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MSc by Research in Environmental Studies

The Impact of Edge-Effects on Aerial Insectivorous Bat Assemblages in the Amazon

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Statement of originality

I declare that, with the exception of any statements to the contrary, the contents of this report/dissertation are my own work, that the data presented herein has been obtained by experimentation and that no part of the report has been copied from previous reports/dissertations, books, manuscripts, research papers or the internet.

Signed ....[redacted]....

Print name... Natalie Yoh ....

Date.... 30th Oct. 2018 ....

Glossary of Terms

Habitat Types

Matrix	The matrix is the disturbed/altered habitat to which the primary forest is adjacent to. In this study, the matrix was composed of secondary regrowth forest.
Edge	The area of two adjoining habitats (e.g. primary forest & matrix) which is influenced by edge-effects
Interior	The area towards the centre of each habitat (primary forest & secondary forest) which is not affected by biotic & abiotic changes associated with the forest edge.

Functional Groups

Open/edge foragers	Species adapted for flying long distances at high speed. These species typically forage in open spaces or along the edge of forest fragments where they do not need high maneuverability (Jenning et al, 2004).
Forest specialists	Species adapted for short, highly-maneuverable flight to enable foraging in densely cluttered environments, usually associated with the interior habitat (Altringham, 1996).

Abstract

Edge effects, the abiotic and biotic changes associated with habitat boundaries, are amongst the most important factors determining a species' distribution in human-modified landscapes. Bats are the second most diverse mammalian order, however many species are not targeted in studies on edge-effects, particularly in tropical forests which suffer the highest rates of deforestation. This study aims to quantify the magnitude and extent of edge effects on Amazonian aerial-insectivorous bats by relying on a suite of theoretical models previously applied to other taxa. Acoustic sampling was conducted across two seasons at the Biological Dynamics of Forest Fragments Project along four 2km transects consisting of primary forest which intersected with secondary forest. As part of this study, the effectiveness of using an automatic classifier to identify species' calls was compared against manual identification using relevant acoustic keys. A total of six models (mean, linear, power, sigmoid, unimodal and cubic) were used to assess the changes in the relative activity of both forest specialist and open/edge forager species in response to edge effects, as well as changes observed at the assemblage level. Responses were assessed for seven individual species, two of which demonstrated a response to edge effects detectable over a minimum extent of 400m - *Centronycteris maximiliani/centralis* and *Pteronotus parnellii* (60KHz). Insect volume was only weakly associated with the activity of these two species, and that of total bat activity, therefore prey availability does not explain activity patterns. Our results suggest edge responses may be more complex than previously considered, however they also imply that a low contrast matrix of mature secondary forest may mitigate the impact of edge effects for many bat species. Therefore, allowing for forest regeneration between forest patches may reduce the extinction pressure on aerial insectivores in tropical fragmented landscapes.

Keywords: *Fragmentation; BDFFP; acoustic monitoring; prey availability; forest regeneration*

Introduction

Tropical Deforestation and its drivers

The conversion of forests to agricultural land and pasture has and continues to be a global phenomenon (Achard *et al.* 2002; Hansen *et al.* 2013). However, contrary to popular belief, global tree cover has increased since the 1980's due to reforestation and afforestation schemes in many temperate regions (Song *et al.* 2018). Unfortunately, the opposite may be true for tropical regions which experience the highest rates of forest loss (Fig. 1). Approximately 600 million hectares of tropical forests have already been lost. This number is expected to rise by 2050 with up to 36% of forest lost within half a century (Wright 2010). As of 2012, approximately 1.1 million hectares has been deforested since 2000 (Hansen *et al.* 2013).

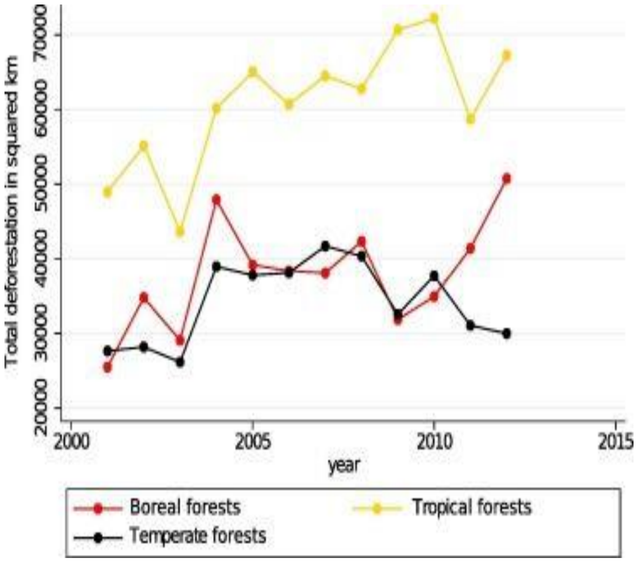

Figure 1 – The sum of country-level deforestation for three climatic types of forests, sourced from Leblois *et al.* (2017). Tropical deforestation accounts for almost half of the total deforestation.

Deforestation is currently the second largest cause of CO_2 release into the atmosphere (D'Amato *et al.* 2017). Not only does this raise concerns for meeting targets to reduce greenhouse gas emissions, but also for reducing biodiversity losses (Leblois, Damette and Wolfersberger 2017; Giam 2017; Wright and Muller-Landau 2006). Despite only constituting ~10% of total land cover (1.8×10^7 km^2) tropical forests support two-thirds of global biodiversity (Raven 1988; Giam 2017), including many endemic species. Hopkins (2005) predicted there could be between 30,000–100,000 endemic plant species in Amazonia alone. Therefore, intensive deforestation in these habitats is a major threat to global biodiversity. Considering the deforestation of tropical forests up until 2010 alone, Rosa *et al.* (2016) predict a current extinction debt of up to 140 forest-specific vertebrate species.

In the Old-World, increased global demand for palm oil has accelerated deforestation across Malaysia and Indonesia since the 1990’s. Approximately 17% of Malaysian and 63% of Indonesian plantations have been converted from tropical forests (Pirker *et al.* 2016). With ever-increasing demand, palm oil cultivation is spreading to other tropical regions increasingly threatening tropical forests in Central and Western Africa, and the Neotropics (Pirker *et al.* 2016; Gollnow and Lakes 2014).

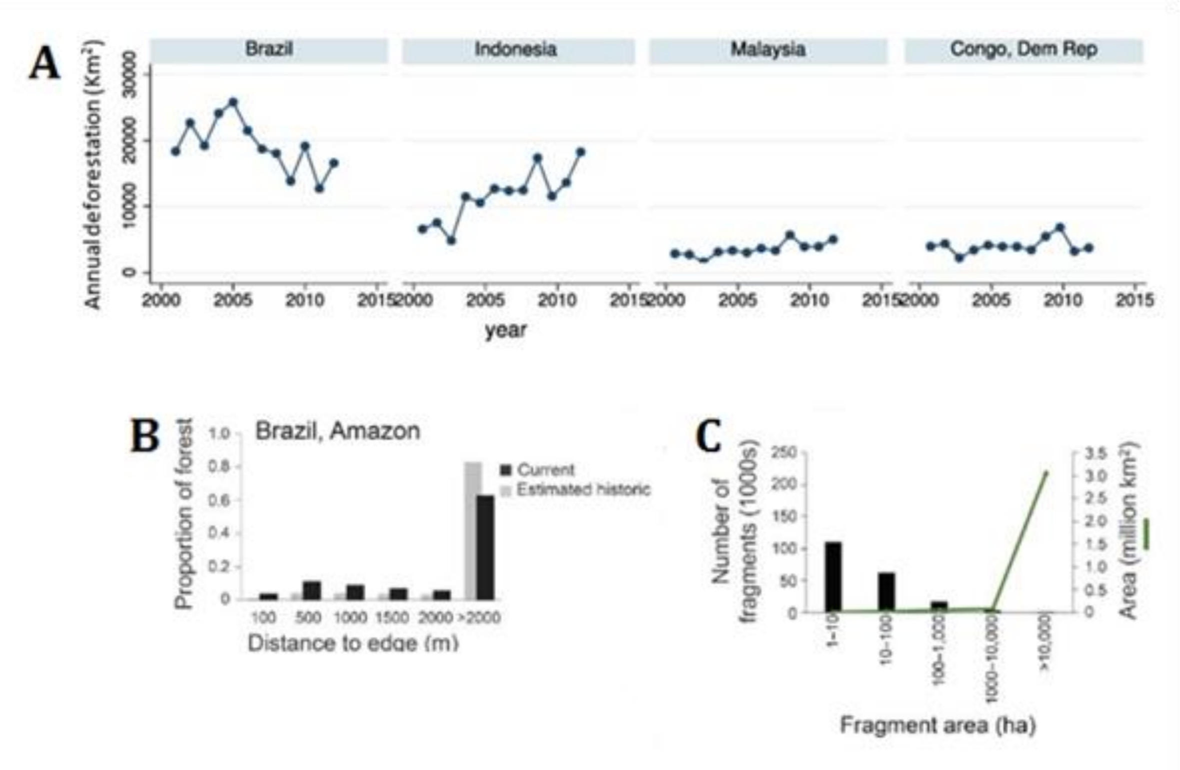

Figure 2 – How deforestation is occurring in the Amazon. A) Tropical deforestation in the four largest developing countries of the tropics from 2001-2012. B) Proportion of forest area in the Brazilian Amazon from an edge in increasing distances categories for both present and estimated historic forest cover. C) Number (per size class) of forest fragment in the Amazon and total area of forest of the corresponding size categories. As the smallest fragments are poorly mapped it is likely the number of 1-10ha fragments is underestimated. Figures adapted from Leblois *et al*. (2017) and Haddad *et al*. (2015).

In the New World, the Amazon is one of the world's most important biological resources; as a biodiversity reservoir (supporting ~25% of global terrestrial species), as a climate regulator (generating 15% of global terrestrial photosynthesis), and as a carbon sink (Aleixandre-Benavent *et al.* 2018; Barros and Fearnside 2016). Over half (52%) of the 4125 forest-dependent tropical vertebrates are found in the Amazon, compared to 38% in SE Asia, and 10% in the Congo Basin (Rosa *et al.* 2016). However, of these regions, the Amazon is expected to have suffered the greatest number of extinctions of forest-dependent vertebrates (Rosa *et al.* 2016) as a result of deforestation.

Deforestation in the Amazon

Brazil continues to experience one of the highest rates of tropical deforestation in the world (Zarin *et al.* 2015; Fig. 2). Since 2015 there has been an increase in deforestation in the Brazilian Amazon (~8,000 km^2 in 2016; Azevedo-Ramos and Moutinho 2018; Barros and Fearnside 2016) following declines of 74% at the turn of the century (from ~19,000 km^2 in 2005 to ~5,000 km^2 in 2014; Azevedo-Ramos and Moutinho 2018). Pressures include industrial logging, mineral extraction, and energy production (Shroder, Sivanpillai and Boekhout van Solinge 2016; Barber *et al.* 2014). However, large-scale clearing for agriculture and conversion to pasture remains the predominant driver of deforestation in the Amazon. Cattle ranching accounts for 60-70% of forest loss (Malhi *et al.* 2008; Aleixandre-Benavent *et al.* 2018). Brazil's exports of beef continue to increase annually (ABIEC 2017). Between January - December 2017, Brazil exported over 1.5 million tonnes of beef, a revenue increase of 17% from 2016 (ABIEC 2017). The country's largest exports include iron ore, soybeans, crude petroleum, and sugar (OEC 2018). Coffee and corn are also significant international products (OEC 2018).

Collectively, soybean exports are currently Brazil's most profitable commodity (World Intergrated Trade Solution 2018) and now accounts for 1/3 of the global production (OEC 2018). Consequently, the greatest rises in deforestation recently have been observed in Mato Grosso (Valdiones *et al.* 2017), a state recognised for its national and international importance for soybean production (Gollnow and Lakes 2014). Although it is typically pasture that is converted for soy plantations, this leads to the displacement of cattle ranches into forested regions elsewhere. Therefore, soy production is often an indirect cause of deforestation (Gollnow and Lakes 2014). This creates conflict between conservation and local people as soy is a valuable contributor to the nation's economic development (Weinhold, Killick and Reis 2013). Despite several successful strategies implemented over the last decade to protect the Amazon forest, 60 - 90% of deforestation has been conducted illegally (Boekhout van Solinge, Sivanpillai and Boekhout van Solinge 2016), and growing economic and political uncertainty is predicted to incite further declines of 40% of the remaining Amazonian forest by 2040 (Carvalho, Domingues and

Horridge 2017; Pailler 2018). A patchwork of small forest fragments (<400ha) currently dominates the landscape due to land clearing for small agricultural holdings (Laurance, Sayer and Cassman 2014) but there are also growing fears that plans to introduce large-scale palm oil plantations in the Brazilian Amazon may intensify this displacement process (Gollnow and Lakes 2014).

Transport infrastructure provides a pathway for this deforestation to occur. Approximately 95% of deforestation in the Amazon occurs within 5.5km of a road or 1km of a navigable river (Barber *et al.* 2014) which includes 43.6% of unprotected land and 10.9% of protected land having been deforested by 2014. Of the 95%, over 80% of deforestation is exclusively linked to roads (Rocha, López-Baucells, *et al.* 2017). This has serious consequences for the longevity of the remaining forest as Barber *et al.* (2014) concluded 35.2% of the Brazilian Amazon was classified as *highly accessible*. Not only does this accessibility facilitate agricultural or industrial expansion, the roads themselves may divide the forest into patches and thus result in the creation of forest edges.

Habitat Fragmentation & Edge-Effects

In the face of widespread deforestation, understanding how habitat fragmentation alters ecological communities is an urgent issue challenging conservation biologists (Laurance *et al.* 2017). Habitat fragmentation is an umbrella term used to group a number of landscape and local scale processes resulting from initial habitat loss (Fahrig 2013; Sodhi *et al.* 2011).

Edge Phenomena

By breaking up continuous habitat, deforestation creates a patchwork of smaller, isolated fragments. Localised extinctions and population declines follow the initial loss of habitat as well as through processes such as reduced habitat connectivity (Didham 2010) and 'crowding effects' (Turner 1996). However, the remaining ecological communities are not fixed. They are subsequently exposed to biotic and abiotic changes associated with the margins of these artificially created fragments (Laurance *et al.* 2017). These changes are known as *edge-effects.* Edge-effects are considered amongst the most important drivers affecting the dynamics and composition of fragmented faunal and floral communities (Laurance *et al.* 2017; Broadbent *et al.* 2008), as they exceed the natural intrinsic variation in conditions, thereby deteriorating the ecosystem and its suitability for the species it previously supported (Murcia 1995; Rocha, López-Baucells, *et al.* 2017). However, due to the diversity of edge-related phenomena, as well as the complexity of biological interactions, the processes governing edge-effects are not yet fully understood despite being one of the most well-studied ecological phenomena of the last 100 years (Ries *et al.* 2017).

Between 35,000 – 50,000km of new edge habitat is created annually in the Brazilian Amazon as a result of deforestation (Broadbent *et al.* 2008), initiating decreases in relative humidity (Cochrane and Laurance 2002), increased exposure to wind stress (Laurance *et al.* 2017), and amplified temperature fluctuations (Murcia 1995). These changes all have consequences, both directly or indirectly, on biotic communities. Abiotic changes such as increased noise pollution, higher temperatures, and decreased humidity have been observed up to 300m either side of a road (Laurance *et al.* 2017). For species, such as terrestrial insectivorous passerines (Ahmed *et al.* 2014; Fletcher 2005) roads themselves create an impassable barrier, reducing connectivity and intensifying the effects of fragmentation (Barber *et al.* 2014).

Edge-effects not only affect populations but also impact community and ecosystem scale processes (Fletcher 2005; Laurance *et al.* 2007). Changes in seed dispersal as a result of edge-effects (Wright 2010), as well as changes to the microclimate, modifies forest composition and structure. Large, established trees die prematurely (Ferreira and Laurance 1997), superseded by early successional plant species. In doing so, the relatively open understory layer becomes densely cluttered. Animal species capable of exploiting these new conditions and resources show an increased abundance and dominance in edge habitat. Butterfly populations of light favoring species have been shown to increase in edge habitat (Leidner *et al.* 2010) at the expense of shade-tolerant species. Similarly, the fruits of pioneer species support a higher abundance of frugivorous bird (Sodhi *et al.* 2011) and bat (Rocha, López-Baucells, *et al.* 2017) species. These replace species specialized for forest interiors, such as understory birds (Sodhi *et al.* 2011; Hansbauer *et al.* 2008) and bats that glean animal prey from vegetation (Rocha, López-Baucells, *et al.* 2017). Both groups exhibit population declines and a decrease in species richness. By negatively impacting multiple trophic levels, edge-effects are one of the key drivers of extinction in fragmented landscapes.

***Magnitude* and *Extent* of Edge-Effects**

Magnitude and extent are two measures by which edge-effects can be quantitively investigated (Ries *et al.* 2017; Ewers and Didham 2006b). The *magnitude* of edge effects is the relative strength of an effect and the *extent* of edge effects, as defined by Ewers and Didham (2006), is the distance to which changes in natural conditions associated with habitat boundaries are present within habitat interiors. Depending on the type of the edge-effect and the species of concern, estimates vary as to what distance edge phenomena penetrate forest interiors (Fig. 3). Most effects are considered to occur between 100-300m from the edge (Laurance *et al.* 2002; Barros and Fearnside 2016). However, some studies have estimated effect distances of 1-10km into forest interiors (Delaval and Charles-Dominique 2006; Murcia 1995; Curran *et al.* 1999). Estimates often vary depending on the focal taxonomic group. Villada-Bedoya *et al.* (2017) observed edge-related changes affected dung beetle abundance over a maximum extent of 420m in the Columbian Andes, however Zurita *et al.* (2012) found *Thamnophilus caerulescens,* a neotropical bird species, was impacted over an extent of 1,300m. Consequently, there is no universally reliable estimate as to what distance from a forest edge a species or specific functional group/guild can be affected (Hansbauer *et al.* 2008).

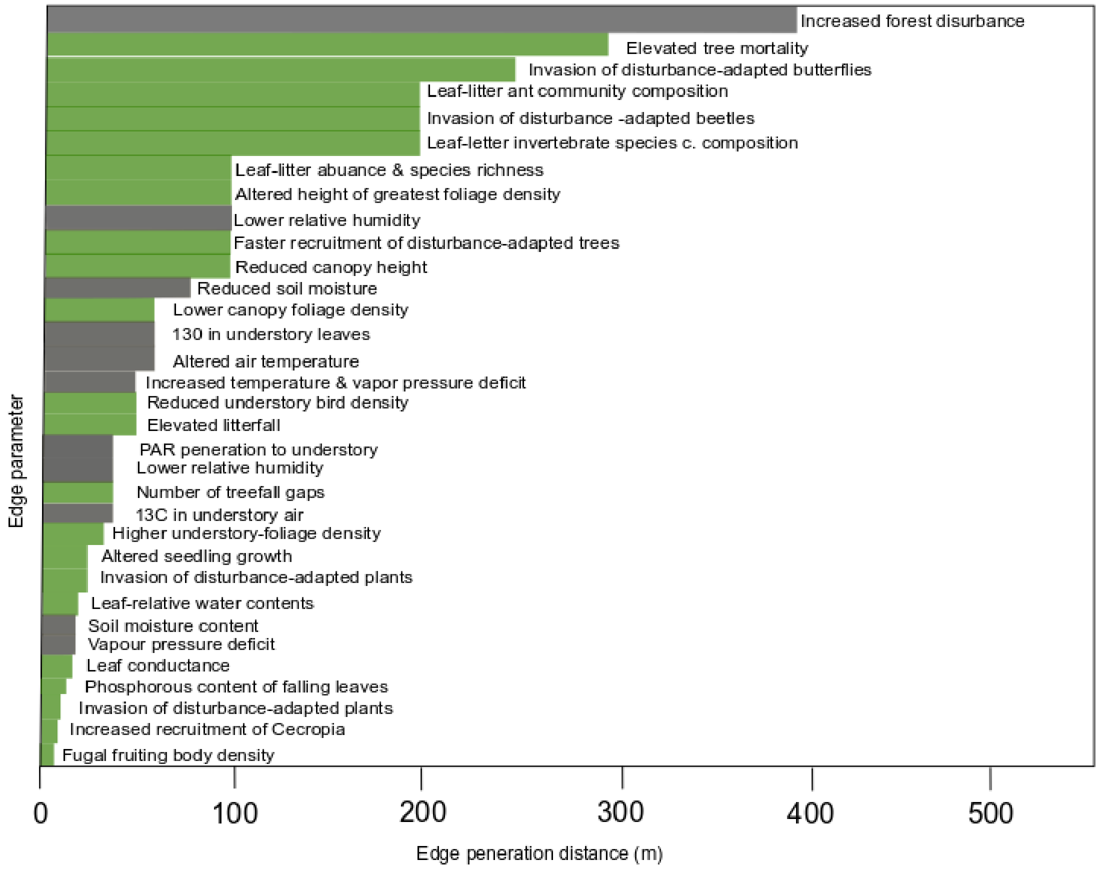

Figure 3 – Figure 3 – Penetration distances for a selection of edge-effect phenomena studied at the Biological Dynamics of Forest Fragments Project (BDFFP) determined by multiple investigators. PAR - photosynthetically active radiation. Grey bars represent abiotic changes to environmental conditions. Adapted from Laurance et al. (2017).

Cumulative effect interactions

Individual edge-related changes do not act in isolation but rather can form complex interactions with each other. As edge-effects are therefore cumulative, the interaction of different effects can often result in further or more dramatic changes in conditions (Porensky and Young 2013; Malcolm 1994; Grass *et al.* 2018). One edge effect that arises as the result of multiple effects interacting is the increased risk of fire in fragmented forests (Cochrane and Laurance 2002; Laurance *et al.* 2017). Increased tree mortality along the edge of fragments results in a diminished canopy which, combined with increased wind pressure and higher temperatures, leads to a decrease in local humidity. These conditions combined with the increased leaf litter and dead-fall along edges quite literally add fuel to the risk of forest fire. The risk is greatly magnified by the accumulation of multiple effects interacting, than if any one of the effects were acting independently. Anthropogenic forest fires are exponentially more common at the boundaries of forest fragments and can result in irreversible damage to tropical forests (Cochrane and Laurance 2002). Differences in the synchronic interactions of different edge-effects can lead to variation in how a habitat, and a species, is impacted by the formation of an edge amongst different sites of occurrence.

Further additive effects transpire in areas of forest which are located near two or more edges (Laurance *et al.* 2007). Therefore smaller or more irregular fragments are more greatly affected by edge effects than larger fragments as they have a higher edge to interior ratio (Forman and Gordon 1986; Benítez-Malvido and Arroyo-Rodríguez 2008). The presence of multiple edges has been shown to affect both an edge effect's magnitude and extent. The extent of edge effects within double-edged fragments has been recorded to penetrate distances of up to 33% greater than at those with a single edge (Fletcher 2005). The quantity of neighbouring forest edges is an important predictor for local phyllostomid bat abundance (Rocha, López-Baucells, *et al.* 2017) and Bobolink (*Dolichonyx oryzivorus*) site fidelity (Fletcher 2005).

Matrix contrast

The matrix surrounding remnant patches is also important in determining an edge-effect's magnitude and extent, as well as a fragment isolation (Ricketts 2001). Low-contrast matrices (e.g. secondary forest) allow for higher dispersal rates than high-contrast matrices (e.g. pasture; Laurance *et al.* 2002; Malcolm 1994). Generalist species are adapted to multiple habitat types and therefore are more capable of exploiting matrices which differ substantially in terms of their structure from the original habitat. Habitat specialists, in contrast, are incapable of traversing any habitat that differs from their primary habitat or are reluctant to do so. Ricketts (2001) demonstrated that specialist Lycaenini butterflies had a low tolerance to either low or high contrast matrices, whereas generalist Argynnini butterflies were indifferent to matrix type. Other species were only tolerant to one of the two matrix types. In this way, the type of matrix acts as a selective filter, only facilitating the dispersal of species between fragments which are able to exploit that type of matrix habitat (Gascon *et al.* 1999).

The structural complexity of the matrix surrounding forest remnants also correlates with the magnitude of edge effects (Baum *et al.* 2004; Vleut *et al.* 2012). Low-contrast matrices mitigate some of these effects by reducing the strength of the gradient of many edge-related changes which are otherwise observed at the boundaries of high contrast matrices (Meyer *et al.* 2016; Rodríguez-San Pedro and Simonetti 2015). They also reduce risk of interacting edge effects that may otherwise occur in remnant patches nested within high-contrast matrices (Porensky and Young 2013). As such, different types of matrices provide substantially different value to biodiversity (Gascon *et al.* 1999). Of the two dominant secondary forest types in the Central Amazon, edge-effects have been shown to be of smaller magnitude in *Cecropia*-dominated forest than in *Vismia*-dominated forest as *Cecropia* trees grow more densely and larger (Laurance *et al.* 2002; Benítez-Malvido and Arroyo-Rodríguez 2008). Not only does the composition of the matrix affect diversity at the species and assemblage level, but it can also determine the effect fragmentation has on ecological processes. Martino (2015) observed that frugivore visitation to fruiting trees differed significantly between low-contrast and high-contrast matrices, therefore disrupting natural seed dispersal processes. As such, fragment size, shape, and matrix composition all play a crucial role in determining the influence of edge effects on community dynamics.

Modelling edge effects

Despite significant interest in edge-phenomena over the past century there is still large variability in the design of edge-related studies, including the length of transects and the scale at which they are sampled (number of distance classes included; Ries *et al.* 2017). Assessing the extent of edge-effects is challenging and requires extensive sampling within a habitat to successfully observe fine-grain landscape changes (Ewers and Didham 2006b; Ries and Sisk 2004). Between 2013-2015 many empirical studies (e.g. Villaseñor *et al.* 2015) utilised short transects (< 500m from edge) with few sample points (< 5). These distances are unlikely to incorporate the full area affected by edge-effects and do not provide adequate spatial detail to successfully determine extent or magnitude. Inaccurate assumptions regarding neotropical herpetofauna responses to edge effects were concluded from studies which did not sample adequate distances to detect edge responses for these species (Schneider-Maunoury *et al.* 2016). In addition, the majority of the studies reviewed by Ries *et al.* (2017) only compared two distance classes (interior and edge), as such they had no means to quantity magnitude or extent in their assessment of edge responses (Ries *et al.* 2017). Only ~30% of the 674 empirical studies reviewed by Ries *et al.* (2017) quantified distance of edge influence in their analysis. Even so, many studies fail to investigate the influence of edge effects on the boundary as a whole, most commonly investigating the effect only on one side of the border (Ewers and Didham 2006b; Ries *et al.* 2017). Edge effects are not mono-directional but impact habitats on both sides of a border (Fernández *et al.* 2002). It is therefore important to consider the total penetration distance/extent rather than focusing on one habitat exclusively in order to fully understand the impact of edge-effects. Of the total studies included in the review only ~12% quantified distance of influence using suitable analytical approaches such as randomization tests, piecewise regression, or Ewers and Didham's (2006) regression models which further reduces the comparability between studies. Magnitude was quantified even more infrequently as it was only included in ~5% of studies. Consequently, although the distance up to which changes occurred may have been investigated, in ~95% of the studies it was not quantitatively assessed resulting in the poor analysis of how much of an effect these changes were having on local populations.

To deduce generalisations of species responses to edge-effects, clear, empirical model designs must be adhered to (Ries *et al.* 2017; Ries and Sisk 2004; Ewers and Didham 2006b). To do so, designs should accommodate sampling points at a fine-scale over large distances (ideally at least >500m from the habitat boundary; Laurance 1991) to ensure that extent and magnitude can be calculated with confidence and sampling points should also be located in the habitats either side of the boundary. Ewers and Didham (2006) proposed five theoretical models to explore species' responses to edge-effects (see methods for model descriptions), individually and as an assemblage, meeting these criteria. These models have also been applied to studies investigating how edge effects effect processes such as seed dispersal (Vespa, Zurita and Bellocq 2014). They examine five potential relationships between edge effects and responses. By testing for potential positive affiliations with edge habitat, as well as incomplete sampling ranges for measuring extent on one or both sides of the habitat boundary, these models provide a valuable tool for empirically investigating edge impact.

Bats & Fragmentation

Bats are often overlooked in conservation research but represent the second most diverse mammalian order, with over 1300 species worldwide (López-Baucells *et al.* 2016). Almost 25% of these are classified as Critically Endangered, Endangered or Vulnerable by the IUCN, predominantly due to habitat loss (Mickleburgh, Hutson and Racey 2002; López-Baucells *et al.* 2016). Bats perform important ecological roles in tropical forests including pollination, seed dispersal, and insect suppression (Kunz *et al.* 2011; De La Peña-Domene *et al.* 2014). They are also considered valuable bioindicators of disturbed forest habitats (Fenton *et al.* 1992; Cunto and Bernard 2012). The Neotropics has the highest bat diversity globally with ~83 genera and ~288 species (Mickleburgh, Hutson and Racey 2002). This comprises species from a variety of feeding guilds including: frugivores, insectivores, carnivores, nectarivores, sanguivores, piscivores and omnivores (Segura-Trujillo, Lidicker and Álvarez-Castañeda 2016). The Amazon alone supports over 200 recognised species with representatives from each of these guilds (López-Baucells *et al.* 2016). The most common diet of Amazonian species is insectivory, the same as that of ancestral bat species (López-Baucells *et al.* 2016; Segura-Trujillo, Lidicker and Álvarez-Castañeda 2016).

Current understanding of tropical bat responses to fragmentation

There have been numerous studies investigating the effects of fragmentation on tropical bat assemblages (reviewed in Meyer et al. 2016), mostly restricted to the Neotropics with isolated studies from the Old World (e.g. Struebig *et al.* 2008; Law, Anderson and Chidel 1999). In the Neotropics, aerial insectivores are poorly sampled due the sensitivity of their biosonar to mist-nets (Marques *et al.* 2013; Meyer 2015), resulting in a dominance of studies focused on phyllostomid bats (Estrada-Villegas, Meyer and Kalko 2010; Meyer, Struebig and Willig 2016; Estrada and Coates-Estrada 2002; Arias-Aguilar *et al.* 2018). This has limited our understanding of fragmentation effects on aerial insectivores, particularly concerning edge-effects.

Bat responses to fragmentation at the assemblage level are complex, as evidenced by conflicting findings across many studies. Multiple studies, including those conducted by Estrada and Coates-Estrada (2002) and Bernard and Fenton (2007), have shown little or no changes in the species richness of tropical bat assemblages in response to fragmentation (Rodríguez-San Pedro and Simonetti 2015). Rodríguez-San Pedro and Simonetti (2015) and Ethier and Fahrig (2011) demonstrated a positive effect on aerial insectivorous bat activity in the temperate forests of Chile and Canada. Both studies hypothesized that fragmentation can benefit many of these species, increasing the habitat complexity as fragmented forests provide a greater set of resources, e.g. for foraging and roosting, and that forest-edges provide beneficial commuting routes (Verboom 1998) Both studies also suggested a positive response by bats to edge habitat; in Ethier and Fahrig (2011) 97.5% of bat passes were recorded at the edge. Higher activity of shrub and canopy frugivores has also been observed in the edge than in the interior of tropical forest fragments due to a higher abundance of fruiting successional plants (Rocha, López-Baucells, *et al.* 2017; Cortés-Delgado and Pérez-Torres 2011).

Other studies contradict the conclusion that forest fragmentation is beneficial to bat assemblages, having shown bats are negatively impacted by fragmentation at the species and assemblage level (Bernard, Albernaz and Magnusson 2010; Meyer *et al.* 2007; Rocha *et al.* 2016; Cunto and Bernard 2012; Struebig *et al.* (2008). For both phyllostomids and aerial-insectivores, higher abundances and number of species have been shown to occur in larger forest fragments compared with smaller ones (Struebig *et al.* 2008; Rocha, López-Baucells, *et al.* 2017; Estrada-Villegas, Meyer and Kalko 2010) with increased species dominance occurring in edge habitat (Rocha, López-Baucells, *et al.* 2017). The results of Ethier and Fahrig (2011) should be interpreted with caution as they do not account for higher detectability within clearings compared to cluttered forest interiors (Stilz and Schnitzler 2012) nor do they consider matrix composition. The authors also classified the forest interior as 50m from the forest edge at which distance the forest may still be affected by edge-effects (Delaval and Charles-Dominique 2006). Similarly, Rodríguez-San Pedro and Simonetti (2015) did not quantify bat activity in the matrix so were unable to compare the effects of fragmentation on bat activity between all three habitats (interior, edge & matrix). The consensus between all of the studies mentioned is varying responses to fragmentation are observed across different bat species.

Although bats are highly mobile, forest cover is an important factor determining whether the matrix is favorable for commuting and foraging (Vleut *et al.* 2012). Ecomorphological factors influence a species' ability to exploit different matrix habitats (Bader *et al.* 2015; García-García, Santos-Moreno and Kraker-Castañeda 2014; Farneda *et al.* 2015). Species which are adapted to foraging in forest interiors may be unable to use high-contrast matrices (such as agricultural land; Bader *et al.* 2015; Farneda *et al.* 2015; Rocha *et al.* 2016), thereby reducing their available range due to a lack of commuting habitat. As such fragments largely enclosed within a low-contrast matrix, e.g. late-stage secondary forest, support a higher diversity of species than partially enclosed patches (Vleut *et al.* 2012). Forest fragments within a low-contrast matrix have a lower magnitude of edge-related changes. For this reason, high-contrast matrices support a lower diversity of insectivorous bat species than secondary forest and forestry plantations (Rodríguez-San Pedro and Simonetti 2015; Struebig *et al.* 2008; Meyer & Kalko 2008). This can be attributed to both abiotic factors - such as increased wind pressure, which reduces the habitat suitability for many prey species - and biotic factors - such as increased detectability by predators. Both can reduce the matrix's suitability for many species, thereby creating a barrier between fragments. Differences in matrix composition and age are likely to account for much of the variability in bat responses across fragmentation studies (Meyer, Struebig and Willig 2016).

Whilst limited, a number of studies have looked at the difference in bat community composition and activity levels between *interior, edge,* and *matrix* habitats (e.g. Ferreira *et al.* 2017; Cortés-Delgado and Pérez-Torres 2011; Rocha *et al.* 2017; Rodríguez-San Pedro and Simonetti 2015). Such studies are often used in conjunction with morphological studies to inform the classification of a species as a forest specialist, open/edge forager, or as a generalist (Delaval and Charles-Dominique 2006). These classifications are helpful for conservationists to better understand how anthropogenic changes are likely to impact particular species. However, as there are no universal estimates as to the degree to which edge effects penetrate unmodified and neighboring modified habitats, these studies often rely on arbitrary definitions of the *edge*'s boundaries (Ries *et al.* 2017).

Few studies to date have investigated how bats respond to edge-effects and existing studies have focused on phyllostomids. These studies suggest that responses of bats to edge effects may be detected up to 3km; the furthest distance recorded within forest fragments compared with responses of any other vertebrate group currently studied (Delaval and Charles-Dominique 2006). However, as with more generalized studies of fragmentation, there have been contradictory findings as to how bats respond to edge-effects. Da Silva, Filho and Lacher (2013) observed lower phyllostomid bat abundance in the edge habitat than in the interior of tropical forest of Southern Brazil. The sampling area for the 'edge habitat' was limited to along the border of two adjacent habitats and therefore they did not quantify the extent of the effect. The interior transects began ~1km into the forest fragment, below the 3km threshold proposed by Delaval and Charles-Dominique 2006). In contrast, Cortés-Delgado & Pérez-Torres (2011) and Rocha *et al.* (2017) found that highest phyllostomid abundance occurred in edge habitat in Colombia and the Amazon. Similar to Da Silva, Filho and Lacher (2013), Cortés-Delgado & Pérez-Torres's (2011) definition of the edge only extended ~50m from the boundary and interior sampling points located >350m from the edge were unlikely to be independent of edge-effects. However, this study identified a significant difference in the value of two different types of edge habitat for these species depending on the forest's structural composition, concluding every edge habitat will not stimulate the same response between species. Along with Delaval and Charles-Dominique (2006), Rocha *et al.* (2017) observed decreased phyllostomid species richness at the forest edge with a dominance of few, generalist species. In Delaval and Charles-Dominique (2006) the edge habitat was defined as the distance up to which species' known to occupy degraded habitats, *Glossophaga soricina* and *Artibeus cinereus*, were recorded. As mentioned, this creates a feedback loop between a specified habitat type being used to determine a species classification, and then species being used to determine a habitat criterion. Both are likely to be influenced by classifications in other localities. By first quantitatively determining the distance threshold of edge effects specifically for a site - and the selected habitats - of interest, researchers can ensure that *interior, edge,* and *matrix* criteria can be used more accurately to reflect the true responses of species. None of the four studies mentioned were able to reliably sample aerial insectivores due to the sampling technique used, however aerial insectivores constituted 1% of the bats captured by Cortés-Delgado & Pérez-Torres's (2011) and six species were analysed by Da Silva, Filho and Lacher (2013), and one species by Rocha *et al.* (2017). The latter included *Pteronotus parnellii* which is an aerial insectivorous species which can be sampled well using mist-netting.

Ecomorphological factors influencing response to fragmentation

Wing shape & roost selection

As a species' tolerance to disturbance can be predicted from its ecological requirements and adaptability, so too can its response to edge effects. Body size, wing loading (body mass divided by wing area), call structure, home range and roost selection are all associated with a bat species' spatial requirements (Kalko and Handley 2001; Pinto and Keitt 2008; García-García, Santos-Moreno and Kraker-Castañeda 2014). Species with a high wing loading trade maneuverability for fast, sustained flight. This enables them to exploit highly-dispersed food resources and to hawk insect prey in the air. However, this morphology restricts their ability to maneuver in highly-cluttered environments such as forest interiors. Therefore, these species are principally associated with open habitat and forest edges (Estrada-Villegas, Meyer and Kalko 2010). On the other hand, species with a low wing loading are well adapted to exploiting resources in the forest interior and maneuvering through dense vegetation in the canopy. However, because of this specialisation they are more likely to be negatively affected by changes to vegetation structure (Pinto and Keitt 2008; García-García, Santos-Moreno and Kraker-Castañeda 2014). Fast-flying, more mobile species are less impacted by fragmentation as they are more capable of exploiting landscape mosaics (Law, Anderson and Chidel 1999; Meyer, Struebig and Willig 2016).

Roost selection is also a significant factor in species' distribution. Although many bat species roost in caves and buildings, most roost in trees and foliage (Kunz 1982). Tree cavity/foliage roosting species are more at risk from the negative impacts of fragmentation than cave-dwelling species as they require suitable habitat within remaining forest patches for roosting as well as for foraging (Struebig *et al.* 2008; Rodríguez-San Pedro and Simonetti 2015; Ethier and Fahrig 2011). This is one way in which a species may need to utilize more than one fragment to meet all of its ecological needs – otherwise known as *landscape supplementation* (Rodríguez-San Pedro and Simonetti 2015). Therefore, an individual is restricted by its ability to commute to and from available roost sites.

Call structure

Different echolocation call structures are utilized by insectivorous species depending on their environment and foraging strategy (Stilz and Schnitzler 2012; Holderied and Von Helversen 2003). Open/edge foragers often utilize low, long, frequency-modulated (FM) calls with narrow bandwidths or FM-QCF (frequency modulated – quasi-constant frequency) calls, both of which can detect prey over large distances. Forest specialists typically use frequent, short, high-frequency FM calls with broader bandwidths (Fig. 4; Russo, Ancillotto and Jones 2018). This call shape allows for a detailed image of the environment necessary to maneuver through vegetation but has a limited detection range (Thomas, Moss and Vater 2004). A combination of its morphology and echolocation call structure therefore determines a species' capability for foraging in different environments.

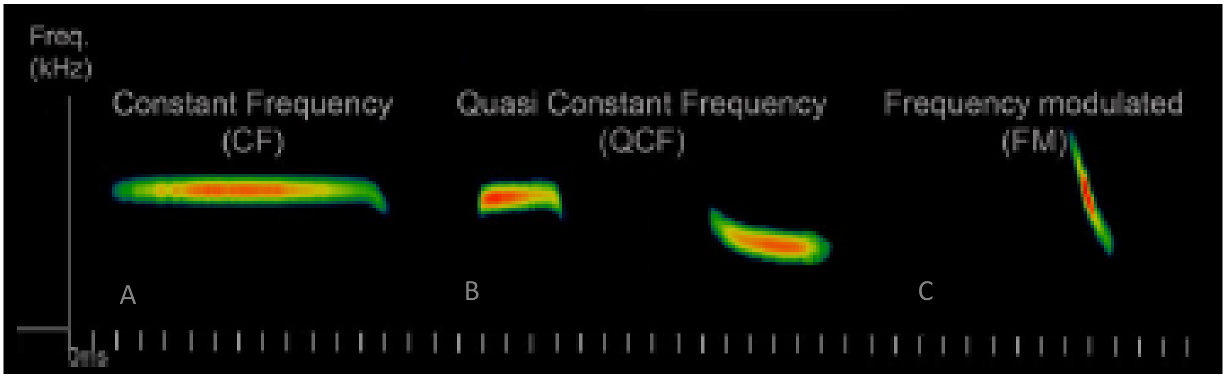

Figure 4 – Example of echolocation call shapes. Families which utilise these call shapes incl. A - Mormoopidae, B – Emballonuridae, Molossidae and Vespertilionidae, C - Furipteridae and Thyropteridae (sourced from López-Baucells et al, 2016).

However, many bat species are highly adaptable. By overlapping high frequency, constant frequency (CF) calls, *P. parnelli* is capable of observing its environment, both in refined detail and over a large distance (Jen and Kamada 1982). Its medium body size allows it to not only exploit forest interior but also traverse open areas depending on prey availability (Estrada and Coates-Estrada 2002), habitat type and risk from predators. In addition to inter-specific variation in call structure, many species are able to adjust their call characteristics to fit their habitat requirements (Russo, Ancillotto and Jones 2018; Kalko and Schnitzler 1993). This intra-specific variation is commonly observed in pipistrelle species (Kalko and Schnitzler 1993) which produce calls with FM and CF components. When foraging in open spaces they produce calls with a narrower FM component but an elongated CF component than when foraging in a cluttered environment. They are also able to adjust the peak frequency of their call (~40-50kHz) depending on the environmental conditions (Kalko and Schnitzler 1993). Therefore, a species response to edge-induced environmental change is often related to its ecological requirements, its dispersal ability or the ability to which it can adapt to such changes. Fundamentally this is often the degree to which it is specialised for a particular habitat type.

Monitoring bat responses

Over the last five years, the development of echolocation call-libraries (Jung, Molinari and Kalko 2014; López-Baucells *et al.* 2016; Arias-Aguilar *et al.* 2018) has rapidly expanded the potential for including aerial insectivores in fragmentation studies. However, the feasibility of such investigations is often limited by the generation of large datasets which require extended post-field analysis (López-Baucells 2018; Russo and Voigt 2016). Thus, acoustic sampling may result in unmanageable acoustic datasets for many researchers interested in studying these species. Including acoustic surveys in these studies is essential as aerial-insectivores make up large fractions of Neotropical bat assemblages (Silva and Bernard 2017; Estrada-Villegas, Meyer and Kalko 2010; MacSwiney, Clarke and Racey 2008), however manual identification of sound recordings is often time-consuming, reliant on experts, and lends itself to identification inconsistencies amongst different analysists (Jennings, Parsons and Pocock 2008). Automated classifiers not only provide a potential solution to these problems but can also reduce the storage requirements for acoustic studies and guarantee consistency across long-term projects (Blumstein *et al.* 2011; Russo, Ancillotto and Jones 2018) saving time, financial, and energy resources. By utilizing the same signal parameters as measured manually by bio-acoustic technicians, machine-based feature-extraction algorithms or neural networks can assign species labels based on pre-determined call characteristics (Parsons and Jones 2000; Armitage and Ober 2010; Zamora-Gutierrez *et al.* 2016; López-Baucells 2018).

However, automation comes with the risk of generating false positives (over estimating species' occurrence) or, more significantly, false negatives (underestimating species' occurrence; Blumstein *et al.* 2011; Russo, Ancillotto and Jones 2018). This may result in the under or overestimation of species' occurrence, as well as the incorrect mapping of a species distribution. As such, many commercial classifiers have been criticized for their low accuracy (Rydell *et al.* 2017; Madhukumar *et al.* 2018). Another issue is that automatic classifiers are often restricted to localities where there are large acoustic datasets available to first train an algorithm. Intrinsically this has limited their use in the tropics where our understanding of bat echolocation is limited (Russo, Ancillotto and Jones 2018; MacSwiney, Clarke and Racey 2008). In order to maximise the potential for this technique to be widely applied, and ensure reliable results are generated, it is of foremost importance that global echolocation call libraries are created for training locality-specific classifiers.

Response to Prey Availability

Diet and food resource distribution are important factors which influence the spatial distribution of many bat species/guilds. In the tropics, fruit abundance is a significant determinant of the distribution of frugivorous bats (Francis 1994; Saldaña-Vázquez 2014; Kalko and Handley 2001). Consequently, it is important to consider whether tropical insectivorous species are equally influenced by the spatial distribution of their prey. Gonsalves *et al.* (2013) found that prey distribution was more important than habitat type in influencing the spatial distribution of aerial insectivores. However, in other localities, the extent of this influence was dependent on spatial constraints of a species (Müller *et al.* 2012) and forest specialist species are typically restricted by habitat type whereas open/edge foragers are capable of using multiple habitats to exploit fluctuating prey abundances (Müller *et al.* 2012; Kusch *et al.* 2004). An inverse relationship between prey availability and insectivorous bat activity was observed by Adams, Law and French (2009) in harvested forests of S.E. Australia. As previously discussed, maneuverability within structural clutter strongly influences the distribution and activity of bat species (Kalko and Handley 2001; Adams, Law and French 2009; García-Morales *et al.* 2016) suggesting the dense understory vegetation of disturbed forests provides unsuitable foraging habitat for aerial-insectivores. Thus, forest structure, as well as the proximity of prey to primary forest (Treitler *et al.* 2016), is perhaps more significant in determining a species distribution rather than prey availability exclusively. Within Neotropical forest interiors, *P. parnellii* is primarily recorded in the understory (Bernard 2001; De Oliveira *et al.* 2015; Herd 1983). However, notably, its morphology and call structure imply that it is capable of exploiting multiple strata (Jennings *et al.* 2004; De Oliveira *et al.* 2015). There is disagreement as to whether this observation reflects maximum prey availability (Appel *et al.* 2017; De Oliveira *et al.* 2015), and therefore foraging behaviour, or whether it is due to their subterranean roosting behaviour (Bernard 2001; Herd 1983). As edge-effects affect insect populations (Foggo and Speight 2001; Villada-Bedoya *et al.* 2017; Leidner *et al.* 2010) it is important to consider whether bat responses to edge-effects reflect changes to forest type or changes to prey availability.

Aims & Objectives

This thesis aimed to use the approach proposed by Ewers and Didham (2006) to assess the *magnitude* and *extent* of edge effects on aerial insectivorous bats in the Amazon. To do so, data collected by Adrià López-Baucells and Maria Mas were used to quantify bat responses to edge effects. This involved modifying an automatic classifier to improve its performance for this bat ensemble. Specifically, the objectives were:

1. To quantify and compare aerial insectivorous bat activity across a habitat gradient (2km transects beginning 1km into the matrix of secondary forest running linear 1km into adjacent primary forest) to determine the *magnitude* and *extent* of edge effects. This was undertaken for individual species/sonotypes, functional groups and for total activity.
2. To use the calculated *extent* of the edge effect to define three habitat categories: interior secondary forest, edge habitat and interior primary forest.
3. To quantify and compare species richness and assemblage composition between these three habitats.
4. To quantify and compare activity of aerial insectivorous bats in relation to insect availability overall and, more specifically, in relation to individual insect orders which are known to be preyed upon by bats.

In doing so, this thesis aimed to address multiple research gaps relating to aerial insectivorous species, thereby increasing our scientific understanding of how landscape fragmentation - and associated edge effects - impact Neotropical bats. To encourage further studies to include these species in Amazonian fragmentation studies the additional aim was:

5. To quantify the performance, in terms of accuracy, of using an automatic classifier for Amazonian aerial insectivores in comparison to manual identification using two confidence thresholds (≥60% and ≥95%)

Hypotheses

i. Forest specialist activity and total bat activity will decrease on both sides of the boundary towards the edge whereas open/edge foragers will exhibit no response to edge effects. This study predicts forest species' responses will cover an extent >~1.5km as no effect has been observed in studies using transects <1km.
ii. Species richness will exhibit a negative response to edge effects in the primary forest but no response in the secondary forest, with two communities present: one in the primary forest and one in the edge/secondary forest.
iii. Edge penetration distance will be larger (>100m) in the primary forest than the secondary forest for all forest specialists.
iv. Forest specialist activity will be significantly lower in the secondary forest than in the primary forest and there will be no difference in the activity of open/edge foragers between the habitats.
v. Total bat activity will exhibit a positive correlation with insect availability across both habitats.

Methods

Study area

Located 80km north of Manaus, Brazil, in the Central Amazon, the Biological Dynamics of Forest Fragments Project (BDFFP) (2024’26”S, 59043’40” W) is the world’s most comprehensive, long-term experimental study into the effects of habitat fragmentation across a broad range of taxa (Laurance et al., 2017; Fig. 5). This includes important observations into how edge effects influence community and landscape dynamics. The primary forest is classified as terra firme forest, with an average tree diversity of 280 species per hectare (Barros & Fearnside, 2016). The canopy height is between 30-45m with emergent trees up to 55m. The primary forest fragments (1, 10, and 100 ha) were experimentally isolated within cattle ranches in the early 1980’s, between 80–650m from continuous forest, however forest regeneration quickly occurred after many were abandoned 5-10 years later due to economic unviability (Bierregaard *et al.* 1992; Gascon *et al.* 1999). Regrowth forest was dominated by *Vismia* spp, in areas that were cleared and burned, or *Cecropia* spp., in areas that were cleared without fire (Mesquita *et al.* 2001). The understory is dominated by palms (Gascon *et al.* 1999) and it is characterised by an average canopy height of 20-25m. The secondary forest at the time of the study was classified as ‘old secondary forest’ using the age classes proposed by Powell *et al.* (2015). The forest has been periodically cleared to ensure fragment isolation was maintained which was scheduled to commence after the survey period in 2013-2014 (Rocha, López-Baucells, *et al.* 2017). Annual average rainfall is between 2.3-2.5m, however a large variation may be experienced between years (1.9-3.5m). The rainy season occurs between November and June (monthly rainfall >250mm) and the dry season occurs between July and October (monthly rainfall <100mm). Average temperature is between 26-30^{o}C and the site covers a low elevational range of 80-160m (Bierregaard *et al.* 1992; de Cássia Guimarães Mesquita 2000; Johnson and Wolfe 2016; Ferreira *et al.* 2017).

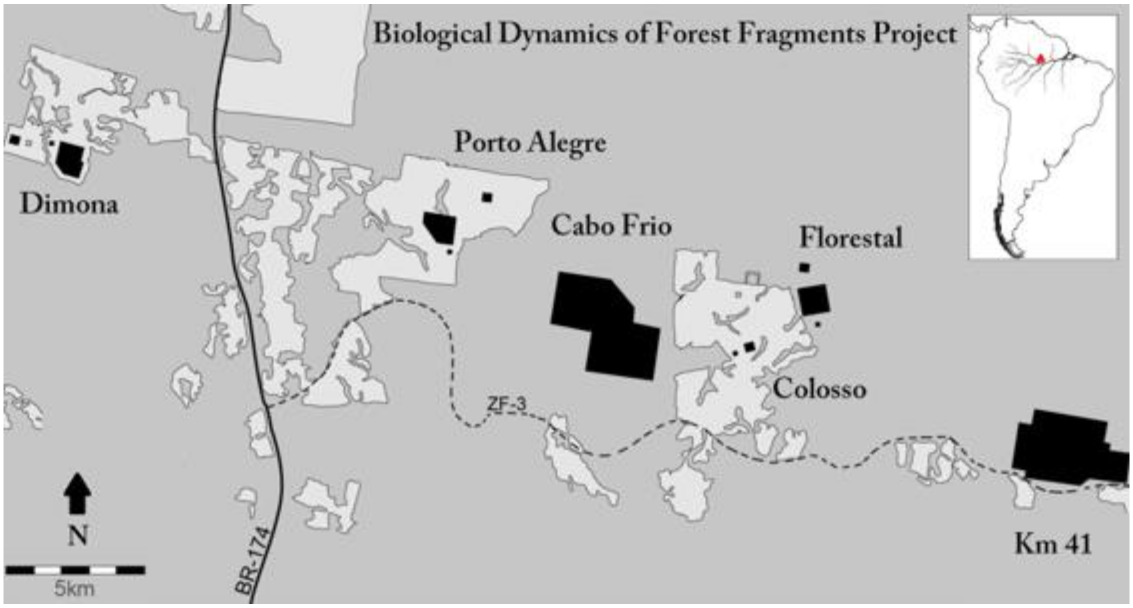

Figure 5 – Map of the BDFFP in the Central Amazon. The black areas represent primary forest sites used in the study, the light grey areas represent secondary forest fragments and the dark grey represents additional continuous primary forest. Transects were located in Dimona and Cabo Frio. Sourced from Rocha *et al* (2017).

Acoustic Surveys

To record bat activity, automatic detectors (Song Meter 2 SM2Bat+, Wildlife Acoustics) with omni-directional microphones (SMX-US Ultrasonic Microphone) were placed every 50m along four, 2km transects for a total of 42 recording stations. Two sites within the BDFFP were used (Cabo Frio and Dimona) to reduce the risk of site bias - two transects at each site (see Appendix I for co-ordinates). Each transect extended through 1km of secondary forest and then continued 1km into the neighbouring primary forest (Fig. 6). Surveys were conducted by Adrià López-Baucells and Maria Mas in the dry season of 2013 and the rainy season of 2014 to prevent seasonal bias. Recordings were saved in WAC format (see Appendix III for further detector settings). As bats are known to favor established flyways for commuting (Law and Chidel 2002; Palmeirim and Etheridge 1985), each transect was established especially for this study.

Figure 6 – Aerial view of the two forest types at Cabo Frio and the sampling points for transects C1 & C2.

At each recording station, one SM2Bat+ detector was placed in the understory - affixed to a tree at breast height (see Appendix II). To ensure the understory was sampled exclusively, plastic dividers were attached to the detectors to create discrete directional microphones (Celis-Murillo, Deppe & Allen, 2009). For this study, the understory was defined to extend from ground to ~ 10m. Hand releases of *P. parnelli* were conducted in both the primary and secondary forest to establish the maximum distance of call detection in each habitat. This species, which has the loudest call of the target species**,** could trigger a detector up to approximately 20m away. Consequently, recording stations situated 50m apart were considered spatially independent sampling points. However, to guarantee maximum point independence, these were rotationally sampled (7 recording stations per rotation) so that actively-recording detectors were 250m apart. Each active detector was programmed to record for 12 hours (18:00-06:00) for three consecutive nights. This amounted to 3,024 recording hours.

Acoustic Analysis

To ensure bat activity was comparable across the study, all recordings were divided into five- second fragments to define a *bat pass* (Torrent et al., 2018). These were used as the measure of bat activity.

Automatic classification

A modified version of the automatic classifier developed by López-Baucells *et al.* (2017) was used to identify species in the acoustic dataset collected. Prior to analysis, the call parameters of an additional acoustic dataset collected by Adrià López-Baucells (2018) were extracted using ScanR (Snapshot Characterization and Analysis Routine) v1.7.4 (Binary Acoustic Technology, USA). This was to increase the number of reference calls available for less common species. All calls were subjected to manual verification prior to their inclusion using the acoustic key in López-Baucells *et al.* (2016). These were used for training the supervised learning algorithm - random forest (Breiman 2001). Random forest has been shown to achieve the highest predictive power against 6 other supervised learning techniques (bagging, support vector, machine, artificial neural network, boosting and linear discriminant analysis; Armitage and Ober 2010) and has performed well for classifying Neotropical bat species (Zamora-Gutierrez *et al.* 2016).

Table 1 - The classification and number of pulses used per sonotype to train the automatic classifier for Amazonian aerial insectivores. Due to difficulties in distinguishing between the three molossid sonotypes (M1, M2 and M3) they have been grouped as a single sonotype (M) for the analysis. No training dataset was available for *Thyroptera sp*. This study species were classified based on the classifications used by Estrada-Villegas, Meyer & Kalko (2010) and information provided by IUCN (2017).

Group	Species/Sonotype	Acronym	Total No. of Pulses for Training Datasets
Forest specialist	*Cormura brevirostris*	CB	40397
	Centronycteris maximiliani/centralis	CM	685227

	Emballonuridae *sp.* (*Saccopteryx gymnura / canescens*)	E1	11068
	Eptesicus brasilensis	EB	125490
	Furipterus horrens	FH	1125
	Pteronotus parnellii (55KHz)	P5	506515
	Pteronotus parnellii (60KHz)	P6	622328
	Pteronotus gymonotus	PG	8362
	Rhynchonycteris naso	RN	417
	Saccopteryx bilineata	SB	510960
	Saccopteryx leptura	SL	262826
	Thyroptera sp.	TT	-
Open/edge forager	*Myotis nigricans*	MRN	455664
	Myotis riparius	MRN	735520
	Molossus molossus	M (1)	11468
	Molossus sp. (*Molossus sinaloae / currentium / Rufus*)	M (2)	23672
	Nyctinomops laticaudatus, Tadarida brasiliensis	M (3)	5141
	Promops nasutus/centralis	P	3714
	Peropteryx kappleri	PK	149007
	Peropteryx macrotis	PM	14176
	Pteronotus personatus	PP	6631

Training datasets of 2000, 3000, 4000, and 5000 pulses were assessed in terms of their performance using accuracy and kappa metrics. This analysis was conducted for all species with sufficient reference calls. For sonotypes with less than 2000 pulses, the maximum number of available files was used for the training dataset (Table 1). The relative importance of each acoustic parameter was also assessed for the most efficient model and the best performing model. The efficiency of a model was determined by the accuracy of classifications relative to model run time. The optimal model was chosen based on efficiency (performance/time taken to conduct analysis). This model was then applied to the dataset using ten acoustic parameters (call duration (Dur), maximum frequency (Fmax), minimum frequency (Fmin), bandwidth (BW), dominant frequency (Fdom), duration of Fdom (Ldom), high end of characteristic (HiFc), low end of characteristic (LowFc), global slope of call (Slope), curvature (Curv) to classify the calls to species level - see Binary Acoustic Technology (2005) for detailed descriptions. To be considered a bat pass, two pulses per species had to be present in each of the files. Once identified, predictions with an accuracy below the 60% threshold (N = 100242) were discarded to reduce noise files and the likelihood of including incorrect identifications (see Appendix IV). Calls which were identified above this threshold were subjected to manual post-validation (N = 235979) to minimize the risk of false negatives and increasing the proportion of species where the probability threshold was low.

Manual post-validation

Manual post-validation on the aforementioned subset of calls was conducted, using Kaleidoscope Viewer 4.0 software (Wildlife Acoustics Incl., USA) with the aid of an echolocation key for bats of the study area (López-Baucells et al., 2016). Call parameters considered include: start/end, maximum/minimum, and peak frequencies, call duration, and call shape. These were measured on the strongest harmonic of each call. Where species identification was not possible (e.g. significant overlap between species), species were identified to mixed-species groups, i.e. sonotype level (Table 1) or calls were excluded from analysis (e.g. calls were faint, <10dB of difference from background noise, or obscured). Feeding buzzes or social calls were not considered so as to allow for comparability with automatically identified calls. To test the reliability of the automatic classifications, post crosschecking was conducted on the files identified to both ≥60% and ≥95% accuracy probabilities (here after referred to as AP60 and AP95). For this, non-paired Wilcoxon Signed-Rank Tests were used. Due to significant deviation between the activity of certain species/sonotypes identified by the automatic classifier and those manually-identified (see Appendix V), the edge-effect analysis was restricted to the manually-identified calls.

Insect sampling

A light trap was mounted in the understory at each of the acoustic sampling points (21 per transect) to quantify insect availability (Appendix II). These traps were mounted for two nights (between 18:00-06:00) per sampling point. To prevent the light traps influencing bat activity recordings (Froidevaux et al, 2018) insect surveys were rotated to ensure that bat activity and insect abundance were not recorded at the same sampling site on the same night. Half of the sampling points were sampled for insects before and half after the bat activity surveys to prevent bias.

Insects collected were subsequently stored in 96% alcohol until later identification in the laboratory. For each sampling point, for each insect order, the number of individuals was determined, as well as total insect volume (length*width*height). This was then used as a measure of insect availability for each order (see Sample *et al.* 1993 for further justification).

Data Analysis

To assess the *extent* of edge effects on aerial insectivorous bat activity at the level of individual species and functional groups (forest species, open space foragers), regression analyses were conducted using the five theoretical models proposed by Ewers and Didham (2006) and subsequently extended upon by Zurita et al. (2012). These were conducted using the stats package in R (version 3.4.4)(R Core Team 2018). Relative bat activity (number of bat passes/survey effort) was used as the dependent variable and distance to the edge was specified as the independent variable. The second-order Akaike Information Criterion, corrected for small sample sizes (AICc), was then used to determine the relative fit of these models. Insufficient data to conduct the regressional analysis (< 120 bat passes across all replicates) were obtained for *Eptesicus brasiliensis,* *Furipterus horrens, Promops nasutus/centralis*, *Peropteryx kappleri, Pteronotus gymnonotus*, *Peropteryx macrotis* and *Pteronotus personatus*.

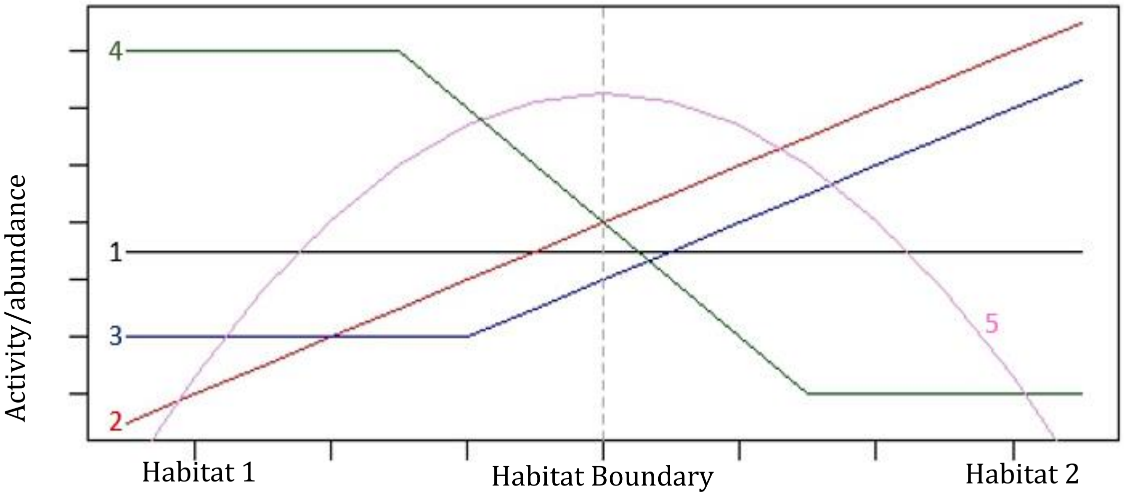

Figure 7 – Visualization of the five models proposed by Ewers and Didham (2006) of species responses to edge effects. 1 – Mean/null model; 2 – Linear model; 3 – Power model; 4 – Sigmoid model; 5 – Unimodal model

Model Descriptions

Model 1 – Mean model

Relative Activity = β0 + ε

Where species exhibit no response to edges as they utilise both habitats equally; this model applies to generalist species.

**ε = error*

Model 2 – Linear model

Relative Activity = β0 + Distance × β1

This model implies that the effect of the edge extends the range of the sampled area of the study.

** β0 & β1 = constants*

Model 3 – Power model

$$\textbf{Relative Activity} = \beta 0 \times e^{\beta 1 \times \text{Distance}} + Y_{\min}$$

This model identifies the uni-directional asymptote response to the edge.

** Y_{min} = the uni-directional asymptote*

Model 4 – Sigmoid model

$$\textbf{Relative Activity} = Y_{\min} + ((Y_{\max} - Y_{\min})/(1 + e^{(\beta 0 - \text{Distance}) \times \beta 1}))$$

Where asymptotes are determined within both habitats in response to the edge. This model implies there is a discrete change in habitat suitability, resulting in a species response which is either gradual or abrupt.

*$Y_{\max}$ & $Y_{\min}$ represent the bi-directional asymptotes

Model 5 – Uni-modal model

$$\textbf{Relative Activity} = Y_{\min} + ((\beta 0 - Y_{\min})/(1 + e^{(\beta 1 - \text{Distance} + \beta 2 \times \text{Distance2}) \times \beta 3}))$$

Where species exhibit a preference for edge habitat.

*β2 & β3 = additional constants

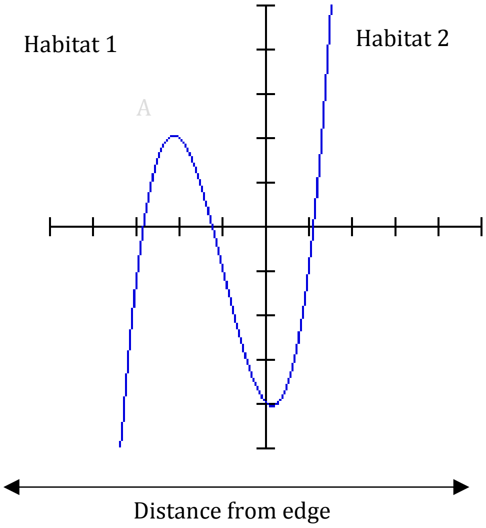

Figure 8 – Visualization of a species distribution following the cubic model repsonse to edge effects. Point A indicates the optimal distance from the edge which favours species activity in habitat 1. No asymptote is reached for habitat 2.

Exploratory analysis revealed that for most species the five theoretical models outlined above were unlikely to fit the data effectively. Therefore, a further, more complex polynomial model was also included to assess whether other models may better explain bat responses to edge-effects. To do so, a third-degree polynomial model was used (model 6 – cubic). This model implies a bi-directional response to edge-effects but indicates only one asymptote is reached (Fig. 8).

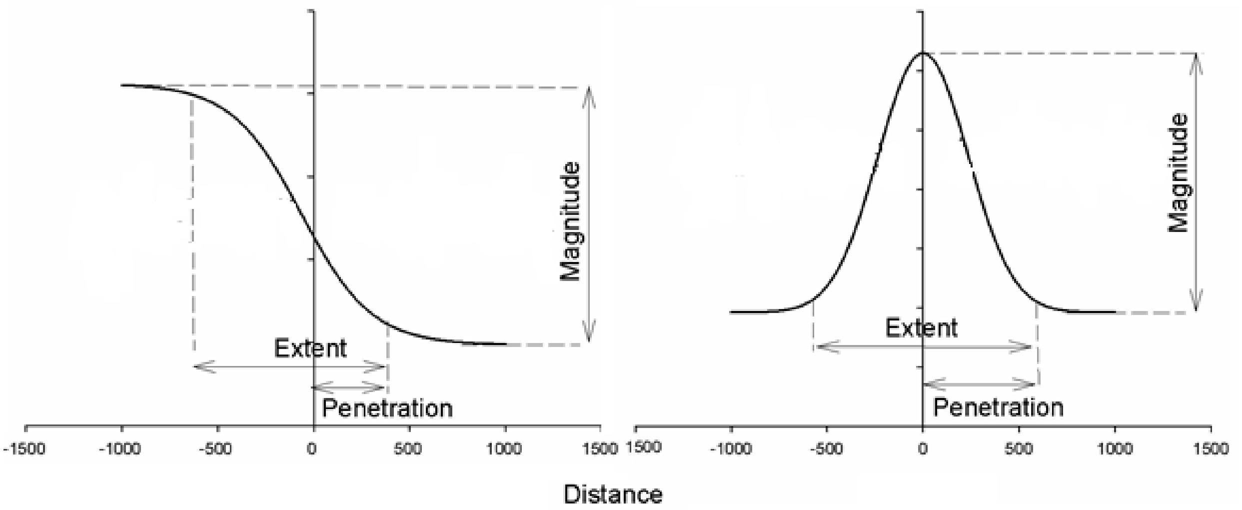

Figure 9 – Visual methodology of how magnitude and extent were calculated for the sigmoid (left figure) and the unimodal (right figure) models (sigmoid function - the distance between the max. and the min. of the second derivative; unimodal function - the distance between the two maxima of the second derivative; adapted from Zurita *et al* (2012).

Unlike the power or sigmoid models, this model indicates there is an optimum distance from the edge which provides the most favorable conditions for at least one habitat type. It also indicates that a response to an edge habitat may not be linear across a habitat (see figure 20 for more information). Following the procedure outlined by Villada-Bedoya et al. (2016) *extent* was calculated as the distance between both inflection points in the sigmoid and unimodal functions (Zurita *et al.* 2012; Ewers and Didham 2006b) (Fig. 9).

By determining the distance threshold of edge effects, considering the mean extent of all species which exhibited a response (N = 2), three habitats were identified: continuous forest interior (continuous forest beyond the distance threshold of edge-effect penetration), edge habitat (area affected by edge effects) and secondary forest (secondary forest beyond the distance threshold of edge-effect penetration). Had all species exhibited a mean or linear response then no habitat comparisons could be examined. If a power model had been identified as best, then only two habitats could have been compared (the habitat with the asymptote and edge habitat). As the data did not meet the assumption necessary for One-Way ANOVA, a Kruskal Wallis test was used to test for differences in activity between these three habitats defined using mean extent for each functional group, total activity, and those species exhibiting an edge-related response. Activity for each habitat was divided by the number of sample points included within each habitat to ensure comparable results (secondary forest = 15 sampling points, edge habitat = 9, continuous forest = 17).

Community Composition

Once the mean extent of edge effect penetration had been determined, Non-Metric Multidimensional Scaling (NMDS) on a Bray-Curtis distance matrix was performed using R package vegan to visualize the species composition of each habitat. Analysis of Similarities (ANOSIM) using the vegan package was used to determine whether compositional differences between habitats were statistically significant. A Kruskal Wallis test was also used to test for differences in species richness between habitats.

Prey Availability

A Shapiro-Wilk normality test showed that the data were not normally distributed (W = 0.235, P-value < 2.2e-16), therefore Spearman's rank correlations were used to test for a relationship between relative bat activity and relative insect volume across the full habitat gradient, and for each of the three habitats as defined above based on the calculated extent of the edge effect. Both relative bat activity and total insect volume were standardized by dividing by the number of sampling stations per habitat.

Results

In total 38,654 bat passes were manually attributed to 18 aerial insectivorous species or sonotypes, including two species/sonotypes of the family Vespertilionidae, seven species/sonotypes of Emballonuridae, four sonotypes of Molossidae (sonotypes M1, M2 and M3 have been grouped for analysis; Table 1), four species of Mormoopidae and one species of Furipteridae. Of these, ten species/sonotypes of forest-specialists were identified and five groups of open/edge foragers. One forest-specialist species, *Rhynchonycteris naso,* which is known to occur locally (López-Baucells *et al.* 2016; Torrent *et al.* 2018) and was included in the classifier was not recorded during this study.

Impact of Edge

Modelling of edge effect magnitude and extent

Regression analysis indicated that five species/sonotypes demonstrated no change in activity in response to edge effects across the habitat gradient using Ewers and Didham's (2006) models (Fig. 10). This included the open/edge forager family Molossidae, three forest-specialist species (*C. brevirostris, P. parnellii* (55KHz) and *S. leptura*), and the forest-specialist genus *Myotis* (Fig. 10). All five also showed no response under the more complex cubic polynomial model (Table 2).

An edge response was identified in two species, *C. maximiliani/centralis* and *P. parnellii* (60KHz), for both of which the sigmoid model provided the best fit when only considering Ewers and Didham's (2006) models (Fig. 10) (Table 2). However, when including the sixth model in the analysis, the cubic polynomial provided the best fit to the data for both species. Both species had greater activity in secondary forest than in primary forest. As these were the only two species to fit a sigmoid or unimodal model they were the only species for which extent and magnitude could be quantified. Extent of the edge effect was calculated as 250m for secondary forest and 150m for continuous forest for both *C. maximiliani/centralis* and *P. parnellii* (60KHz), resulting in a total affected area of 400m. Of the two, *P. parnellii* (60KHz) was more greatly impacted by edge-effects as magnitude was calculated as 94.76% for *C. maximiliani/centralis* and 99.91% for *P. parnellii* (60KHz). It was not possible to obtain a power model AICc value for *S. bilineata* as start values could not be determined and the species therefore was removed from the analysis.

Table 2 – The corresponding AICc values for each model fit for all species, individual species, functional groups and species richness. The Ewers and Didham (2006) model of best fit is highlighted in grey. Where the Cubic model provided a better overall fit, values are in bold. See Table 1 for species abbreviations. O/E = Open/edge forager species

Species/ Sonotype /Group	**Model**						**Penetration Distance (m)**		**Strength of edge effect**	
	Mean	Linear	Power	Sigmoid	Unimodal	Cubic	Secondary Forest	Primary Forest	Magnitude	Extent (m)
All Species	522.11	523.46	523.48	523.40	525.92	**518.29**				
CB	178.24	178.75	178.37	178.62	180.52	182.63				
CM	488.46	489.14	489.46	488.03	491.21	**486.55**	250	150	94.76%	400
Molossidae	122.47	123.79	123.91	122.92	126.21	124.69				
MRN	205.24	206.85	207.55	207.13	208.59	208.90				
P5	390.49	392.47	392.48	392.47	394.90	395.26				
P6	392.39	391.30	391.07	390.50	392.97	**380.57**	250	150	99.91%	400
SL	261.38	262.08	262.22	262.06	264.49	267.04				
Forest Sp.	521.44	522.79	522.81	522.73	525.25	**517.62**				
O/E Sp.	211.72	213.92	214.02	213.92	216.32	218.52				
Sp. richness	169.37	171.57	171.57	171.57	172.70	**163.24**				

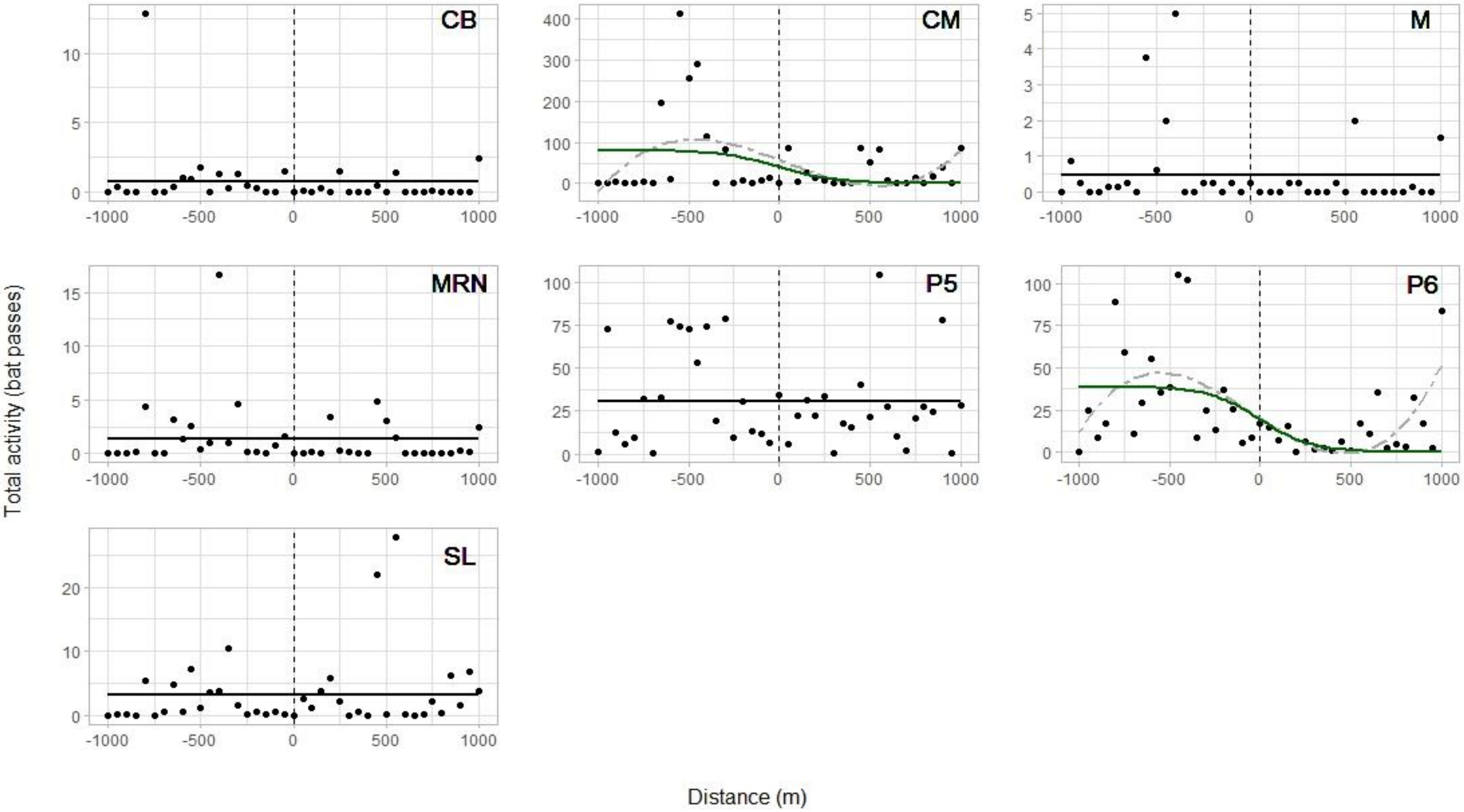

Figure 10 – The activity of each species/sonotype and the corresponding models of best fit proposed by Ewers and Didham (2006). Mean distribution models are represented in black (5 species/sonotypes) and a sigmoid distribution are represented in green (2 species). A further polynomial distribution provided the best overall fit for two species (represented by a dashed grey line). Both species exhibited a sigmoid distribution when considering only Ewer & Didham's models. Minus values on the X-axis indicates the distance within the secondary forest whereas positive values indicate the distance into the primary forest.

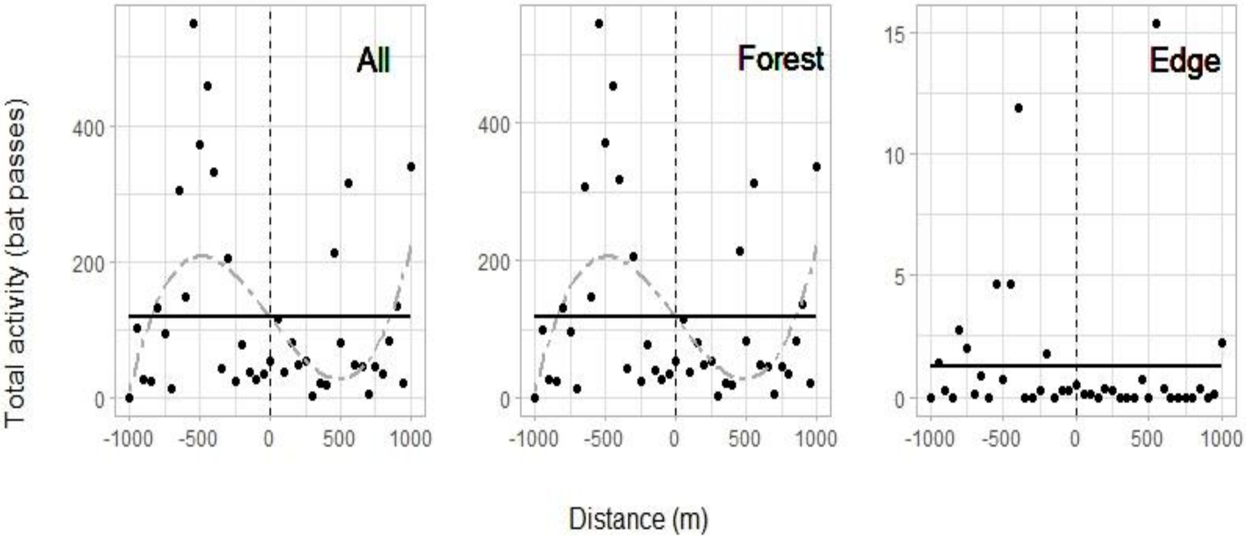

Figure 11 – Plots represent the total activity for all species and the total activity of both functional groups (forest specialists & open/edge foragers) as well as the corresponding models of best fit. All three groups exhibited a mean distribution (shown in black) when considering Ewers and Didham (2006) models, however a cubic polynomial provided the best overall fit for total activity and forest-specialists (represented by a dashed grey line). Minus values on the X-axis indicates the distance within the secondary forest whereas positive values indicate the distance into the primary forest

There was no response to edge-effects observed in the total activity of both functional groups, forest-specialists or open/edge foragers, or for all species collectively using Ewers and Didham's (2006) models. However, a response was detected with the inclusion of the cubic model, which provided the best fit overall for total activity and total activity of forest-specialists (Fig. 11; Table 2). Activity of both of these groups peaked 500m from the edge within the secondary forest, decreasing both towards the interior of the secondary forest and up to 500m into the primary forest.

Habitat Comparison

There was no significant difference in the activity of *C. maximiliani/centralis* (K-W = 0.34, DF = 2, P = 0.85) between the three habitats. *P. parnellii* (60KHz) exhibited a significant difference in activity (K-W = 10.72, DF = 2, P = 0.005) with the highest activity occurring in the secondary forest and the lowest in the primary forest. The largest variation in activity of both species was observed within the secondary forest (Fig. 12).

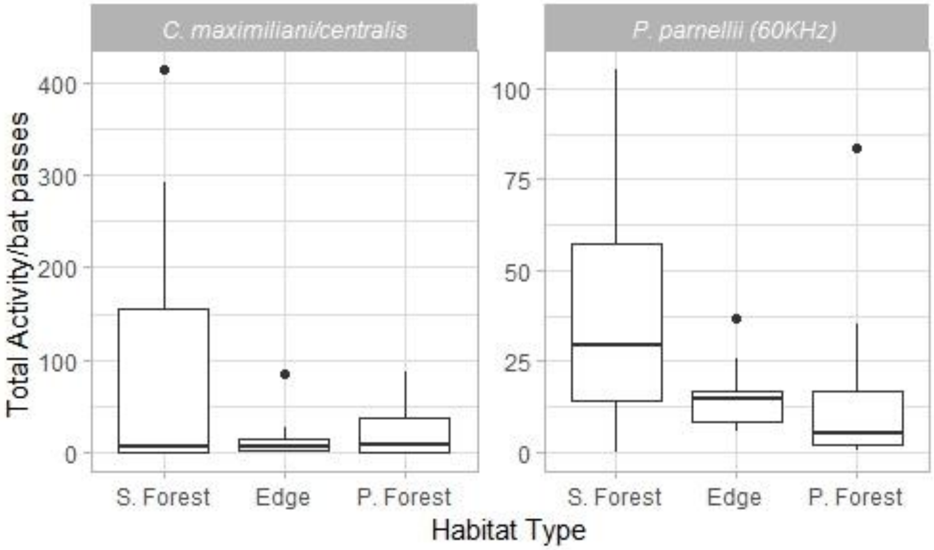

Figure 12 – Mean average bat activity per habitat for both species exhibiting a sigmoid response to edge effects.

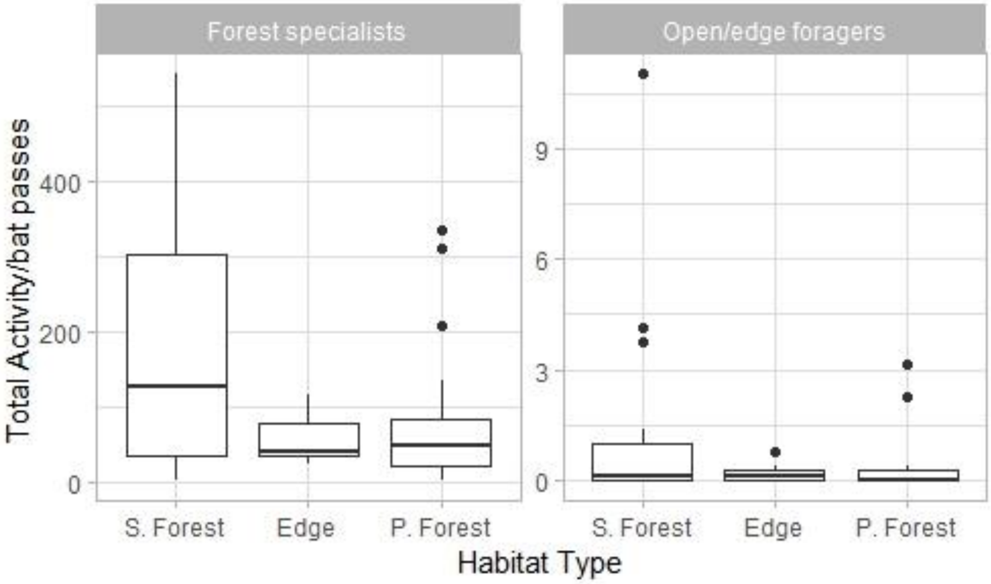

Figure 13 – Mean average activity recorded for both functional groups within the 3 habitats.

When considering these habitat boundaries for all species, no significant difference in the activity of open/edge foragers (K-W = 3.36, DF = 2, P-value = 0.42) was observed. There was also no significant difference in the activity of forest-specialists (K-W = 3.36, DF = 2, P

= 0.19) between the three habitats, however there is a possible trend as the highest activity occurred in the secondary forest and the least in the edge habitat. The same pattern was observed when considering total bat activity (F = 3.45, DF = 2, P =0.18; Fig. 13). Forest-specialists were much more frequently recorded than open/edge foragers throughout this study.

Species Richness & Community Composition

Tested against each of the first five theoretical models, species richness followed a mean model and therefore exhibited no response to edge. However, with the inclusion of the sixth model, the cubic polynomial provided the best fit indicating a response in species richness to edge effects (Fig. 14; Table 2) with the greatest number of species predicted to occur 300-400m into the secondary forest and increasing beyond 500m from the edge in the primary forest. The number of species in each habitat also showed no significant difference (K-W = 2.33, DF = 2, P = 0.31), though no species were recorded in the edge habitat along the second Dimona transect during the dry season (Fig. 15).

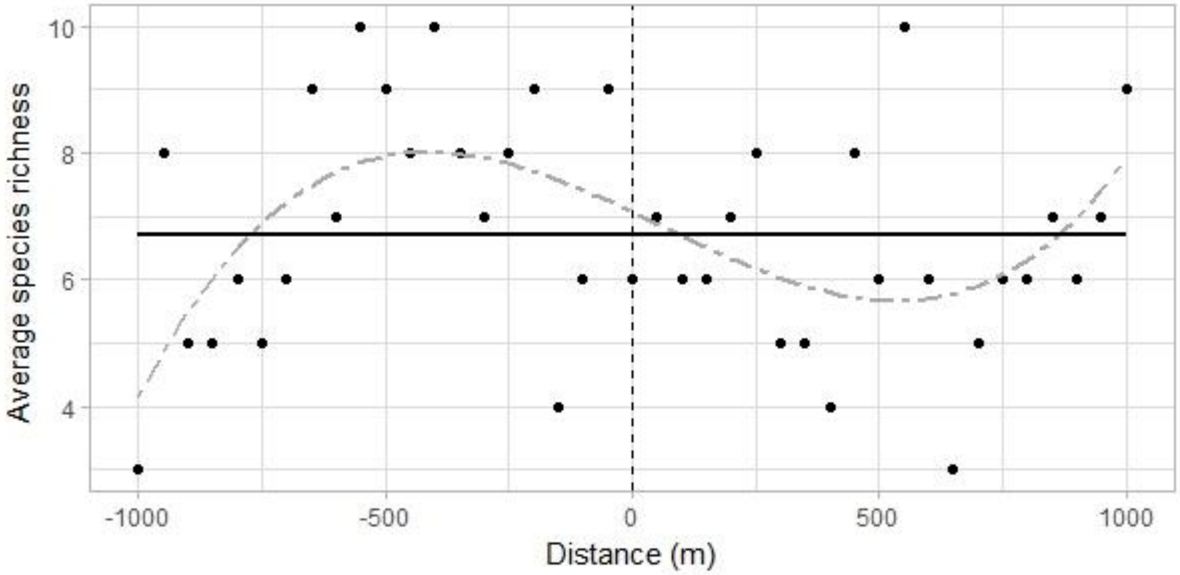

Figure 14 – Plot showing variation in species richness with increasing distance from the forest edge. Of the Ewers and Didham (2006) models the mean model provided the best fit (shown in black), however a cubic polynomial model provided the best overall fit (represented by a dashed grey line). Minus values on the X-axis indicates the distance within the secondary forest whereas positive values indicate the distance into the primary forest.

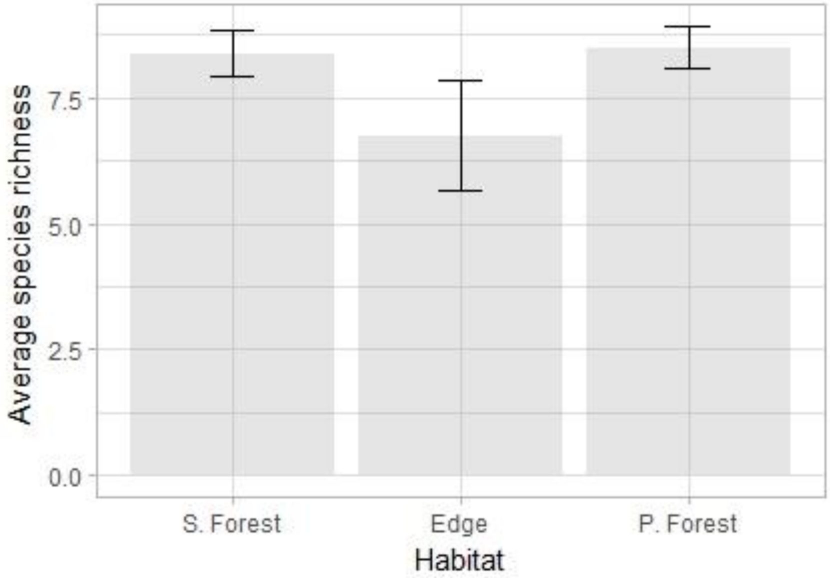

Figure 15 –Mean species richness (no. of species) recorded per habitat with a SD.

There was no significant difference in species composition between the three habitats (R = 0.071, P = 0.072; Fig. 16). This was also true for forest specialists (R = 0.073, P = 0.074) but insufficient data was obtained to analyse the community composition of open/edge foragers.

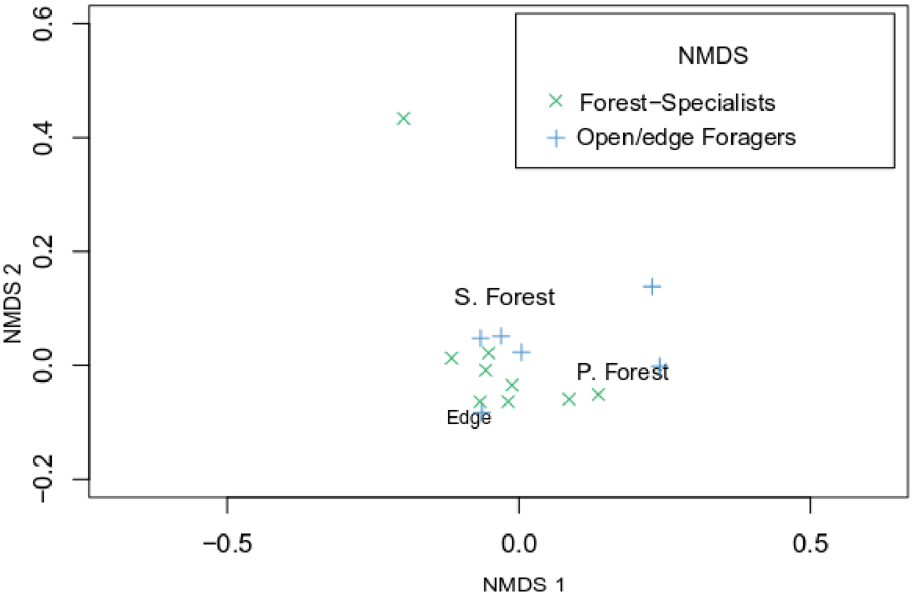

Figure 16 –The relationship between each functional group and habitat type.

Prey distribution

Insect samples included individuals from nine orders. Approximately 81% of total insect volume belonged to the two orders Coleoptera and Hymenoptera. A significant positive association was present between total bat activity and total insect volume however they were not strongly correlated (rho = 0.560, N = 259, P < 0.0001). A weak association was identified between total bat activity and the total volume of four insect orders: Homoptera (rho =0.134, N = 509, P = 0.0148), Isoptera (rho =0.176, S = 484, P-value = 0.001), Lepidoptera (rho =0.116, N = 520, P = 0.036) and Orthoptera (rho =0.193, N = 475, P = 0.005). Collectively these four orders equate to ~11.5% of the total insect volume sampled (3.36%, 2.93%, 3.17% and 2.28% respectively; Fig. 17). When combined, a weak association was observed between this group and total bat activity (rho = 0.12, N = 518, P = 0.03). No relationship was obtained for the remaining five orders sampled (see Appendix VI).

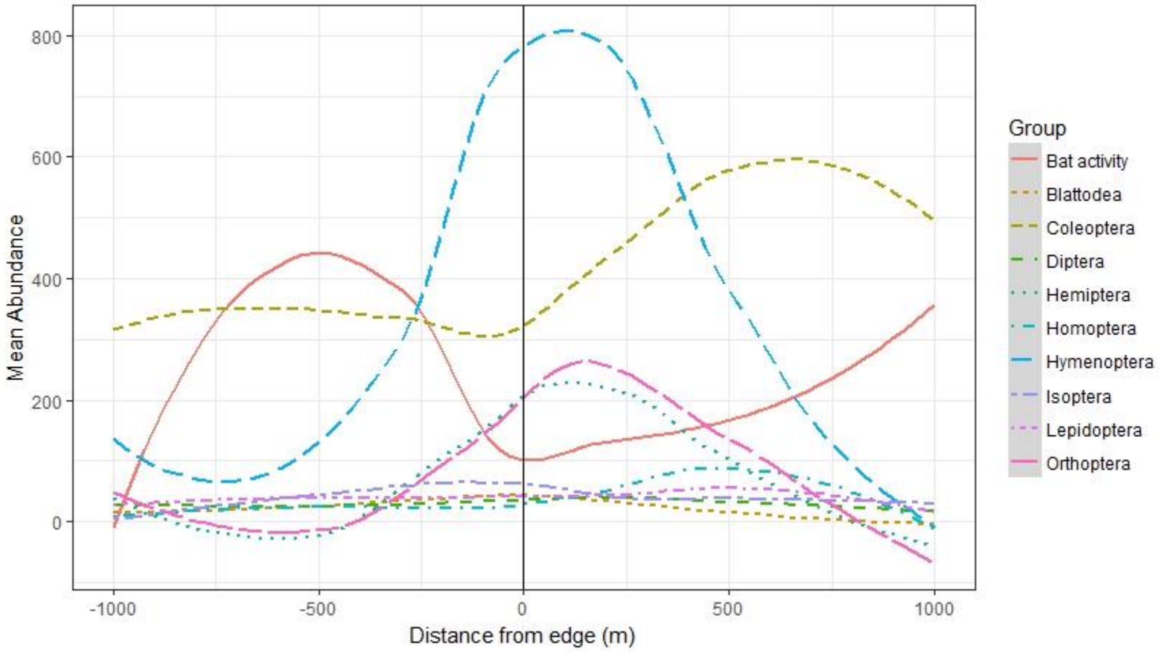

Figure 17 – The relationship between mean bat activity (no. of bat passes) and mean abundance of insect occurrence (total volume) by Order. Curves fitted using a loess polynomial regression.

Random Forest Classifier

Performance of the training set

Of the four models tested, the 4000-pulse training model presented the most consistent performance for both metrics - accuracy and kappa, whereas the 2000-pulse model showed the greatest variation in performance (Fig. 18). The 4000-pulse model exhibited the highest accuracy and kappa values (Fig. 18). However, there was relatively little difference overall between the performance of all four models. The variables which were most informative for both the classifier algorithm using the 2000-pulse and 4000-pulse model were the "High end of characteristic", followed by the "Slope" and the "Maximum frequency". "Minimum frequency" demonstrated a greater importance in the 2000-pulse model (Fig. 19).

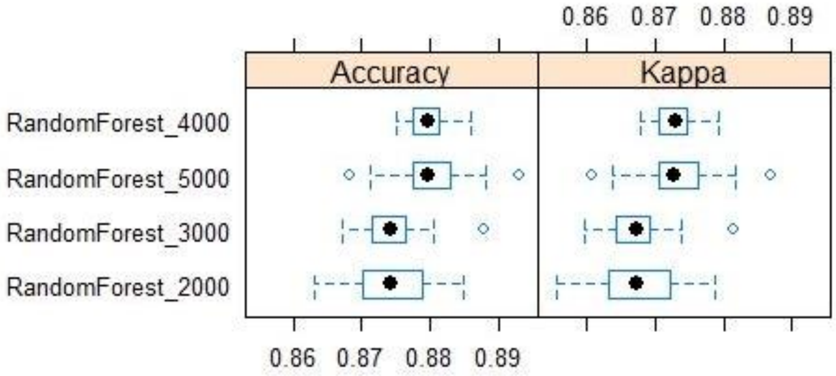

Figure 18 – Classifier performance determined using accuracy and kappa metrics

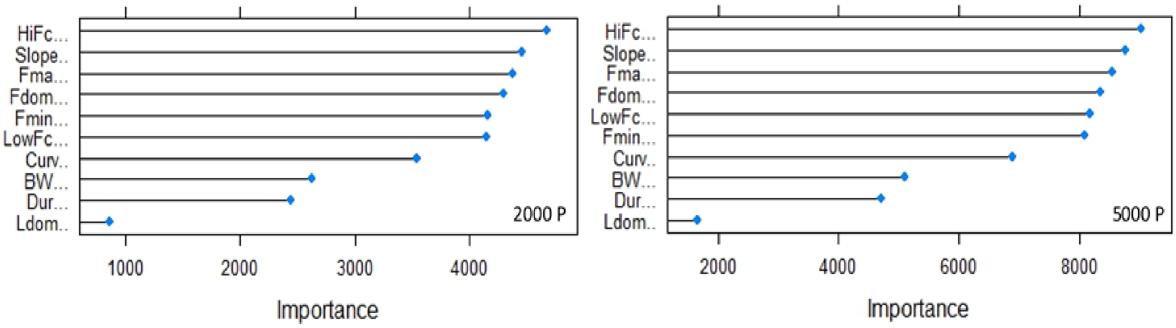

Figure 19 – Importance of each variable in the algorithm when trained with two datasets; one built with 2000 reference pulses and one with 5000 reference pulses per species.

Comparison of classification method

Overall, the automatic classifier using AP60 generated similar results to those when classifying the species calls manually (W = 123,260, P = 0.87; Fig. 20). There was no significant difference in the activity of all species combined or of eight forest-specialist species/sonotypes (Table 1) when classified manually or using AP60 (Appendix V). However, the classifier significantly overestimated the activity of molossids using this accuracy probability (W = 140, P <0.01). In contrast, when restricted to using AP95 the automatic classifier significantly underestimated bat activity by >12,000 bat passes (W = 96,400, P <0.01). At this accuracy probability the classifier significantly underestimated the activity of four forest-specialist species: *C. brevirostris, C. maximiliani/centralis, S. bilineata* and *S. leptura* (Fig. 20).

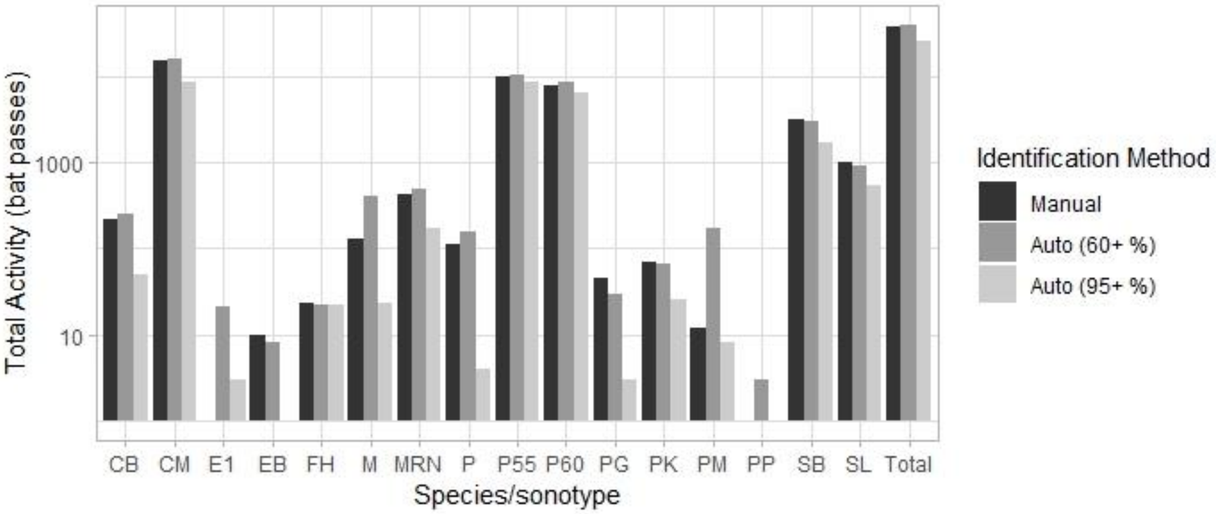

Figure 20 – The number of files identified per sonotype dependent on identification method and accuracy. Automatic classifications have been divided into two accuracy thresholds; those above 60% confidence and those above 95% confidence. See Table 1 for species acronyms.

Sample sizes were too small to statistically test for a difference between the identification methods for six species/sonotypes: *F. horrens, P. personatus, P. nasutus/centralis, P. macrotis, P. kappleri* and *S. gymnura / canescens*. Similar results were observed between the classifier at both accuracy probabilities and those manually identified for *F. horrens* and *P. personatus* (Appendix V). The classifier using AP95 largely underestimated the activity of *P. nasutus/centralis* whereas the classifier using AP60 largely overestimated the activity of *P. macrotis.* Although not significantly different, the classifier at AP95 only identified 17.69% of the molossid activity manually identified (W = 36, P = 0.15; Fig. 12).

Discussion

Overall the results indicate aerial insectivorous bat responses to edge effects at the BDFFP are more complex than originally hypothesized at the beginning of this study. The pattern of forest specialist activity and total bat activity was not as linear as hypothesized (increasing from the edge on either side) but rather exhibiting different responses on either side of the boundary. Forest specialists were also recorded more frequently in the secondary forest which could not be explained as a correlation with insect availability. Extent was substantially less than predicted by Delaval and Charles-Dominique (2006) for phyllostomid bat species and edge effects were evident at greater distances within the secondary forest than in the primary forest. Edge effects also appeared to have no impact on species richness or community composition at this site.

Responses to Edge-effects

Ewer & Didham's (2006) models indicated that overall bat activity was unaffected by edge effects, as was the activity of both functional groups and that of several species: *C. brevirostris*, *S. leptura*, *M. nigricans/riparius* and *P. parnellii* (55KHz). Forest-specialists were more greatly impacted by edge-effects than open/edge foragers none of which exhibited a response to edge-effects using the six models within this study. Although no response was detected using Ewers and Didham's (2006) models for forest specialists or total activity, the cubic model provided the best fit for both groups suggesting edge effects did influence activity. It is important to note that forest-specialists constitute the vast majority of total activity (>98%) and therefore the distribution of overall activity reflects nearly entirely the distribution of forest-specialists. Considering a maximum extent of 2km (transect length), forest-specialists showed a preference for secondary forest over primary as the highest activity was recorded in this habitat. In the secondary forest, forest-specialist activity peaked at 500m but subsequently continued to decline towards the interior of the secondary forest and no activity was predicted beyond 1km into the secondary forest. On the contrary, forest-specialist activity was lowest 500m from the edge into the primary forest. However, from this point, it continued to increase and was expected to surpass the peak activity observed in the secondary forest >1km into the primary forest. This model suggests the response to edge-effects may not be as straightforward as proposed by Ewers and Didham (2006). The results imply that edge-effects do not only differ in terms of magnitude between distances within each habitat (as described in the linear, power, sigmoid and unimodal models) but also in how they impact populations and communities.

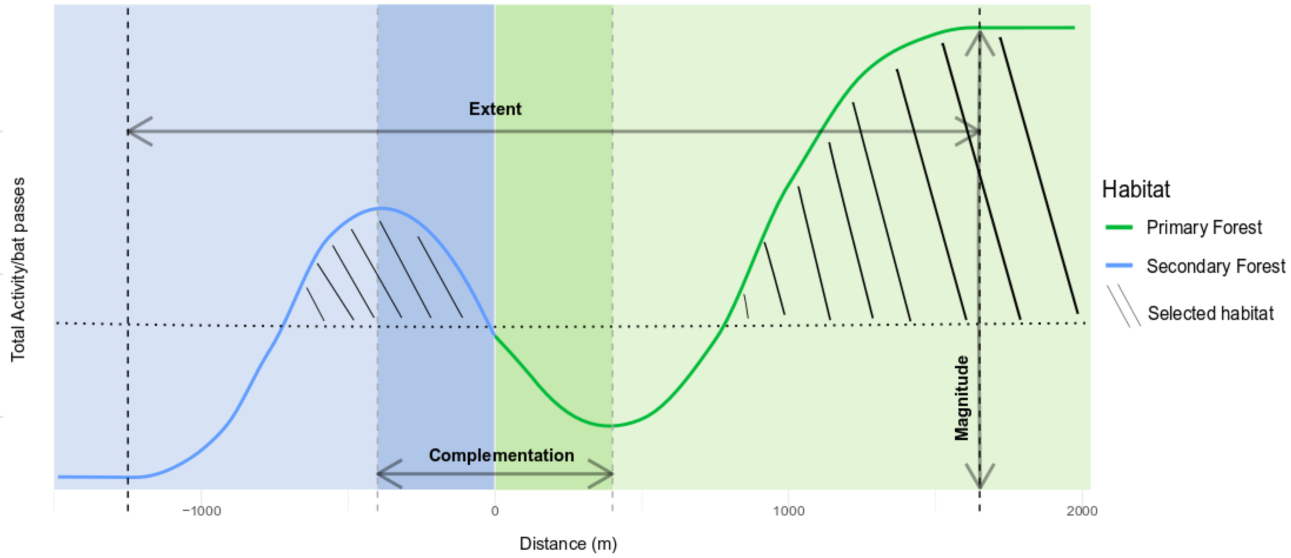

Figure 21 – Hypothetical representation of bat responses to edge-effects using the cubic model. Extent is proposed as the difference between the second asymptotes of each habitat and magnitude is proposed as the difference in activity between these two points. The complementation zone is the area between the second asymptotes of each habitat. x-values represent the distance from the edge in the secondary forest; positive x-values represent the distance from the edge in the primary forest.

This is supported by the activity of *C. maximiliani/centralis* whose peak activity was recorded at ~550m from the edge in the secondary forest (Fig. 10). It could therefore be interpreted that this species showed a preference for the interior of the secondary forest which was not supported by the comparison of activity for each of the three habitats. The secondary forest exhibited the highest variation in activity for this species compared to edge and primary forest, and it was rarely recorded farther than 800m into the interior of the secondary forest. This is also true for *P. parnellii* (60KHz) whose activity peaked at 600m from the edge in the secondary forest. Unlike *C. maximiliani/centralis, P. parnellii*

(60KHz) did show a significant preference for secondary forest compared to the primary forest during the habitat comparison. However as with *C. maximiliani/centralis,* this habitat also experienced the highest variability in activity compared to the other habitats. Using the cubic model, extent would be calculated at >1000m for *C. maximiliani/centralis* and >1100m for *P. parnellii* (60KHz) (over double the extent calculated based on the sigmoid model) and would intrinsically alter the areas of forest being compared. By using this new measure of extent, the model may indicate that the edge does provide benefits to bats within the matrix up to a certain distance from the boundary as suggested by Rodríguez-San Pedro and Simonetti (2015) and Ethier and Fahrig (2011) as its suitability is improved due its proximity to the primary forest. These positive effects may attract bats from the neighbouring primary forest whose suitability has decreased from its proximity to the matrix. This area is shown as the *Complementation Zone* in Fig. 21. However, the magnitude of these benefits may decrease beyond this threshold ultimately returning to natural activity levels in the secondary forest at the limit of edge-effects. To test this hypothesis, further surveys along transects spanning greater distances would be required. This model may provide a better taxon-specific explanation of how bats are affected due to the larger home ranges of these species compared to the invertebrates and passerines studied by Ewers and Didham (2006) and Zurita *et al.* (2012). An extent greater than the range sampled could also explain why *Thyroptera tricolor* was not recorded through-out the sampling period. Due to its roosting ecology and small home ranges this species is highly habitat specific to undisturbed primary forest (Chaverri and Kunz 2011). However, as this species also produces short-range, FM calls it is also possible that further acoustic sampling would be required to detect the species.

Four of the seven species/sonotypes whose responses were investigated had very low relative sample sizes (a mean of <150 bat passes per transect), all of which demonstrated no response to edge effects. Where possible, Zurita *et al.* (2012) suggested an inclusion threshold of >30 records on both sides of the habitat boundary which was not achieved for three of these species/sonotypes: *C. brevirostris*, Molossidae and *M. nigricans/riparius* (although the latter did reach this threshold within the secondary forest). This may explain why no response was detectable. By also pooling the three Molossid groups, this could have also camouflaged individual species responses. *S. leptura* did exceed the threshold (41 mean bat passes in the secondary forest and 87.5 mean bat passes in the primary forest) however this low sample size may explain why no response was detected despite this species being twice as abundant in the primary compared to the secondary forest. Ewers and Didham's original tests of their five models was performed using sample sizes >6000 per group. Small sample sizes and consequent parameter reductions compromise the validity and accuracy of these models potentially leading to an inaccurate assessments of a response (Ewers and Didham 2006b). Further sampling would be required to investigate whether the current sample sizes available provide an accurate representation of how these species are affected by edge effects.

As Ewers and Didham (2006) models did not show a response between the species richness to edge-effects it challenges the hypothesis that bats are examples of habitat complementation (Dunning, Danielson and Pulliam 1992). Habitat complementation is the key process thought to underpin the distribution of mobile species, such as insectivorous bats, in heterogeneous landscapes and this guild has been shown to utilise different resources across forest landscape mosaics in temperature regions (Charbonnier *et al.* 2016). However, the sigmoid model did not indicate that the edge habitat was providing important commuting or foraging habitat. However, the cubic model infers that increased activity in edge habitat may not occur directly on the habitat border and therefore it does not dismiss the role of resource mixing at habitat boundaries. This process may increase the number of species naturally occurring in secondary forest to better reflect that of the primary forest. However, there was no evidence of distinct communities present in any of the habitats, including edge habitat. As the mature secondary forest provides a low-contrast matrix it is unlikely to provide the differences in ecological conditions needed to support species associated with non-forested habitats. Open/edge foragers are classified as such due to their perceived association with open and edge habitat however no response to edge effects were observed for molossids. Small sample sizes were obtained for these species as molossids typically forage in clear, open areas and therefore neither primary nor secondary forest provides ideal habitat for these species. Increased activity would be expected in a higher contrast matrix consisting of agricultural land or urban areas (Jung *et al.* 2016). To ensure the species' recorded during the study provide an accurate reflection of the species richness for these habitats, species accumulation curves could be used to ensure sufficient sampling was undertaken (Moreno and Halffter 2000).

Considering both the sigmoid and cubic model, the maximum extent of edge effects on aerial insectivorous bat species in this study was between 400-1100m; substantially less than the 3km proposed by Delaval and Charles-Dominique (2006) for phyllostomid bats and most forest-specialist aerial insectivores showed no response to edge effects. Approximately 90% of the 104 neotropical herpetofauna species examined by Schneider-Maunoury *et al.* (2016) exhibiting a response to edge effects and almost 60% of the forest specialists in this study showed changes in abundance >200m into primary forest interior. The low number of forest specialist species exhibiting a response in this study, as well the short penetration distance within the primary forest, is likely due to the low contrast matrix at the BDFFP as secondary forest maturation has been shown to increase habitat suitability for forest-specialist bat species between fragments (Rocha *et al.* 2018). Barnes *et al.* (2014) and Vespa, Zurita and Isabel Bellocq (2014) found that not only did matrix composition affect the magnitude of edge effects calculated using Ewers and Didham's (2006) models but also which model provided the best fit and thus what response was being observed. The low contrast matrix at the site is also thought to explain the unimodal response to edge effects exhibited by three forest bird species at the BDFFP, as the edge provides additional resources to two of the species typically classified as forest interior species (Powell *et al.* 2015). The same pattern was observed for forest interior passerines in the Atlantic forests of Brazil (Hansbauer *et al.* 2008; Zurita *et al.* 2012), and Zurita *et al.* (2012) also observed differences in the magnitude of two sigmoid responses of these species between two matrix types (lower magnitude = low contrast).

The traditional classification of a species as 'edge favouring' or 'edge avoidant' has been challenged by Ries and Sisk (2010) on the grounds that edge responses are not idiosyncratic, but rather a species response is likely to vary depending on the type of edge. Species which were considered edge sensitive in previous studies have been shown to ignore edges where both habitats are considerably favorable (Ries and Sisk 2010) which may partially explain this reduction. As suggested by Powell *et al.* (2015), it could also be that the old secondary forest has reached the point of recovery where edge effects can no longer be detected. To confirm either hypothesis', resampling the transects after the matrix is scheduled to be clear-cut would provide an insightful comparison between low and high contrast matrices in determining edge effect extent and magnitude. This study was predominantly restricted to *Vismia* regrowth (A López-Baucells 2018, personal communication), therefore further studies could also investigate whether extent and magnitude were comparable with a matrix dominated by *Cecropia* regrowth. This would enable land-users to clear the forest in a manner (with or without the use of fire) which would minimize its effects on bat communities.

Secondary forest provides significant value to tropical biodiversity (Chazdon 2014; Rocha *et al.* 2018), however, López-Baucells (2018) demonstrated that aerial-insectivorous bat assemblages still have not fully recovered after 15 years of forest regrowth. Even after ~30 years of maturation, the secondary forest does not reflect the same phyllostomid bat assemblage as primary forest (Rocha *et al.* 2018). Using the sigmoid model, Zurita *et al.* (2012) also calculated edge effect extent to approximately 300m whether the matrix either comprised forest plantation or open agricultural areas. Despite the similar extent between both habitat types, extent could not be used in isolation to explain edge effect responses effect, magnitude was much greater in the high-contrast matrix than in the low-contrast matrix. The magnitude of edge effects for both species in this study for which it could be calculated were >90% (Table 2) suggesting edge effects are still able to highly disrupt natural activity patterns of these species despite the low-contrast matrix. As such, at this maturity secondary forest cannot provide a sufficient replacement for primary forest. Understanding the factors - both extrinsic (e.g. matrix contrast) and intrinsic (e.g. body size) - that underpin edge sensitivity, including unresponsiveness, is essential to predicting the vulnerability of species whose ecology is relatively unknown (Ries and Sisk 2010).

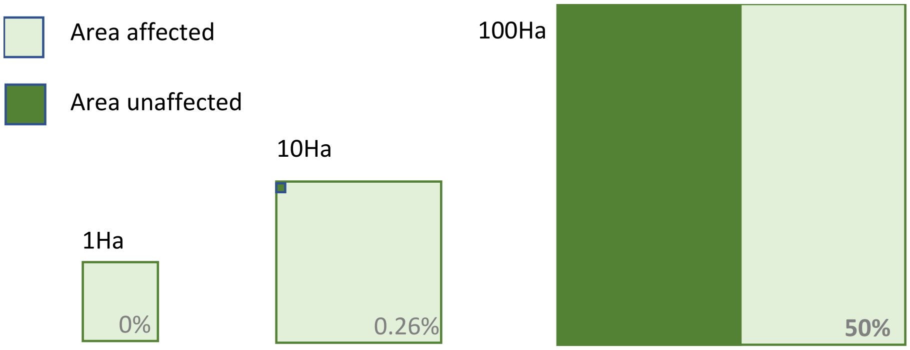

Figure 22 – Relative area of each fragment size which remains unaffected by edge-effects considering the sigmoid model. There is no area of any of the three fragments which are unaffected considering the cubic model.

If the sigmoid model provides the most accurate estimate of extent, then only fragments ≥10ha contain primary forest interior. However, if the cubic model is more accurate then there is no area within any of the BDFFP fragments that remains un-affected by edge effects (Fig. 22). This is an important consideration for future studies comparing the interior, edge and matrix of BDFFP fragments as it may be there is no interior to a fragment. This may also explain why contrary to previous studies on other taxa (Grass *et al.* 2018; Collinge 1996; Laurance *et al.* 2007), aerial insectivorous bat activity at the BDFFP is independent of fragment size (López-Baucells 2018) and why studies which only consider fragments <100ha do not observe substantial differences in bat activity between different fragment sizes (e.g. Ortêncio-Filho, Lacher and Rodrigues 2014). The Adolpho Ducke Forest Reserve, of the Instituto Nacional de Pesquisas da Amazônia (INPA), comprises 10,000ha of lowland terra firme forest; the same forest type as found in the BDFFP (Rodrigues *et al.* 2017). This fragment is 100 times larger than the largest of those in the BDFFP and is surrounded by a variety of different matrix types (e.g. urban, agricultural). Studies into edge effects at this location could be used in tandem with the BDFFP to address several aspects of edge responses otherwise still unanswered, such as if whether the cubic model provides a better representation of edge-effect extent in larger fragments. It can also provide a wider scope for investigating the influence of matrix contrast. It is very important that land managers understand the minimum size fragments required to ensure they provide refuge for forest species.

Prey availability

Unlike previous studies (Gonsalves *et al.* 2013; Müller *et al.* 2012), the results indicate that prey distribution is not a significant predictor of bat activity. Neotropical bat species are known to predominantly feed on insects from Lepidoptera, Coleoptera, Diptera and Orthoptera (Fleming, Hooper and Wilson 1972; Bernard 2002; LaVal and Rodríguez-H. 2002), although members from the genus *Molossus* in Costa Rica also prey on Hymenoptera (LaVal and Rodríguez-H. 2002) and *P. parnellii* is known to consume Isoptera (Bernard 2002). Small beetles were the predominant component of fecal samples of aerial insectivorous bats observed by Bernard (2002). The former four orders made up 56% of the insects sampled however only Lepidoptera and Orthoptera, both of which were sampled in small densities, were shown to correlate with bat activity (Appendix VI). Neither of these groups were more abundant in areas of peak bat activity within the secondary forest and therefore do not explain the increase in bat activity at these sampling points. The high habitat specificity and high proportion of endemism of tropical invertebrates likely result in their high edge sensitivity across studies (Foggo and Speight 2001). Lepidoptera, which have been shown to respond negatively to disturbance (Dodd *et al.* 2012) and which are selected by both open/edge foragers and forest specialists (LaVal and Rodríguez-H. 2002), were more abundant in the primary forest, as were Coleoptera. Therefore this study supports previous research by Adams (2012), Müller *et al.* (2012) and Kusch *et al.* (2004) that indicates habitat suitability is more important to forest specialist bats rather than insect availability.

The feeding ecology of many neotropical insectivores is poorly understood (Bernard 2002; LaVal and Rodríguez-H. 2002)(but see Fenton *et al.* 1999, Pio *et al.* 2010 and Whitaker, Findley and Findley 1980) and a species diet is often inferred from limited fecal samples. Therefore, our understanding as to the type of insects selected for, as well as in what relative concentrations, is also limited. There are further complications when examining the relationship between activity and prey availability. Light traps are considered a relatively unbiased method of monitoring tropical entomofauna (Hirao, Murakami and Kashizaki 2008), however capture rates can be influenced by weather conditions, lunar cycles, vegetation density, a species dispersal ability and daily movement patterns (Hirao, Murakami and Kashizaki 2008; Jonason, Franzén and Ranius 2014; Appel *et al.* 2017; Bowden 1982). Lepidoptera are a key component of many insectivorous bats diets (Bernard 2002; Dodd *et al.* 2012; Freeman 1979; Freeman 1981) but their abundance in light traps fluctuates depending on nightly temperature and humidity (Jonason, Franzén and Ranius 2014), therefore a large sampling effort is required to adequately assess their distribution and abundance - potentially larger than that used for this study.

Another consideration should be that higher bat activity in the presence of higher insect volume does not necessarily infer higher predation rates. Therefore, it could be that patterns in bat activity indicate foraging activity is highest in the secondary forest, despite lower prey availability, or contrastingly that foraging is occurring in the primary forest where maximum prey is available and that other factors explain the peak in activity within the secondary forest (e.g. commuting or roost availability). To examine this further, the occurrence of feeding buzzes (the temporary increase in echolocation call repetition rate upon insect pursuit and capture; Griffin, Webster and Michael 1960) could be used to investigate predation events (see Torrent *et al.* 2018). This would provide a clearer understanding of how bats foraging behaviour may have altered in response to edge effects. It was not possible to examine the relationship between feeding buzzes and prey availability in this study as insufficient feeding buzzes were recorded. This method also cannot be used in conjunction with automatic classifiers which are unable to detect feeding buzzes.

This study also does not investigate temporal variation in bat responses to prey availability. As bat activity and insect volume were quantified nightly, it cannot be determined whether bat activity was occurring synchronously with insect captures within each night. Neotropical insectivorous bat activity peaks during the first three hours after sunset (Brown 1968), therefore it is possible insect captures were occurring during times of minimal bat activity. This could obscure the true relationship between activity and prey availability. Furthermore, the importance of prey abundance is likely to vary between the sexes during the breeding season, as female bats have been shown to be spatially constrained in other regions due to the high energy demands of pregnancy and lactation (Barclay 1991). Consequently reproductively-active females may exhibit a higher correlation with prey abundance compared with males, juveniles and non-reproductively active females. This demand may also affect how each sex responds to edge effects. Rocha *et al.* (2017) found two frugivorous neotropical species exhibited sex-specific responses to fragmentation, where it was suggested the distribution of reproductively-active females during the breeding season was significantly influenced by food resource availability. The use of acoustic sampling in this study did not allow for sex-specific differences in edge effect extent or magnitude to be examined, nor determine sex-specific responses to insect availability. It is important to consider variation in how different sexes and age classes respond to edge effects as a greater impact on reproductively-active females (compared to other individuals) will have a greater impact on overall reproductive success, and thus have greater negative consequences for a population's fitness.

Further considerations

Although the models utilized throughout this study go part the way to explaining bat responses to edge effects, they are limited by the assumption of a positive linear relationship between abundance and fitness parameters (e.g. survival, breeding success; Terraube *et al.* 2016). Each inherently fails to consider how fitness parameters may be affected (e.g. bat-ectoparasite interactions; Bolívar-Cimé *et al.* 2018), independent of abundance, in edge habitat. Without also considering these small-scale impacts the full picture of edge effect responses is not wholly examined. Investigations into edge effects, such as this, have also been predominately confined to the understory (Delaval and Charles-Dominique 2006; da Silva, Filho and Lacher 2013; Cortés-Delgado and Pérez-Torres 2011). The canopy and understory provide significantly different microclimates, varying in conditions such as food resource availability, light intensity and wind pressure (Bernard 2001; Foggo and Speight 2001). Approximately ~60-70% of all tropical mammals and >50% of all tropical diversity occurs in the canopy (Bernard 2001). Edge effects are unlikely to occur simultaneously between strata as the effects they induce are not synchronous. Therefore the response by biota is likely to differ between them (Didham and Ewers 2014; Stone, Catterall and Stork 2018; Foggo and Speight 2001;

Adams, Law and French 2009). Changes to microclimatic conditions caused by edge effects are likely to be exaggerated in the canopy as this habitat not only interfaces with the matrix but also the understory and atmosphere (Foggo and Speight 2001). Thus, there are multiple dimensions compounded by multiple, divergent effects.

Studies investigating bat activity have consistently demonstrated that bat abundance and diversity is greater in canopy than the understory in both the Paleo – and Neotropics (Francis 1994; Bernard 2001; Adams, Law and French 2009; Adams 2012; Navarro 2014; Gregorin *et al.* 2017). This includes species which occur exclusively in the canopy (Gregorin *et al.* 2017). Few studies have investigated the vertical stratification of aerial insectivorous bats in the Amazon as, as with other Neotropical bat studies, vertical stratification studies are biased towards phyllostomids (João *et al.* 2010; Rex *et al.* 2011; Bernard 2001; Kalko and Handley, Jr. 2001). However, investigations so far coincide with trends observed for phyllostomid assemblages as Marques, Ramos Pereira and Palmeirim (2016) recorded double the diversity of species within the canopy compared to the understory. Depending on forest structure, the canopy also supports a higher diversity and abundance of flying insects and the presence of distinct communities have been identified between these vertical strata (Sutton, Ash and Grundy 1983). This highlights a need to consider the potential response variation exhibited between different strata and their corresponding communities. Reflecting on the disparity between the microclimate, edge effect diversity, and bat and insect diversity within the understory and canopy, studies such as this cannot deduce the impact of edge effects on the aerial insectivorous bat community as a whole. The inclusion of canopy sampling is critical to determining the spatial distribution of these species and that of their prey. For this reason, the extent and magnitude of edge effects calculated in this study are only applicable to the understory aerial insectivorous bat assemblage.

Methodological comparison

The automatic classifier successfully generated reliable data for overall bat activity and for the individual activity of many forest-specialist species. Unexpectedly, using an AP60 better reflected the activity of all but three species/sonotypes (Molossidae, *P. macrotis* and *S. gymnura/canescens*) compared to using an AP95. Collectively, these species/sonotypes only constituted 0.37% of the total activity however their activity was over-estimated almost four-fold using AP60 (from 153 bat passes identified manually to 601 bat passes automatically identified). Molossids produce low-frequency calls, with high design plasticity (Jung, Molinari and Kalko 2014; Madhukumar et al. 2018), which can be easily confused with or camouflaged by other background noises, such as insects. The AP95 failed to detect over 80% of manually identified molossids and therefore these species cannot reliably be monitored using either accuracy probability. The three most abundant sonotypes constituted over 86% of the total activity recorded (*C. maximiliani/centralis* - 40%, *P. parnellii* (55KHz) – 26%, *P. parnellii* (60KHz) – 20.3%) and the AP65 provided results which were not significantly different to those manually identified. All three sonotypes exhibit little intra-specific variation (López-Baucells et al. 2016; Jennings et al. 2004) and are emitted at frequencies much higher than common background noise. Consequently, they can be easily identified by the classifier. As such the classifier may be used to reduce the number of calls that require manual validation by removing the highly abundant species which it can reliably identify, thereby reducing the time needed to analyse acoustic data for Amazonian species.

By using the classifier to filter files which were not attributed to a species with AP60 an unknown number of bat calls were cleaned from the dataset. Intrinsically these undetected calls will be biased towards species which are more difficult for the classifier to categorize (e.g. molossids). However, it is my belief that by using a relatively low accuracy probability, such as ≥60%, the time saving benefits of this method outweigh this risk of missed calls in the analysis of extensive datasets. Further research could compare intermittent accuracy thresholds to determine if there is an interval that more effectively reflects true bat activity than ≥60%. Overall our results mirror those of Zamora-Gutierrez et al. (2016) and support their conclusion that aerial insectivorous bat species of megadiverse countries can be reliably monitored using bioacoustic surveys.

Conclusion

Ewers and Didham's (2006) models provide a valuable, quantitative framework for identifying patterns amongst edge-related responses. However, as proposed by other researchers (Zurita *et al.* 2012; Schneider-Maunoury *et al.* 2016), this tool may need adapting to explain the responses of all taxonomic groups to edge effects, as well as to explain subsequent changes to ecological processes. Further work should build upon these models to include additional non-linear responses species may demonstrate depending on traits which impact how a species responds to fragmentation, such as dispersal ability and degree of habitat specialization, as these models may not be universal across taxa (Ewers and Didham 2006a). This study highlights the importance of considering responses on both sides of the habitat boundary, as the activity of at least two species differed depending on the habitat being examined. This is despite the relative similarity between primary and old secondary forest compared with higher contrast matrices. In keeping with Powell *et al.* (2015) and previous studies at the BDFFP (Laurance *et al.* 2011), the findings of this study suggest secondary forest regeneration at the site may have reached a critical recovery point, thereby reducing the impact of edge effects on these species – particularly at the assemblage level. However, as edge effects are still evident, the aerial insectivorous bat community is still impacted by the fragmentation and its corresponding edge effects despite the maturity of the secondary forest regrowth. Nonetheless it provides a buffer against the extremities of these effects and low contrast matrices may provide a method by which to mitigate the dangers of edge effects in already fragmented environments (Laurance *et al.* 2011; Barnes *et al.* 2014).

The threat posed by edge-effects continues to rise as tropical communities become ever increasingly fragmented. Over a quarter of the Brazilian Amazon is currently known to be affected by edge effects (Vedovato *et al.* 2016; Fig. 22) and globally almost three quarters of all forest is situated within 1km of an edge (Haddad *et al.* 2015). Therefore, understanding the impact that edge effects have on global and tropical forests ecosystems is essential for safe-guarding forest-dependent species. Research into the impacts of deforestation continues to rise (Aleixandre-Benavent *et al.* 2018; Ries *et al.* 2017) and projects such as the BDFFP, the Stability of Altered Forest Ecosystems (SAFE) Project

(Ewers *et al.* 2011) and the Wog Wog fragmentation project (Debinski and Holt 2001) provide a platform for comparing edge effect responses within - and between - taxa on a global scale. By doing so fragmentation research aims to identify the underlying trends governing edge sensitivity and species-specific responses. This will only be achieved by the use of standardized, empirical studies into edge effect magnitude and extent (Ries *et al.* 2017). Understanding habitat fragmentation is of critical importance in order to establish successful policies which balance the conservation of biodiversity with managing social and economic security, particularly for small-holding owners.

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Appendix

Appendix I – Co-ordinates of each sampling point of the four transects and corresponding habitat type.

Co-ordinate X	Co-ordinate Y	Sampling point	Habitat Type	Distance from the edge (m)
-59.8876	-2.39154	C1-100	Secondary forest	100
-59.8955	-2.39157	C1-1000	Habitat boundary	0
-59.896	-2.39158	C1-1050	Primary forest	50
-59.8964	-2.39158	C1-1100	Primary forest	100
-59.8969	-2.39158	C1-1150	Primary forest	150
-59.8973	-2.39159	C1-1200	Primary forest	200
-59.8978	-2.39159	C1-1250	Primary forest	250
-59.8982	-2.39159	C1-1300	Primary forest	300
-59.8987	-2.39158	C1-1350	Primary forest	350
-59.8992	-2.39159	C1-1400	Primary forest	400
-59.8996	-2.3916	C1-1450	Primary forest	450
-59.888	-2.39153	C1-150	Secondary forest	150
-59.9001	-2.39159	C1-1500	Primary forest	500
-59.9005	-2.3916	C1-1550	Primary forest	550
-59.901	-2.3916	C1-1600	Primary forest	600
-59.9014	-2.39161	C1-1650	Primary forest	650
-59.9018	-2.3916	C1-1700	Primary forest	700
-59.9023	-2.3916	C1-1750	Primary forest	750
-59.9027	-2.39161	C1-1800	Primary forest	800
-59.9032	-2.39161	C1-1850	Primary forest	850
-59.9036	-2.39162	C1-1900	Primary forest	900
-59.9041	-2.39162	C1-1950	Primary forest	950
-59.8885	-2.39153	C1-200	Secondary forest	200
-59.9044	-2.39163	C1-2000	Primary forest	1000
-59.8889	-2.39154	C1-250	Secondary forest	250
-59.8894	-2.39155	C1-300	Secondary forest	300
-59.8898	-2.39156	C1-350	Secondary forest	350
-59.8903	-2.39155	C1-400	Secondary forest	400
-59.8907	-2.39156	C1-450	Secondary forest	450
-59.8871	-2.39153	C1-50	Secondary forest	50
-59.8912	-2.39155	C1-500	Secondary forest	500
-59.8916	-2.39155	C1-550	Secondary forest	550
-59.8921	-2.39155	C1-600	Secondary forest	600
-59.8925	-2.39156	C1-650	Secondary forest	650
-59.893	-2.39156	C1-700	Secondary forest	700

-59.8934	-2.39156	C1-750	Secondary forest	750
-59.8939	-2.39157	C1-800	Secondary forest	800
-59.8943	-2.39157	C1-850	Secondary forest	850
-59.8948	-2.39157	C1-900	Secondary forest	900
-59.8952	-2.39157	C1-950	Secondary forest	950
-59.8876	-2.38537	C2-100	Secondary forest	100
-59.8956	-2.38546	C2-1000	Habitat boundary	0
-59.8961	-2.38546	C2-1050	Primary forest	50
-59.8965	-2.38547	C2-1100	Primary forest	100
-59.897	-2.38547	C2-1150	Primary forest	150
-59.8974	-2.38548	C2-1200	Primary forest	200
-59.8979	-2.38548	C2-1250	Primary forest	250
-59.8983	-2.38549	C2-1300	Primary forest	300
-59.8988	-2.38549	C2-1350	Primary forest	350
-59.8992	-2.38549	C2-1400	Primary forest	400
-59.8997	-2.38549	C2-1450	Primary forest	450
-59.8881	-2.38538	C2-150	Secondary forest	150
-59.9001	-2.3855	C2-1500	Primary forest	500
-59.9006	-2.3855	C2-1550	Primary forest	550
-59.901	-2.38551	C2-1600	Primary forest	600
-59.9015	-2.38552	C2-1650	Primary forest	650
-59.9019	-2.38552	C2-1700	Primary forest	700
-59.9024	-2.38552	C2-1750	Primary forest	750
-59.9028	-2.38553	C2-1800	Primary forest	800
-59.9033	-2.38553	C2-1850	Primary forest	850
-59.9037	-2.38553	C2-1900	Primary forest	900
-59.9042	-2.38554	C2-1950	Primary forest	950
-59.8885	-2.38538	C2-200	Secondary forest	200
-59.9046	-2.38554	C2-2000	Primary forest	1000
-59.889	-2.3854	C2-250	Secondary forest	250
-59.8894	-2.38541	C2-300	Secondary forest	300
-59.8899	-2.3854	C2-350	Secondary forest	350
-59.8903	-2.3854	C2-400	Secondary forest	400
-59.8908	-2.3854	C2-450	Secondary forest	450
-59.8872	-2.38535	C2-50	Secondary forest	50
-59.8912	-2.38541	C2-500	Secondary forest	500
-59.8916	-2.38542	C2-550	Secondary forest	550
-59.8921	-2.38543	C2-600	Secondary forest	600
-59.8925	-2.38543	C2-650	Secondary forest	650
-59.893	-2.38543	C2-700	Secondary forest	700
-59.8934	-2.38542	C2-750	Secondary forest	750

-59.8938	-2.38542	C2-800	Secondary forest	800
-59.8943	-2.38544	C2-850	Secondary forest	850
-59.8947	-2.38546	C2-900	Secondary forest	900
-59.8952	-2.38546	C2-950	Secondary forest	950
-60.101	-2.32796	D1-100	Secondary forest	100
-60.1087	-2.32548	D1-1000	Habitat boundary	0
-60.1091	-2.32534	D1-1050	Primary forest	50
-60.1096	-2.3252	D1-1100	Primary forest	100
-60.11	-2.32506	D1-1150	Primary forest	150
-60.1104	-2.32492	D1-1200	Primary forest	200
-60.1108	-2.32478	D1-1250	Primary forest	250
-60.1113	-2.32464	D1-1300	Primary forest	300
-60.1117	-2.32451	D1-1350	Primary forest	350
-60.1121	-2.32436	D1-1400	Primary forest	400
-60.1126	-2.32424	D1-1450	Primary forest	450
-60.1014	-2.32782	D1-150	Secondary forest	150
-60.113	-2.32409	D1-1500	Primary forest	500
-60.1134	-2.32395	D1-1550	Primary forest	550
-60.1139	-2.32382	D1-1600	Primary forest	600
-60.1143	-2.32366	D1-1650	Primary forest	650
-60.1147	-2.32354	D1-1700	Primary forest	700
-60.1151	-2.32343	D1-1750	Primary forest	750
-60.1156	-2.32327	D1-1800	Primary forest	800
-60.116	-2.32314	D1-1850	Primary forest	850
-60.1164	-2.32298	D1-1900	Primary forest	900
-60.1169	-2.32283	D1-1950	Primary forest	950
-60.1019	-2.32769	D1-200	Secondary forest	200
-60.1173	-2.3227	D1-2000	Primary forest	1000
-60.1023	-2.32754	D1-250	Secondary forest	250
-60.1027	-2.32741	D1-300	Secondary forest	300
-60.1031	-2.32726	D1-350	Secondary forest	350
-60.1036	-2.32713	D1-400	Secondary forest	400
-60.104	-2.32699	D1-450	Secondary forest	450
-60.1006	-2.3281	D1-50	Secondary forest	50
-60.1044	-2.32686	D1-500	Secondary forest	500
-60.1049	-2.32672	D1-550	Secondary forest	550
-60.1053	-2.32658	D1-600	Secondary forest	600
-60.1057	-2.32644	D1-650	Secondary forest	650
-60.1061	-2.3263	D1-700	Secondary forest	700
-60.1066	-2.32616	D1-750	Secondary forest	750
-60.107	-2.32602	D1-800	Secondary forest	800

-60.1074	-2.32589	D1-850	Secondary forest	850
-60.1078	-2.32575	D1-900	Secondary forest	900
-60.1083	-2.32559	D1-950	Secondary forest	950
-60.0996	-2.32353	D2-100	Secondary forest	100
-60.1073	-2.32107	D2-1000	Habitat boundary	0
-60.1077	-2.32096	D2-1050	Primary forest	50
-60.1082	-2.3208	D2-1100	Primary forest	100
-60.1086	-2.32067	D2-1150	Primary forest	150
-60.109	-2.32054	D2-1200	Primary forest	200
-60.1094	-2.3204	D2-1250	Primary forest	250
-60.1099	-2.32026	D2-1300	Primary forest	300
-60.1103	-2.32013	D2-1350	Primary forest	350
-60.1107	-2.31998	D2-1400	Primary forest	400
-60.1112	-2.31984	D2-1450	Primary forest	450
-60.1	-2.3234	D2-150	Secondary forest	150
-60.1116	-2.31971	D2-1500	Primary forest	500
-60.112	-2.31957	D2-1550	Primary forest	550
-60.1125	-2.31943	D2-1600	Primary forest	600
-60.1129	-2.3193	D2-1650	Primary forest	650
-60.1133	-2.31915	D2-1700	Primary forest	700
-60.1137	-2.31901	D2-1750	Primary forest	750
-60.1142	-2.31889	D2-1800	Primary forest	800
-60.1146	-2.31875	D2-1850	Primary forest	850
-60.115	-2.31861	D2-1900	Primary forest	900
-60.1154	-2.31849	D2-1950	Primary forest	950
-60.1005	-2.32326	D2-200	Secondary forest	200
-60.1159	-2.31834	D2-2000	Primary forest	1000
-60.1009	-2.32311	D2-250	Secondary forest	250
-60.1013	-2.32299	D2-300	Secondary forest	300
-60.1017	-2.32284	D2-350	Secondary forest	350
-60.1022	-2.32272	D2-400	Secondary forest	400
-60.1026	-2.32259	D2-450	Secondary forest	450
-60.0992	-2.32366	D2-50	Secondary forest	50
-60.103	-2.32246	D2-500	Secondary forest	500
-60.1035	-2.32231	D2-550	Secondary forest	550
-60.1039	-2.32216	D2-600	Secondary forest	600
-60.1043	-2.32203	D2-650	Secondary forest	650
-60.1047	-2.32189	D2-700	Secondary forest	700
-60.1052	-2.32176	D2-750	Secondary forest	750
-60.1056	-2.32162	D2-800	Secondary forest	800
-60.106	-2.32149	D2-850	Secondary forest	850

-60.1064	-2.32135	D2-900	Secondary forest	900
-60.1069	-2.32122	D2-950	Secondary forest	950

Appendix II – An example of SM2 deployment (left) and light-trap setup (right). Sourced from Mas (2014).

Appendix III– Additional detector settings used to record bat activity.

Additional Detector Settings	
HPF left	Fs/32
Div ratio	16
File format	WAC0
Sample rate	384000
Channel	Mono-L
Compression	7%

Appendix IV – The number of files identified to the three accuracy thresholds for each transect**.**

Season	Location	Transect	<60%	>60%	>95%
1	Cabo Frio	1	6539	14829	8270
		2	15521	44992	28178
	Dimona	1	10814	34051	20813
		2	5122	19484	12400
2	Cabo Frio	1	9847	13590	7465
		2	23487	62123	34411
	Dimona	1	21051	21844	12221
		2	7861	25066	15006
	Total		100242	235979	138764

Appendix V – The number of bat passes per species/sonotype as calculated using three methods: manually identification, automatically classified to a 60% confidence and automatically classified to a 95% confidence. Highlighted values indicate a significant difference between a classifier results compared with manual identification.

Species/ sonotype	**Manual**	**Auto (60+ %)**	**W-Value**	**P-Value**	**Auto (95+ %)**	**W-Value**	**P-Value**
Total	38654	40323	123260	0.87	26466	96400	<0.01
Cormura brevirostris	224	251	293.5	0.72	50	143	0.04
Centronycteris maximiliani/ centralis	15487	15917	3321	0.49	8607	3211	<0.01
Emballonuridae sp. (*Saccopteryx gymnura / canescens*)	1	21	-	-	3	-	-
Eptesicus brasilensis	10	8	22	0.52	1	1	1
Furipterus horrens	23	22	-	-	22	-	-
Molossidae	130	411	140	<0.01	23	36	0.15
Myotis nigricans/ riparius	431	491	471	0.59	169	490	<0.01
Promops nasutus/centralis	111	154	-	-	4	-	-
Pteronotus parnellii (55KHz)	10059	10293	5414	0.99	8811	5635	0.3
Pteronotus parnellii (60KHz)	7870	8569	5203	1	6468	57345	0.13
Pteronotus gymonotus	45	30	9	0.7865	3	-	-
Peropteryx kappleri	70	65	57.5	0.86	26	11	0.46
Peropteryx macrotis	12	169	-	-	8	-	-
Pteronotus personatus	1	3	-	-	1	-	-
Saccopteryx bilineata	3164	3016	1807.5	0.72	1728	1152	<0.01
Saccopteryx leptura	1016	903	1570	0.73	542	848	0.02

Appendix VI – The table shows the correlation between total bat activity and insect volume by insect Order. Total relative volume represents the volume of each insect Order.

Insect Order	Total relative Volume	Rho	N	P-Value
Blattodea	1277	0.0914	534	0.098
Coleoptera	69519	0.0714	546	0.1974
Diptera	4775.5	0.0456	561	0.4106
Hemiptera	3791	0.0136	580	0.8056
Homoptera	4919	0.1345	509	0.0148
Hymenoptera	49860	0.1029	528	0.0626
Isoptera	4289.5	0.1763	484	0.0013
Lepidoptera	4637	0.1161	520	0.0357
Orthoptera	3340	0.1926	475	0.0045