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ORIGINAL ARTICLE

Weak edge effects on trees in Bornean rainforest remnants bordering oil palm

Jake A. Anderson[1] | Colin J. McClean[2] | Sarah Sim[3] | Nathalie Pettorelli[4] | Ahmad Jelling[5] | Joseph Tangah[6] | Jane K. Hill[1]

[1]Department of Biology, Leverhulme Centre for Anthropocene Biodiversity, University of York, York, UK

[2]Department of Environment and Geography, University of York, York, UK

[3]Unilever Safety and Environmental Assurance Centre, Unilever R&D, Sharnbrook, UK

[4]Zoological Society of London, Institute of Zoology, London, UK

[5]South East Asia Rainforest Research Partnership, Danum Valley Field Centre, Sabah, Malaysia

[6]Sabah Forestry Department, Forest Research Centre, Sabah, Malaysia

Correspondence
Jake A. Anderson, Department of Biology, Leverhulme Centre for Anthropocene Biodiversity, University of York, York YO10 5DD, UK.
Email: jaa563@york.ac.uk

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Abstract

Many tropical forests are dominated by edge habitat, with consequences for forest structure, carbon stocks, and biodiversity. However, edge effects are highly variable and context-dependent, and are poorly quantified in oil palm landscapes. We studied edge effects in 10 lowland rainforest remnants bordering mature oil palm plantations on Borneo, by surveying 0.2 ha plots along transects running perpendicular to the forest edge (ten 1.6 km transects, 5-6 plots per transect; 57 plots in total). We examined how edge proximity affected plot-level forest structure (canopy cover, number and size of stems ≥10 cm diameter), aboveground carbon stocks, microclimate (air temperature and light intensity), and tree community composition and richness. The largest trees were significantly smaller (up to 21% reduced diameter) in plots near edges, and plot-level carbon was up to 30% lower (model-fitted average = 64.7 Mg ha^{-1} at 50 m from the edge, versus 92.3 Mg ha^{-1} at 1600 m), with the strongest effects within 300m of edges. However, these significant effects of edge proximity were relatively small in the context of existing variation, with distance-from-edge explaining <13% of the total variability in maximum tree size or carbon. In addition, there were generally no effects of edge proximity on any other component of forest structure, composition or diversity, and only a weak effect on microclimate. We conclude that limited edge effects in this system may reflect low structural contrast between forest and mature oil palm, and limited invasion of pioneer trees from plantations, which diminished edge influence in highly heterogeneous forest remnants.

Abstract in Malay is available with online material.

KEYWORDS
agricultural expansion, biodiversity, carbon storage, forest fragmentation, forest structure, microclimate, tropical trees

1 | INTRODUCTION

Agricultural expansion has caused widespread loss of tropical rainforests, which support an outstanding diversity of species and provide valuable ecosystem services (Lewis et al., 2015). This expansion is predicted to continue in the coming decades to provide food and resources for a growing human population (Laurance et al., 2014). Deforestation for agriculture causes a reduction in forest area and increased fragmentation of remaining forest, with consequences for biodiversity and key ecosystem functions such as carbon storage

(Haddad et al., 2015). Forest fragmentation creates edges, where abiotic and biotic changes ("edge effects") can drive significant ecological changes within remnants (Laurance et al., 2002; Pfeifer et al., 2017). Approximately 20% of remaining tropical forest is within 100m of an edge (Brinck et al., 2017); it is therefore critical that we understand the impacts that edges have on rainforest tree communities, both to quantify the environmental impacts of agricultural expansion and to devise management strategies to limit detrimental effects.

Forest edges are typically hotter, drier, brighter and windier than interior forest, with increased vulnerability to desiccation and fire (Laurance et al., 2002). Abiotic changes lead to biotic edge effects, such as elevated tree recruitment and mortality, causing rapid community turnover (Laurance et al., 2006). This typically manifests in declines of slow-growing, late successional species with higher wood densities, whilst fast-growing pioneers with lower wood densities, better suited to the disturbed conditions at edges, become more dominant (Tabarelli et al., 2012). Thus, long-term compositional shifts can occur, resulting in taxonomically and functionally distinct tree communities at forest edges (Santos et al., 2008), changes to stand-level structure (e.g., stem number, stem size, and canopy density) (Broadbent et al., 2008) and reduced species richness (Oliveira et al., 2004), but not always (Ibáñez et al., 2014). Increased mortality of large and high wood density trees can cause declines in aboveground biomass and carbon (de Paula et al., 2011), but edge effect magnitude is highly variable, and can be mediated by structural contrast with the adjacent matrix (i.e., land cover) type (Melito et al., 2018).

Not only do edge effects vary in magnitude, but also it is often unclear how far they permeate into the forest. Many studies report penetration distances of less than 500m, albeit with considerable variation in exact distances (Broadbent et al., 2008). Estimates from remotely-sensed data, however, indicate that biomass losses of >10% can penetrate at least 1.5km into the forest, but this is highly variable among regions (Chaplin-Kramer et al., 2015). Hence, variable edge effects are commonly reported (Ries et al., 2004); this may in part be due to variable study designs but is also due to the context-dependent nature of edge effects (Ries et al., 2017). Landscape composition and configuration exert a strong influence on edge effect magnitude and penetration depth, and also define the ecological context within which to assess their significance (Harper et al., 2005). Given that forest fragmentation is becoming increasingly common (Fischer et al., 2021), and that remaining forest patches are important refuges for wildlife and contribute to carbon stocks in agricultural landscapes (Fleiss et al., 2020), it is important to examine edge effects across a range of human-modified landscapes.

To date, there has been relatively little research on rainforest edges that border oil palm (*Elaeis guineensis*) plantations. This is surprising given that palm oil is the world's most consumed vegetable oil (Meijaard et al., 2020), with plantations estimated to cover over 20M ha globally (Descals et al., 2021) and with around half of all new plantations occupying land converted from forest (Meijaard et al., 2018). Oil palm is a perennial crop that can reach over 13m in height in industrial plantations, forming a closed canopy with a stable understory microclimate (Luskin & Potts, 2011). It may therefore buffer the severity of edge effects in neighboring forest (Fitzherbert et al., 2008), explaining the lack of edge effects found by Fleiss et al. (2020) in forest remnants within plantations. However, remotely-sensed data from Borneo suggest that edge effects may have large impacts on aboveground carbon (AGC) in forest remnants, resulting in average declines of 22.5% up to 114m from oil palm plantations (Ordway & Asner, 2020). Similarly, Nunes et al. (2021) found that forest within 300m of oil palm plantations had reduced canopy growth during the 2015-16 El Niño event. In addition, there is evidence of increased stem turnover and reduced biomass accumulation up to 448m from edges in oil palm landscapes (Qie et al., 2017), suggesting that biomass loss may be due to compositional shifts toward low wood density taxa. However, Qie et al. (2017) also included edges bordering other matrix types in their study, such as inhabited areas, clear cut logging, regenerating forest and logging roads. Thus, it is unclear if there are changes in plant community composition or diversity in edges bordering oil palm, and there is also a lack of consensus on the magnitude and scale over which edge effects may operate.

The growth of the palm oil industry is expected to continue (Meijaard et al., 2020), and it is important to consider edge effects when quantifying the environmental impacts of oil palm expansion. Edge effects can account for 19% of palm oil production greenhouse gas (GHG) emissions, but are typically not included in GHG footprint studies (Lam et al., 2019); these will benefit from robust estimates of AGC loss at edges. In addition, the Roundtable on Sustainable Palm Oil (RSPO) has Zero-Deforestation Commitments and requires patches of forest with "High Conservation Values" (e.g., high biodiversity) and "High Carbon Stocks" to be conserved (Rosoman et al., 2017; RSPO, 2018). Estimates of carbon stocks and biodiversity levels could be significantly enhanced with better understanding of edge effects within oil palm landscapes, potentially enabling better conservation and management practices and outcomes.

In this study, we conducted field surveys to quantify edge effects on rainforest tree communities in forest remnants bordering mature oil palm plantations in Sabah, Malaysian Borneo. Forests in this region contain some of the highest levels of AGC of any tropical forests (Asner et al., 2018) and are important biodiversity hotspots (Myers et al., 2000). However, Sabah has lost approximately 40% of its forest cover since 1973 (Gaveau et al., 2014) and the remaining forest is highly fragmented within oil palm plantation landscapes, with plantations now accounting for >20% of Sabah's land cover (MPOB, 2019). We quantify changes in plot-level forest structure, AGC and microclimate at increasing distances into forest remnants from edges bordering plantations, and examine how the composition and diversity of tree communities change, up to 1.6km from edges. We studied effects over these distances because edge influence can persist up to 1.5km from edges (Chaplin-Kramer et al., 2015). We test the hypotheses that edge plots contain fewer and smaller stems and have lower AGC stocks than interior plots, and also have reduced canopy cover, higher temperatures, and higher light levels.

We also test the hypothesis that tree community composition near edges is distinct from forest interior plots, with taxonomic and functional shifts toward low wood density pioneer trees, the loss of some taxa, and lower tree richness.

2 | METHODS

2.1 | Study region and field sites

We studied 10 lowland (<500 m a.s.l.) mixed dipterocarp rainforest remnants in the State of Sabah, Malaysian Borneo (Figure S1; Table S1), between June and October 2019. All sites were forest reserves protected from disturbance (i.e., timber logging and hunting), containing interior forest areas at least 1.6 km from any edges, except Site 6 which only had interior forest 1 km from edges. Whilst detailed management histories of sites are not available, most have likely been selectively logged at variable intensities in the past (Gaveau et al., 2014). However, there has been no commercial logging in any site since at least 1984, when they were formally declared as protected areas, although many may have experienced low levels of encroachment (e.g., felling and hunting) (Stride et al., 2018). Edges were 19–49 years old (mean = 36 years), and bordered by large expanses of mature oil palm plantations. Neighboring palms were on average 12.6 m tall (SD = 3.75 m) and 7.5 m apart, with varied understory vegetation typical of mature plantations (Luke et al., 2019).

2.2 | Vegetation surveys

We placed a single transect in each site, running perpendicular from the edge to the interior and >800 m from any other edges, to avoid influence from multiple edges (Porensky & Young, 2013). Transects were >4 km apart to avoid spatial autocorrelation. Forest edge was defined as the point where natural vegetation became taller than 5 m in height (UN FAO, 2012); however, edges were usually characterized by a hard boundary between natural forest and oil palm at our sites, sometimes separated by minor plantation tracks. Transects comprised six circular plots (25 m radius, 0.2 ha) spaced to concentrate sampling effort close to the edge (Figure S1c), where the greatest effect of edge proximity was expected. Transects at three sites contained only five plots, either due to small remnant size or because natural features made the final plot inaccessible. In total, we sampled 57 plots (total area of 11.2 ha).

Within each plot, we used a nested survey design to maximize sampling efficiency (Figure S1d) and followed standard protocols (Marthews et al., 2014; Phillips et al., 2016) to inventory live trees (including palms) above 10 cm diameter at breast height (dbh). Trees were identified to genus level, or to species when known (23.1% of stems), either in the field or in consultation with botanists at Danum Valley Field Centre herbarium. Tree height was estimated by eye, always by the same person (AJ). AJ's estimates have been validated against the "tangent method", which is commonly used to estimate tree height (Larjavaara & Muller-Landau, 2013), and were closely correlated (Fleiss et al., 2020), giving us confidence in our estimates.

2.3 | Forest structure and microclimate measures and AGC estimation

For each plot we calculated the total number of individual stems sampled, and the mean and maximum dbh (cm) and height (m), to characterize plot-level forest structure. We also measured canopy density using a spherical crown densiometer, taking four readings (N, E, S, and W) from the plot center then converting these to a single plot-level measure (proportion cover from 0–1). We measured mean daily air temperature (°C) and mean daytime light intensity (lum/ft^2) within each plot, using Hobo® loggers (see Appendix S1 for details).

We assigned wood density (g/cm^3) values to each stem at the finest taxonomic level available, using the Global Wood Density Database (Chave et al., 2009; Zanne et al., 2009), then used published allometric equations (Chave et al., 2014; Goodman et al., 2013) to produce plot-level AGC (Mg C ha^{-1}) estimates (see Appendix S1 for details).

2.4 | Tree diversity and community composition measures

As a measure of functional composition, we calculated plot-level community-weighted mean (CWM) wood density (g/cm^3), using mixed-resolution wood density values (12.9% of stems at species level, 82.4% at genus level, 4.6% at family level) and plot-level abundance weightings. Wood density is a functional trait linked to growth strategy, with lower-wood density trees typically having faster growth rates, increased light preference and earlier successional status (Slik, 2005). We used genus-level data for analyses of taxonomic composition, and calculated plot-level genus richness (number of genera) as our measure of tree diversity. We worked at genus level because there are challenges with reliably identifying trees to species in Borneo, and analyzing genus-level data can give more reliable results than species-level identifications (Slik et al., 2003), whilst also increasing sampling efficiency to give greater sample sizes (Imai et al., 2014). Genus-level data are also commonly used in studies of disturbance-driven floristic changes (Laurance et al., 2006; Michalski et al., 2007; Slik et al., 2008). Furthermore, patterns of floristic richness and composition are highly correlated between taxonomic levels in Borneo forests, making fragmentation and disturbance effects detectable at multiple taxonomic resolutions (Ganivet et al., 2020; Imai et al., 2014; Stride et al., 2018), and wood density is a highly taxonomically-conserved trait, with 72.5% of species-level variation explained at the genus-level (Slik, 2006). Our analyses of taxonomic and functional composition and diversity are therefore robust to genus-level information.

2.5 | Data analysis of forest structure, AGC, and microclimate

We conducted all analyses in R version 4.0.2 (R Core Team, 2020), using mixed-effects models to test for edge effects on: number of trees (stems per plot), mean and maximum tree dbh (cm), mean and maximum tree height (m), canopy density (proportion cover from 0–1), AGC (Mg ha^{-1}), mean daily temperature (°C), and mean daytime light intensity (lum/ft^2) (nine models in total; Table 1). Data were analyzed at plot level, using the lme4 package (Bates et al., 2015). Maximum dbh and mean daytime light intensity were both ln-(natural log) transformed to improve model fits, based on diagnostic plots. For all models, we used ln-transformed distance of plots from the forest edge as our fixed effect in order to linearize predicted edge-response curves, following Ibanez et al. (2017), which is appropriate given our concentrated sampling effort closer to the edge. We fitted models with appropriate error distribution families and link functions (Table 1) to ensure model assumptions were met and included "site" as a random intercept in all models to account for site-level variation in response variables.

2.6 | Community composition and diversity analyses

We used the same modelling procedure to test for edge effects on plot-level CWM wood density and genus richness (two models; Table 1). To evaluate taxonomic similarity between plots in relation to edge proximity, we computed a Bray–Curtis dissimilarity matrix of all plots (Magurran, 2004), based on relative abundances of genera. We then performed an ordination using non-metric multidimensional scaling (NMDS) with 1000 iterations, using the R vegan package (Oksanen et al., 2020). We used a permutational multivariate analysis of variance (PERMANOVA) to assess differences in plot-level community composition between the six distance classes (treated categorically for this analysis), with 999 permutations to calculate significance.

To determine whether some taxa may be lost from edges even in the absence of detectable edge effects on plot-level richness or community composition, we pooled data from the 10 sites into 3 distance classes: "edge" (50 m + 100 m plots), "intermediate" (200 m + 400 m plots), and "core" (800 m + 1600 m plots). We used a randomization approach to generate a random (abundance-based) distribution of genera amongst categories (Appendix S1), then used a chi-square goodness-of-fit test to determine if the actual distribution of genera differed from what we would expect by chance (i.e., our randomization approach). If compositional shifts are resulting in the loss or gain of genera at edges (as distinct communities form), we would expect to see more genera unique to each individual distance class, and fewer genera found in all three classes, than predicted by chance alone. To confirm that our results are robust to the taxonomic resolution of our data, we also repeated all diversity and composition analyses on higher-resolution subsets of our data as a sensitivity analysis (Appendix S1).

3 | RESULTS

In total, we surveyed 2403 individual stems from 57 plots at 10 sites, representing 138 genera (Table S3) and 54 families. We found high levels of heterogeneity among plots. For example, AGC varied from 11.3 to 255.9 Mg ha^{-1} (mean = 81.9 Mg ha^{-1} ± 44.4), and genus richness varied from 8 to 31 genera per plot (mean = 20 genera ± 4.8). There was also high floristic dissimilarity between plots according to Bray–Curtis index scores (mean = 0.8 ± 0.11, on a 0–1 scale).

TABLE 1 Summary of mixed-effects models used to analyze the effect of ln-(natural log) transformed distance-from-edge on plot-level variables, with site included as a random intercept in all models

Response variable	Error family (link function)	β (±SE)	p	R^2_M	R^2_C
Stem number	Negative binomial (log link)	0.01	.74		
Mean dbh (cm)	Gamma (log link)	0.001	.94		
ln(Max dbh (cm))	Gaussian (identity link)	**0.07 (±0.02)**	**.004**	**0.13**	**0.20**
Mean height (m)	Gamma (log link)	0.02	.23		
Max height (m)	Gaussian (identity link)	**3.4 (±1)**	**.002**	**0.10**	**0.50**
Canopy density (proportional)	Binomial (identity link)	−0.0002	.96		
Aboveground carbon (Mg ha^{-1})	Gamma (log link)	**0.103 (±0.05)**	**.027**	**0.05**	**0.27**
Mean daily temperature (°C)	Gaussian (identity link)	**−0.05 (±0.02)**	**.02**	**0.005**	**0.95**
ln(Mean daylight intensity (lum/ft^2))	Gamma (log link)	−0.01	.20		
CWM wood density (g/cm^3)	Gamma (identity link)	0.005	.12		
Genus richness	Poisson (log link)	−0.007	.79		

Note: Models with a significant effect of distance ($p < .05$) are denoted in bold. Marginal (R^2_M) and conditional (R^2_C) R^2 values are given for these models, representing the proportion of variance explained by the fixed effect (ln-distance), and the entire model, respectively.

3.1 | Variation in forest structure, AGC, and microclimate with distance from edge

We found a significant effect of distance-from-edge on some components of forest structure, with maximum tree height, maximum dbh and AGC declining closer to edges (Table 1). Model-predicted values showed a 26.2% decrease in maximum height in plots at 50 m (mean = 32.9 m) versus 1600 m (mean = 44.6 m; Figure 1a; $p < .01$), and a similar decrease (21.3%) in maximum dbh (65.9 cm compared with 83.7 cm; Figure 1b; $p < .01$). The loss of very large trees in plots near edges resulted in a 29.9% decline in plot-level AGC (from 92.3 to 64.7 Mg ha^{-1} in plots at 1600 m vs. 50 m; Figure 1c; $p < .05$). Edge effects on these three variables weakened with distance, with more than half of the change occurring within approximately 300 m of the edge. Edge proximity explained only 13% of the total variance in maximum dbh, 10% of total variance in maximum height, and 5% of total variance in AGC (Table 1 R^2_M). Hence, whilst significant, distance-from-edge explained only a small proportion of the total variation in these three variables. There was no effect of edge proximity on any other structural variable we measured (mean height, mean dbh, number of stems, canopy density; Table 1; Figure S2).

Edge plots were marginally hotter, but there was no significant effect of edge proximity on mean daytime light intensity (Table 1; Figure S2f). Model-predicted values showed a significant but small temperature increase from 25.54°C at 1600 m to 25.71°C at 50 m ($p < .05$; Figure 1d), and edge proximity explained only 0.5% of the total variance. There was a large effect of site in the model ($R^2_C = 0.95$), likely because sites were sampled on different days.

3.2 | Community composition and diversity

There was no significant effect of distance-from-edge on plot-level genus richness (Table 1; Figure 2b). There was also no evidence of plots clustering by distance in the NMDS ordination (Figure 2a), and results of the PERMANOVA supported this conclusion ($R^2 = 0.07$, $p = .98$), indicating that edge communities were not taxonomically distinct from forest interior communities. There was no significant effect of distance-from-edge on CWM wood density (Table 1; Figure S2e), indicating that there was also no edge effect on tree functional composition. This lack of edge effects on tree richness or composition was supported by analyses on data pooled into three distance classes (edge, intermediate, and core); there was no significant difference between the observed distribution of genera among distance classes and their expected random abundance-based distribution ($\chi^2(6) = 7.47$, $p = .3$). Sensitivity analyses generally showed no qualitative change in results, and whilst a minority did give significant results indicative of possible edge effects, these were biologically weak and were driven entirely by outlier plots or rare (<1 individual/ha) species (Appendix S1). Thus, our findings are robust to the taxonomic resolution of our data, and we conclude that distance-from-edge generally had no effect on tree diversity or community composition.

4 | DISCUSSION

4.1 | Edge effects on the largest trees and AGC

We found reduced AGC in forest edges bordering oil palm plantations, with a 30% reduction in predicted plot-level AGC from 1600 m to 50 m (Figure 1c). This is similar to estimates from remotely-sensed data, with Ordway and Asner (2020) reporting AGC declines of up to 30% in some edges. Given the absence of edge effects on stand-level structure and composition, but declines in maximum tree dbh and height, we conclude that AGC loss is driven primarily by edge effects on large trees (i.e., those over 70 cm dbh; Slik et al., 2013; Figure 1b). Thus, decline in biomass and AGC occurred independent of any compositional shifts, as observed elsewhere (Silva et al., 2021), probably because large trees make up a small proportion of stems but make a disproportionately large contribution to biomass (Slik et al., 2013).

Large trees (e.g., Figure S5) are commonly among the worst affected by edge effects (Laurance et al., 2000). They are highly susceptible to wind damage and canopy desiccation (Gora & Esquivel-Muelbert, 2021), which tend to be higher near edges and can cause increased mortality (Magnago et al., 2015). Indeed, the largest trees on Borneo are sensitive to drought-induced mortality (Phillips et al., 2010) and are typically found in sheltered areas where wind speeds are low (Jackson et al., 2021). Thus, abiotic changes at edges can reduce forest biomass (Qie et al., 2017). Many edges in our study were created after commercial logging had ceased, but subsequent encroachment and felling of large trees could also have contributed to the observed patterns, if removal rates have been higher near edges, where trees are more accessible. Nonetheless, even if logging has contributed to tree mortality at edges, we argue that this is still an edge-related effect, given that it results from edge creation and maintenance (Ries et al., 2017). Our finding that the largest trees are smaller at edges (21% reduced dbh, 26% reduced height) may therefore indicate increased mortality (via abiotic effects or edge-facilitated felling), and/or inhibited growth (Nunes et al., 2021), of the largest trees near plantations.

Over half of the observed reduction in AGC and maximum tree size occurred within approximately 300 m from the edge (Figure 1), supporting studies that found edge effects within 300–500 m of edges (Nunes et al., 2021; Ordway & Asner, 2020; Qie et al., 2017). Small forest remnants will increasingly dominate many fragmented tropical landscapes (Taubert et al., 2018), and remnants without interior forest areas further than 300m from edges may therefore experience severe degradation of the large tree stand and associated carbon stocks. Effects on the largest trees could also have wider consequences, given their importance for numerous ecosystem processes and the many species they support (Pinho et al., 2020), and their loss may also have contributed to the small increase in understory temperature we observed near edges.

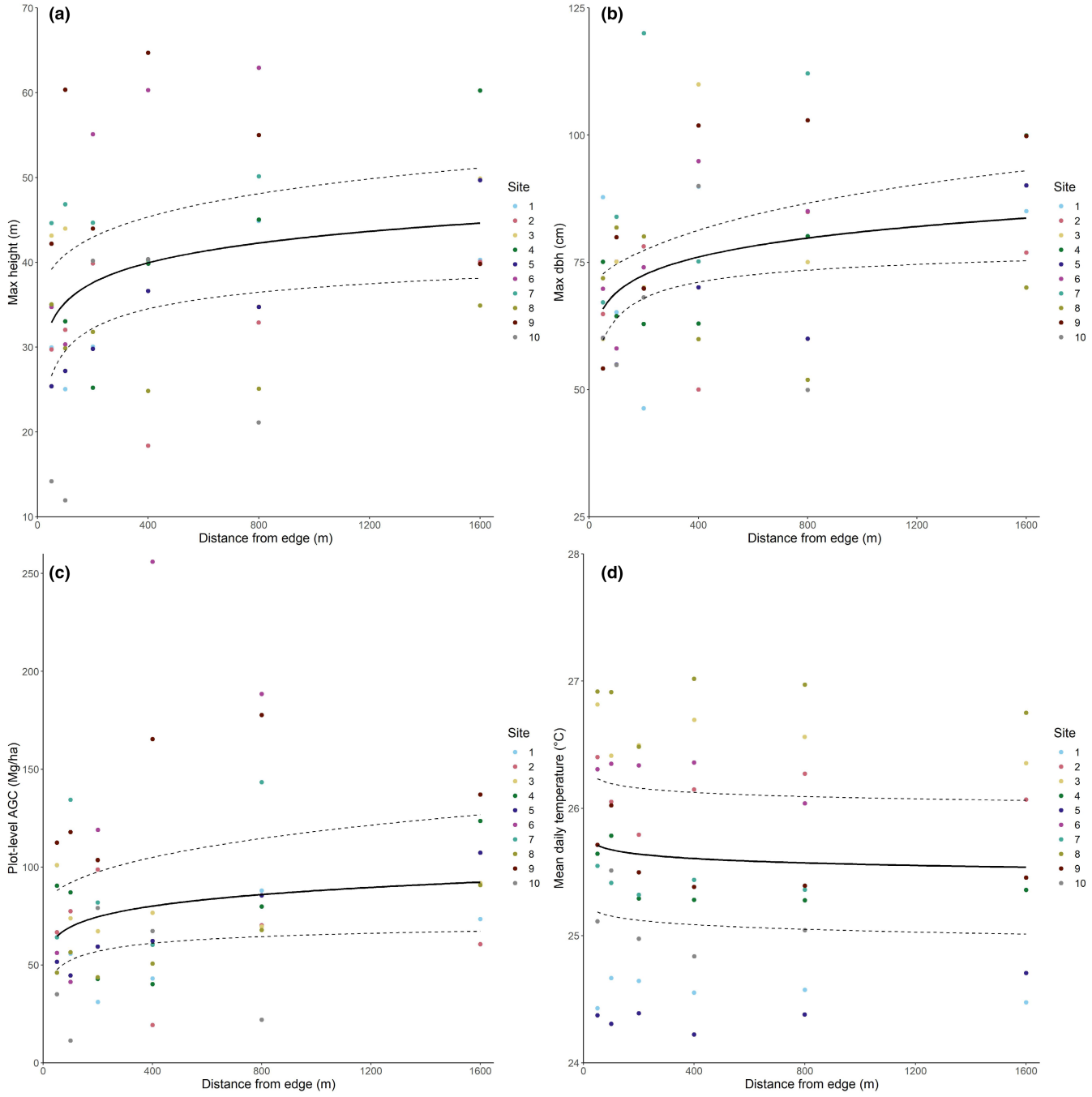

FIGURE 1 Significant effect of edge proximity (ln-transformed) on (a) maximum height (m), (b) maximum dbh (cm), (c) AGC (Mg ha^{-1}), and (d) mean daily temperature (°C), with 95% confidence intervals. Relationships are plotted against untransformed distance in order to visualize the non-linear edge effect. All models include "site" as a random intercept but only a single trend line is presented here for each model, using predicted values for the entire sample, to aid visualization of the effect (see Figure S3 for individual trend lines for each site). Maximum dbh was ln-transformed prior to analysis, therefore the exponents of predicted values were taken to make results more interpretable. Minor jitter applied to all figures to aid visualization of overlapping data points. See Table 1 for model structures, coefficients and significance values

4.2 | Weak edge influence—the importance of local context

Contextualizing the influence of edge effects against existing variability within a system is essential to evaluate their relative importance (Harper et al., 2005). Whilst distance-from-edge caused a significant and meaningful decline in both AGC and maximum tree size ($p < .05$, .01 and .01, respectively; Table 1), these effects were relatively small in the context of the high baseline heterogeneity within the forest. Distance-from-edge explained only 13%, 10%, and 5% of the total variation in maximum dbh, maximum height, and AGC, whilst including site as a random effect in the models

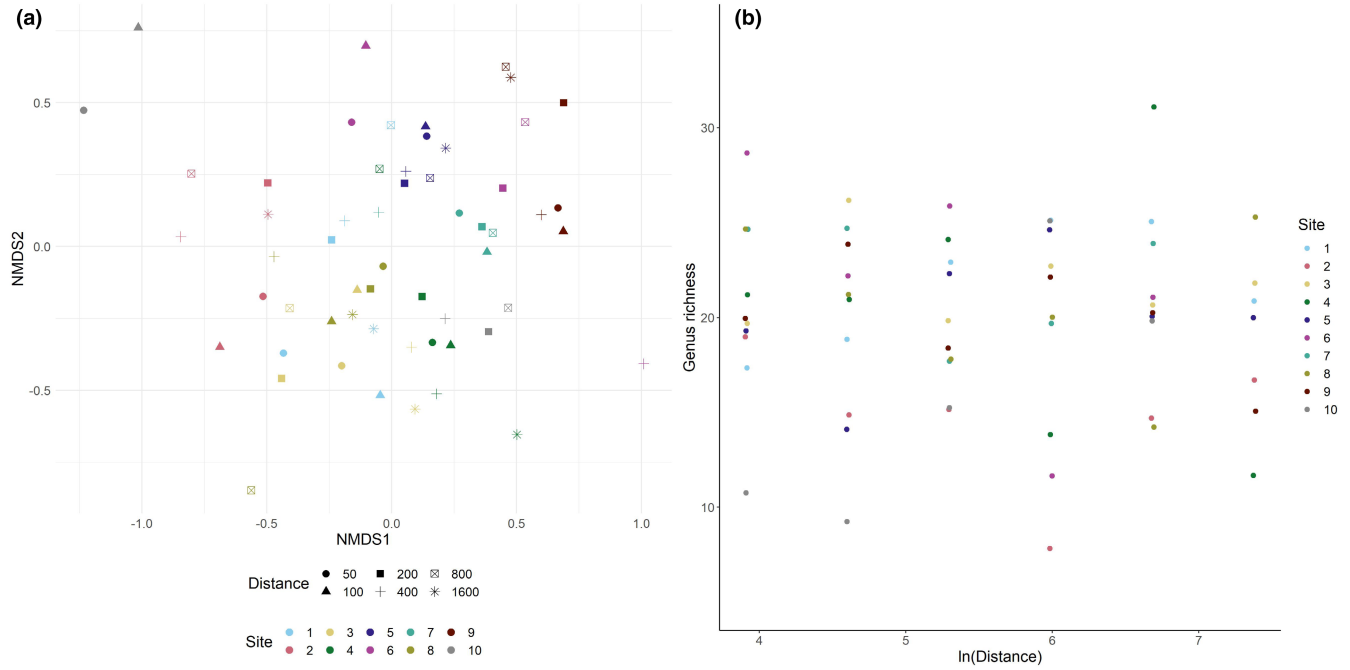

FIGURE 2 (a) Non-metric multidimensional scaling (NMDS) of plot genus composition, using Bray–Curtis index scores based on relative abundances (stress = 0.25), (b) No effect of edge proximity (ln-transformed) on plot-level genus richness, with minor jitter applied to aid visualization of overlapping data points (see Table 1 for model structure, coefficients, and significance value)

accounted for an additional 7%, 40%, and 22% of variation, respectively (Table 1 R^2 values). Thus, the ecological importance of edge influence in our study system is low compared with other drivers of variation, such as inter-site differences in factors such as disturbance (e.g., from selective logging) or topography, which can outweigh fragmentation effects (Fleiss et al., 2020; Liu & Slik, 2014). In addition, contrary to our hypotheses, many effects found in other systems were absent. We generally found no effect of edge proximity on community composition or tree diversity, no effect on most forest structural variables (e.g., stem number and canopy density), and only a weak effect on microclimate (<0.2°C increase in temperature). Thus, overall edge effects do not appear to be as dominant here as in other systems (Laurance et al., 2018). We think this finding is unlikely to be due to the taxonomic resolution of our data, because analyses on a subset of stems identified to species-level support our conclusions (Appendix S1). Other studies have shown that the adjacent matrix is a key determinant of ecological change within forest fragments, and has a mediating influence on fragmentation effects (Driscoll et al., 2013; Hatfield et al., 2020; Kupfer et al., 2006), and so, the nature of the oil palm matrix (i.e., its structure, composition and extent) is likely to be an important factor in explaining the limited influence of edges in our study.

The average height of palms bordering our sites was 12.6 m; at this height, plantations have typically developed closed canopies and some level of understory complexity (Luskin & Potts, 2011). Thus, compared with forest bordering open habitats such as pastureland (Laurance et al., 2002) or annual crops such as sugarcane (Santos et al., 2008), structural contrast is maintained at relatively low levels at these plantation-forest edges. Structural contrast directly mediates the strength of abiotic gradients at edges, which control the magnitude and distance of effects on tree communities (Arroyo-Rodríguez et al., 2017; Mesquita et al., 1999), thus palm maturation may have provided a buffer against edge influence. For example, plantations are typically only around 2.8°C hotter than forest once mature (Luskin & Potts, 2011); hence the very small increase in temperature we observed near edges, which may also have been buffered by vegetation regrowth "sealing" the forest edge (Didham & Lawton, 1999) and may only occur over very short distances (Ewers & Banks-Leite, 2013). Oil palm plantations may also act as a barrier to the dispersal of disturbance-adapted trees into forest edges, thus minimizing compositional shifts. Study systems in which tree communities experience strong edge effects often contain many small, degraded forest remnants in close proximity to one another (Benchimol & Peres, 2015; Laurance et al., 2002; Magnago et al., 2017; Santos et al., 2008), which can act as a source of seed rain and facilitate the spread of pioneer trees into edges (Jesus et al., 2012), and trees within the matrix can also act as a source of propagule pressure (Nascimento et al., 2006). However, management practices that prevent the establishment of mature trees within monoculture oil palm plantations, and the isolation of forest remnants within the plantation landscape (Figure S1; Scriven et al., 2015), will probably limit pioneer tree seed rain into edges, given that the maximum dispersal distance of most trees in the region is 100–1000 m (Corlett, 2009). Hence, the composition and configuration of forest remnants and the plantation landscape have likely mediated the ecological influence of edges in this study system. This suggests that mature tree communities in remnants within these oil palm landscapes may have some resilience to fragmentation effects, although it is important to

note that edge effects can vary considerably even within the same study system, for example, due to variation in local topography, soil type, climate, or patch geometry (Laurance et al., 2007; Ordway & Asner, 2020), and it is therefore possible that effects may be more severe in other edges bordered by oil palm.

4.3 | Potential time lags in edge effects

The average age of edge formation in our study was around 36 years, and so, we conclude that there are long-term consequences of edge creation for the largest rainforest trees and AGC. However, it is unclear if these edge effects are ongoing or if they are residual effects following high mortality shortly after edge creation. There is little variation in edge age amongst our sites, which are biased toward older edges created 46–49 years ago (Table S1); therefore, any conclusions about the temporal dynamics of effects are limited. However, there is evidence that AGC loss increases with edge age (Ordway & Asner, 2020), suggesting that edge effects may continue to impact the largest trees in our study, particularly in the younger edges established 19 years ago. Mortality at edges could also increase if management practices within plantations (e.g., periodic replanting) increase structural contrast at edges, or if edge effects are worsened by droughts, which are becoming more frequent and severe due to climate change (Cai et al., 2018; Nunes et al., 2021). Thus, edge effects on large trees may worsen, and forest remnants within oil palm landscapes could experience long-term decays of carbon stocks.

Although we found no edge effects on the composition or diversity of trees in our plots, edge effects may be present in younger cohorts smaller than our 10 cm dbh stem threshold. Edge effects on seedlings and saplings can occur independently of effects on adult trees, for example, due to their establishment post-edge creation or due to altered biotic interactions during early life stages (Krishnadas et al., 2019; Luskin et al., 2017; Slik et al., 2011). Stride et al. (2018) found that forest area and isolation effects reduced richness of tree seedlings but not adult trees in Bornean forest remnants, signaling a potential extinction debt. It is therefore possible that compositional shifts, loss of diversity, and greater reductions of carbon could occur in these edges in the future. Further research on younger tree cohorts is needed to determine whether there are potential time lags, which may pose a threat to the long-term integrity of small remnants. Studies should also seek to determine the temporal dynamics of edge effects on mature trees and any potential impacts of plantation management, such as palm replanting.

4.4 | Conclusions and implications for sustainable oil palm landscapes

Whilst edge proximity explained relatively little of the total plot-level variation within this system, it nevertheless caused a significant decline in maximum tree size and AGC; therefore, edge effects do have implications for the future of sustainable oil palm landscapes. Adoption of sustainability criteria, such as the retention of forest patches that support "High Conservation Values" or "High Carbon Stocks" within plantations (Rosoman et al., 2017; RSPO, 2018), can boost local carbon stocks by 20% (Fleiss et al., 2020). However, their long-term persistence and integrity must be considered; for this reason, there are recommendations to prioritize the conservation of forest remnants with "core" areas >200 ha (Lucey et al., 2017; recognizing the detrimental effects of edges). Most remnants within plantations fall well short of this target (Scriven et al., unpublished data), and an edge penetration distance of around 300 m, as indicated by this study, would compromise the ability of small or irregularly shaped forest remnants to maintain carbon stocks, and the associated biodiversity that high-carbon forests support (Fleiss et al., 2020). Thus, if oil palm agriculture is to become sustainable as the industry continues to grow, it is important that these effects are taken into account when developing sustainability criteria, to ensure the long-term integrity of forest remnants.

Overall, however, our results, like those of Fleiss et al. (2020) and Stride et al. (2018), suggest that fragmentation effects on mature tree communities in oil palm landscapes may be weak relative to existing levels of variation within forest remnants. Thus, tree communities in these landscapes may be less vulnerable to fragmentation effects than those in other agricultural landscapes, with remnants possibly maintaining their integrity in the longer term. We suspect that this is probably because of the current configuration and composition of the oil palm matrix (extensive and mature) and the forest remnants themselves (isolated and heterogeneous). However, given that edge effects can vary even within the same study system (Ordway & Asner, 2020), it is possible that effects may be more severe in other edges bordered by oil palm, such as those bordered by young palms or in close proximity to additional edges, and effects may also become more severe if there are time lags. Thus, whilst we conclude that strong edge effects are not ubiquitous, and are absent from some edges bordering oil palm, future research should seek to understand the patterns and drivers of spatial and temporal variability in these effects at a landscape scale, in order to inform the management of sustainable oil palm landscapes into the future.

AUTHOR CONTRIBUTIONS

JAA, CJM, SS, NP, and JKH were involved in project conceptualization and administration. CJM, SS, NP, and JKH assisted with supervision, and SS with funding acquisition. JAA, CJM, SS, NP, JKH, and AJ designed methodology. JAA and AJ collected the data. JT assisted with project administration and resources in Malaysia. JAA analyzed the data and led writing of the original draft, with all authors contributing to reviewing and editing the paper.

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CONFLICT OF INTEREST

The corresponding author confirms on behalf of all authors that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: doi: 10.5061/dryad.gqnk98sqj (Anderson et al., 2022).

ORCID

Jake A. Anderson https://orcid.org/0000-0002-3375-4074
Colin J. McClean https://orcid.org/0000-0002-5457-4355
Sarah Sim https://orcid.org/0000-0002-0833-0253
Nathalie Pettorelli https://orcid.org/0000-0002-1594-6208
Jane K. Hill https://orcid.org/0000-0003-1871-7715

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