Citation for final published version:

Scriven, Sarah, Gillespie, Graeme, Laimun, Samsir and Goossens, Benoit 2018. Edge effects of oil palm plantations on tropical anuran communities in Borneo. Biological Conservation 220 , pp. 37-49. 10.1016/j.biocon.2018.02.006

Publishers page: http://dx.doi.org/10.1016/j.biocon.2018.02.006

Edge effects of oil palm plantations on tropical anuran communities in Borneo.

Sarah A. Scriven[1,2*], Graeme R. Gillespie[3,4*], Samsir Laimun[5], Benoît Goossens[1,5,6,7]

*These authors contributed to the work equally

[1]Organisms and Environment Division, Cardiff School of Biosciences, Cardiff University, Cardiff, United Kingdom

[2]Department of Biology, University of York, York YO10 5DD, UK

(sarah.scriven@york.ac.uk)

[3]School of Biosciences, University of Melbourne, Parkville, Victoria, Australia

[4]Department of Environment and Natural Resources, Palmerston, Northern Territory, Australia (Graeme.Gillespie@nt.gov.au)

[5]Danau Girang Field Centre, c/o Sabah Wildlife Department, Kota Kinabalu, Sabah, Malaysia (goossensbr@cardiff.ac.uk)

[6]Sabah Wildlife Department, Kota Kinabalu, Sabah, Malaysia

[7]Sustainable Places Research Institute, Cardiff University, Cardiff, United Kingdom

Keywords

Amphibians, habitat fragmentation, oil palm agriculture, rainforest, deforestation, Southeast Asia

Running title: Edge effects on anurans

Corresponding author: Graeme Gillespie

Number of words in the Abstract: 266

Number of words in the main body of the paper: 7189

Abstract

The expansion of industrial agriculture (oil palm) has significantly reduced lowland tropical diversity through direct loss or alteration of habitat, leading to habitat fragmentation and edge effects. Edge effects can have serious impacts on species diversity and community dynamics. To assess the effect of oil palm plantation edges on anuran communities in Sabah, Malaysian Borneo, we surveyed anuran species and measured structural habitat and landscape parameters at 74 sites spread across forest and plantation habitats along the Kinabatangan River. We then evaluated how anuran species richness and assemblage composition varied in relation to these environmental parameters. Relative species richness was higher at forest sites, compared to oil palm plantation sites. Plantation sites were dominated by wide-ranging terrestrial species, and assemblage composition varied mostly in relation to standing surface water. Forest habitats supported both more endemic and arboreal species. Variability on anuran assemblage composition in forest habitats was greatest in relation to distance to forest edge followed by canopy density, which was also partially correlated with forest edge distance. Moreover, anuran species richness in forest habitats declined as proximity to the forest-plantation interface increased, and as canopy density decreased. Our study provides further evidence that oil palm plantations provide little conservation benefit to anurans. Furthermore, oil palm plantations appear to have adverse pervasive impacts on amphibian diversity considerable distances into adjacent forest areas. These findings suggest that in order for small patches or narrow corridors of retained forest in landscapes managed for oil palm to maintain biodiversity values in the long term, their sizes and widths need to adequately account for the considerable influence of edge effects.

Introduction

Conversion of tropical forests to intensive plantation forestry or agriculture has negative impacts on biodiversity, and oil palm plantations are no exception (Fitzherbert 2007, 2008; Danielsen et al., 2008; Foster et al., 2011). Direct negative effects (e.g., a decline in species richness, or changes in community composition) of oil palm plantation establishment on tropical forest biodiversity have been documented for a range of biota, including mammals (Danielsen and Heegaard 1995; Maddox et al., 2007; Bernard et al., 2009), birds (Peh et al., 2006; Azhar et al., 2011), amphibians (Gillespie et al., 2012; Faruk et al., 2013) lizards (Glor et al., 2001; Gallmetzer and Schulze, 2015), various insect groups (Chung et al., 2000; Davis and Philips, 2005; Koh and Wilcove, 2008; Brühl and Eltz, 2010; Fayle et al., 2010) and other invertebrates (Hassall et al., 2006), and plants (Danielsen et al., 2008).

In addition to the direct effects of habitat loss and alteration from conversion of rainforests to plantations, there are a range of indirect and pervasive effects on biodiversity that may manifest themselves over time. These include downstream effects of hydrological and nutrient changes in waterways and catchments (Dudgeon et al., 2006), as well as habitat fragmentation and edge effects on adjacent remaining forest areas (Fitzherbert et al., 2007, 2008; Danielsen et al., 2008). Habitat loss and fragmentation are likely to exacerbate the impacts of anthropogenic climate change on tropical species (Nowakowski et al., 2017), and may also result in genetic erosion, leading to a reduction in breeding populations (e.g., see Goossens et al., 2005). Edge effects may also have a number of ecological consequences, including microhabitat alterations resulting from changes in temperature, humidity, wind or light penetration (Laurence et al., 2002; Fischer and Lindenmayer 2007; Broadbent et al., 2008); invasive species, that may cause habitat disturbance (Ickes et al., 2005), competition, predation (Rajaratnam et al., 2007), or introduction of disease (Arroyo-Rodríguez and Dias 2010); and increased human access for resource extraction, such as hunting, timber harvesting and other resource extraction (McMorrow and Talip, 2001; Fitzherbet et al., 2008).

Detrimental edge effects in tropical forests from roads, agriculture and silvicultural plantations have been documented for various biota, including mammals (Lidicker 1999; Goosem 2000), birds (Watson et al., 2004; Moradi et al., 2009), invertebrates (Didham et al., 1996) and plants (Hoang et al., 2010). However, evidence of major adverse forest edge effects on amphibians and reptiles is more ambiguous (Gardner et al., 2007a), with a number of studies finding either no effect (Gascon 1993; Biek et al., 2002; Toral et al., 2002), a weak effect (Demaynadier and Hunter 1995), or species-specific effects with no overall change in richness (Schlaepfer and Gavin, 2001; Lehtinen et al., 2003). To date, few studies have examined edge effects on tropical forests from oil palm plantations (Fitzherbert et al., 2008; Yaap et al., 2010; Lucey and Hill 2012). Understanding these pervasive effects is important for the conservation of biodiversity in remnant forest patches that have high conservation value, many of which occur in highly fragmented landscapes.

The expansion of oil palm plantations has significantly reduced lowland tropical amphibian diversity through direct loss or alteration of habitat (Gillespie et al., 2012; Faruk et al., 2013; Gallmetzer and Schulze, 2015). Oil palm plantations have lower amphibian species richness, more disturbance-tolerant species and less endemic species (Gillespie et al., 2012; Faruk et al., 2013; Gallmetzer and Schulze 2015; Konopik et al., 2015). These differences in richness and changes to community composition in oil palm plantations compared to forest habitats are underpinned by marked differences in both habitat structure and microclimate characteristics. Oil palm plantations lack microhabitats important for many forest amphibian species and are subject to a greater microclimatic flux (Chung et al., 2000; Peh et al., 2006; Luskin and Potts 2011; Gillespie et al., 2012). Important microhabitats for amphibian reproduction, foraging and shelter may be absent or limited within plantations, excluding many forest-dwelling species. However, quantification of impacts of forest conversion to oil palm plantations on amphibian communities is limited.

Forest amphibian communities persisting in forests within close proximity to plantations are also potentially highly vulnerable to pervasive edge effects, such as changes in abiotic conditions (see Urbina-Cardona et al., 2006; Dixo and Martins 2008). The reproductive strategies of many rainforest amphibians are potentially highly sensitive to microclimatic and microhabitat perturbations (Heatwole and Taylor, 1987; Wells, 2007; Bickford et al., 2010). Oil palm plantations are typically colonized by highly dispersive anuran species with more generalized ecological requirements (Gillespie et al., 2012; Faruk et al., 2013), which may in turn penetrate adjacent forests and compete with, or predate on, forest species. Elevated population densities of other species, such as leopard cat (*Prionailurus bengalensis*) and bearded pig (*Sus barbatus*), may increase predation on anurans or cause habitat alterations near forest edges (Peters 2000; Ickes et al., 2005). Given that pervasive edge effects may permeate substantial distances into adjacent forest habitats for some taxa (e.g., Broadbent et al., 2008), it is likely that such effects may detrimentally affect forest amphibian communities residing in these fragmented landscapes. Oil-palm induced edge effects and their influence on tropical amphibian communities have received little attention, and so there is currently limited understanding of how species richness and diversity change in relation to plantation edge proximity.

We evaluated the influence of forest/oil palm plantation edges on anuran diversity by collecting empirical data on anuran species richness and assemblage composition from 74 sites located within lowland rainforest and adjacent oil palm plantations in Malaysian Borneo. Using a repeated sampling design, we collected data from both edge and interior habitats (~20 m and 100-500 m from the forest/plantation interface, respectively) within secondary forest and established plantations. We then examined differences in anuran species richness and assemblage composition between oil palm plantations and adjacent forest in relation to a number of site-specific structural habitat parameters and local-landscape parameters, including the distances from forest/plantation interfaces. Based on findings from previous studies that have compared amphibian species richness and community composition between oil palm plantations and forest habitats (see Gillespie et al., 2012; Faruk et al., 2013), we hypothesized that: (i) forest sites would support more species than plantation sites, and (ii) plantation sites would support distinct communities of anurans compared to forest habitats, mostly comprising of generalist, widespread (i.e., non-endemic) terrestrial species. Some rainforest species are known to be detrimentally affected by agricultural edges (Urbina-Cardona et al., 2006; Schneider-Maunoury et al., 2016), and anuran communities in particular may be sensitive to changes in habitat structure that result from oil-palm induced edges (Gillespie et al., 2015). Hence, we also hypothesized that: (iii) species richness would increase in forest habitats with increasing distance from the forest/plantation interface; and (iv) both structural habitat and local-landscape parameters (i.e., proximity to the forest-plantation interface) would strongly influence anuran community composition and species richness within both habitat types.

Methods

Study Area

Fieldwork was conducted along the Kinabatangan River in Northeast Borneo, within the Malaysian state of Sabah (5◦10’-5◦50’N; 117◦40’-118◦30’E) (Fig. 1). The climate is warm, wet and humid with mean monthly temperatures throughout the year ranging from 21-34°C. Mean annual precipitation is usually between 2600-3600 mm and there are seasonal floods between November and March (Sooryanarayama, 1995), which can extend through to May (Gillespie et al., 2012). A large portion of the Kinabatangan floodplain is classified as extreme lowland forest and is flat, low (10-20 m a.s.l.) and poorly drained (Azmi, 1998). Due to logging between the mid 1950’s and early 1990s, the lowland forest of the Kinabatangan floodplain is almost exclusively regenerating secondary forest (McMorrow and Talip, 2001).

Over the past two decades much of the remaining lowland forest of the Kinabatangan floodplain has been converted to oil palm plantations (Abram et al., 2014). These alterations have left only remnant patches of forest, scattered amongst a matrix of vast oil palm monocultures, along with several small villages, and other agricultural lands (Gillespie et al., 2012; Abram et al., 2014). These forest patches form a partially fragmented corridor, extending from the coastal mangrove swamps for approximately 70 km upstream to the dry-land foot hill forests (Gillespie et al., 2012). This corridor includes the 27,960 ha Lower Kinabatangan Wildlife Sanctuary (LKWS), gazetted in 2005 (Abram et al., 2014), 10,000 ha of private and state forests and 15,000 ha of Virgin Jungle Reserves (VJRs) (Ancrenaz et al., 2004).

Site Selection and Local-Landscape Parameters

We established 39 transects, each 120m long, in secondary forest in LKWS and adjacent forest areas, and 35 transects of the same length in oil palm plantations. Transects were spread over a reach of approximately 100 km of the Kinabatangan floodplain and surrounding oil palm plantations (Fig. 1).

Transects were placed at varying distances from 100–500 m from the Kinabatangan River. All transects were a minimum distance of 500 m from each other. Within each habitat type (forest or plantation), transects were placed either approximately 20 m from the forest/plantation edge, or between 100 and 500 m from this edge. Where possible, transects ran parallel to the habitat edge irrespective of their distance from the edge. Distances to forest/plantation edges were measured using a GPS. We therefore recorded two local-landscape parameters at each transect for inclusion in our analyses: straight line distance to the Kinabatangan River and the straight line distance to the nearest forest/oil palm plantation edge.

Habitat Parameters

We measured 12 structural habitat parameters considered potentially influential on tropical anuran diversity as evidenced in previous studies (see Gardner et al., 2007b; Wanger et al., 2010; Gillespie et al., 2015). We chose parameters that were indicative of habitat variability in canopy, mid strata, understory and forest floor of both forest and plantation habitats. Canopy cover and tree circumference are indicative of relative disturbance levels in tropical forest habitats and influence ectotherm species composition (Vitt et al., 1998; Whitfield and Pierce 2005); understory vegetation density contributes to habitat structural complexity, which in turn has been shown to influence anuran diversity (Wanger et al., 2009; Gillespie et al., 2015); and fallen logs and leaf litter contribute to heterogeneity of forest floor microhabitats, which can also influence amphibian communities (Gardner et al., 2007b; Wanger et al., 2009).

The number of trees and their mean circumference and variance (at 1.5 m high) were recorded. The number and mean diameter of logs and fallen trees (diameter ≥ 0.1 m) were measured at their points of interception with each transect. Canopy density along each transect was measured by taking a digital photo of the canopy from 1.5 m height (using a Nikon Coolpix P100 digital camera, Kaiser RA1, Kaiser, Germany) at every 20 m interval. Saved images (3648 x 2736 pixels) were analyzed using IMAGE*J* software (National Institute of Health, USA). In order to reduce unevenness in picture tone before manual thresholding, all images were converted to an 8-bit grey scale. Thresholding then allowed the conversion of pixels with a grey scale lower than the threshold to black (representing the canopy) and those pixels with a grey scale higher than the threshold were converted to white (representing the sky). The canopy density, or number of dark pixels measured by IMAGE*J*, was then converted into a percentage against the total number of pixels in each image. Mean canopy density and variance in canopy density per transect was also calculated. Understory vegetation density was estimated at 1.5 m height at 20 m intervals along each transect, using a 2 m graduated pole with 50 black bands. In alternate directions, the pole was held horizontally above the ground at a 5 m distance perpendicular to each transect; the number of black bands not obscured by vegetation was recorded by a second observer on the transect. The gradient was also measured in this manner using a clinometer. Forest litter cover (leaves, twigs, small branches < 0.1 m diameter etc.) were measured at the same 20 m intervals, across the same alternate 5 m distances using a tape measure. Values for each of these parameters were averaged for each transect.

Availability of suitable breeding habitat influences local distribution of anurans (Wells, 2007). Many anuran species in the LKWS region reproduce in waterbodies on, or near the forest floor, with variable levels of ephemerality (Gillespie et al., 2012; Inger et al., 2017). Seasonal availability of ephemeral breeding sites is likely to influence frog activity patterns and detection levels, both spatially and temporally (see Wells, 2007). To account for the potential influence of this variability we measured the relative extent of standing water during each survey at each site. Surface water availability was measured by recording the total length of all ground surface water bodies intercepting each transect (max. = 120 m) immediately after every survey. The mean value was calculated across the three repeated surveys at each site and used as a covariate in analyses. Our transects were linear, so measuring the relative extent of standing water along each transect enabled us to account for local effects of water variability across both space and time during the study. The presence/absence of streams within 10m of each transect was also recorded.

Anuran Sampling

Data were collected between February and July 2011, spanning the wet and dry seasons. To reduce seasonal sampling effects, each transect was sampled three times throughout this period, with repeat censuses a minimum of 28 days apart. Transects were surveyed after 1830 hrs, with two people searching visually and acoustically for anurans. All encounters within 5 m either side of each transect were recorded. Leaf litter, logs, branch piles, tree trunks and understory vegetation were inspected as observers moved along each transect. Amphibians were identified following the nomenclature of Haas et al. (2011) and later revised following that of Inger et al., (2017). Two or three transects were sampled each evening, with all sampling completed by approximately 2200 hrs. The time of evening at which each transect was sampled was rotated across replicates to reduce systematic bias from time-related effects.

Species Composition

All statistical analyses were implemented using R statistical software version 3.0.2. Patterns of variation in anuran community composition across forest and plantation habitats were explored using non-metric multidimensional scaling (NMDS) ordination, with Jaccard’s distance measure for binary (presence/absence) data and the subsequent dissimilarity matrix of pairwise dissimilarities between sampling sites (Oksanen, 2013). Twenty random starting configurations were used and the final configuration had the lowest residual stress. In order to reduce residual stress, we used a three dimensional NMDS plot, and residual stress of the final ordination plot was 0.106.

We used the function ‘envfit’ in the R package *vegan* (Oksanen, 2013) to overlay environmental parameters ($P > 0.05$) onto the NMDS plots, without disrupting the original ordinations. Overlaying environmental parameters onto NMDS ordinations using envfit generates correlation coefficients (represented as linear vectors on the ordination plots), R^2 values and significance values based on the probability that 999 random permutations of environmental parameters would give a better fit than the true environmental parameters. We overlaid 12 structural habitat parameters and two local-landscape parameters (distance from edge and distance to river) onto the NMDS ordination. Distance to edge was calculated as the straight line distance into forest from the habitat edge, hence sites inside plantations were assigned negative values in the ordination. The presence/absence of streams within the transect survey area was treated as a categorical variable (i.e., centroids), whilst all other parameters were continuous (i.e., linear vectors).

Species Richness

Generalized additive models (GAMs) (Wood, 2006) were used to examine the effect of environmental parameters on anuran richness. GAMs use non-linear smooth terms to describe the relationship between the dependent variable and each predictor variable, whereby the fitted algorithm selects an optimal level of complexity for each non-linear (smooth) term. Each smooth term is described by the effective degrees of freedom (edf), and if edf = 1, this corresponds to a linear relationship between the dependent variable (i.e., anuran richness) and the predictor variable (Wood, 2006). We fitted GAMs using the R package *mgcv* (Wood, 2011). Pairwise Spearman's correlation analysis of environmental parameters revealed that many were collinear (see Dormann et al., 2013). For those variable pairs with coefficients > (±) 0.6, one variable was selected that was thought to have the greatest potential influence on anuran species richness, and the others were subsequently excluded from the analyses. The resultant set of seven parameters was included in the GAMs, which comprised the two local-landscape parameters: distance to edge and distance to river; and five structural habitat parameters: canopy density, understory density, litter cover, gradient and surface water.

We used backward stepwise selection to determine the most important predictors in our GAMs on anuran richness in all habitats, forest habitats and plantation habitats. We started with a global model where all predictor variables were fitted with a smooth term. Predictor variables with an edf = 1 were simplified to linear terms within the model. The least significant predictor variables within each GAM were successively dropped until the AIC (Akaike's Information Criterion) of the model no longer improved. This resulted in a final model which included the most important structural habitat and local-landscape effects on species richness. The partial effects of each significant predictor variable were plotted to examine the shape of the response curve.

Results

Twenty seven anuran species from five families were detected (Table 1). Of these, 25 species were recorded at forest sites, eight of which were not found at plantation sites. Seventeen species were found at plantation sites, two of which were not found at forest sites. Of the 11 Bornean-endemic species detected, five were restricted to forest sites. One endemic species, *Rhacophorus harrissoni*, was detected on a single occasion in a plantation site near the forest edge (Table 1). Relative species richness (i.e., the number of species found at each site) was higher at forest sites (mean = 10.82 (SE ± 0.36) species per transect), compared to oil palm plantation sites (mean = 7.26 (SE ± 0.35) species per transect). Forest habitats also supported more endemic species, averaging 3.59 (SE ± 0.03) species per transect, compared to only 0.63 (SE ± 0.03) per plantation transect.

Anuran assemblage composition

Forest sites were strongly differentiated from plantation sites by most of the structural habitat parameters that we measured (Fig. 2; Appendix 1). Differences between forest and plantation sites were most strongly explained by tree circumference, litter cover, tree density and log density. Forest sites were characterised by high litter cover, understorey vegetation density, tree density, log density and canopy cover, all of which had relatively low values at plantation sites. Plantation sites were also characterised by highly variable canopy cover, high tree circumference, and greater extent of standing surface water (Fig. 2c).

Anuran species varied markedly in their level of affinity with either forest or plantation habitats (Fig. 2b & c). Species strongly associated with forest sites comprised a range of both arboreal (e.g., *Metaphrynella sundana and Polypedates colletti*) and terrestrial species (e.g., *Microhyla perpava* and *Ingerophrynus divergens*), whereas species strongly associated with plantations were mostly terrestrial, such as *Hylarana erythraea, Fejervarya cancrivora,* and *F. limnocharis* (Fig. 2a and b; Table 1). Six species showed no strong associations with either forest or plantation sites: *H. glandulosa, H. nicobariensis, H. meganesa, Kaloula baleata, Limnonectes paramacrodon* and *Polypedates macrotis.*

Forest sites varied with respect to distance from forest edge, variance in canopy cover, tree density, log density and canopy density (Appendices 2 & 3). Log and canopy densities tended to be higher at sites further from forest edges, whereas variability in canopy density was higher at sites near forest edges (Appendix 3). The lack of clustering of anuran species in the centre of the NMDS plot (Appendix 3) suggests that the occurrence of most species was influenced by these parameters. However, the greatest variability on anuran assemblage composition was in relation to canopy density and distance to forest edge (Appendices 2 & 3). Several species, such as *Chaperina fusca, L. paramacrodon, M. sundana, Polypedates colletti* and *P. otilophus*, were restricted to forest interior sites. Conversely several species were found only at forest edges, namely *H. erythraea, K. baleata* and *Polypedates leucomystax*.

Plantation sites varied significantly only with respect to extent of surface water and log density (Appendices 4 & 5). The lack of clustering of anuran species in the centre of the NMDS plot (Appendix 5) suggests that the occurrence of most species was influenced by these parameters.

Anuran assemblage composition varied mostly in relation to availability of standing surface water (Appendix 5). Proximity to forest edge was marginally insignificant (Appendix 4).

Species Richness

Across plantation and forest habitats, the best supported GAM for the influence of environmental parameters on anuran richness included canopy density and distance to edge (Table 2). Canopy density had a linear negative relationship with anuran richness (Fig. 3a), whilst the relationship between distance to edge and species richness was non-linear, and complex (Fig. 3b). Overall, species richness was lower at plantation sites compared to forest sites. In plantations, species richness tended to increase somewhat as distance from the forest/plantation edge increased, but there was a much higher increase in species richness with proximity to the forest/plantation edge. Species richness continued to rise at forest sites with increased distance from plantations (Fig. 3b).

Discussion

Biodiversity conservation in intensively managed landscapes is contingent upon the magnitude and nature of both direct and indirect disturbance effects. Expansion of oil palm plantations is a major cause of habitat loss and associated biodiversity in tropical regions (Fitzherbert et al., 2008a; Pirker et al., 2016). In support of our first and second hypotheses, we found further evidence that oil palm plantations support lower species richness, fewer endemic species and mostly disturbance-tolerant species compared to rainforest habitats, and provide little overall benefit to conservation of Bornean anuran diversity.

To date, indirect effects of oil palm plantations on biodiversity have had far less evaluation than direct impacts. To our knowledge, our study provides the first evidence of edge effects from oil palm plantations on anuran diversity in adjacent forest landscapes. Moreover, our results suggest that changes in forest anuran diversity associated with plantation edges may extend up to 4 km into adjacent forest. In contrast to the findings of our study, Gardner et al. (2007a) found little support amongst nine studies for impacts of edge effects on either amphibians or reptiles across various tropical regions. However, none of these studies examined effects of oil palm plantations. Oil palm plantations may have different biotic and abiotic edge effects on adjacent forest habitats, such as less protection from wind exposure (e.g., Ferrante et al., 2017). A number of the studies reviewed by (Gardner et al., 2007a) sampled habitat fragments surrounded by heterogeneous matrices of different levels of fragmentation and intensities of agriculture and silviculture, which may have in-part confounded inferences of edge effects *per sé*. The impacts of edges on species diversity in adjacent forest habitats likely depend upon the size, quality and spatial extent of forest fragments within a specific agricultural system, and the structural contrast between the forest habitat and adjacent altered environment (Ferrante et al., 2017; Pfeifer et al., 2017). Nevertheless our findings build on those of Schneider-Maunoury et al. (2016) who found pronounced effects on forest amphibians and reptiles up to 1 km from forest edges in Neotropical landscapes adjacent to agricultural matrices of pasture, secondary regrowth and plantations (including palm groves, cocoa plantations and *Eucalyptus* plantation forests). Similarly, in a recent global study examining the impact of edge effects on amphibians, forest-core habitats supported more amphibian species than forest-edge, matrix-core and matrix-edge habitats (Pfeifer et al., 2017). Collectively these findings suggest that tropical anuran communities are sensitive to edge effects from adjacent agricultural development, but that the nature and magnitude of these effects may vary substantially amongst different types of agricultural edges and how they are managed, as well as the broader level of habitat fragmentation/connectivity and disturbance in surrounding landscapes.

Consistent with our third hypothesis, amphibian species richness in forest habitats declined as proximity to the forest-plantation interface increased. Forest sites further from plantation edges tended to have more arboreal species (e.g., *M. sundana*), and more litter-dwelling and direct-developing species compared with sites closer to plantation edges (Table 1). In forest habitats presence of endemic species also declined with increasing proximity to forest-plantation edges (Fig. 2b). Disturbance-tolerant anuran species were present in forest habitats close to plantation edges but were encountered much less frequently in forest areas further from the forest/plantation interface (Fig. 2b).

Several mechanisms may underpin the detrimental edge effects of oil palm plantations on forest anurans in lowland Borneo. The creation of abrupt habitat edges alters forest structure and composition, both at the forest edge itself (Didham and Lawton, 1999) and within interior forest habitats (Mesquita et al., 1999). Large trees often die off within 300 m of forest edges (Laurance et al., 2000), leaving numerous canopy gaps that are often filled by disturbance-adapted vines, weeds and pioneer species (Laurance et al., 2002; Laurance et al., 2006). These changes in turn lead to reduced moisture and increased maximum daily temperatures (Didham and Lawton, 1999; Pohlman et al., 2009; Hardwick et al., 2015). Amphibians are especially vulnerable to these altered microclimates (Lehtinen et al., 2003), as they are sensitive to desiccation in drier environments and depend upon a variety of aquatic microhabitats for reproduction. Changes in forest structure and composition, accompanied by disruptions in plant–animal interactions (Rodríguez-Cabal et al., 2007), can also alter the community composition and abundance of many different faunal groups (Goosem, 2000; Laurance et al., 2002; Laurance, 2004; Lehtinen et al., 2003; Watson et al., 2004). Such changes can often lead to invasion of disturbance-adapted animal species, including reptiles (Schlaepfer and Gavin, 2001), birds (Hagan et al., 1996), pigs (Peters, 2000) and other mammals (Kinnaird et al., 2003), which may predate or compete with amphibians. Pesticides and fertilizers are often used intensively in oil palm plantations with potentially serious implications for nearby streams and wetlands (Obidzinski et al., 2012). How these substances affect tropical amphibian assemblages are unknown. However, given the dependence of many anuran species on aquatic habitats and their sensitivities to pesticides (Bidwell and Gory, 1995; Brühl et al., 2013), many species may be adversely affected by residual chemical runoff into forests near oil palm plantations. We did not evaluate chemical residues or runoff in this study; hence this is topic may warrant further research.

Consistent with our fourth hypothesis, we found that amphibian diversity was influenced to various degrees by both structural habitat and landscape parameters. Our findings suggest that amphibian species richness increased, and species composition changed with variability in canopy density. Canopy density within forest habitats also tended to increase with distance from forest-plantation edges, possibly suggesting lower levels of selective logging and other direct human disturbances further from plantations and associated road networks. Human disturbance levels in tropical forests are typically strongly related to human access (Laurance et al., 2009; Bhat et al., 2011; Kodandapani et al., 2014). Thus, in this landscape, plantations and associated road networks may facilitate human access to forest edges, increasing encroachment and forest habitat disturbance. Other studies have found that tropical amphibian species richness may vary with respect to relatively low levels of human disturbance (e.g., Gillespie et al., 2015). Therefore interactions may exist between edge effects *per sé* and other anthropogenic disturbance processes operating in forests facilitated by access provided by plantations, which in turn may contribute to the large distance over which changes in anuran diversity were observed.

Biodiversity conservation in Southeast Asia is becoming increasingly dependent on landscapes with varying levels and patterns of habitat retention, and habitat patches with varying levels of anthropogenic disturbance (Sodhi et al., 2010; Giam et al., 2011). A greater understanding is needed of the relationships between these disturbance processes and biodiversity change in order to determine management priorities and practices (Sodhi et al., 2010; Gillespie et al., 2015). The effects of forest conversion to oil palm plantations and/or their management are likely having significant and pervasive effects on amphibians, and probably other biota, that extend well beyond plantation boundaries.

Current or modified management practices of oil palm plantations in themselves are unlikely to improve their biodiversity conservation value for many taxa (Edwards et al., 2010; Faruk et al., 2013). Therefore biodiversity conservation in oil palm-managed landscapes is likely to be largely dependent upon retention of forest patches and corridors (e.g., High Conservation Value (HCV) areas: see http://www.rspo.org). However, for such retained areas to maintain biodiversity values in the long term, their sizes and widths need to adequately account for the considerable influence of edge effects. These considerations are most pertinent in high biodiversity-value regions where forest conversion to oil palm plantations is expanding (Pirker et al., 2016), such as the island of New Guinea (Fitzherbert et al., 2008). Our findings, along with those of Schneider-Maunoury et al. (2016), provide snapshots of patterns of amphibian biodiversity in space at specific times in fragmented tropical forest landscapes. However, on-going monitoring is required to evaluate how these amphibian assemblages continue to change through time and what the ultimate effects of these landscape changes will be on biodiversity in remaining rainforest habitats.

Acknowledgements

We thank Sabah Wildlife Department for allowing us to carry out research in the Lower Kinabatangan Wildlife Sanctuary. We also thank Mark Rampangajouw, Danica Stark and Luke Evans for logistical help during fieldwork, and are grateful to Anton Saroto, Eddie Ahmad, Rodi Tenquist-Clarke and Rob Colgan for help with field sampling. Hefin Jones provided helpful advice and comments on early drafts of the manuscript, and Michael Scroggie and Joanne Lello provided statistical advice. We are grateful to Cardiff University for awarding S. Scriven with the 125 Scholarship award, and the Blue School Wells for their bursary awarded to S. Scriven from the Governor's Grant Fund. This project also received funding from Houston Zoo and Danau Girang Field Centre.

References

Arroyo-Rodríguez, V. and Dias, P.A., 2010. Effects of habitat fragmentation and disturbance on howler monkeys: a review. American Journal of Primatology 72, 1-16.

Azhar, B., Lindenmayer, D.B., Wood, J., Fischer, J., Manning, A., McElhinny, C., Zakaria, M., 2011. The conservation value of oil palm plantation estates, small holdings and logged peat swamp forest for birds. Forest Ecology and Management 62, 2306-2315.

Bernard, H., Fjeldsa, J. & Mohamed, M., 2009. A case study on the effects of disturbance and conversion of tropical lowland rain forest on the non-volant small mammals in north Borneo: management implications. Mammal Study 34, 85–96.

Bhat, D.M., Hegde1, G.T., Shetti, D.M, Patgar, S.G., Hegde1, G.N., Furtado, R.M, Shastri, C.M, Bhat, P.R., Ravindranath, N.H., 2011. Impact of disturbance on composition, structure, and floristics of tropical moist forest in Uttara Kannada District, Western Ghats, India. Ecotropica 17: 1–14.

Bidwell, J.R., Gorrie, J.R., 1995. Acute Toxicity of a Herbicide to Selected Frog Species. Prepared for the Western Australian Department of Environmental Protection, Perth. Curtin Ectotoxicology Program, Curtin University of Technology.

Broadbent, E.N., Asner, G.P., Keller, M., Knapp, D.E., Oliviera, P.J.C., Silva, J.N., 2008. Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. Biological Conservation 141, 1745–1757.

Brühl, C.A., Eltz, T., 2010. Fuelling the biodiversity crisis: species loss of ground dwelling forest ants in oil palm plantations in Sabah, Malaysia (Borneo). Biodiversity Conservation 19, 519–529.

Brühl, C.A., Schmidt, T., Pieper, S., Alscher, A., 2013. Terrestrial pesticide exposure of amphibians: An underestimated cause of global decline? Scientific Reports, 1135.

Chung, A.Y.C., Eggleton, P., Speight, M.R., Hammnd, P.M., Chey, V.K., 2000. The diversity of beetle assemblages in different habitat types in Sabah. Malaysian Bulletin of Entomology Research 90, 475–496.

Danielsen, F., Beukima, H., Burgess, N.D., Parish, F., Brühl, C.A., Donald, P.F., Murdiyaso, D., Phalan, B., Reijnders, L., Struebig, M., Fitzherbet, E.B., 2008. Biofuel Plantations on Forested Lands: Double Jeopardy for Biodiversity and Climate. Conservation Biology 23, 348–358.

Danielsen, F., Heegaard, M., 1995. Impact of logging and plantation development on species diversity: a case study from Sumatra. In Management of tropical forests: towards an integrated perspective (ed. O. Sandbukt). Oslo, Norway: University of Oslo, Centre for Development and the Environment.

Davis, A.L.V., Philips, T.K., 2005. Effect of deforestation on a southwest Ghana dung beetle assemblage (Coleoptera: Scarabaeidae) at the periphery of Ankasa Conservation Area. Environmental Entomology 34, 1081–1088.

Didham, R.K., Ghazoul, J., Stork, N.E., Davies, A.J., 1999. Insects in fragmented forests: a functional approach. Trends in Ecology and Evolution. 11, 255-260.

Didham, R.K., Lawton, J.H., 1999. Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. Biotropica 31, 17–30.

Dixo, M., Martins, M., 2008. Are leaf-litter frogs and lizards affected by edge effects due to forest fragmentation in Brazilian Atlantic forest? Journal of Tropical Ecology 24, 551-4.

Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.I., Knowler, D.J., Soto, D., Stiassny, M.L.J., Sullivan, C.A., 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. Biological reviews of the Cambridge Philosophical Society 81, 163–182.

Edwards, D.P., Hodgson, J.A., Hamer, K.C., Mitchell, S.L., Ahmad, A.H., Cornell, S.J., Wilcove, D.S., 2010. Wildlife-friendly oil palm plantations fail to protect biodiversity effectively. Conservation Letters 3, 236–242.

Faruk, A., Belabut, D., Ahmad, N., Knell, R.J., Garner, T.W.J., 2013. Effects of oil-palm plantations on diversity of tropical anurans. Conservation Biology 27, 615–624.

Fayle, T.M., Turner, E.C., Snaddon, J.L., Chey, V.K., Chung, A.Y.C., Eggleton, P., Foster, W.A., 2010. Oil palm expansion into rain forest greatly reduces ant biodiversity in canopy, epiphytes and leaf-litter. Basic Applied Ecology 11, 337–345.

Ferrante, L., Baccaro, F.B., Ferreira, E.B., Sampaio, M.F., Santos, T., Justino, R.C., Angulo, A., 2017. The matrix effect: how agricultural matrices shape forest fragment structure and amphibian composition. Journal of Biogeography 44, 1911-1922.

Fischer, J., Lindenmayer, D.B., 2007. Landscape modification and habitat fragmentation: a synthesis. Global Ecology and Biogeography. 16, 265–280.

Fitzherbert, E.B., Struebig, M.J., Morel, A, Danielsen, F., Brühl, C.A, Donald, P.F. Phalan, B., 2008. How will oil palm expansion affect biodiversity? Trends in Ecology and Evolution 23, 538-545.

Fitzherbert, E.B., Struebig, M.J., Phalan, B., Morel, A., 2007. Biodiversity and Oil Palm: an objective review. Biodiversity and Oil Palm Network.

Foster, W.A., Snaddon, J.L., Turner, E.C., Fayle, T.M., Cockerill, T.D., Farnon Ellwood, M.D., Broad, G.R., Chung, A.Y.C., Eggleton, P., Khen, C.V., Yusah, K.M., 2011. Establishing the evidence base for maintaining biodiversity and ecosystem function in the oil palm landscapes of South East Asia. Philosophical Transactions of the Royal Society B 366, 3277-3291.

Gallmetzer, N., Schulze, C.H., 2015. Impact of oil palm agriculture on understory amphibians and reptiles: A Mesoamerican perspective. Global Ecology and Conservation 4, 95–109.Gardner, T.A., Barlow, J., Peres, C.A., 2007a. Paradox, presumption and pitfalls in conservation biology: The importance of habitat change for amphibians and reptiles. Biological Conservation 138, 166-179.

Gardner, T.A., Barlow, J., Peres, C.A., 2007a. Paradox, presumption and pitfalls in conservation biology: The importance of habitat change for amphibians and reptiles. Biological Conservation 138, 166-179.

Gardner, T.A., Ribeiro Jr., M.A., Barlow, J., Ávila-Pires, T.A.S., Hoogmoed, M., Peres, C.A., 2007b. The value of primary, secondary and plantation forests for a neotropical herpetofauna. Conservation Biology 21, 775–787.

Gillespie, G.R., Ahmad, E., Evans, A., Ancrenaz, M. Goossens, B., Scroggie, M., 2012. Relative value of secondary forests and non-forest habitats for amphibians in Borneo. Biological Conservation. 152, 136-144.

Gillespie, G. R., Howard, S., Stroud, J. T., Ul-Hassanah, A., Campling, M., Lardner, B., Scroggie, M., Kusrini, M. 2015. Factors influencing herpetofaunal species richness and assemblage structure along a forest disturbance gradient in Sulawesi, Indonesia. Biological Conservation 192, 161–173.

Glor, R.E., Flecker, A.S., Benard, M.F., Power, A.G., 2001. Lizard diversity and agricultural disturbance in a Caribbean forest landscape. Biodiversity Conservation 10, 711-723.

Goosem, M. 2000. Effects of tropical rainforest roads on small mammals: edge changes in community composition. Wildlife Research 27, 151–163.

Goossens, B., Chikhi, L., Jalil, M.F., Ancrenaz, M., Lackman-Ancrenaz, I., Mohamed, M., Andau, P., Bruford, M.W. 2005. Patterns of genetic diversity and migration in increasingly fragmented and declining orang-utan (*Pongo pygmaeus*) populations from Sabah, Malaysia. Molecular Ecology 14, 441–456.

Hagan, J.M., Vander Haegen, M.W., McKinley, P.S., 1996. The early development of forest fragmentation effects on birds. Conservation Biology 10, 188–202.Hardwick, S.R., Toumi, R., Pfeifer, M., Turner, E.C., Nilus, R., Ewers, R.M., 2015. The relationship between leaf area index and microclimate in tropical forest and oil palm plantation: forest disturbance drives changes in microclimate. Agricultural and Forest Meteorology 201, 187–195.

Hassall, M., Jones, D.T., Taiti, S., Latipi, Z., Sutton, S.L., Mohammed, M., 2006. Biodiversity and abundance of terrestrial isopods along a gradient of disturbance in Sabah, East Malaysia. European Journal of Soil Biology 42, 197–207.

Houlahan, J.E., Findlay, C.S., 2003. The effects of adjacent land use on wetland species richness and community composition. Wetlands 26, 79–96.

Hoang, V.S., Baas, P., Keßler, P.J.A., Slik, J.W.F., Ter Steege, H., Raes, N., 2010. Hunan and Environmental influences on plant diversity and composition in Ben En Nation Park, Vietnam. Journal of Tropical Forest Science 23, 328-337.

Ickes, K., Paciorek, C.J., Thomas, S.C., 2005. Impacts of nest construction by native pigs (*Sus scrofa*) on lowland Malaysian rain forest saplings. Ecology 86, 1540-1547.

Inger, R.F., Stuebing, R.B., Graffe, T.U., Dehling, J.M., 2017. *A Field Guide to the Frogs of Borneo.* Third Edition. Natural History Publications, Kota Kinabalu.

Kinnaird, M.F., Sanderson, E.W., O’Brien, T.G., Wibisono, H.T., Woolmer, G., 2003. Deforestation trends in a tropical landscape and implications for endangered large mammals. Conservation Biology 17, 245–257.

Kodandapani, N., Satheesh, N., Ashutosh, S.S., Raj Kumar, K., 2014. Human dimensions of forest degradation in the Sathyamangalam landscape. Asian Nature Conservation Foundation, Sathyamangalam Forest Division, Center for Advanced Spatial and Environmental Research, Bangalore, India.

Koh, L.P., Wilcove, D.S., 2008. Is oil palm agriculture really destroying tropical biodiversity? Conservation Letters 1, 60–64.

Konopik, O., Steffan-Dewenter, I., Grafe, T.U., 2015. Effects of logging and oil palm expansion on stream frog communities on Borneo, Southeast Asia. Biotropica 47, 636-643.

Laurance, S.G.W., 2004. Responses of understory rain forest birds to road edges in central Amazonia, Ecological Applications 14, 1344–1357.

Laurance, W.F., Delamonica, P., Laurance, S.G., Vasconcelos, H.L., Lovejoy, T.E., 2000. Rainforest fragmentation kills big trees. Nature 404, 836.

Laurance, W.F., Goosem, M., Laurance, S.G.W., 2009. Impacts of roads and linear clearings on tropical forests. Trends in Ecology and Evolution 24, 659-669.

Laurance, W.F., Lovejoy, T.E., Vasconselos, H.L., Bruna, E.M., Didham. R.K., Stouffer, P.C., Gascon, C., Bierregaard, R.O., Laurance, S.G., Sampaio, E., 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. Conservation Biology 16, 605–618.

Laurance,W.F., Nascimento, H.E.M., Laurance, S.G., Andrade, A.C., Fearnside, P.M., Ribeiro, J.E.L., Capretz, R.L., 2006. Rain forest fragmentation and the proliferation of successional trees. Ecology 87, 469–482.

Lehtinen, R.M., Ramanamanjato, J., Raveloarison, J.G., 2003. Edge effects and extinction proneness in a herpetofauna from Madagascar, Biodiversity Conservation 12, 1357–1370.

Lidicker W.Z., 1999. Responses of mammals to habitat edges: an overview. Landscape Ecology 14, 333-343.

Lucey, J. M., Hill, J.K., 2012. Spillover of insects from rain forest into adjacent oil palm plantations. Biotropica 44, 368–377.

Luskin, M.S., Potts, M.D., 2011 Microclimate and habitat heterogeneity through the oil palm lifecycle. Basic and Applied Ecology 12, 540-551.

Maddox, T.M., Gemita, E., Wijamukti, S., Selampassy, A., 2007. The conservation of tigers and other wildlife in oil palm plantations. Jambi Province, Sumatra, Indonesia. ZSL Conservation Report No 7. Zoological Society of London, London, United Kingdom.

McMorrow, J. and Talip, M.A., 2001. Decline of forest area in Sabah, Malaysia: relationship to state policies, land code and land capability. Global Environmental Change 11, 217-230.

Mesquita, R.C.G., Delamonica, P., Laurance, W.F., 1999. Effect of surrounding vegetation on edge-related tree mortality in Amazonian forest fragments. Biological Conservation 91, 129–134.

Moradi, H.V., Zakaria, M., Mohd, A.B., Yusof, E., 2009. Insectivorous birds and environmental factors across an edge-interior gradient in tropical rainforest of Malaysia. International Journal of Zoological Research 5, 27-41.

Nowakowski, A.J., Watling, J.I., Whitfield, S.M., Todd, B.D., Kurz, D. J., Donnelly, M.A. 2017. Tropical amphibians in shifting thermal landscapes under land use and climate change. Conservation Biology 31, 95-105.

Obidzinski, K., R. Andriani, H. Komarudin, and A. Andrianto. 2012. Environmental and social impacts of oil palm plantations and their implications for biofuel production in Indonesia. *Ecology and Society* 17, 25. doi.org/10.5751/ES-04775-170125

Peh, K.S.H., Sodhi, N.S., de Jong, J., Sekercioglu, C.H., Yap, C.A.M., Lim, S.L.H. 2006. Conservation value of degraded habitats for forest birds in southern Peninsular Malaysia. Diversity and Distributions 12, 572-581.

Peters, H.A., 2000. *Clidemia hirta* invasion at the Pasoh forest reserve: an unexpected plant invasion in an undisturbed tropical forest. Biotropica 33, 60–68.

Pfeifer, M., Lefebvre, V., Peres, C.A., Banks-Leite, C., Wearn, O.R., Marsh, C.J., Butchart, S.H., Arroyo-Rodríguez ,V., Barlow, J., Cerezo, A., Cisneros., L., 2017. Creation of forest edges has a global impact on forest vertebrates. Nature 551, 187-191.

Pirker, J., Mosnier, A., Kraxner, F., Havlik, P., Obersteiner, M., 2016. What are the limits to oil palm expansion? Global Environmental Change 40, 73–81.

Pohlman, C.L. et al. (2009) Temporal variation in microclimatic edge effects near powerlines, highways and streams in Australian tropical rainforest, Agricultural and Forest Meteorology 149, 84–95.

Rajaratnam, R., Sunquist, M., Rajaratnam, L., Ambu, L. 2007. Diet and habitat selection of the leopard cat (*Prionailurus bengalensis borneoensis*) in an agricultural landscape in Sabah, Malaysian Borneo. Journal of Tropical Ecology 23, 209–217.

Rodrı´guez-Cabal, M., Aizen, M.A., Novaro, A.J., 2007. Habitat fragmentation disrupts a plant-disperser mutualism in the temperate forest of South America. Biological Conservation 139, 195–202.

Schlaepfer, M.A., Gavin, T.A., 2001. Edge effects on lizards and frogs in tropical forest fragments. Conservation Biology 15, 1079–1090.

Schneider-Maunoury, L. Lefebvre, V., Ewers, R.M., Medina-Rangel, G.F., Peres, C.A., Somarriba, E., Urbina-Cardona, N., Pfeifer, M., 2016. Abundance signals of amphibians and reptiles indicate strong edge effects in Neotropical fragmented forest landscapes. Biological Conservation 200, 207–215.

Sodhi, N.S., Koh, L.P., Clements, R., Wanger, T.C., Hill, J.K., Hamer, K.C., Clough, Y., Tscharntke, T., Posa, M.R.C., Lee, T.M., 2010. Conserving Southeast Asian biodiversity in human-modified landscapes. Biological Conservation 143, 2375–2384.

Urbina-Cardona, J.N., Olivares-Pérez, M., Reynoso, V.H., 2006. Herpetofauna diversity and microenvironment correlates across a pasture–edge–interior ecotone in tropical rainforest fragments in the Los Tuxtlas Biosphere Reserve of Veracruz, Mexico. Biological Conservation 132, 61-75.

Vitt, L.J., Avila-Pires, T., Caldwell, J.P., Oliveira, V.R., 1998. The impact of individual tree harvesting on thermal environments of lizards in Amazonian rain forest. Conservation Biology 12, 654-64.

Wanger, T.C., Saro, A., Iskandar, D.T., Brook, B.W., Sodhi, N.S., Clough, Y., Tscharntke, T., 2009. Conservation value of cacao agroforestry for amphibians and reptiles in South-East Asia: combining correlative models with follow-up field experiments. Journal of Applied Ecology 46, 823-32.Wanger, T.C., Iskandar, D.T., Motzke, I., Brook, B.W., Sohdi, N.S., Clough, Y., Tscharntke, T., 2010. Effects of land-use change on community composition of tropical amphibians and reptiles in Sulawesi, Indonesia. Biological Conservation 24, 795–802.

Watson, J.E.M., Whitacker, R.J., Dawson, T.P., 2004. Habitat structure and proximity to forest edge affect the abundance and distribution of forest-dependent birds in tropical coastal forests of southeastern Madagascar. Biological Conservation 120, 311-327.

Wells, K.D. 2007. *The Ecology and Behavior of Amphibians*. University of Chicago Press, Chicago, USA.

Whitfield, S.M., Pierce, M.S., 2005. Tree buttress microhabitat use by a Neotropical leaf-litter herpetofauna. Journal of Herpetology 39, 192-8.

Yaap, B., Struebig, M.J., Paoli, G., Koh, L.P. 2010. Mitigating the biodiversity impacts of oil palm development. CAB Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources 5, No. 019. doi: 10.1079/PAVSNNR20105019

List of Figures

Figure 1. Lower Kinabatangan River Floodplain and sampling sites; inset shows location on Borneo. Grey shaded areas are forest and adjacent unshaded areas are oil palm plantations; black triangles represent survey sites and red circles represent villages. All forest sites were located within the Lower Kinabatangan Wildlife Sanctuary (LKWS).

Figure 2. Non-metric multidimensional scaling (NMDS) ordination diagrams (first two axes) for all forest and plantation sites: (a) sampling sites: o = forest sites: Δ= plantation sites; (b) species, refer to Table 1 for species abbreviations; and (c) direction and magnitude (vector length) of significant ($P > 0.05$) fitted environmental parameters overlaid into the ordination space, refer to Table 2 for environmental parameter abbreviations.

Figure 3. Partial effects of significant parameters retained in the final GAM for overall species richness in all habitat types. (a) Distance to edge; b) canopy density. The values on the *y*-axes are centred on zero and based on partial residuals, and thus indicate the relative influence of each explanatory variable on the prediction. Dashed lines are ± 2 standard errors.

List of Appendices

Appendix 1. Fitted environmental vectors in the NMDS ordination of anuran assemblage similarity across all sites.

Appendix 2. NMDS loadings and P values for habitat parameters at forest sites.

Appendix 3. NMDS ordination diagrams (first two axes) for forest sites. (a) Species, refer to Table 1 for species abbreviations; (b) direction and magnitude (vector length) of significant ($P > 0.05$) fitted environmental parameters overlaid into the ordination space, refer to Table 2 for environmental parameter abbreviations.

Appendix 3. Partial effects of significant parameters retained in the final GAM for overall species richness in all habitat types: (a) distance to edge; b) canopy density. The values on the *y*-axes are centred on zero and based on partial residuals, and thus indicate the relative influence of each explanatory variable on the prediction. Dashed lines are ± 2 standard errors.

Appendix 4. NMDS loadings and P values for habitat parameters at plantation sites.

Appendix 5. NMDS ordination diagrams (first two axes) for plantation sites. (a) Species, refer to Table 1 for species abbreviations; and (b) direction and magnitude (vector length) of significant ($P > 0.05$) fitted environmental parameters overlaid into the ordination space, refer to Table 2 for environmental parameter abbreviations.