Living at the edge: influence of forest edge types on tropical owls

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General Abstract

Owls are charismatic animals that play essential functional roles in ecosystems. Due to their nocturnal habits and cryptic nature, we understand little about the ecology and conservation status of many owl species and communities. Despite a global movement to understand the effects of habitat change on biodiversity, effects on owls have been largely ignored, especially in the tropics. Studies from temperate regions suggest that some species are able to adapt to habitat modifications while others suffer but information on their response to habitat edges is poorly known. In this study, I investigated whether owl abundances are influenced by habitat edges in a lowland rainforest-agriculture mosaic of Dehing Patkai Elephant Reserve in north-eastern India. I sampled owls systematically using call playback and compared owl encounters at 23 sites (group of three playback sampling stations each), distributed in forest habitats adjacent to small roads, large roads, paddy fields and tea fields. To check if habitat explained owl abundances at edges, I collected few habitat attributes at these sites. I examined responses of the entire owl communities, diet guilds as well as individual species. I detected 11 species of owls with Oriental Scops Owl (OSO) *Otus sunia*, Asian Barred Owlet (ABO) *Glaucidium cuculoides*, Collared Scops Owl (CSO) *Otus lettia* and Brown Hawk Owl (BHO) *Ninox scutulata* encountered most frequently. I found that owl encounters increased with increasing tree density. On average, owls occurred at similar abundances in all edge habitats, but responses to various edge types varied between owl species. OSO and CSO (insectivores) were unaffected by large roads whereas ABO and BHO (diet generalists) decreased at large road edges, indicating that large active roads may affect some owl species but not all. Both insectivorous owls together were not affected by edges, but separately showed strong and contrasting responses to certain edges. OSO was least abundant at paddy edges and was positively correlated with tree density, but CSO in contrast benefitted from paddy and tea edges correlating positively with liana density (increasing disturbance). This study shows that rainforest owls are most abundant in dense forests, and that they are sensitive to edge effects but differ considerably in their response to edges.

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General Introduction

Owls have been a source of mystery, folklore and mythology in many cultures (Marcot et al., 2000). Despite their popularity and charisma, so little is known about them, possibly due to their nocturnal and cryptic behaviour which makes them difficult to study (Borges et al., 2004; Sekercioglu, 2010). But why is it important to study owls? Owls play important functional roles as predators in natural ecosystems and provide service to humans by controlling pest populations (Kross et al., 2016; Mehta et al., 2018; Norrdahl & Korpimäki, 1995; Wiens et al., 2014; Zabel et al., 1995). In this era of global change (Keenan et al., 2015), some of these functional roles may be threatened and it is important that we understand how owls are affected by human-induced change.

As forests are being converted into agriculture and other land uses, studies show that a huge number of the taxa have suffered declines in populations and shrinking distributions (Haddad et al., 2015; Holmes & Sherry, 2001). Owls have also shown to be affected by such changes (Hinam & Clair, 2008; Dayananda et al., 2016). But, vast majority of studies that explore the effects of habitat change on owl communities come from the species poor temperate regions (Alivizatos et al., 2005; Appleby et al., 1999; Forsman et al., 2004; Franklin et al., 1996; Hamer et al., 2007; Holt, 1997; Redpath, 1995). Studies that focus on owl ecology and conservation are particularly scarce in tropical regions where, ironically, owl communities are the most diverse, and where the impacts of land use changes are most adverse (Alba-Zúñiga et al., 2009; Borges et al., 2004; Holt, 1993; Ibarra et al., 2012; Jayson & Sivaram, 2015; Dayananda et al., 2016; Sekercioglu, 2010). Studies have shown that most owls need large tracts of intact forests to thrive in (Franklin et al., 2000; Ganey et al., 1999; Hayward & Garton, 1988; Kajtoch et al., 2015). Although some species have adapted to thrive in modified environments (Vazhov et al., 2016), most owl species appear to respond negatively. Owls have been known to suffer a reduction in foraging efficiency and breeding success (Hinam & Clair, 2008), changes in home range size (Redpath, 1995) and have even been known to completely abandon altered habitats (Martínez & Zuberogoitia, 2004a).

Owl species that have adapted to use altered habitats include Tawny Owl *Strix aluco*, Little Owl *Athene noctua*, Long-eared Owl *Asio otus*, and Barred Owl *Strix varia*, which are wide ranging species and use forests as well as agricultural areas (Alba-Zúñiga et al., 2009; Framis et al., 2011; Redpath, 1995; Vazhov et al., 2016). Barn owls *Tyto alba* and Spotted Owlets *Athene brama* do well in urban areas (Ali & Santhanakrishnan, 2012; Hindmarch & Elliott, 2015). Owls of open areas like Indian Eagle Owls *Bubo bengalensis* and Short eared Owls *Asio flammeus* nest in agriculture (Pande & Dahanukar, 2011; Vazhov et al., 2016). One of the major adaptations that allows owls to thrive in such areas is the ability to utilize the abundant prey often available in these disturbed habitats. Barn Owls, Spotted Owlet and even the critically endangered Forest Owlet *Heteroglaux blewitii* feed on rodents around agriculture (Hindmarch & Elliott, 2015; Kross et al., 2016; Mehta et al., 2018) and Tawny Owls are known to shift diet to birds and bats as they use more agriculture and urban areas (Galeotti et al., 1991; Lesiński et al., 2009). Other species have utilized human structures to nest and breed (Ramsden, 1998). Due to the flexible nature of their life history, habitat needs and generalist diets, these owls are able to survive in altered habitats, but unfortunately not all species have such flexible life histories.

Owl species that have responded adversely to habitat modifications include the symbolic Spotted Owl *Strix occidentalis* which has now become the flagship of owl conservation world over. Spotted Owl is known to be strictly associated with old growth forests (Ganey & Balda, 1989; Gutierrez, 1996) and require forest interior habitats (Franklin et al., 2000; Phillips et al., 2010). Rufous legged Owls *Strix rufipes* and Austral Pygmy Owls *Glaucidium nana* are also restricted to primary forests (Ibarra et al., 2012). Some owl communities are so specific to certain forest types that any change in habitat can lead to changes in the owl community (Borges et al., 2004). A study found that in a fragmented landscape, four of eight owl species were only restricted to larger fragments and did not occur at all in small disturbed fragments (Dayananda et al., 2016). But adaptable owl species can also be affected by change. Species like Powerful Owls *Ninox strenus* and Little Owls which are adaptable still need specific nesting trees to breed which are not always available in agriculture and urban areas (Framis et al., 2011; Isaac et al., 2014). Barn Owls have suffered severe declines in populations due to increase in road networks (Martínez & Zuberogoitia, 2004a; Toms et al., 2001). In some regions increase in traffic led to the abandoning of nest sites (Hindmarch et al., 2012).

Owls therefore show mixed responses to habitat change based on their life histories, but also based on how habitat has been altered. Perhaps one of the most common artefacts of habitat change is the creation of habitat edges (Broadbent et al., 2008), or the creation of zones of abrupt transition between habitats (Ries & Sisk, 2004). Such habitat edges result in various organisms being affected by edge effects (Pfeifer et al., 2017; Ries et al., 2004). Some of these effects arise because edges have different properties from habitat interiors in terms of temperature, light, vegetation and resources (Ries et al., 2004; Ries & Sisk, 2004). When a species benefits from an edge, it is termed as a positive edge effect, but when it suffers or is disadvantaged, then it is termed as a negative edge effect (Ries & Sisk, 2004). Studies have shown that forest edges have both positive and negative edge effects on bird communities (Gates & Gysel, 1978; Heske et al., 1999; Paton, 1999). Generalist birds seem to grow in abundance at forest edges because they are able to access resources from multiple habitats (Watson et al., 2004). Specialists often suffer because of the loss of habitat (Morante-Filho et al., 2015), and bird communities in general may suffer from reduced nesting success due to disturbance and predation (Paton, 1999).

The few studies that focus on the effect of edges on owl communities suggest that there are both positive and negative effects of edges. Many owls include edge habitat in their home ranges (Bolboacă et al., 2013; Eyes et al., 2017; Franklin et al., 2000; Hindmarch et al., 2017). Some populations of Spotted Owl have been shown to preferentially select edge habitats in their home ranges whereas others have shown neutral or negative associations with abrupt edges (Eyes et al., 2017; Franklin et al., 1996; Phillips et al., 2010). In a forest-agriculture matrix, Great Horned Owl *Bubo virginianus* and Long-eared Owl showed higher usage of forest edges (Grossman et al., 2008; Martínez & Zuberogoitia, 2004b) while Powerful Owls did not show any preference (Cooke et al., 2006). Tawny Owls selected forest edges to avoid competition from the larger Ural Owls *Strix uralensis* which inhabited forest interiors (Kajtoch et al., 2015). Similarly, Little Owls avoided forest edges due to presence of Tawny Owls (Michel et al., 2016). Road edges have shown to have negative effect on many owls (Hindmarch et al., 2012; Santos et al., 2013; Silva et al., 2012). Barn Owls, Tawny Owls and Little Owls have been shown to avoid road side habitats (Hindmarch et al., 2012; Silva et al., 2012). What these studies suggest is that the response to habitat edges by owls is species and context specific.

How would we expect owl communities and species in the tropics to respond to habitat edges? The answer is still unclear because previous studies are from temperate areas and have unearthed few generalities. We may expect owls to benefit because they can access prey from both forests and agriculture by occupying edge habitat (Mehta et al., 2018; Ries & Sisk, 2004).

Moreover, studies show that the prey species themselves increase near edges (Bedford & Usher, 1994; Machado & Maltchik, 2010; Watson et al., 2004) and additionally spill-over from adjacent agricultural patches (Rand et al., 2006). However we may expect some negative effects as well, as excessive use of pesticides in agricultural fields can be detrimental for owls (Gervais et al., 2003; Hegdal & Colvin, 1988). Some negative effects may also arise from human activities and disturbance at edges (Kociolek et al., 2011; Mason et al., 2016; Reijnen & Foppen, 2006), including the noise of traffic which can cause a reduction in foraging efficiency (owls hunt through auditory cues), and direct mortality due to traffic (Hindmarch et al., 2012; Mason et al., 2016; Santos et al., 2013; Senzaki et al., 2016). So, while individual species can be affected in many ways, are there generalities in how owl communities respond to various edges, both overall and in terms of their dietary specialization and body size? Even for a wide-ranging species, its responses to habitat and edges can be very different in different parts of the world. There can be differences in preferred prey and where its available, requirement of habitat and available vegetation. In addition, tropics have more diverse community of owls and behavioural adaptations to avoid competition might also shape different responses in the tropics from temperate systems. In the tropics where forests are being converted rapidly into agriculture and intense road networks are being laid, studies on how owls respond can be of conservation value.

In this study, I try to partly address this gap in knowledge by exploring relationships between owl communities and habitat edges in the rich tropical lowland rainforest – agriculture system of the Dehing Patkai Elephant Reserve, Assam, India. Rainforests in this region are fragmented and are located in a mosaic of paddy and tea cultivation, and road networks, creating many abrupt edges (hard edges) with forest. With high owl diversity and many hard edges, this landscape provided an excellent opportunity to understand more about owls.

Chapter 1: Living at the edge: influence of forest edge types on tropical owls in a rainforest-agriculture mosaic in north-eastern India?

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Abstract

We understand little about the ecology of owls due to their nocturnal habits and cryptic nature. Despite a global movement to understand the effects of habitat change on biodiversity, effects on owls have been largely ignored, especially in the tropics. In this study, I investigated whether owl abundances are influenced by habitat edges in a lowland rainforest-agriculture mosaic in north-eastern India. I sampled owls systematically using call playback and compared owl encounters (as an index of owl abundance) in habitats adjacent to small roads, large roads, paddy fields and tea fields. I detected 11 species of owls with Oriental Scops Owl (OSO) *Otus sunia*, Asian Barred Owlet (ABO) *Glaucidium cuculoides*, Collared Scops Owl (CSO) *Otus lettia* and Brown Hawk Owl (BHO) *Ninox scutulata* encountered most frequently. I found that owl encounters increased with increasing tree density. On average, owls occurred at similar abundances in all edge habitats, but responses to various edge types varied between owl species. OSO and CSO (insectivores) were unaffected by large roads whereas ABO and BHO (diet generalists) decreased at large road edges, indicating that large active roads may affect some owl species but not all. Both insectivorous owls together were not affected by edges, but separately showed strong and contrasting responses to certain edges. OSO was least encountered at paddy edges and was positively correlated with tree density, but CSO in contrast benefited from paddy and tea edges correlating positively with liana density (increasing disturbance). This study shows that rainforest owls are most abundant in dense forests, and that they are sensitive to edge effects but differ considerably in their response to edges.

Key words: Edge effects, Oriental Scops Owl, Tea plantation, Asian Barred Owlet, Collared Scops Owl, Brown Hawk Owl, Paddy-field

Introduction

Owls are charismatic species that play important functional roles in many ecosystems (Korpimäki & Norrdahl, 1989; Millon et al., 2014). They act as avian predators in the ecosystem and keep prey populations in balance (Korpimäki & Norrdahl, 1989; Kross et al., 2016; Millon et al., 2014; Pande & Dahanukar, 2011). To humans, they perform a great service by controlling populations of rodents in agricultural fields, as rodents are major prey of many owl species, thereby reducing crop loss and disease spread (Arlettaz et al., 2010; Hindmarch et al., 2017; Kross et al., 2016; Pande & Dahanukar, 2011). Despite their importance, owls remain understudied due to their nocturnal and cryptic behaviour (Borges et al., 2004; Sekercioglu, 2010). Consequently, our understanding of their ecology, and how owl species and communities respond to habitat change is still limited.

Studies show that owls can either benefit from habitat change or be negatively affected, based on the species and the type of change (Vazhov et al., 2016). Adaptable species like Barn Owl *Tyto alba*, Spotted Owlet *Athene brama* and Tawny Owl *Strix aculo* thrive in agricultural and urban areas by predating on abundant prey like rodents and insects, even shifting to a diet of birds and bats in some regions (Ali & Santhanakrishnan, 2012; Galeotti et al., 1991; Hindmarch & Elliott, 2015; Lesiński et al., 2009). Some species have adapted by using human structures for nesting and roosting (Ramsden, 1998). Owls of open areas like Short-eared Owl *Asio flammeus*, Indian Eagle-Owl *Bubo bengalensis*, Little Owl *Athene noctua* and Burrowing Owl *Athene cunicularia* have readily adapted to use agricultural lands as suitable habitats (Green & Anthony, 1989; Pande & Dahanukar, 2011; Vazhov et al., 2016).Some owls have shown themselves to be so adaptable that their breeding success is higher in urban and rural areas than in natural habitats (Solonen & Ursin, 2008; Tomé et al., 2008).

But many species have not been able to adapt successfully to change (Franklin et al., 2000; Ganey et al., 1999; Hayward & Garton, 1988; Kajtoch et al., 2015). Some reasons may include the loss of specialized nesting habitats, insufficient prey and a general sensitivity to various forms of disturbance (Hinam & Clair, 2008; Martínez & Zuberogoitia, 2004a). Owls like the Spotted Owl *Strix occidentalis* require large tracts of intact forest and strictly avoid human modified areas (Franklin et al., 2000; Gutierrez, 1996; Phillips et al., 2010). Balsas Screech Owl *Megascops seductus*, though able to stay in agriculture, is found in very low numbers when compared to forests (Alba-Zúñiga et al., 2009). Some adaptive species like Barn Owl have suffered population declines due to an increase in road networks and associated disturbance (Hindmarch et al., 2012; Mason et al., 2016; Silva et al., 2012; Toms et al., 2001). One study from south China found that some species entirely avoided small forest fragments (Dayananda et al., 2016).

Owl species with different life histories, therefore, respond differently to habitat change, with even the same species showing variable responses based on the form of change. Since impacts are so context-specific, it is important to understand relationships between owls and habitats in a variety of ecosystems across the world. Currently, most studies on owls come from species-poor temperate regions where the focus has often been on single species rather than on communities (Alivizatos et al., 2005; Appleby et al., 1999; Forsman et al., 2004; Franklin et al., 1996; Hamer et al., 2007; Holt, 1997; Redpath, 1995). A large information gap exists in the tropics, which harbour the most diverse owl communities (Alba-Zúñiga et al., 2009; Borges et al., 2004; Holt, 1993; Ibarra et al., 2012; Jayson & Sivaram, 2015; Dayananda et al., 2016; Sekercioglu, 2010) but are also a hotspot for rapid land use change. When natural habitat is modified, habitat edges are created that are subject to 'edge effects' (Ries et al., 2004), which can in turn strongly influence biodiversity including birds (Barbaro et al., 2012; Holmes & Sherry, 2001; Murcia, 1995). An understanding of edge effects on owl abundances and communities can be a powerful tool for their conservation in the tropics.

But how are owls affected by habitat edges? Owls appear to respond to edges like they respond to habitat change in general – both positively and negatively depending on the context. Spotted Owls have been known to select edges between forest types but to avoid hard edges near agriculture (Eyes et al., 2017; Alan B Franklin et al., 2000; Phillips et al., 2010). Some species like Great Horned Owl and Long-eared Owl preferentially hunt at edges (Grossman et al., 2008; Martínez & Zuberogoitia, 2004b), or others like Boreal Owl *Aegolius funereus* breed more successfully at edges (Hakkarainen et al., 1996), but Barn Owl, Tawny Owl and Little Owl avoided forest edges created by roads (Forman & Alexander, 1998; Hindmarch et al., 2012; Silva et al., 2012). Responses can even be driven by interspecific competition where larger species that prefer interiors relegate small species to habitat edges (Kajtoch et al., 2015; Michel et al., 2016). Studies, however, are once again largely limited to temperate regions, are scarce, and have usually focused on one or two species (Alivizatos et al., 2005; Appleby et al., 1999; Forsman et al., 2004; Franklin et al., 1996; Hamer et al., 2007; Holt, 1997; Redpath, 1995).

In this study, I address this gap in knowledge by examining the effects of habitat edges on owl communities in the tropical evergreen rainforests of Dehing Patkai Elephant Reserve (DPER), India. Rainforests in DPER are fragmented, surrounded by paddy and tea plantations that create many sharp edges with the forest, and cut by many major roads and forest mud roads. In a system with the following four edge types – (a) Paddy edge, (b) Tea edge, (c) Large Road edge and (d) Small Road edge – I asked the following questions:

1) How are owl communities (abundance and richness) influenced by edge effects and habitat variables?

2) Do different species and guilds respond differently based on life histories and habitat preferences?

Methods

Study Area

I conducted this study in Dehing Patkai Elephant Reserve (DPER) in eastern Assam. DPER is situated at the base of the Eastern Himalaya contains some of the last remaining lowland rainforests of north-east India and is one of the most diverse landscapes in the country. Dominated by the state tree of Assam, 'Hollong' *Dipterocarpus macrocarpus*, these forests are multi-storied with a high canopy and trees reaching heights beyond 50 m. DPER contains over 359 species of birds as recoded on eBird (Sullivan et al., 2009), 49 species of mammals and is famous for supporting the highest diversity of cats (seven species) in the world (Kakati, 2017). It is also home to globally-threatened species like White-winged Wood Duck *Asarcornis scutulata*, Austen's Brown Hornbill *Anorrhinus austeni*, and Hoolock Gibbon *Hoolock hoolock*. DPER is also rich in owls with over 13 species documented and consequently serves as one of the most important sites for owl tourism in north-east India. The rainforests of DPER have however severely shrunk in the past decades due to excessive logging, mining and conversion to agriculture and now persist as fragments within a human-modified landscape (Chatterjee, 2008; Das, 2019).

Various land use types that occur alongside forests in the DPER landscape are often associated with different intensities of use, which can in turn affect owls differently. My study sites in DPER included Jeypore Reserve Forest, Dehing Patkai Wildlife Sanctuary and Upper Dehing East Block which are characterized by a matrix of large forest patches, paddy fields, tea plantations and human settlements. Several major roads pass through DPER that connect major cities in Assam and Arunachal Pradesh. Moreover, a large number of un-tarred and mud roads either connect villages or are used by the forest department. Small forest roads are usually associated with low disturbance, with surrounding forests resembling interiors. Large roads on the other hand are more intensely used with moderate traffic passing through them, which mostly consists of heavy trucks. But the forests on either side of these roads are usually as good as forests around small roads. Paddy fields form very stark edges with forests as vegetation sharply terminates at the physical edge. Paddy fields remain fallow from late December to May and are mostly managed only during sowing and harvesting season. Tea estates on the other hand are intensely managed throughout the year with trimming and plucking of tea bushes along with use of pesticides to control damage from insects. Structurally, the major difference between tea and paddy field is the presence of old shade trees in tea estates which may act as an extension of forest habitat. As people live near agricultural fields, forest edges near agriculture are more disturbed/degraded than those near roads because those edges provide local communities with important resources such as firewood. With many habitat edges and different agriculture types, road networks and high owl diversity, this landscape was apt for the study.

Study Design

I visualized the landscape on Google Earth and identified large roads, forest edges with paddy fields and forest edges with tea plantations. I also identified small roads (not discernible on Google Earth) by surveying on foot. I chose 24 sites based on accessibility and safety, six associated with each of four edge types – a) Large road edge b) Small road edge c) Paddy field edge d) Tea edge. At each site, 100 m inside the physical edge, I located three "sampling stations" (where owls were counted) separated by at least 250 m from each other that were together referred to as a "group" (**Figure 1**). Each 'group' was separated from the others by at least 500 m (**Figure 2**). I, with the help of my field assistants made trails to reach each sampling station and marked them using bright coloured ribbons at intervals of five to ten metres to allow easy access in the night.

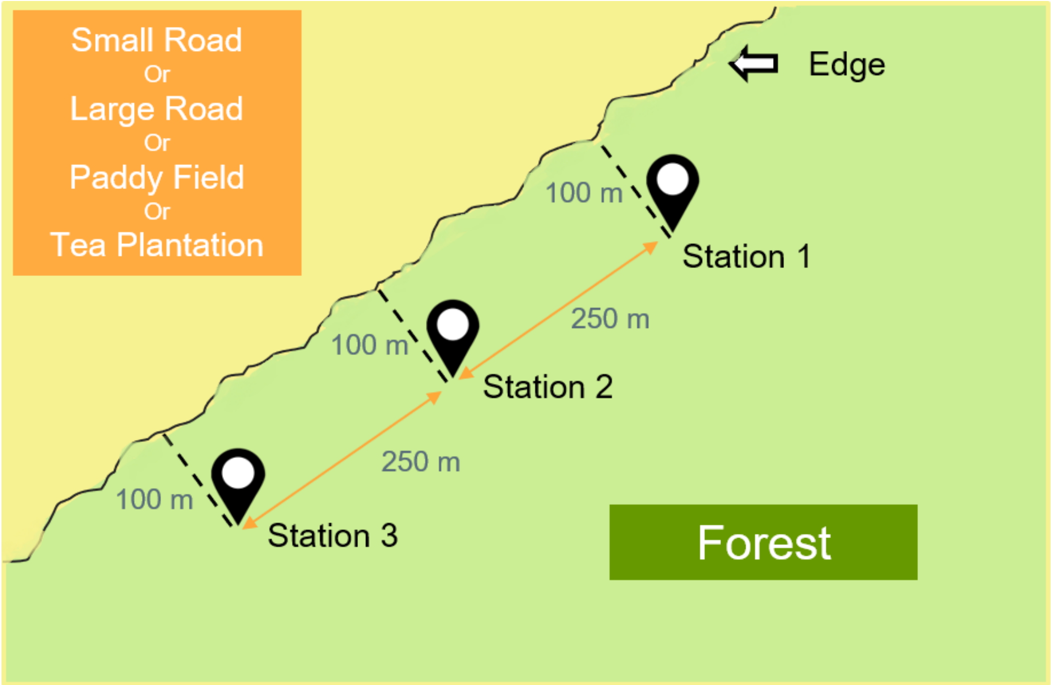

Figure 1: Sampling design, arrangement of sampling stations in a group

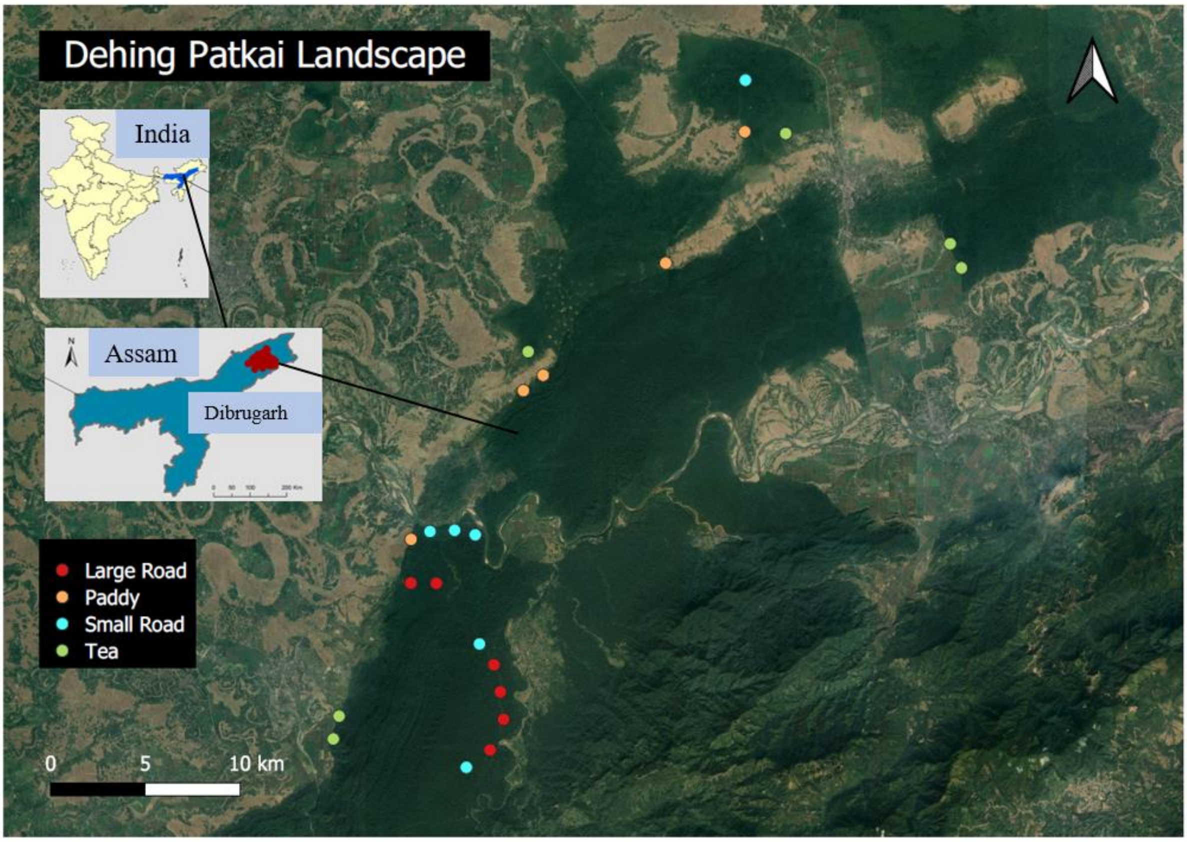

Figure 2: Map of Dehing Patkai Landscape with distribution of sampled groups. (Made on QGIS with base map from Google satellite) (Map not to scale)

Counting owls

One of the reasons owls and owl communities are so understudied is because they are difficult to detect and observe in the dark. But owls can also be detected by their distinctive vocalizations. As they do not always vocalize, owls can be more efficiently detected by eliciting a response through the playback of their calls (Alba-Zúñiga et al., 2009; Iñigo & Luisa Fernanda, 1998; Johnson et al., 1981; Navarro et al., 2005). This method works well for owls because they are territorial and playback is now a well-established technique (Johnson et al., 1981). Call playback has been used to census, find densities and to study habitat use by owls (Alba-Zúñiga et al., 2009; Borges et al., 2004; Hayward & Garton, 1988; Redpath, 1994). Call playback has been used in tropical systems to look at owl communities with success (Borges et al., 2004; Dayananda et al., 2016). I used playback to detect owl species in this study.

I focused on six relatively common forest owl species. These included two small, insectivorous owls - Oriental Scops Owl *Otus sunia* and Collared Scops Owl *Otus lettia* (Leadprathom et al., 2009; Toyama et al., 2011), two diet generalist owls – Asian Barred Owlet *Glaucidium cuccoloides* and Brown Hawk Owl *Ninox scutulata*, and two relatively specialized owls – Oriental Bay Owl *Phodilus badius* and Spot-bellied Eagle-Owl *Bubo nipalensis* (König & Weick, 2008) (**Table 1**). Oriental Scops owl is an insectivore and is the smallest of the six. Asian Barred Owlet and Brown Hawk Owl are common in both human habitation and forests and are diet generalists, feeding on a variety of prey including birds, rodents, amphibians and insects (König & Weick, 2008). Oriental Bay Owl is a rare owl species known for its habit to perch on vertically slanting branches. Spot-bellied Eagle Owl is the largest owl in India and mostly feeds on arboreal mammals like the giant squirrel, primates, birds and other large taxa (König & Weick, 2008). These species are vocaly identifiable and are vocally most active during breeding season which ranges from February to May/June (König & Weick, 2008). I pre-selected good recordings of all six species from www.xeno-canto.org to use for playback experiments at each "sampling station" (used owl calls belong to: Anderson, 2016; Boesman, 2017,2018; Lad, 2009; Lambert, 2019; Tosinthiti, 2014).

My assistants and I began sampling for owls around sunset. All sampling was carried out between 1600 hrs and 2100 hrs. All night samplings were conducted between 26th December and 18th March. We used flashlights to navigate our way to reach the sampling station. Before beginning any sampling session, we checked whether any elephant was in the vicinity for safety reasons. Once cleared for safe sampling, we turned our torches off and started our sampling session. The whole session (34 minutes) was divided into three parts; 1) period of initial listening for five minutes where I noted all unsolicited calls, 2) period of call playback for 24 minutes using a portable Bluetooth speaker (JBL Flip) where I played calls of the six owl species and waited for responses, 3) period of late listening for five minutes to detect owls that responded late to the call playback.

Initial listening: I silently listened for all unsolicited calls of owls for five minutes. If any calls were heard, I noted the species and the number of individuals. I inferred that more than one individual was calling when calls were either in duets or were simultaneously heard from different directions. This initial period of listening was essential to ensure sufficient time for owls to settle down following the disturbance associated with our approach to the sampling station.

Call playback: This session immediately followed the initial listening period. Calls were played at 50 - 70 decibels (loudness at a distance of 1 m) such that they fell in the loudness range of real owl calls and were not too loud. Calls were audible to the human ear until a distance of 100 m (tested on field). I played the call of each species for two minutes followed by two minutes of silence to hear responses. The session therefore lasted 24 minutes for six species, solicited in ascending order of their body size - Oriental Scops Owl, Asian Barred Owlet, Collared Scops Owl, Oriental Bay Owl, Brown Hawk Owl and finally Spot-bellied Eagle Owl. I wanted to minimize the possibility of biasing detection of smaller owl species by first playing calls of potential predators in the larger owls. After the call and response period for each species finished, we further listened for five minutes to note late responders. I noted all species that called and the respective number of individuals.

Species of owls in question			
Common Name	**Scientific Name**	**Size**	**Guild**
Oriental Scops Owl	*Otus sunia*	19 cm	Insectivore
Asian Barred Owlet	*Glaucidium cuculoides*	23 cm	Generalist
Collared Scops Owl	*Otus lettia*	23-25 cm	Insectivore
Oriental Bay Owl	*Phodilus badius*	29 cm	Specialist
Brown Hawk Owl	*Ninox scutulata*	32 cm	Generalist
Spot-bellied Eagle Owl	*Bubo nipalensis*	63 cm	Specialist

Table 1. List of species in question

To check if habitat explained owl abundances at edges, I collected few habitat attributes at each sampling station. I marked a 25 m by 25 m quadrat with the sampling station at the centre which I further sub-divided in two 25 m by 12.5 m sub-plots. Within each sub-plot, I measured a) tree density or the number of trees > 10 cm in girth b) average girth at breast height (GBH) c) average tree height d) percentage liana cover or the number of trees with lianas divided by total number of trees. All measures were finally aggregated to the level of a quadrat and averaged when required to get a single value for the group. I used a measuring tape to obtain GBH values in cm and a range finder to obtain height. Tree density would indicate whether owls used more dense patches. Girth and height would indicate whether owls used older forest areas. Lianas are assumed to indicate disturbance (Campbell et al., 2018; van der Heijden & Phillips, 2008), so a correlation with liana cover would indicate a correlation with disturbance.

Analysis

I used encounters from systematic call playback as an index of owl abundance. I could only sample five out of the six groups associated with paddy edges, which meant that I sampled 23/24 groups overall. Of these 23 groups, eight groups that were sampled earliest were replicated again during the breeding season. I then selected the sampling replicate closest to the breeding season (Feb-March) for each group. I calculated encounters per 'group' for each species using the number of individuals encountered (aggregated over the three stations). As the data did not fit the assumptions of generalised linear models, I bootstrapped owl encounters to arrive at mean owl encounters and 95% confidence intervals across all edge types. Because small road edges were most similar to contiguous forest, we considered small roads as a control and compared other edge types to small roads.

I estimated species diversity at each edge type using the Shannon-Weiner diversity index from package vegan in R 4.0 (Oksanen et al., 2013; R Core Team, 2020). Due to logistic constraints, I obtained habitat covariates only for 12 groups which included six large road edges, five small road edges and one paddy edge. Due to the limited sample size, I first visually examined every scatterplot for any relationship between encounters and habitat variables. I then used linear models to explore relationships between encounters and the habitat covariates i.e. average tree density, average tree height and average percentage of liana cover. I disregarded girth because girth and height were strongly correlated.

In all analyses, we examined responses of the entire owl community, of diet guilds as well as of each individual species

Results

I encountered 340 individuals of owls belonging to 10 species across all sampling replicates but encountered 298 belonging to nine species in the 23 selected replicates. Among all species, Oriental Scops Owl *Otus sunia*, Asian Barred Owlet *Glaucidium cuculoides*, Collared Scops Owl *Otus lettia* and Brown Hawk Owl *Ninox scutulata*, were the most frequently encountered (**Table 2**).

Code	Species	Scientific Name	Number of encounters
ABO	Asian Barred Owlet	*Glaucidium cuculoides*	84
BHO	Brown Hawk Owl	*Ninox scutulata*	71
OSO	Oriental Scops Owl	*Otus sunia*	64
CSO	Collared Scops Owl	*Otus lettia*	45
MSO	Mountain Scops Owl	*Otus spilocephalus*	18
CO	Collared Owlet	*Glaucidium brodiei*	7
OBO	Oriental Bay Owl	*Phodilus badius*	3
BFO	Brown Fish Owl	*Ketupa zeylonensis*	3
SBEO	Spot-bellied Eagle Owl	*Bubo nipalensis*	1
BWO	Brown Wood Owl	*Strix leptogrammica*	0

Table 2. Number of encounters for each owl species.

Small roads had the highest species richness with eight species followed by large road edges, paddy edges and tea edges (**Table 3**). Tea edges had the least species richness with just four species. Asian Barred Owlet and Brown Hawk Owl were abundant at all edge types except large road edges. Oriental Scops Owl on the other hand was abundant at all edge types except paddy edges. Collared Scops Owl was most abundant at paddy and tea edges (**Table 3**). I also found that the Shannon-Weiner diversities of each edge type followed the same order as species richness, with small roads being most diverse (**Table 3**).

Image 1: Four most encountered species in the study; Oriental Scops Owl (Top-left); Collared Scops Owl (Top-right); Asian Barred Owlet (Bottom-left); Brown Hawk Owl (Bottom-right)

Edge Type	ABO	BHO	OSO	CSO	MSO	CO	OBO	BFO	SBEO	Total Species	Shannon Diversity
SR	22	18	19	5	10	3	3	1	0	**8**	**1.7569**
LR	8	9	20	9	6	4	0	0	1	**7**	**1.7203**
PE	26	17	7	16	2	0	0	2	0	**6**	**1.4823**
TE	30	27	18	15	0	0	0	0	0	**4**	**1.3479**

Table 3. Edge type wise distribution of encounters. LR= Large road edge, PE= Paddy edge, SR= Small road edge, TE=Tea edge

Owls occurred at similar abundances (in terms of encounters, henceforth all terms of abundance/abundant refer to this) and richness at all edge types but mean encounters (approximately 9) and richness (3) were lowest at large road edges (**Figure 3**). Only for small roads, large roads, and a single paddy edge, I found that owl encounters correlated with tree density ($R^2 = 0.38$) but not with liana density (**Figure 4**). Both small roads and large roads had similar tree densities (**Figure 4**).

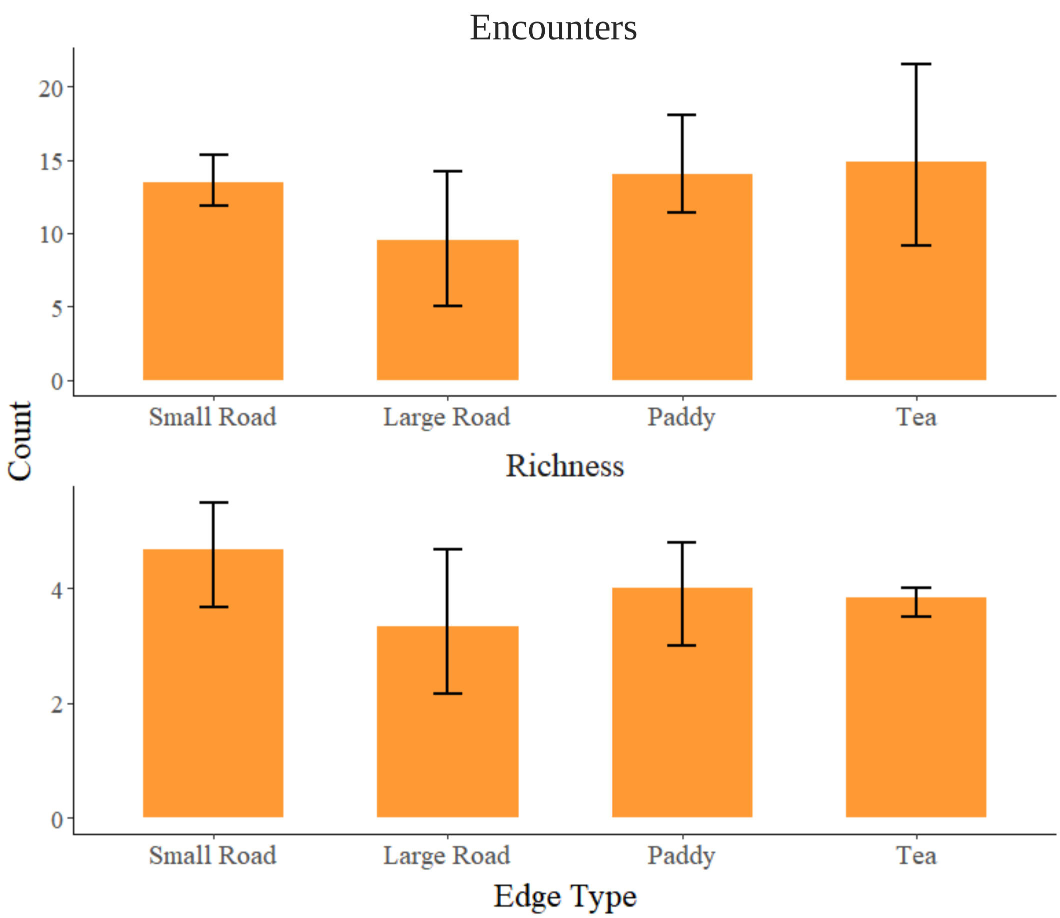

Figure 3: (Top) Mean owl encounters per group across all edge types with 95 % confidence intervals; (Bottom) Mean number of species encountered per group across all edge types. N = 23 (6 Small Roads, 6 Large Roads, 5 Paddy edges, 6 Tea edges)

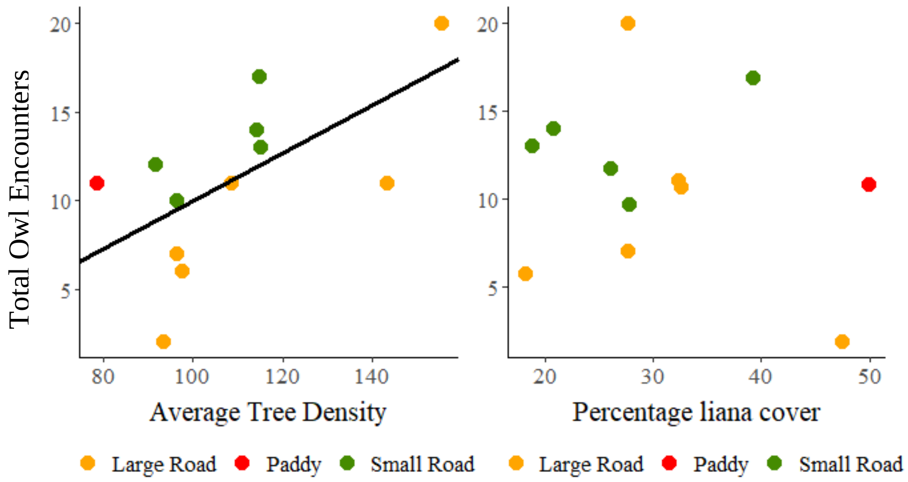

Figure 4: Owl encounters at each group with respect to average tree density (left) and percentage liana cover (right). Best fit lines are only shown where visual correlations are apparent. $R^2 = 0.38$ for the plotted line (Tree density). N = 12

I investigated whether insectivorous owls (Oriental Scops Owl and Collared Scops Owl) were differently affected by edges as compared to diet generalist owls (Asian Barred Owlet and Brown Hawk Owl). I found that insectivorous owls were equally abundant at all edge types, but diet generalist owls were significantly less abundant at large road edges (approximately 60% lower, **Figure 5**). Encounters of insectivorous owls correlated strongly with tree density (R^2 = 0.428) but not with liana density whereas the diet generalist owls did not show any relationships with habitat variables (**Figure 6**).

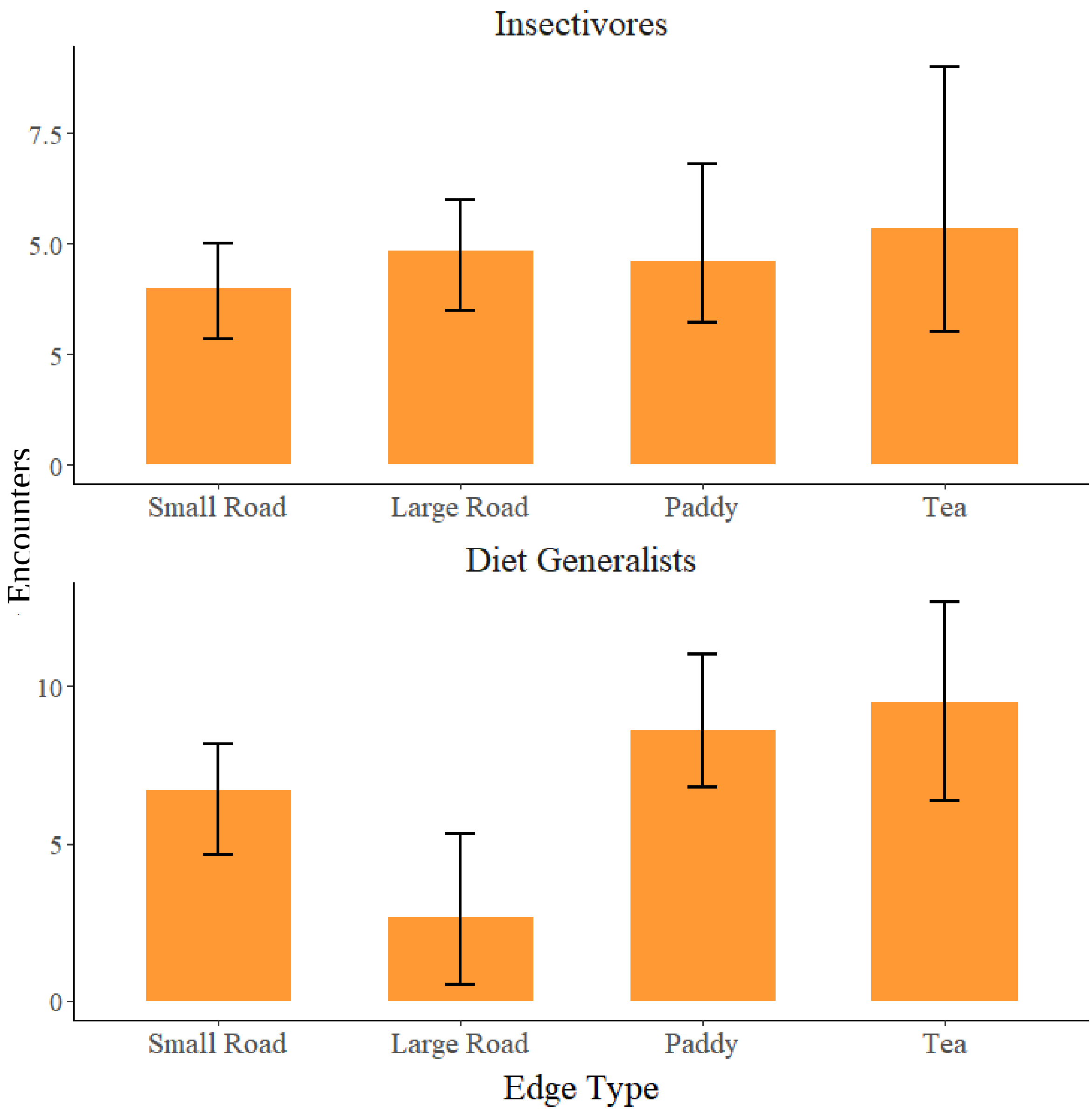

Figure 5: Mean encounters of diet generalist and insectivorous owls across all edge types with 95% confidence intervals. N = 23 (6 Small roads, 6 Large Roads, 5 Paddy edges, 6 Tea edges)

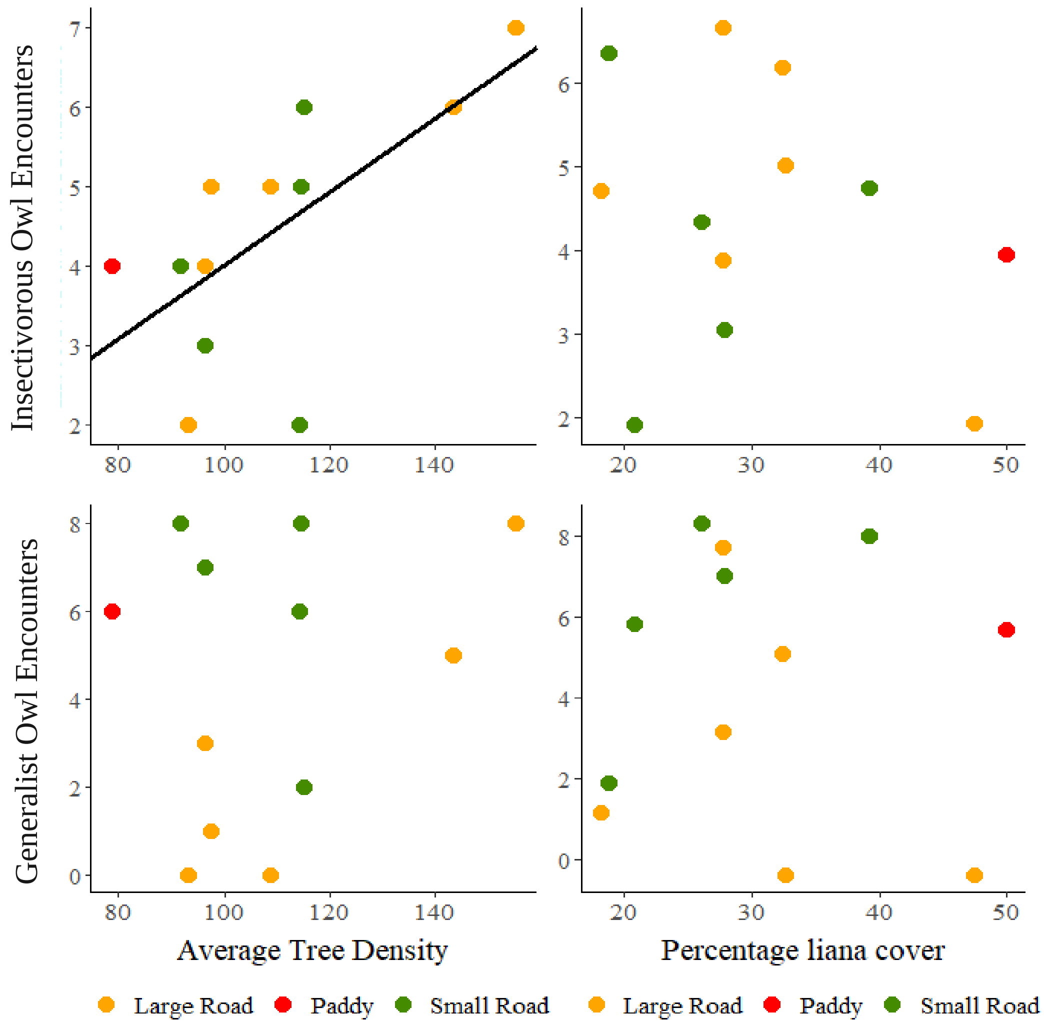

Figure 6: Encounters of generalist and insectivorous owls as a function of habitat variables. Best fit lines are only shown where visual correlations are apparent; R^2 = 0.43 for the plotted line. N = 12

Although the two insectivorous owls together did not show any edge habitat associations, the two species individually showed markedly different responses to edge types (**Figure 7**). Oriental Scops Owl was significantly less abundant at paddy edges (approximately 50% lower) whereas Collared Scops Owl was most abundant at paddy and tea edges (approximately 50% higher). Both species occurred at similar densities at tea edges but while OSO dominated at road edges, CSO dominated at paddy edges. Additionally, OSO encounters were correlated with tree density (R^2 = 0.66) and I encountered six more OSO individuals in the densely forested edges than the least dense forest edge. CSO was correlated with liana density and the edge with the highest liana cover had about 4 more CSO individuals than with the least liana cover (R^2 = 0.33) (disturbance) (**Figure 8**).

On the other hand, both generalist owls (Asian Barred Owlet and Brown Hawk Owl) were least abundant at large roads (approximately 60% lower), mirroring the pattern they showed in combination (**Figure 7**). Neither species showed any association with habitat (**Figure 8**).

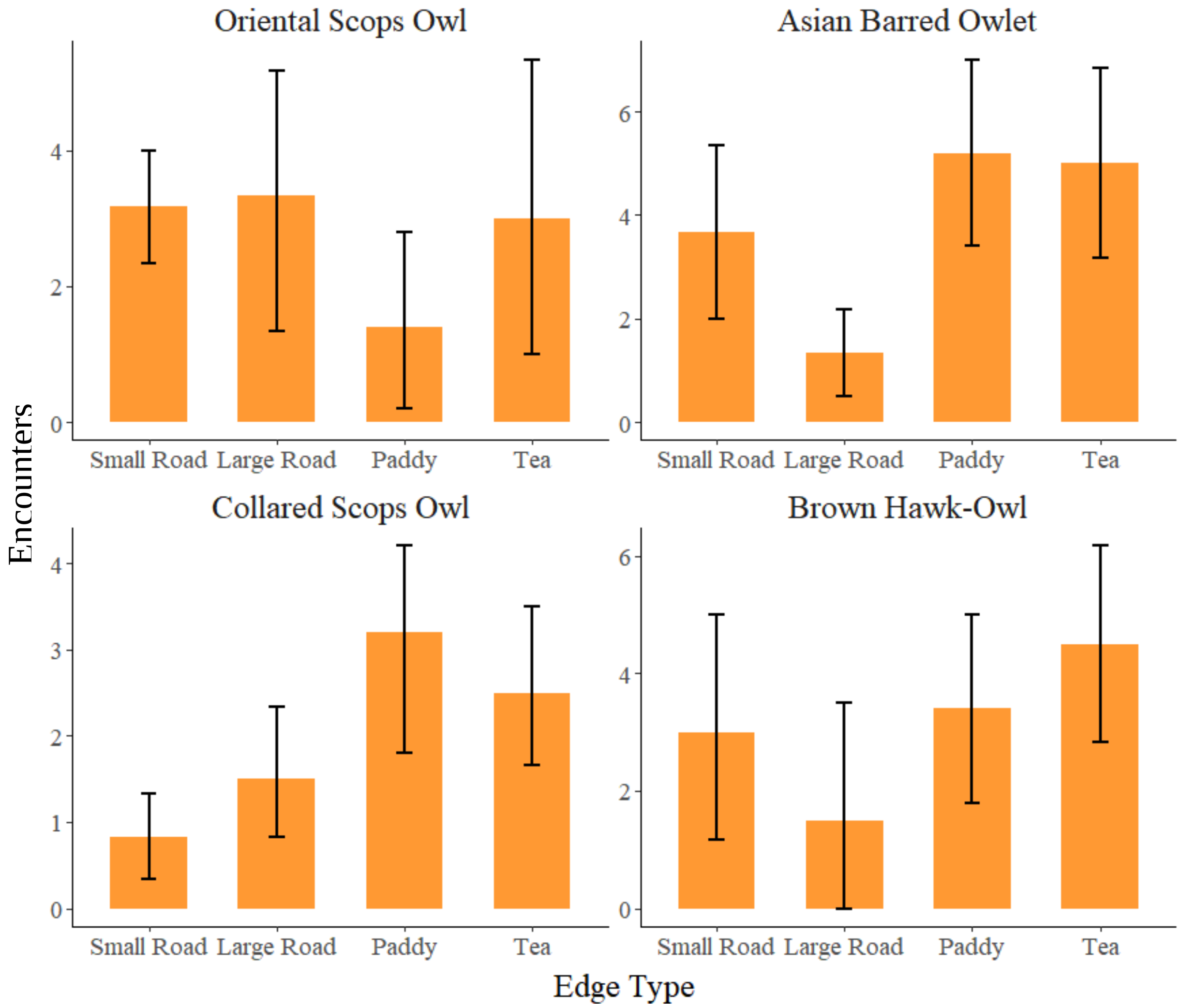

Figure 7: Mean encounters of Oriental Scops Owl, Asian Barred Owlet, Collared Scops Owl and Brown Hawk Owl across all edge types with 95 % confidence intervals. N = 23 (6 Small Roads, 6 Large Roads, 5 Paddy edges, 6 Tea edges)

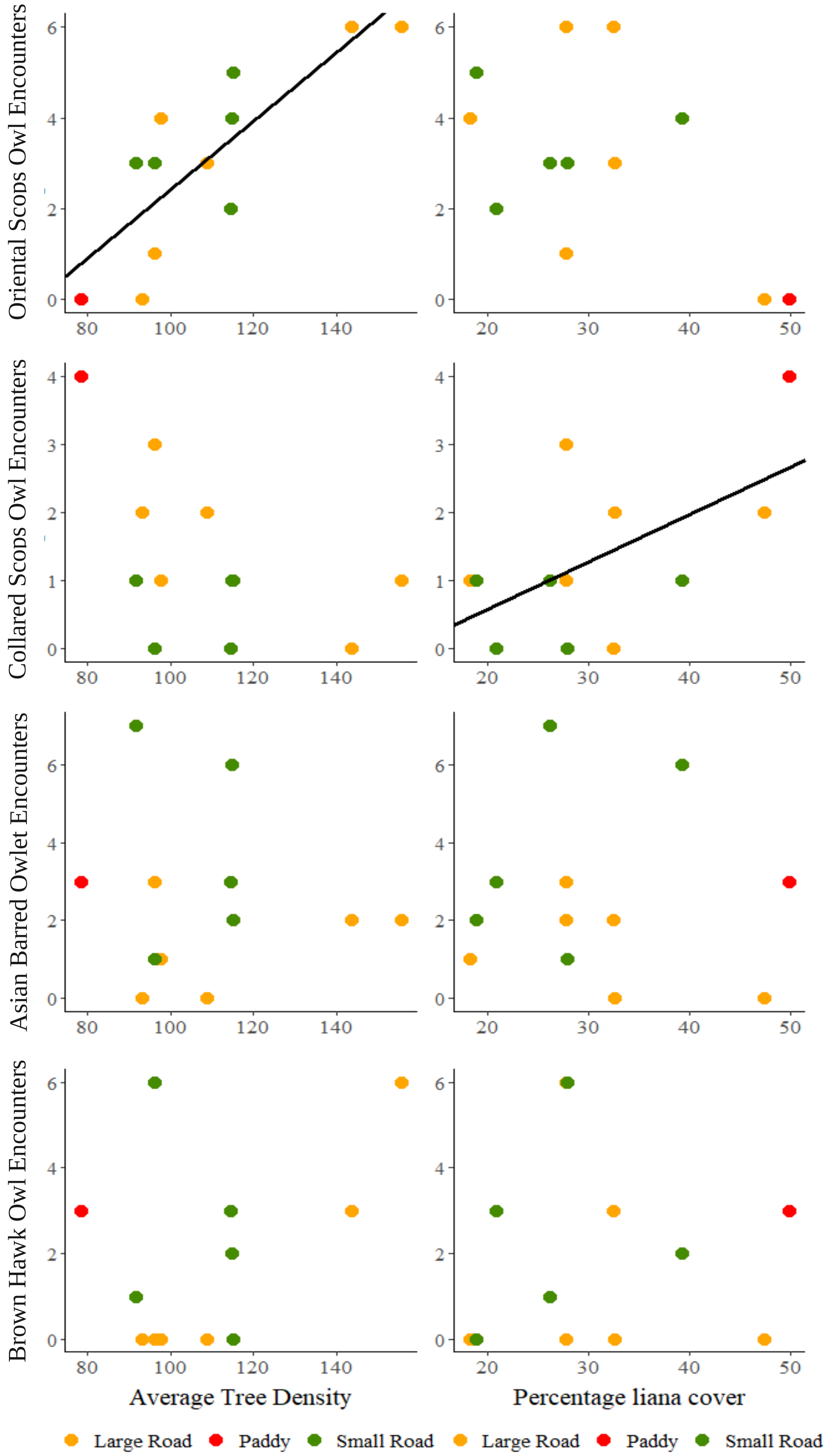

Figure 8: Relationships between the encounters of the four most abundant owl species and habitat variables. Best fit lines are only shown where visual correlations are apparent. $R^2 = 0.66$ for plotted line for OSO (Tree density). $R^2 = 0.33$ for plotted line for CSO (liana cover).

Owls	Edge Type	Mean Abundance	Confidence Interval
Total Owls	Small Roads	13.5	11.67 – 15.16
	Large Roads	9.33	5.16 – 14
	Paddy	14	11.4 – 18
	Tea	15	9.16 – 20.83
Insectivores	Small Roads	4	3 – 5
	Large roads	4.83	3.5 – 6.00
	Paddy	4.6	3.2 – 6.80
	Tea	5.33	2.82 – 8.67
Generalists	Small Roads	6.83	4.67 – 8.33
	Large Roads	2.66	0.5 – 5
	Paddy	8.6	6.8 – 11
	Tea	9.67	6.16 – 12.66
Oriental Scops Owl	Small Roads	3.16	2.33 – 4
	Large Roads	3.33	1.5 – 5.16
	Paddy	1.4	0.2 – 2.8
	Tea	3	1 – 5.33
Collared Scops Owl	Small Roads	0.83	0.33 – 1.33
	Large Roads	1.5	0.66 – 2.33
	Paddy	3.2	1.8 – 4.2
	Tea	2.5	1.66 – 3.5
Asian Barred Owlet	Small Roads	3.67	2 – 5.33
	Large Roads	1.33	0.5 – 2.33
	Paddy	5.2	3.4 – 6.8
	Tea	5	3.16 – 6.83
Brown Hawk Owl	Small Roads	3	1.66 – 4.67
	Large Roads	1.5	0 – 3.5
	Paddy	3.4	1.6 – 5
	Tea	4.5	3 – 6.16

Table 4: Mean encounters and 95 % confidence intervals of total owls, guilds and species in question. Highlighted rows represent edges with significantly different abundance than other edge types. N = 23 (6 Small Roads, 6 Large Roads, 5 Paddy edges, 6 Tea edges)

Discussion

I recorded 11 owl species during the course of the study, including one incidental observation of Spotted Owlet *Athene brama* in the agricultural area adjacent to the forest. This is therefore one of the most diverse owl communities recorded from a single forest system in tropics. Dayananda et al., (2016) found eight species in fragmented South East Asian tropical forests while studies in the Amazon forests recorded six to seven species (Borges et al., 2004). The only other study to find a comparable number of owl species was a study in the Western Ghats by Jayson & Sivaram, (2015), where 12 species of owls were recorded in two protected areas. Most studies in temperate regions have reported smaller owl communities despite larger extents of study areas, with the largest community reported from the vast Altai region with nine species (Hayward & Garton, 1988; Vazhov et al., 2016). Given this diverse owl community within such a small study area, the Dehing Patkai landscape is definitely a hotspot for owl diversity conservation.

Asian Barred Owlet, Brown Hawk Owl, Oriental Scops Owl and Collared Scops Owl were the most abundant species in the study area. Though widely distributed across south and South East Asia, Oriental Scops Owl and Brown Hawk Owl are considered to be relatively rare and elusive owls (Jayson & Sivaram, 2015; Dayananda et al., 2016; Sullivan et al., 2009) but can be locally abundant (via eBird, Sullivan et al., 2009) . Asian Barred Owlet is considered rather common across its range and seems to occupy all habitats (König & Weick, 2008), which may explain why it was the most abundant species in the fragmented Dehing Patkai landscape. Another study in south China also found Asian Barred Owlet to be the most common owl in the community and unaffected by fragmentation (Dayananda et al., 2016). Collared Scops Owl is another widely distributed species with very limited information on its ecology (Leadprathom et al., 2009; Sullivan et al., 2009; Toyama et al., 2011) but the high abundances may again be explained by a general tolerance for disturbance, a feature also seen in its sister species, Indian Scops Owl *Otus bakkamoena* (Jayson & Sivaram, 2015; Sharma et al., 2018). With so little information available on the ecology of tropical owls and owl communities, this study provides baseline information both into their general ecology and their response to habitat edges.

I found that aggregated owl richness and diversity was highest at small roads, followed by large roads, paddy edges and tea edges, corresponding broadly with the expected gradient of increasing disturbance. However, when examined with uncertainty, owl encounters and richness was similar across all edges, but encounters was positively correlated with tree density. Despite these broad similarities, further investigations revealed that individual species and species guilds responded strongly and differently to certain habitat edges. Such variable responses are expected because the owls recorded in this study have different life histories, and therefore different diet and habitat requirements (Barbaro et al., 2012; Crooks et al., 2004; Watson et al., 2004). We found large owls like Spot-bellied Eagle Owl, Brown Fish Owl and Brown Wood Owl to be generally uncommon in the fragmented landscape, and rarely detected at paddy and missing at tea edges (most disturbed). Studies in Western Ghats and south China also found Spot-bellied Eagle Owl and Brown Wood Owl to be restricted to less disturbed larger fragments (Jayson & Sivaram, 2015; Dayananda et al., 2016), possibly also due to their need of larger prey which is more common in larger fragments (Zabel et al., 1995)

I found that insectivore encounters did not differ across edge types, possibly indicating that insect/arthropod prey is not a limiting resource at any of these habitat edges (Kotze & Samways, 2001). Studies have found insect populations to be rather higher at edges but also not all species respond positively to prey availability (Bedford & Usher, 1994; Fretz, 2002; Šálek et al., 2010; Wirth et al., 2008). But the two species comprising this guild, Oriental Scops Owl (OSO) and Collared Scops Owl (CSO), showed strong and contrasting responses. OSO strongly avoided paddy edges while CSO was most abundant at paddy and tea edges. OSO showed a positive correlation with tree density which suggest that it needs dense vegetation to thrive. Another study in the Western Ghats suggested their association with tall and older forests (Jayson & Sivaram, 2015). Paddy edges are usually near settlements, where local requirements of resources like firewood can cause a reduction in tree density (Rüger et al., 2008; Shankar et al., 1998), in turn causing OSO to avoid these edges. CSO on the other hand was positively correlated with increasing liana cover which is an indicator of disturbance (Campbell et al., 2018; van der Heijden & Phillips, 2008). Paddy and tea edges are highly disturbed (from field observations of direct disturbance and high liana cover, data could not be collected due to COVID restrictions) but may be preferred by CSO because agricultural edges can contain supplementary prey that spills-over from agricultural fields (Rand et al., 2006), and due to the potential lack of competition from larger owl species (Kajtoch et al., 2015; Michel et al., 2016) or other owls sensitive to such edges (Hayward & Garton, 1988; Kajtoch et al., 2015; Michel et al., 2016; Ries, Fletcher, et al., 2004; Sergio et al., 2007) such as OSO.

Both species of diet generalist owls, Asian Barred Owlet and Brown Hawk Owl, and the guild as a whole, exhibited identical responses to habitat edges. ABO and BHO occurred at similar abundances at small road edges, paddy edges and tea edges but were negatively affected by large road edges especially ABO. Because neither the guild as a whole, nor the two species separately, showed any correlations with habitat variables, reasons for their avoidance of large roads may be independent of habitat but a consequence of other factors like vehicular movement. Possible consequences of vehicular movement may include 1) a change in hunting/social behaviour due to traffic noise (Mason et al., 2016; Senzaki et al., 2016), 2) mortality from collisions in high traffic areas (Hindmarch et al., 2017; Santos et al., 2013; Silva et al., 2012), 3) less prey (Fahrig & Rytwinski, 2009; Forman & Alexander, 1998), which is unlikely because diet generalist owls can shift to alternate prey when their preferred prey is scarce (Ali & Santhanakrishnan, 2012; Galeotti et al., 1991; Hindmarch & Elliott, 2015; Lesiński et al., 2009; Pande & Dahanukar, 2011).

We often consider owls to be generally sensitive to traffic noise. Though this study did not look at effects of traffic noise, but speculate from this study that adverse impacts of traffic may be species and life history specific, rather than broadly generalizable. Although Asian Barred Owlet and Brown Hawk Owl were negatively affected by large roads, both insectivorous owls were as abundant at large road edges (with traffic and vehicular noise) as at small road edges (not used often by vehicles), possibly indicating that traffic noise does not impede their ability to find insect prey (Ali & Santhanakrishnan, 2012; Martínez & Zuberogoitia, 2004b). Other studies have also shown that owls are not always affected by noise from industries (Shonfield & Bayne, 2017). But Tawny Owls have been shown to be adversely affected by roads and traffic due to traffic disturbance and collisions (Santos et al., 2013; Silva et al., 2012). So, in order to really understand the impacts of large road networks on an owl community and a general ecosystem, we may need to separately examine impacts on each species and their functional roles in the ecosystem. We know that the absence of Barn Owls can cause rapid increase in rodent populations (Kross et al., 2016), but the consequences of low densities of ABO and BHO (as in this study) are difficult to predict until we understand their ecologies and functional roles better.

Overall, this study provides a peek into the largely unknown ecology of Asian tropical owls and their relationship with the ever-changing forests that they live in. My study suggests that owl species and guilds are indeed sensitive to edge effects, and that intensive land use change can predictably and adversely influence owl densities. Rare and elusive owl species like Oriental Bay Owl *Phodilus badius* and Spot-bellied Eagle Owl *Bubo nipalensis* may be the first to vanish with further land-use change in the region, resulting not just in the loss of aesthetic value, but in the loss of a budding local tourism economy to which these owls are central. Our understanding of tropical owls is still in its infancy and further studies in diverse landscapes like Dehing Patkai will slowly help us unravel the mysterious world of owls.

General Summary

Owl play essential functional roles in ecosystems but are poorly understood due to their nocturnal habits. Despite a global movement to understand the effects of land-use change on biodiversity, effects on owls have been largely ignored, especially in the tropics. Studies from temperate regions suggest that certain species of owls can adapt to habitat changes and thrive but many others suffer. Such changes to forested landscapes introduce forest owls to a variety of habitat edges whose effects on tropical owl communities is largely unknown. In this study, I investigated whether owl abundances are influenced by habitat edges in a lowland rainforest-agriculture mosaic of Dehing Patkai Elephant Reserve in north-eastern India. These rainforests are surrounded by paddy and tea cultivation, which in combination with major roads create different edge types varying in intensity of human use. I sampled owls systematically using call playback and compared owl encounters in edge habitats adjacent to small roads, large roads, paddy fields and tea fields.

I detected 11 species of owls with Oriental Scops Owl *Otus sunia*, Asian Barred Owlet *Glaucidium cuculoides*, Collared Scops Owl *Otus lettia* and Brown Hawk Owl *Ninox scutulata* encountered most frequently. Owls were most abundant in denser habitats. Cumulatively, least disturbed small road edges supported the highest owl richness and diversity whereas the most disturbed tea edges supported the lowest. All edge types supported similar abundances of owls but every edge type affected each owl species and diet guild differently. Diet generalists (ABO and BHO) were negatively affected at large road edges while insectivores (OSO and CSO) were unaffected. As a guild, insectivores did not differ in abundances across edge types but at species level, OSO and CSO showed contrasting trends. OSO did badly at the paddy edges and selected dense forested areas while CSO benefitted from paddy and tea edges and selected more disturbed habitats characterized by higher liana cover.

My study suggests that owl species and communities are indeed affected by habitat edges. Cumulatively, agricultural edges support the fewest species of owls which suggests that further conversion of forests to agriculture or other intensive land-uses may negatively affect owl richness. My results also suggest that some owl species strongly avoid large roads, which indicates that growing road networks both in this landscape and elsewhere can have profound impacts on owl communities. I did not explore how edge ecosystems may have changed in response to changing owl communities but potential consequences include proliferation of prey

including rodents, which can in turn cause considerable damage in agricultural landscapes. This aspect is certainly worth further research.

What I could not investigate in this study, except to a small degree, are the ecological mechanisms that drive these responses. I was not able to sample extensively and collect vegetation data for all edge types because my field work was stalled by potentially dangerous elephants, by protests against the Citizenship Amendment Act (CAA) and finally (once and for all) by the COVID 19 pandemic. Apart from the detailed habitat data, data on prey availability, noise levels and pesticide use in agriculture would allow future studies to look deep into the mechanisms that influence owl abundance in this landscape. The Dehing Patkai landscape is one of the last remaining lowland rainforest systems, supporting innumerable threatened and rare species along with an extremely diverse owl community. But in the face of severe threats, only focused research and conservation efforts in the area can help sustain the diversity it contains.

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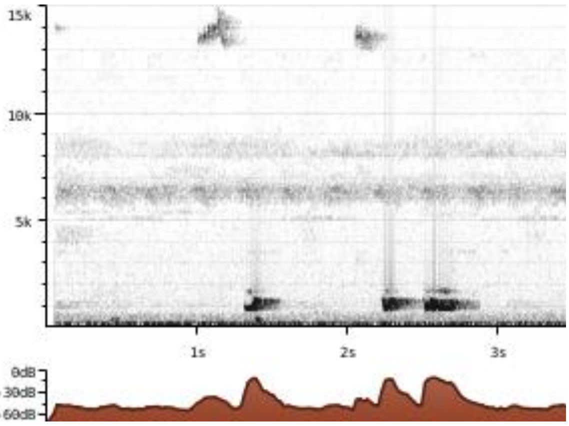
Appendix

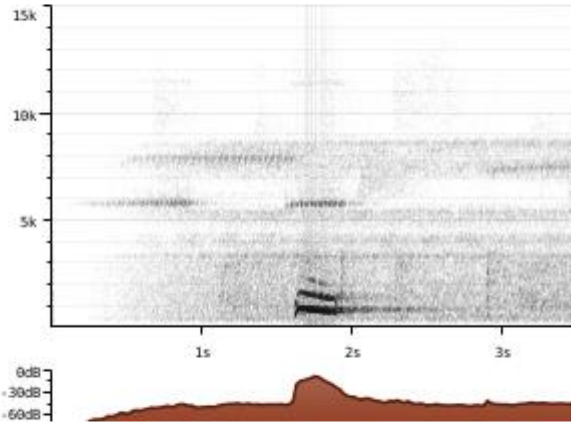
Spectrograms of the calls used in call playback

Calls and Spectrograms were taken from xeno-canto.org. Spectrograms have been cropped for the purpose of visualization. Y axis represent the frequency in khz and X axis represent time in seconds. Below the spectrogram is the decibel level of call recording.

- Oriental Scops Owl (XC214019 by Pankaj Lad) and Collared Scops Owl (XC315138 by Marc Anderson)

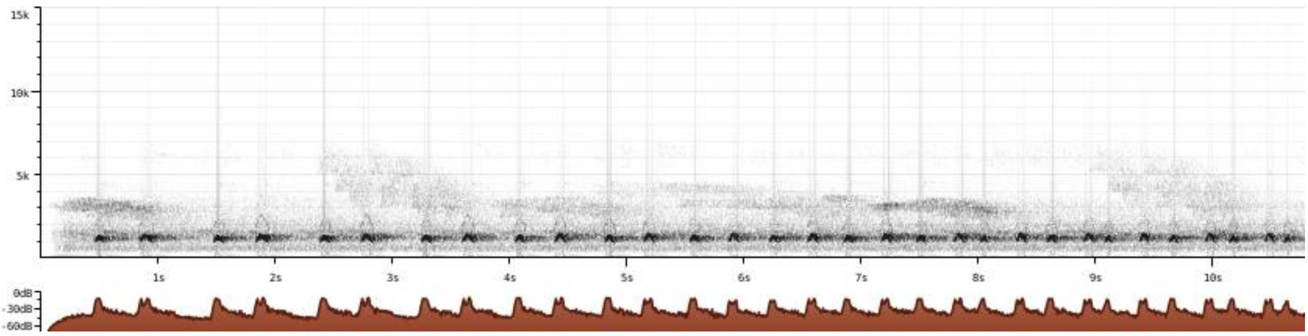


Oriental Scops Owl

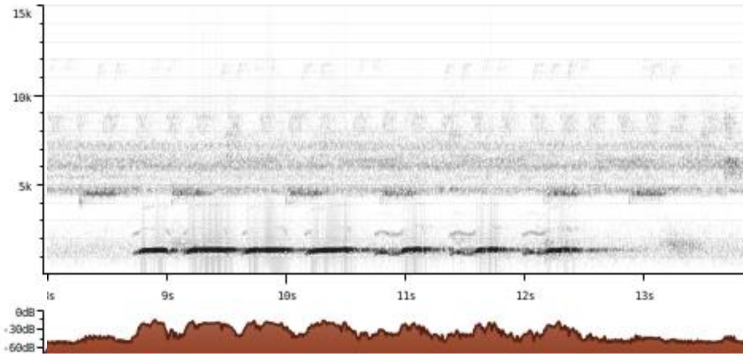


Collared Scops Owl

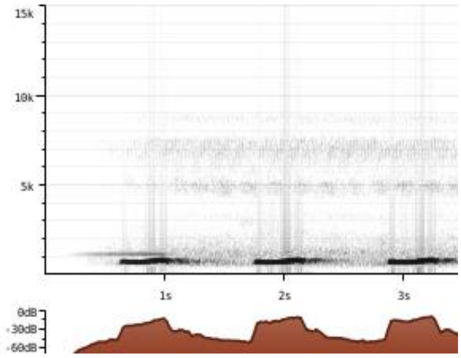
- Asian Barred Owlet (XC426587 by Peter Boesman)



- Oriental Bay Owl (XC492693 by Frank Lambert) and Brown Hawk Owl (XC369356 by Peter Boesman)



Oriental Bay Owl



Brown Hawk Owl

- Spot-bellied Eagle Owl (XC188474 by Chan Tosinthiti)