\omicron}, \Delta\Phi_{\sigma\nu\beta.total}, \Delta\Phi_{\sigma\nu\beta.\nu\epsilon\tau}$, and $\Delta\Phi_{\sigma\nu\beta.\rho\alpha\tau\iota\omicron}$), for the m -th river catchment. All predictors were scaled to facilitate model convergence. We parameterised the models with a Bayesian approach using the same settings as with our individual-level models. While Bayesian techniques are generally more robust to small sample sizes (Kery, 2010), we sought to improve the accuracy of our findings by repeating our parameterising procedure 100 times. We used a different random subset of individual-level pairwise data (i.e., 75% of total pairwise comparisons) for the calculation of ΔW by repeating the randomised draws at the start of every iteration. We recorded the following indices for model comparison: 1) mean slope coefficients values (β_1) describing the relationship between ΔW and the predictor variables; 2) WAIC and LOO as measures of model parsimony (Vehtari et al., 2017); and 3) Root Mean Square Error (RMSE) as a measure of model error. We calculate

(3) using residuals between predictions made using β_1 coefficients (parameterised using the training data subset) and observed values in the testing data subset.

Results

Forest cover change over two decades

Changes in forest cover over time were highly variable (Fig. 2; Table 1). Forest loss was most extensive in the Endau catchment, occurring in approximately 23 percent of its total area. Conversely, the Nee Soon catchment gained forest cover (0.2 km² net gain) in the ~25 years between sampling occasions.

Changes in freshwater food webs over time

Temporal trends in *allochthony* are best described by the *univariate ‘Temporal’ model* ($allochthony = 0.06 - 0.01time$) (Supplementary Table 2). While the model describes a decrease in *allochthony* over time (negative slope term on *time*), this relationship is not statistically important (95% Bayesian credible interval of slope term overlaps with zero) (Supplementary Fig. 1, 2). Conversely, trends in *TP* are best described by ‘*Size*’ *controlled ‘Location’ interaction model* ($TP = 1.79 + 0.14size + 0.27drainage - 0.44time + 0.17drainage*time$). The interaction coefficient between *catchment* and *time* is statistically different from zero (95% credible interval: 0.08–0.21), suggesting that differences in *TP* over time was not consistent across catchments (Fig. 3, Supplementary Fig. 1).

Forest loss as a driver of food web change

The first part of our findings suggests that *allochthony* did not change over time, so we focussed on *TP* for our second research question. We found that the mean pairwise difference in *TP* (ΔTP) was best predicted by the ratio of forest loss:gain in the immediate upstream area ($\Delta\Phi_{sub.ratio}$) (Table 2). Further, slope coefficients describing the relationships between ΔTP and candidate predictors were negative for all six forest loss metrics, and positive for predictors unrelated to forest loss (Fig. 4).

Discussion

Overall, our findings suggest that catchment forest loss is associated with a reduction in the trophic position of apex predators, which we interpret as a general shortening of food chain lengths (Wolkovich et al., 2014). Decreases in food chain lengths are commonly driven by resource limitation because the number of viable successive trophic steps (i.e., predator-prey interactions) are limited by the total metabolic energy in a food web (Doi et al., 2009; Takimoto & Post, 2013). While terrestrial inputs into fresh waters have been shown to diminish with forest loss (Tanentzap et al., 2014), we do not believe that limitation of terrestrial resource subsidies is the primary driver of the changes observed. This is because average *allochthony* levels (~7%) and its temporal invariance (Supplementary Fig. 1, 2), both suggest that terrestrial inputs are a relatively unimportant basal resource in the freshwater food webs that we studied, reinforcing shifting perceptions about the subject (Takimoto et al., 2008).

Despite this, there are some plausible mechanisms through which reductions in terrestrial subsidies can result in resource limitations. Firstly, the contribution of terrestrial inputs to overall resources may not necessarily be commensurate with their importance as a direct food source. For example, Hobbs et al. (2006) found growth rates to be higher in aquatic invertebrates feeding on a mix of leaf litter and algae when compared to individuals subsisting exclusively on either. The experimental data also show that the proportion of terrestrial carbon assimilated remained low in the mixed-diet treatment, at a value similar to those recorded in our study (~6%), despite the apparent positive effect on consumer growth (Hobbs et al., 2006). Secondly, terrestrial organic matter can also serve functions which are unrelated to nutrition. For example, terrestrial detritus adds mechanical structure and refugia to freshwater ecosystems—both beneficial to aquatic primary (Brothers et al., 2013) and secondary (Sass et al., 2006) production.

Although we found forest loss to be predictive of changes in food webs over time, the relative performance of the different forest loss metrics (Table 2; Fig. 4) suggests intricacies in our generalised conclusion. Here,

we found that food web changes were better predicted by forest loss in the upstream catchment area than by overall forest loss across the entire catchment basin. This is unsurprising, as a majority of terrestrial subsidies are likely to enter stream systems with groundwater/runoff from the upstream catchment. We also found that the ratio between forest loss and forest gain (i.e., net change in forest cover) was a better predictor of food web changes than total forest lost (Table 2), suggesting that the impacts of deforestation may be attenuated by re-forestation. However, an increase in TP was recorded only in the Danum catchment, where upstream forest cover comprised part of a protected conservation area and was relatively unchanged over time (Fig. 2; Table 1). While sample size is limiting, it seems that as with most measures of environmental health (e.g., species diversity), freshwater food webs benefit more from forest preservation than from forest restoration (Hobbs et al., 2006), at least within the time interval (~ 20 years) of our study (Chazdon, 2008).

We note two possible confounding factors in our study, specimen body-size and substantial differences in catchment basin areas. The susceptibility of larger individuals to anthropogenic disturbances (Walters & Post, 2008) and a strong positive correlation between trophic position and body size (Brose et al., 2005) means that there may be a feasible alternative driving mechanism to the one we proposed. Specifically, forest loss could result in the loss of larger individuals (Walters & Post, 2008), hence lowering trophic positions of apex predators overall (Brose et al., 2005). While this may be the case where loss or similar anthropogenic impacts causes a reduction in trophic positions (Wilkinson et al., in revision), it is not likely to be relevant to our study. Here, our data show that fish individuals collected from both *before* and *after* were of comparable sizes (Supplementary Fig. 3).

Another factor likely to complicate the interpretation of our findings is the influence of ecosystem (or catchment) size on food web structure (Takimoto & Post, 2013). This is partially accounted for by our longitudinal study design because unlike cross-sectional studies, our primary response variable is less prone to conflation with baseline variations between survey locations. Thus, we were able to determine if observed trends in a response variable (e.g., food web structure) were driven by differences in the intensity of a disturbance regime (e.g., forest loss) independently of ecosystem size driven starting conditions (Takimoto & Post, 2013). We also found that when tested as predictors of food web change, ecosystem size performed more poorly than forest loss metrics measured at an equivalent spatial scale (i.e., whole catchment or immediate upstream area of catchment; Table 2).

Conclusion

We show with a novel combination of approaches that forest loss affects freshwater food webs *via* indirect resource limitations. Our observations also add to a growing body of evidence indicating that terrestrial subsidies are a less important basal resource than autochthonous aquatic production. From a conservation perspective, our findings reinforce the conventional wisdom advocating the preservation of intact forests (Gibson et al., 2011). While this ideal may appear unfeasible in the face of rapid urbanisation and expanding human populations, our observations suggest that we may be able to limit the impacts of anthropogenic development within river catchments by prioritising the preservation (or restoration) of forest cover upstream of more sensitive freshwater habitats. More importantly, our study reveals the impacts of forest loss on food webs at a decadal temporal scale which may not be apparent in the short term because of compensatory effects of buffering mechanisms (e.g., trophic redundancy (Chua et al., in revision), food web complexity (Brose et al., 2005)). It is paramount that we do not underestimate the importance of responsible land-use planning as longer-term impacts can sometimes be overlooked.

Acknowledgements

We gratefully acknowledge an AcRF Tier 1 grant from the Singapore Ministry of Education (National University of Singapore (NUS) Grant No. R-154-000-A32-114). KWJC was supported by the NUS President's Graduate Fellowship and CLW was supported by funding from the Faculty of Science, NUS. We thank the Economic Planning Unit in the Prime Minister's Department of Malaysia (UPE 40/200/19/3440) and the Sabah Biodiversity Council, Yayasan Sabah, Danum Valley Conservation Management Committee and SEARPP (JKM/MBS.1000-2/2JLD.3(9)) for granting us permission to conduct field surveys. We acknowl-

edge Kelvin Lim Kok Peng and other staff at the Lee Kong Chian Natural History Museum, NUS, for their assistance in accessing specimen collections. We thank Chris Yarnes from the University of California Davis for help with sample analysis.

References

- Barlow J, Lennox GD, Ferreira J, Berenguer E, Lees AC, MacNally R, et al. (2016). Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature* , 535: 144–147.
- Brett MT, Bunn SE, Chandra S, Galloway AWE, Guo F, Kainz MJ, et al. (2017). How important are terrestrial organic carbon inputs for secondary production in freshwater ecosystems? *Freshwater Biol* , 62: 833–853.
- Brook BW, Sodhi NS, & Ng PKL (2003). Catastrophic extinctions follow deforestation in Singapore. *Nature* 424: 420–423.
- Brose U, Cushing L, Berlow EL, Jonsson T, Banasek-Richter C, Bersier LF, et al. (2005). Body size of consumers and their resources. *Ecology* , 86(9): 2545.
- Brothers SM, Hilt S, Meyer S, & Kohler J (2013). Plant community structure determines primary productivity in shallow, eutrophic lakes. *Freshwater Biol* , 58(11): 2264–2276.
- Chazdon RL (2008). Beyond deforestation: restoring forests and ecosystem services on degraded lands. *Science* . 320: 1458–1460.
- Chikaraishi Y, Ogawa NO, Kashiyaama Y, Takano Y, Suga H, Tomitani A, et al. (2009). Determination of aquatic food-web structure based on compound-specific nitrogen isotopic composition of amino acids. *Limnol Oceanogr-Meth* , 7: 740–750.
- Choi B, Ha S-Y, Lee JS, Chikaraishi Y, Ohkouchi N, & Shin K-H (2017) Trophic interaction among organisms in a seagrass meadow ecosystem as revealed by bulk $\delta^{13}\text{C}$ and amino acid $\delta^{15}\text{N}$ analyses. *Limnol Oceanogr* , 62: 1426–1435.
- Choy SC, Latif SA, & Yung YN (1996). Resource use in a freshwater fish community of a tropical rainforest stream in northern Borneo. In Edwards DS, Booth WE, & Choy SC (Eds.) *Tropical Rainforest Research—Current Issues* . Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 307–314.
- Chua KWJ, Liew JH, Wilkinson CL, Ahmad AB, Tan HH, & Yeo DCJ (in revision). Land-use change erodes trophic redundancy in tropical forest streams: evidence from amino acid stable isotope analysis. *J Anim Ecol* .
- Chua KWJ, Tan HH, & Yeo DCJ (2019). Loss of endemic fish species drives impacts on functional richness, redundancy, and vulnerability in freshwater ecoregions of Sundaland. *Biol Conserv* , 234: 72–81.
- Chua KWJ, Liew JH, Shin KH, & Yeo DCJ (2020). Effects of ethanol preservation and formalin fixation on amino acid stable isotope analysis ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and its ecological applications. *Limnol Oceanogr-Meth* .
- Digel C, Curtsdotter A, Riede J, Klarner B, & Brose U (2014). Unravelling the complex structure of forest food webs: higher omnivory and more trophic levels. *Oikos* , 123: 1157–1172.
- Doi H, Chang KH, Ando T, Ninomiya I, Imai H, & Nakano SI (2009). Resource availability predict food chain length in pond ecosystems. *Oikos* , 118: 138–144.
- Giam X (2017) Global biodiversity loss from tropical deforestation. *P Natl Acad Sci USA* 114(23): 5775–5777.
- Giam X, Hadiaty RK, Tan HH, Parenti LR, Wowor D, Sauri S, Chong KY, Yeo DCJ, & Wilcove DS (2015). *Conserv Biol* 29(5): 1357–1367.
- Gibson L, Lee TM, Koh LP, Brook BW, Gardner TA, Barlow J, Peres CA, Bradshaw CJA, Laurance WF, Lovejoy TE, & Sodhi NS (2011). Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*

478: 378–381.

Grieve A & Lau DCP (2018). Do autochthonous resources enhance trophic transfer of allochthonous organic matter to aquatic consumers, or vice versa? *Ecosphere* , 9(6): e02307.

Guo F, Kainz MJ, Valdez D, Sheldon F, & Bunn SE (2016). High-quality algae attached to leaf litter boost invertebrate shredder growth. *Freshw Sci* , 35: 1213–1221.

Hetherington ED, Kurlle CM, Ohman MD, & Popp BN (2019). Effects of chemical preservation of bulk and amino acid isotope ratios of zooplankton, fish, and squid tissues. *Rapid Commun Mass Sp* , 33: 935–945.

Hobbs RJ, Arico S, Aronson J, Baron JS, Bridgewater P, Cramer VA, Epstein PR, et al. (2006). Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecol Biogeogr* , 15(1): 1–7.

Holt RD & Loreau M (2001). Biodiversity and ecosystem functioning. The role of trophic interactions and the importance of system openness. In: Kinzig APK, Pacala SW, & Tilman D (eds.). *The Functional consequences of biodiversity* . Princeton University Press. Pp. 246–262.

Jarvis A, Reuter HI, Nelson A, & Guevara E (2008). Hole-filled SRTM for the globe Version 4. Accessed: January 2019. <http://srtm.csi.cgiar.org>.

Kery M (2010). *Introduction to WinBUGS for ecologist* . Academic Press.

Lau DCP, Goedkoop W, & Vrede T (2013). Cross-ecosystem differences in lipid composition and growth limitation of a benthic generalist consumer. *Limnol Oceanogr* , 58: 1149–1164.

Lau DCP, Leung KMY, & Dudgeon D (2009). Are autochthonous foods more important than allochthonous resources to benthic consumers in tropical headwater streams? *J N Am Benthol Soc* , 28: 426–439.

Lawrence D & Vandecar K (2015). Effects of tropical deforestation on climate and agriculture. *Nat Clim Change* , 5: 27–36.

Lawton RO, Nair US, Pielke Sr. RA, & Welch RM (2001). Climatic impact of tropical lowland deforestation on nearby montane cloud forests. *Science* , 294(5542): 584–587.

Lehner B & Grill G (2013). Global river hydrogeography and network routing: baseline data and new approaches to study the world’s large river systems. *Hydrol Process* , 27(15): 2171–2186.

Liew JH, Chua KWJ, Arsenault E, Thorp JH, Suvarnaraksha A, Ahmad A, et al. (2019). Quantifying terrestrial carbon in freshwater food webs using amino acid isotope analysis: Case study with an endemic cavefish. *Methods Ecol Evol* . 10.1111/2041-210X.13230.

Liew JH, Giam X, Clews E, Tan KYW, Tan HH, Kho ZY, & Yeo DCJ (2018). Contrasting changes in freshwater fish assemblages and food webs follow modification of tropical waterways. *Ecol Freshw Fish* , 27(4): 1114–1125.

Liew JH, Jardine TD, Lim RBH, Kwik JTB, Tan HH, Kho ZY, et al. (2018). Bottom-up influences on tropical freshwater food webs support the ‘environmental filtering’ hypothesis. *Limnol Oceanogr* , 63(5): 1877–1890.

Lindsay JB (2016). Whitebox GAT: A case study in geomorphometric analysis. *Comput Geosci* , 95: 75–84.

Loke LHL & Todd PA (2016). Structural complexity and component type increase intertidal biodiversity independently of area. *Ecology* , 97: 383–393.

MacKenzie RA (2008). Impacts of riparian forest removal on Palauan streams. *Biotropica* , 40(6): 666–675.

Maina J, de Moel H, Zinke J, Madin J, McClanahan T, & Vermaat JE (2013). Human deforestation outweighs future climate change impacts on sedimentation on coral reefs. *Nat Commun* , 4: 1986.

- Malhi Y, Gardner TA, Goldsmith GR, Silman MR, & Zelazowski P (2014). Tropical forests in the Anthropocene. *Annu Rev Environ Resour* , 39: 125–159.
- McHugh PA, McIntosh AR, & Jellyman PG (2010). Dual influences of ecosystem size and disturbance on food chain length in streams. *Ecol Lett* , 13(7): 881–890.
- Miettinen J, Chi C, & Liew SC (2012). Two decades of destruction in Southeast Asia’s peat swamp forests. *Front Ecol Environ* , 10(3): 124–128.
- Morris RJ (2010) Anthropogenic impacts on tropical forest biodiversity: a network structure and ecosystem functioning perspective. *Philos T R Soc B*, 365: 3709–3718.
- Myers SM, Gaffikin L, Golden GD, Ostfeld RS, Redford KH, Ricketts TH, et al. (2013). Human health impacts of ecosystem alteration. *P Natl Acad Sci USA* , 110(47): 18753–18760.
- Naman SM, Rosenfeld JS, Kiffney PM, & Richardson JS (2018). The energetic consequences of habitat structure for forest stream salmonids. *J Anim Ecol* , 87(5): 1383–1394.
- Parnell AC (2016). SIMMR: A stable isotope mixing model.
- Parnell AC, Phillips DL, Bearhop S, Semmens BX, Ward EJ, Moore JW, Jackson AL, Grey J, Kelly DJ, & Inger R (2013). Bayesian stable isotope mixing models. *Environmetrics* , 24(6): 387–399.
- Plummer M (2016). rjags: Bayesian graphical models using MCMC. Rpackage version 4.6. <https://CRAN.R-project.org/package=rjags>.
- Ramankutty N, Gibbs HK, Achard F, Defries R, Foley JA, & Houghton RA (2006). Challenges to estimating carbon emissions from deforestation. *Glob Change Biol* , 13(1): 51–66.
- Ruddiman WF (2013). The Anthropocene. *Annu Rev Earth Pl Sci* , 41: 45–68.
- Sass GG, Kitchell JF, Carpenter SR, Hrabik TR, Marburg AE, & Turner MG (2006). Fish community and food web responses to whole-lake removal of coarse woody habitat. *Fisheries* , 31(7): 321–330.
- Takimoto G & Post DM (2013). Environmental determinants of food-chain length: A meta-analysis. *Ecol Res* , 28: 675–681.
- Takimoto G, Spiller DA, & Post DM (2008). Ecosystem size, but not disturbance, determines food-chain length on islands of the Bahamas. *Ecology* , 89(11): 3001–3007.
- Tanentzap AJ, Szkokan-Emilson EJ, Kielstra BW, Arts MT, Yan ND, & Gunn JM (2014). Forests fuel fish growth in freshwater deltas. *Nat Commun* , 4: 4077.
- Vannote RL, Minshall GW, Cummins JW, Sedell JR, & Cushing CE (1980). The river continuum concept. *Can J Fish Aquat Sci* , 37: 130–137.
- Vehtari A, Gelman A, & Gabry J (2017). Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Stat Comput* 27(5): 1413–1432.
- Walsh R, He S, & Yarnes CT (2014). Compound-specific $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis of amino acids: a rapid, chloroformate-based method for ecological studies. *Rapid Commun Mass Sp* , 28: 96–108.
- Walters AW & Post DM (2008). An experimental disturbance alters fish size structure but not food chain length. *Ecology* , 89(12): 3261–3267.
- Wilkinson CL, Chua KWJ, Fiala R, Liew JH, Kemp V, Ewers RM, et al. (in revision). Conversion to oil-palm alters freshwater trophic ecology in Borneo. *Ecology*
- Wilkinson CL, Yeo DCJ, Tan HH, Fikir AH, & Ewers RM (2018). Land use change leads to significant loss of freshwater fish species and functional richness in Sabah, Malaysia. *Biol Conserv* , 222: 164–171.

Wolkovich WM, Allesina S, Cottingham KL, Moore JC, Sandin SA, & de Mazancourt C (2014). Linking the green and brown worlds: The prevalence and effect of multichannel feeding in food webs. *Ecology* 95(12): 3376–3386.

Table captions

Table 1 Summary of changes in forest cover over time across river catchments surveyed.

Table 2 Summary of predictive model parsimony (mean WAIC and LOO) and accuracy (RMSE) of forest loss metrics as well as ‘null’ variables (i.e., predictor variables unrelated to forest loss). Lower values (denoted by asterisks) suggest greater parsimony (WAIC and LOO) or predictive accuracy (RMSE).

Figure captions

Figure 1 Four river catchments surveyed in Southeast Asia (Malaysia and Singapore). Catchment boundaries are highlighted in blue. Inset depicts Singapore and its surrounding areas.

Figure 2 Changes in land-use cover over time across the four catchments surveyed: Danum (top-left); Endau (top-right); Nee Soon (bottom-left); and NSFPF (bottom-right). Red pixels represent catchment area associated with forest loss while green pixels represent catchment area associated with forest gain. Black circles represent the exact sites where fish specimens were collected. All sites were sampled in both the *before* and *after* time points.

Figure 3 Probability distribution of pair-wise intra-specific differences in TP between the before and after time points.

Figure 4 Distribution (average and standard deviation) of mean slope coefficients describing the relationship between mean intra-specific change in TP over time (Δ TP) and various ‘null’ variables (filled circles) as well as forest loss metrics (empty circles). Mean slope coefficients were parameterised over 100 iterations of generalised linear models using a Bayesian approach (see Methods).

Tables

Table 1

Catchment	Total Area (km ²)	Temporal Range (duration [years])	Forest Cover Lost (km ²)	Forest Cover Gained (km ²)	Catchment Area upstream of sampling points (km ²)	Forest cover lost upstream of sampling points (km ²)	Forest cover gained upstream of sampling points (km ²)
Danum	4066	1996–2015 (19)	487.0	299.0	539	1.70	6.30
Endau	4482	1998–2018 (20)	1042.0	155.0	106	34.90	3.60
Nee Soon	5	1990–2015 (25)	0.2	0.4	1	0.06	0.04
NSPSF	2607	1991–2018 (27)	278.0	89.0	37	3.50	0.40

Table 2

Predictors	Mean WAIC	Mean LOO	Mean Model Fit (RMSE)
Catchment area (A_{total})	9.4	10.0	0.38
Upstream area ($A_{\text{sub.total}}$)	5.9*	6.7	0.36
Water quality change (ΔQ)	8.8	9.4	0.35
Total catchment forest loss ($\Delta\Phi_{\text{total}}$)	9.1	9.5	0.35
Net catchment forest loss ($\Delta\Phi_{\text{net}}$)	9.0	9.4	0.35
Catchment forest-cover change ratio ($\Delta\Phi_{\text{ratio}}$)	8.9	9.5	0.35
Total upstream forest loss ($\Delta\Phi_{\text{sub.total}}$)	8.8	9.5	0.33
Net upstream forest loss ($\Delta\Phi_{\text{sub.net}}$)	8.8	9.5	0.33
Upstream forest-cover change ratio ($\Delta\Phi_{\text{sub.ratio}}$)	6.2	6.4*	0.29*

Figures

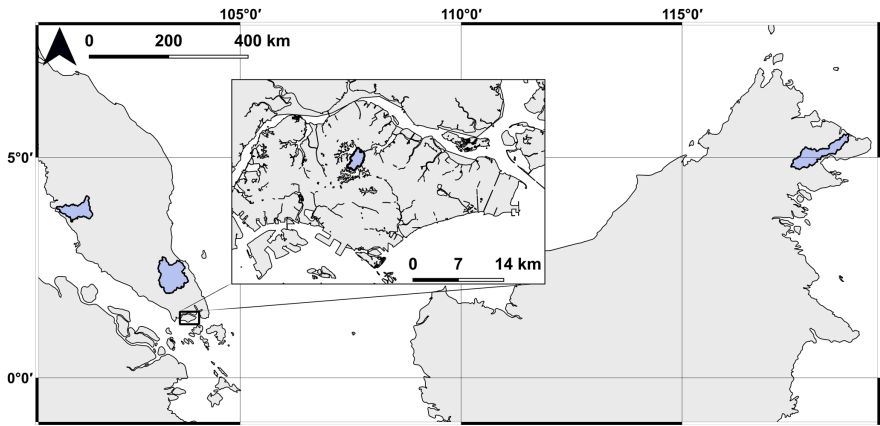


Fig. 1

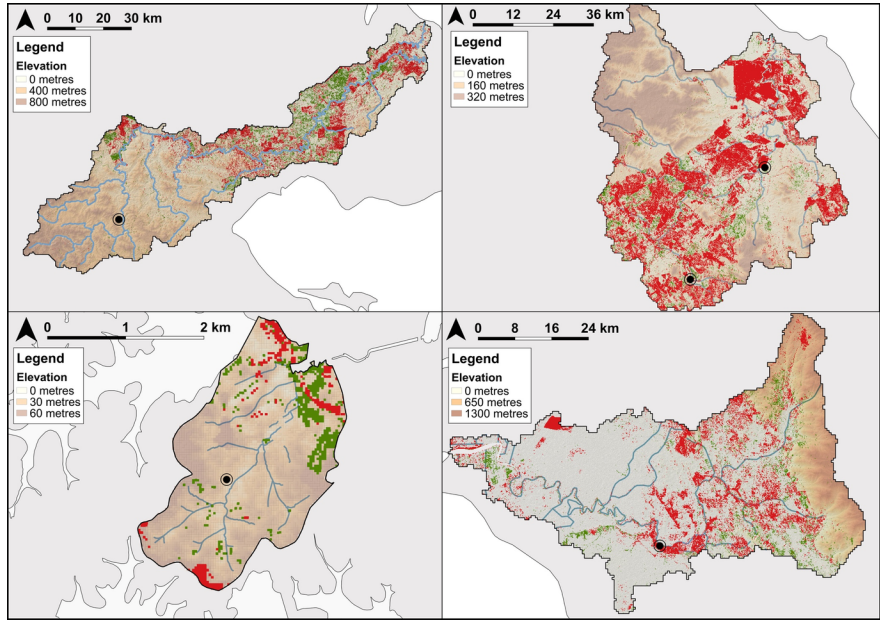


Fig. 2

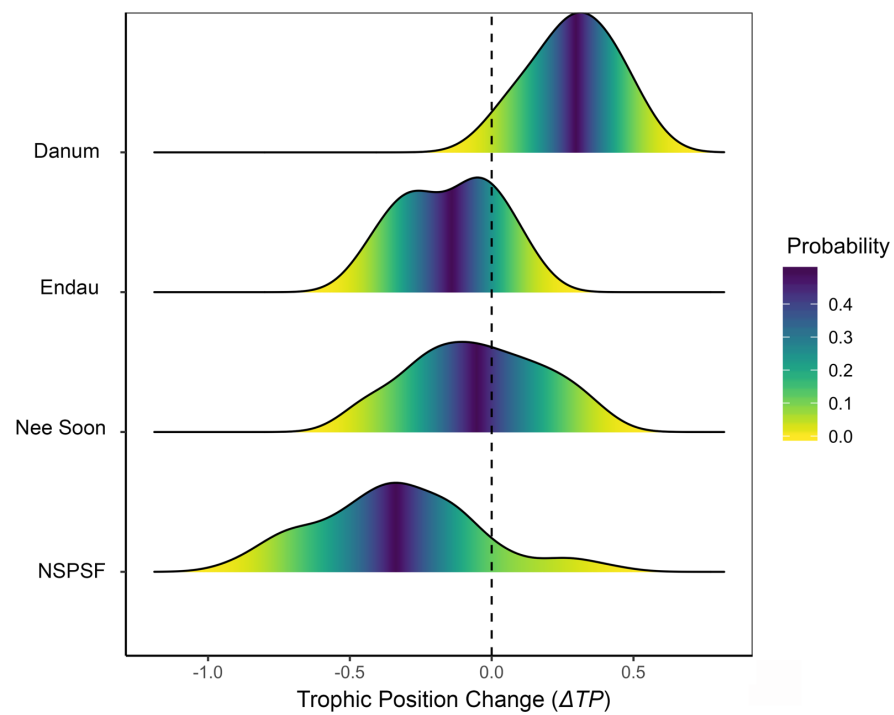


Fig. 3

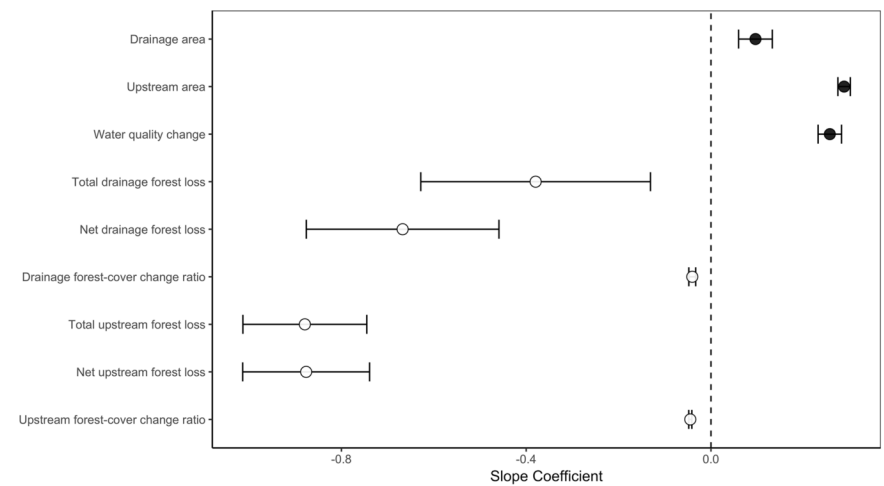


Fig. 4

