INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA – INPA
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EFEITOS DAS CARACTERÍSTICAS DE LAGOS DE ÁGUA PRETA SOBRE A OCORRÊNCIA E A ABUNDÂNCIA DE AVES PISCÍVORAS NO ARQUIPÉLAGO DE ANAVILHANAS, RIO NEGRO, AMAZÔNIA CENTRAL, BRASIL

RENATA DA SILVA XAVIER

Manaus, Amazonas

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Sinopse:

Estudou-se, em nível populacional, a influência das características de lagos de água preta sobre a ocorrência e a abundância de aves piscívoras no Arquipélago de Anavilhanas, Rio Negro, Amazônia Central, Brasil. Modelos múltiplos lineares e múltiplos logísticos foram utilizados para testar os efeitos de nove variáveis, sendo quatro físicas, duas químicas, duas geográficas e uma biótica, sobre a distribuição e abundância de doze espécies de aves. Os dados foram coletados entre novembro-dezembro de 2007, em 45 lagos do arquipélago.

Palavras-chave:

Aves aquáticas, PARNA Anavilhanas, variáveis limnológicas

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RESUMO

Foi avaliada, em nível populacional, a influência das características de lagos de água preta sobre a ocorrência e abundância de 12 espécies de aves piscívoras na Amazônia Brasileira. A principal hipótese foi que as variações locais nas características dos lagos deveriam influenciar a ocorrência e abundância de populações de diversas aves aquáticas em um sistema tropical de águas pretas (igapó). Foi testada a hipótese complementar de que as variações no grau de isolamento dos lagos influenciariam a ocorrência e abundância de aves aquáticas nos lagos. Os levantamentos de aves foram conduzidos entre os meses de novembro-dezembro de 2007, em 45 lagos distribuídos em ilhas no Arquipélago de Anavilhanas, ao longo de 100 km no Rio Negro, Amazônia Central, Brasil. Modelos múltiplos lineares e múltiplos logísticos foram utilizados para testar os efeitos de nove variáveis, sendo quatro físicas, duas químicas, duas geográficas e uma biótica, sobre a ocorrência e abundância de doze espécies de aves piscívoras. Foi encontrado que a profundidade do lago e a transparência da água influenciaram a ocorrência e abundância do martim-pescador-grande (*Megaceryle torquata*) e a abundância da águia-pescadora (*Pandion haliaetus*), da garça-moura (*Ardea cocoi*) e da garça-branca-pequena (*Egretta thula*). O isolamento do lago influenciou a ocorrência do trinta-réis-anão (*Sternula superciliaris*) e do socozinho (*Butorides striata*), e a riqueza de habitats ao longo das margens dos lagos influenciou a maioria das espécies de aves piscívoras. Os resultados indicam que as características limnológicas e físicas de lagos são determinantes da variação espacial na abundância e ocorrência de aves piscívoras em sistemas de lagos de água preta na Amazônia Central Brasileira.

Palavras-chave: Amazônia, Anavilhanas, aves aquáticas, aves piscívoras, características de lagos, uso do habitat.

ABSTRACT

Effects of black water lake features on the occurrence and abundance of fish-eating birds in the Anavilhanas Archipelago, Rio Negro, Central Amazonian, Brazil

The influence of blackwater lakes characteristics on the occurrence and abundance of 12 fish-eating birds species in the Brazilian Amazon at the population level was evaluated. The central hypothesis was that local variations in lake characteristics should influence the occurrence and abundance of aquatic bird population in a tropical blackwater flooded forest system. An additional hypothesis was tested, the variation in the degree of isolation of the lakes, influence the occurrence and abundance of lake-living waterbirds. Bird surveys were conducted from November to December 2007 in 45 lakes within islands along 100 km of the Anavilhanas Archipelago, Rio Negro, Central Brazilian Amazonia. Multiple linear and multiple logistic statistical models were used to test the effects of nine variables, four physical, two chemical, two geographical, and one biotic, on the occurrence and abundance of 12 species of fish-eating birds. It was found that lake depth and water transparency influenced the occurrance and abundance of Ringed-Kingfisher (*Megaceryle torquata*) and abundance of Osprey (*Pandion haliaetus*), Cocoi Heron (*Ardea cocoi*) and Snowy Egret (*Egretta thula*). Lake isolation influenced the occurrence of Yellow-billed Tern (*Sternula superciliaris*) and Striated Heron (*Butorides striata*), and habitat richness has affected most of the fish-eating birds species. The results indicate that lake limnological and physical attributes are determinants of spatial variation in abundance and occurrence of fish-eating birds in the blackwater lake systems in central Brazilian Amazon.

Key words: Amazonia, Anavilhanas, fish-eating birds, habitat use, lake characteristics, waterbirds.

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INTRODUÇÃO GERAL

A dispersão de populações e, em consequência, as mudanças na composição de comunidades, podem resultar da ligação entre processos operando em escalas locais e regionais (Ricklefs e Schluter 1993). Além disso, as espécies abundantes localmente tendem a ter distribuição mais extensa, com a substituição de indivíduos resultando de imigração de um pool regional de espécies, como o previsto pela Teoria Neutra, ou influenciado por fatores ecológicos locais, como previsto pela Teoria de Nicho (Thompson e Townsend 2006). O debate nesse arcabouço teórico, sobre qual processo é mais importante, ainda persiste.

Populações e comunidades são influenciadas por mudanças ambientais no habitat de maneiras distintas. As populações são mais sensíveis às alterações ambientais e fatores ecológicos locais, enquanto comunidades são mais influenciadas por processos regionais (Supp e Ernest 2014). As espécies que compõem uma comunidade respondem às alterações no habitat, principalmente com base nas demandas de seus nichos. As comunidades podem apresentar uma dinâmica compensatória entre as populações que as compõem, o que as tornam menos sensíveis aos distúrbios do que populações de espécies. Os fatores que podem afetar negativamente a população de uma determinada espécie, podem criar condições favoráveis ao estabelecimento de populações de novas espécies, cujos requisitos de nicho sejam atendidos nas novas condições criadas. Essas predições foram apenas recentemente confirmadas, para grupos de invertebrados e vertebrados, inclusive para aves (Supp e Ernest 2014).

Em uma escala local, as populações são influenciadas pelas características do habitat (Durães *et al.* 2005, Josens *et al.* 2009) e o aumento na complexidade estrutural ambiental implica diversas maneiras de exploração dos recursos, permitindo a um maior número de espécies realizarem seus nichos (Bazzaz 1975). As variações na heterogeneidade de habitats também podem influenciar a composição de assembleias de espécies, uma vez que as variações nas características do habitat determinam quais espécies podem ocorrer em determinado local, dependendo da disponibilidade de locais para abrigo, reprodução e alimentação (Silva *et al.* 2010) (veja Lassau e Hochuli 2004, Durães *et al.* 2005). A heterogeneidade em ambientes terrestres geralmente é baseada na estrutura física da vegetação, que serve como base para o estabelecimento da vida animal (Huston 1979), ou na estrutura física do ambiente estudado (Lassau e Hochuli 2004).

Em áreas úmidas, as variações nos atributos da paisagem, como variações na profundidade da água, no tamanho ou área do ambiente aquático e no grau de isolamento, também influenciam a composição de assembleias de espécies nos ambientes aquáticos (Accordi e Hartz 2006, Gawlik e Crozier 2007, Johnson *et al.* 2007, Sebastián-González e Green 2014, Guadagnin *et al.* 2009, Gimenes e Anjos 2006). Áreas úmidas são importantes para a biota, pois fornecem habitats para espécies de vários grupos taxonômicos, além de serem consideradas um dos ecossistemas mais produtivos do mundo (Blanco 1999, Gatto *et al.* 2008), contribuindo também para a biodiversidade (Junk *et al.* 2014). Atualmente as áreas úmidas estão sendo consideradas entre as mais ameaçadas no mundo (Junk *et al.* 2014). A Convenção Sobre Áreas Úmidas de Importância Internacional enfatizou a importância de áreas úmidas como habitats para aves aquáticas, pois estas áreas servem de sítios de alimentação, nidificação e refúgio para estas aves, além de oferecerem abrigo durante o período de muda e migração anual (Blanco 1999, Gatto *et al.* 2008, Scherer *et al.* 2011). Existem diversas terminologias que se referem às aves aquáticas, porém neste trabalho utilizaremos o conceito proposto pela Convenção Ramsar, considerando aves aquáticas como “aves ecologicamente dependentes de áreas úmidas” (Accordi 2010).

Cerca de 20% do território brasileiro é coberto por diversos tipos de áreas úmidas (Junk *et al.* 2014). Considerando somente a Bacia Amazônica, várzeas (água-branca) e igapós (água-preta) cobrem aproximadamente três quartos dos 800.000 km^2 de habitats aquáticos associados com os rios amazônicos de tamanho médio e grande (Melack e Hess 2010). Ambas várzea e igapó têm alta diversidade de plantas herbáceas (Piedade *et al.* 2010), além de serem as florestas mais ricas em espécies do planeta (Pires e Prance 1985, Ayres 1993, Wittmann *et al.* 2006). Porque os sistemas de água-branca têm maior produtividade (Melack e Forsberg 2001), a riqueza de espécies de aves aquáticas e as abundâncias de indivíduos nas populações são esperadas serem diferentes daquelas de águas-pretas e apresentarem gradientes na composição de espécies, por exemplo, devido às diferenças entre lagos, nas características físicas (forma, profundidade, transparência da água), riqueza de habitats e produtividade (Cintra 2012, Cintra 2015). O que ainda precisa ser estabelecido é como as populações de aves aquáticas respondem individualmente às variações nas características físico-químicas e biológicas e sob escala local e regional.

Na Amazônia brasileira os principais sistemas aquáticos existem de acordo com os tipos de rios: rios de água preta, rios de água clara ou cristalina, e rios de água branca ou barrenta. A variação na coloração também representa variações físico-químicas nas águas dos rios da bacia Amazônica, como pH, transparência, condutividade e quantidade de nutrientes (Sioli 1985, Cintra 2012). Rios de água branca possuem maiores quantidades de nutrientes em suspensão do que rios de água cristalina e preta, devido à alta carga de sedimento que é transportada em suas águas, enquanto os rios de água preta são os mais pobres em nutrientes, sendo mínima a quantidade de sedimento transportada em suas águas (Sioli 1985, Melack e Hess 2010).

As aves aquáticas desempenham importantes funções nos sistemas ecológicos dos quais fazem parte, uma vez que podem dispersar organismos e sementes, que eventualmente podem se aderir à plumagem ou serem regurgitados e defecados por estas aves, além de contribuírem para a ciclagem de nutrientes nos ecossistemas aquáticos (Soares e Rodrigues 2009). De acordo com Blanco (1999), cerca de 30% de toda a energia consumida pelas aves é liberada para o ambiente em forma de resíduos. Além disso, estas aves são consideradas predadoras de topo em cadeias alimentares ecológicas nos ecossistemas aquáticos e podem controlar as populações de níveis tróficos inferiores (Steinmetz *et al.* 2003).

A abundância e a composição de espécies de aves aquáticas apresentam variações sazonais e anuais, tanto numa escala local quanto numa escala regional (López de Casenave e Filipello 1995, Romano *et al.* 2005, Josens *et al.* 2009). As flutuações nas abundâncias das espécies de aves podem ser explicadas pelos processos populacionais (por exemplo, variações nas taxas de natalidade e mortalidade) e também por processos de migração dentro e entre habitats (Blake e Loiselle 1991, Poulin *et al.* 1993, Josens *et al.* 2009). Localmente, a abundância de aves aquáticas depende das características do habitat, como a profundidade da água, o tamanho do corpo d’água, os atributos físicos e químicos e também do isolamento geográfico do corpo d’água (Canepuccia *et al.* 2007, González-Gajardo *et al.* 2009, Josens *et al.* 2009, Sebastián-González e Green 2014). Zonas úmidas cujas concentrações de nutrientes são maiores (produtividade maior) geralmente apresentam abundâncias de aves e riqueza de espécies maiores (Hoyer e Canfield 1994, Josens *et al.* 2009).

Inúmeros estudos buscaram compreender as relações das espécies de aves aquáticas com os atributos de seus habitats, principalmente no Hemisfério Norte. Na Dinamarca, foi demonstrado que o nível da água influencia a abundância de patos, sendo que a abundância das espécies aumentava com a elevação do nível da água (Boertmann e Riget 2006). Uma relação semelhante foi encontrada em estudo realizado no Canadá, onde foi demonstrado que a abundância de *Ixobrychus exilis* (Aves: Ardeidae) reduziu drasticamente após a redução do nível da água do lago, devido ao rompimento de um dique. A abundância da espécie aumentou um ano após o reparo do dique, quando o nível da água retornou à normalidade, demonstrando que o nível da água é um fator determinante da abundância desta espécie (Jobin *et al.* 2009). Porém, a profundidade dos corpos d'água não influencia positivamente todas as espécies de aves aquáticas, como demonstrado em um outro estudo na província de Manitoba, Canadá, onde quatro espécies tiveram um aumento em suas densidades à medida que a profundidade da água aumentava, enquanto a densidade de duas outras espécies reduziu com o aumento da profundidade (Baschuk *et al.* 2012).

Além da profundidade, o tamanho do corpo d'água (área), atributos físico-químicos e vegetação marginal são fatores determinantes da abundância das espécies de aves aquáticas. Em um estudo realizado em sistemas lacustres no estado de Wisconsin, Estados Unidos, foi demonstrado que o tamanho do lago e o pH da água são fatores determinantes da riqueza de espécies de aves piscívoras, sendo que os lagos maiores e com pH elevado apresentaram a riqueza de espécies mais alta (Newbrey *et al.* 2005). Em outro estudo realizado no estado da Flórida, Estados Unidos, evidenciou-se que as abundâncias de três espécies de aves aquáticas (*Ixobrychus exilis*, *Porphyrio martinica* e *Aramus guarauna*), que também ocorrem em território brasileiro, aumentavam em lagos com maior e mais diversa cobertura vegetal em suas margens (Alexander e Hepp 2014). Além disso, também foi demonstrado em um estudo no estado de Mississippi, Estados Unidos, que a presença de *Ixobrychus exilis* e *Podilymbus podiceps* (outra espécie com ocorrência no Brasil) estava relacionada ao tipo de cobertura vegetal do sistema aquático estudado, sendo que estas espécies ocuparam os sítios com predominância de vegetação aquática emergente e estando ausentes daqueles sítios com cobertura vegetal lenhosa (Darrah e Krementz 2010).

Na América do Sul, alguns estudos também demonstraram como as características do habitat influenciam a ocorrência e abundância de aves aquáticas. Um trabalho realizado na Argentina mostrou que a ocorrência de *Phalacrocorax gaimardi* estava relacionada à profundidade e à produtividade da costa, sendo que a espécie estava ausente nos locais cuja profundidade era maior e presente nas áreas mais próximas à costa onde a produtividade era alta (Millones e Frere 2012). Uma correlação forte entre a produtividade do sistema aquático e a abundância das espécies de aves aquáticas também foi encontrada em um estudo no lago Los Padres, Argentina, mostrando que a abundância das aves aquáticas aumentou à medida que as concentrações de Nitrogênio e Fósforo aumentaram no lago (Josens *et al.* 2009). González-Gajardo *et al.* (2009), em seu trabalho no Chile, evidenciaram a área da zona úmida e as flutuações no nível da água como as variáveis mais importantes na determinação da abundância das aves aquáticas.

No Brasil, as aves aquáticas têm sido objetos de estudo há anos, principalmente na região sul e sudeste. Os estudos conduzidos no Brasil com aves associadas aos ambientes aquáticos abordaram aspectos de comportamento (Gimenes e Anjos 2007, Henrique e Piratelli 2008, Moralez-Silva *et al.* 2010), dieta (Naves e Vooren 2006), reprodução (Gianuca 2007, Hogan *et al.* 2010, Rodrigues *et al.* 2010), uso do habitat (Alves *et al.* 2012, Pinto *et al.* 2013, Scherer *et al.* 2013) e levantamento de espécies em diversas regiões do país (Dias e Burguer 2005, Rodrigues e Michelin 2005, Accordi e Barcellos 2006, Araujo *et al.* 2006). Outros trabalhos avaliaram a composição e estrutura da assembleia de aves aquáticas em ambientes naturais (Rubim 2013) e artificiais (Scherer *et al.* 2011), e também como a composição e abundância de espécies variam em função dos atributos do habitat e da paisagem circundante (Guadagnin e Maltchik 2007, Guadagnin *et al.* 2009).

Apesar da grande área correspondente às áreas úmidas na Amazônia brasileira, poucos estudos foram realizados com aves aquáticas na região (veja Krannitz 1989, Cintra *et al.* 2007a, Cintra 2012, Zarza *et al.* 2013, Cintra 2015). O estudo realizado em 54 lagos de água branca nas Reservas de Desenvolvimento Sustentável Mamirauá e Amanã (Amazonas, Brasil) mostrou que a composição de espécies de aves aquáticas pode variar entre lagos distribuídos sobre uma grande área, uma vez que as características físico-químicas de cada corpo d’água também podem variar espacialmente. As assembleias de aves aquáticas e aves piscívoras, um subgrupo das aves aquáticas e investigado separadamente destas, apresentaram comportamentos diferentes em relação à forma dos lagos de água branca investigados neste estudo. Foi demonstrado que a riqueza e abundância de aves aquáticas diminuíam à medida que a forma do lago ficava mais complexa (de arredondada à dendrítica), contrariando a hipótese central do estudo, pois era esperado que lagos com formas complexas abrigassem maior diversidade de espécies. As abundâncias das aves piscívoras não foram influenciadas pelo formato dos lagos, entretanto a riqueza de espécies também foi menor nos lagos cujos formatos eram mais complexos. O padrão encontrado poderia ser entendido levando em consideração a competição por espaço por aves aquáticas em épocas de escassez de recursos alimentares (por exemplo, peixes por estarem dispersos em função do período de cheias). Em lagos alongados as distâncias entre as margens dos lagos são menores, permitindo que uma dada ave territorial (garça, martim-pescador e outros) alcance rapidamente a margem oposta para defender seu território em caso de um outro indivíduo aparecer, dificultando assim o estabelecimento de novos colonizadores. O resultado é a redução local na abundância e riqueza de espécies (Cintra *et al.* 2007a).

Em sistemas aquáticos de água preta, como no Arquipélago de Anavilhanas, na Amazônia Central, dois estudos foram realizados com assembleias de aves, incluindo diversas variáveis ecológicas (Cintra *et al.* 2007b, Cintra 2012). O trabalho pioneiro fez o levantamento da avifauna presente nas ilhas do Parque Nacional de Anavilhanas e na porção de floresta de terra-firme adjacente, também pertencente à unidade de conservação (Cintra *et al.* 2007b). A composição da assembleia de aves dessas duas áreas do parque foram comparadas e o grau de similaridade entre elas foi avaliado, encontrando-se diferenças significativas, havendo espécies de ocorrência restrita às ilhas e outras restritas à floresta de terra-firme, evidenciando os efeitos das características espaciais do habitat sobre a composição de espécies (Cintra *et al.* 2007b).

Em um estudo mais recente realizado no Arquipélago de Anavilhanas, foi investigado como a composição da assembleia de aves aquáticas se comportava em relação às características físico-químicas dos lagos que existem nas ilhas (Cintra 2012). De uma forma geral, a composição da assembleia de aves aquáticas variou ao longo dos gradientes ecológicos do Arquipélago, como a profundidade dos lagos, riqueza de habitats marginais, grau de isolamento e transparência da água. A riqueza e abundância das aves aquáticas foram maiores nos lagos mais rasos, provavelmente por causa da maior facilidade para as espécies detectarem e capturarem as presas nesses locais. Como esperado, em lagos mais próximos às margens do rio a riqueza de espécies foi maior, devido à proximidade com uma possível fonte colonizadora, confirmando predições da Teoria de Biogeografia de Ilhas de MacArthur e Wilson (Losos e Ricklefs 2009, Gotelli 2009, Townsend *et al.* 2010). Um resultado inesperado foi a diminuição da riqueza de espécies em águas cuja transparência era maior. O contrário era o esperado, pois a transparência poderia favorecer as espécies visualmente orientadas no sucesso de forrageio. O atributo mais importante relacionado à riqueza e abundância de aves aquáticas foi a riqueza de habitats marginais, representada pela variação espacial nos tipos de micro-habitat (vegetação) nas bordas dos lagos. Nos lagos onde havia maior riqueza de habitats, o número de espécies e de indivíduos também foi maior. Diferente do trabalho realizado em lagos de água branca, a assembleia de aves aquáticas não foi influenciada pelo formato dos lagos, talvez porque em Anavilhanas a maioria dos lagos tem formato similiar, tendem a ser elípticos, e análises para o subgrupo das aves piscívoras não foram realizadas neste estudo (Cintra 2012).

A maioria dos trabalhos realizados na região foram conduzidos a nível de assembleias de espécies (Cintra *et al.* 2007a, Cintra 2012, Cintra 2015) e, como demonstrado no trabalho de Cintra *et al.* (2007a), as assembleias de aves aquáticas e assembleias de aves piscívoras, podem responder diferentemente às variações nos atributos do habitat em sistemas de água branca na Amazônia, mostrando diferenças no uso do habitat pelas espécies. Em sistemas aquáticos de água preta ainda é pouco conhecido, a nível populacional, como e quais das espécies de aves piscívoras são influenciadas pelas variações nas características dos lagos. Além disso, foi demonstrado em um estudo recente que populações são mais sensíveis às variações no habitat do que assembleias de espécies (Supp e Ernest 2014). Neste estudo, realizado a partir de dados publicados com comunidades de animais terrestres (aves, mamíferos, répteis, aracnídeos e insetos) em todos os continentes, demonstrou-se que comunidades eram mais resistentes aos efeitos de manipulações naturais e artificiais no ambiente, pois tendiam a apresentar uma dinâmica compensatória entre as populações de espécies que a compunham. Contrastando com os resultados a nível de comunidades, as espécies responderam rapidamente às manipulações (Supp e Ernest 2014). Trabalhos realizados a nível de assembleias de espécies podem obscurecer como as populações de aves aquáticas respondem individualmente às mudanças ambientais e ecológicas (Rubim 2013). Portanto, compreender as relações entre as variações simultâneas de mais de um fator ecológico em relação a variações nas abundâncias de cada espécie de ave aquática, avaliando as influências de atributos de lagos em populações, é importante para conhecer mais especificamente se existem padrões de uso de habitat por elas. Esse tipo de informação ajuda a guiar ações e políticas de manejo em ambientes naturais protegidos e aqueles manejados pelo homem, além de fornecer dados sobre a qualidade ambiental, devido à presença ou ausência de certas espécies no sistema estudado (Rodrigues e Michelin 2005). O presente estudo é um dos primeiros trabalhos que analisa em nível populacional como as características de lagos de água preta, localizados exclusivamente em ambientes de água preta (igapó), influenciam a ocorrência e abundância de espécies de aves piscívoras.

As aves piscívoras são amplamente distribuídas na bacia amazônica, além de serem boas colonizadoras e oportunistas no uso de ambientes aquáticos (Stotz *et al.* 1996, Cintra 2012). Portanto, a previsão central deste estudo é que haverá pouca variação na ocorrência e abundância das aves piscívoras ao longo dos lagos no Arquipélago de Anavilhanas.

Entretanto, os lagos variam em seus atributos limnológicos, riqueza de habitats e grau de isolamento. Porque as espécies de aves piscívoras diferem em suas preferências e habilidades de colonizar e usar esse complexo sistema com lagos de água preta, relações diretas no nível local são previstas, entre outras, o aumento na abundância de aves com aumento em cada um dos atributos dos lagos (transparência da água, produtividade, e riqueza de habitats), e a nível regional aumento na abundância das aves em lagos mais isolados.

OBJETIVO GERAL

Avaliar os efeitos das características ambientais de lagos de água preta sobre a ocorrência e abundância das espécies de aves piscívoras no Arquipélago de Anavilhanas.

OBJETIVOS ESPECÍFICOS

1) Registrar as espécies de aves piscívoras presentes nos lagos do Arquipélago e determinar suas as abundâncias;

2) Avaliar os efeitos de nove variáveis, sendo quatro físicas (profundidade, transparência da água, forma e área do lago), duas químicas (concentrações de nitrogênio e fósforo), duas geográficas (distância da margem do rio e distância do lago mais próximo) e uma biótica (riqueza de habitas marginais), sobre a ocorrência e abundância das espécies de aves piscívoras.

3) Testar duas hipóteses: (1) As variações locais nas características dos lagos devem influenciar a ocorrência e abundância de populações de diversas aves aquáticas em um sistema tropical de águas pretas (igapó), composto de lagos de águas pretas; (2) As variações no grau de isolamento dos lagos, a nível regional dentro do arquipélago, influenciam a ocorrência e abundância de aves aquáticas nos lagos.

Capítulo 1

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Effects of Black Water Lake Features on the Occurrence and Abundance of Fish-eating Birds in the Anavilhanas Archipelago, Rio Negro, Central Amazonian, Brazil

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Abstract.–The influence of blackwater lakes characteristics on the occurrence and abundance of 12 fish-eating birds species in the Brazilian Amazon at the population level was evaluated. The central hypothesis was that local variations in lake characteristics should influence the occurrence and abundance of aquatic bird population in a tropical blackwater flooded forest system. An additional hypothesis was tested, the variation in the degree of isolation of the lakes, influence the occurrence and abundance of lake-living waterbirdsl. Bird surveys were conducted from November to December 2007 in 45 lakes within islands along 100 km of the Anavilhanas Archipelago, Rio Negro, Central Brazilian Amazonia. Multiple linear and multiple logistic statistical models were used to test the effects of nine variables, four physical, two chemical, two geographical, and one biotic, on the occurrence and abundance of 12 species of fish-eating birds. It was found that lake depth and water transparency influenced the occurrance and abundance of Ringed-Kingfisher (*Megaceryle torquata*) and abundance of Osprey (*Pandion haliaetus*), Cocoi Heron (*Ardea cocoi*) and Snowy Egret (*Egretta thula*). Lake isolation influenced the occurrence of Yellow-billed Tern (*Sternula superciliaris*) and Striated Heron (*Butorides striata*), and habitat richness has affected most of the fish-eating birds species. The results indicate that lake limnological and physical attributes are determinants of spatial variation in abundance and occurrence of fish-eating birds in the blackwater lake systems in central Brazilian Amazon.

Key words.–Amazonia, Anavilhanas, fish-eating birds, habitat use, lake characteristics, waterbirds.

WATERBIRDS IN ANAVILHANAS

The analysis of relationships between the number of species or species richness at the local level, and that of the regional assemblages in which they are embedded, is central to ecology (Ricklefs and Schluter 1993; Willig *et al.* 2003). In addition, locally abundant species may often have more extensive distributions, with the replacement of individuals via immigration from a regional pool of species, as predicted by the Neutral theory, or influenced by local ecological factors as predicted by Niche theory. The theoretical debate over which process is more important, influencing the variation in abundance of individuals and species composition in a community, still persists (Thompson and Townsend 2006).

Populations and communities are influenced by environmental changes in the habitats they occur: populations are more sensitive to environmental changes and local ecological factors, while communities are more strongly influenced by regional processes (Supp and Ernest 2014). The species that make up a community respond to changes in habitat, based mainly on the demands of their niches. The potential for compensatory dynamics between the populations of the various species that compose them, means that communities are generally less sensitive to overall disturbance than populations of individual species. Factors that may negatively impact the population of one species, can create favorable conditions for the establishment of new populations of another whose niche requirements are better met by the newly-created conditions. Such ideas have been recently confirmed for a variety of invertebrate and vertebrate taxa, including birds (Supp and Ernest 2014).

Wetlands are biotically important because they provide habitats for species of various taxonomic groups, and are considered among the most productive ecosystems in the world (Blanco 1999; Gatto *et al.* 2008). Hence they are very important for maintaining biodiversity (Junk *et al*. 2014). Currently loss of wetland is extremely rapid and they are widely considered among the most endangered habitats in the world (Junk *et al*. 2014).

Some 20% of Brazilian territory is covered by wetlands of various forms (Junk *et al.* 2014). In the Amazon basin, seasonally-flooded forests and associated vegetation on white-water (várzea) and blackwater (igapó) rivers constitute approximately three-quarters of the 800.000 km^2 of aquatic habitats associated with medium- and large-sized Amazonian rivers (Melack and Hess 2010). Both várzea and igapó have high diversity of herbaceous plants (Piedade *et al*. 2010), and are the most species-rich forests in the planet (Pires and Prance 1985; Ayres 1993; Wittmann *et al*. 2006). Because white-water systems have higher productivity than those involving black-water (Melack and Forsberg 2001), it is expected that (i) within communities, the number of species of waterbirds and their individual abundance will differ between the two systems, and that (ii) within systems there will be gradients in species composition due to differences in lake physical characteristics (shape, depth, water transparency), habitat richness and productivity (Cintra 2012; Cintra 2015). What still needs to be established is how waterbird populations individually respond to changes in the physical-chemical and biological characteristics at the local and regional scale.

Waterbirds play important roles in the ecological systems. This includes dispersing organisms and seeds (either by adherence to plumage or feet, or their regurgitation or defecation), and contribution to nutrient cycling in aquatic ecosystems (Soares and Rodrigues 2009). According to Blanco (1999), about 30% of the energy consumed by waterbirds is released back into the environment as waste. Furthermore, waterbirds are considered top predators in aquatic ecosystem food chains, with capacity to control populations of species at lower trophic levels (Steinmetz *et al.* 2003).

A study of 54 whitewater lakes in the Mamirauá and Amanã sustainable development reserves (Amazonas state, Brazil), showed that the species composition of waterbird communities can vary between lakes, and that this is associated with spatial-variance in physical characteristics of the water bodies (Cintra *et al.* 2007). The authors found that waterbirds and the assemblage of fish-eating birds showed different responses to the shape of the investigated white-water lakes. For waterbirds, species richness and bird abundance decreased as lake shape became more complex (rounded to dendrictic). This was contrary to the central hypothesis of the study, which predicted that lakes with complex shapes would support higher bird species diversity. However, for fish-eating birds, abundance was not influenced by lake shape, though species richness was lower in lakes whose shapes were more complex. This unexpected pattern could be explained in terms of competition for space by waterbirds in times of food shortage (e.g., fish are more dispersed during floodings). In elongated lakes, distances between the banks of the lakes are smaller, allowing a given territorial bird (herons, kingfishers and others) to reach the opposite bank quickly to defend its territory in the event that another individual appears, so hindering establishment of new settlers. The result is a local reduction in the abundance and species richness in long-thin to dendrictic lakes (Cintra *et al*. 2007).

In blackwater aquatic ecosystems, how physical-chemical characteristics of lakes on islands of the Anavilhanas Archipelago, Central Amazonia, affect waterbird community composition was studied by Cintra (2012). In general, the waterbirds community composition has varied over the ecological gradients of the archipelago, as lake depth, lake margin habitat richness, degree of lake isolation and lake water transparency. Waterbird richness and abundance were greater in shallower lakes, probably because it was easier to detect and catch prey in such locations. As expected, bird species richness in lakes closer to the river was higher, as the river provided a source of potential colonizers, confirming predictions of the Island Biogeography theory of MacArthur and Wilson (Gotelli 2009; Losos and Ricklefs 2009; Townsend *et al*. 2010). An unexpected result was the decrease in species richness in lakes with water of greater transparency. The opposite was expected because greater transparency could favor foraging success in visually-oriented species. The most important attribute associated with waterbird richness and abundance was richness of lakeshore habitats (in terms of the spatial variation in vegetation micro-habitat types along the lakes margins). In lakes where there was a greater micro-habitat richness, the numbers of waterbird species and individuals were higher. Unlike the waterbird communities on white-water lakes, the blackwater waterbird community was not influenced by the lake shape, possibly because in Anavilhanas lakes are largely elliptical, and analysis for the subgroup of fish-eating birds were not performed by Cintra (2012).

Most studies in the Amazon region have been conducted at the species assemblage level and the communities of waterbird and fish-eating birds, may respond differently to changes in habitat atributes, both in Amazonian white- and black-water systems, illustrating differences in habitat use by species concerned (Cintra *et al*. 2007; Cintra 2012; Cintra 2015). Blackwater aquatic systems are still little known at the avian population level, and it is not known how waterbird populations are influenced by variations in the characteristics of lakes, nor which species of fish-eating birds are most affected. Therefore, it is important to understand the relationships between abundance of each species of waterbird, and several, simultaneously varying, ecological factors in lake-based systems. Of particular importance is to do this for patterns of habitat usage and for patterns of habitat change. This type of information helps guide management actions and policies in protected natural environments and those managed by man, as well as providing data on environmental quality due to the presence or absence of certain species in the studied system (Rodrigues and Michelin 2005). Accordingly, and for the first time in the Brazilian Amazon, this study looks at the population level whether the characteristics of blackwater lakes, located exclusively in blackwater environments (igapó flooded forest), influence the occurrence and abundance of species of fish-eating birds.

Since habitat features (lakes) influence waterbird species abundance on a local scale and because species populations are probably more sensitive to habitat attributes than species assemblages, we evaluated the effects of limnological and geographical atributes of blackwater lakes on occurrence and abundance of species of fish-eating birds in the Anavilhanas Archipelago, Brazilian Amazonia. In the current study, the fish-eating bird species investigated comprised of cormorants, anhingas, egrets, herons, osprey, terns and kingfishers. The aims of our study were: 1) identify and determine the abundances of species of fish-eating birds present on the archipelago lakes; 2) evaluate the effects of nine variables - four physical (depth, water transparency, lake shape and lake area), two chemical (nitrogen and phosphorus concentrations), two geographical (distance from the river margins, and distance to nearest neighboring lake) and biotic (lake marginal habitat richness) on the occurrence and abundance of species of fish-eating birds.

Based on these variables, we test two hypotheses: (1) local variations in lake characteristics should influence the occurrence and abundance of populations of fish-eating birds in a tropical blackwater lakes system within black-water flooded forest (igapó); (2) changes in the degree of lake isolation, and their location within the archipelago, influence the occurrence and abundance of waterbirds populations.

Fish-eating birds are widely distributed in the Amazon basin, and are strong colonizers and largely opportunic in their use of aquatic environments (Stotz *et al*. 1996; Cintra 2012). Consequently, a key prediction of this study is that there will be little variation in the occurrence and abundance of fish-eating birds between the lakes of the Anavilhanas Archipelago. However, the lakes vary in their limnological attributes, habitats richness composition at their margins and degree of isolation. Because the species of fish-eating birds differ in their preferences and abilities to colonize and use this complex blackwater lakes system, direct relationships at the local level are predicted, including an increase in bird abundance of with an increase in the following attributes - water transparency, productivity and lake habitat richness, and, at the regional level, an increase in the abundance of birds in more isolated lakes.

METHODS

Study Area

The study was carried out in the lakes of the Anavilhanas Archipelago, the second biggest fresh water archipelago in the world (Fig. 1, between 2°03’ S and 3°02’ S, 60°22’ W and 61°12’ W). The archipelago is located in the channel of Rio Negro, and is part of the Anavilhanas National Park, the southern border of which is located 40 km northwest of Manaus, the Amazonas state capital (Nakazono and Piedade 2004; Scabin *et al.* 2011; Cintra 2012), then extending for 100 km upstream (Nakazono and Piedade 2004). Currently the park is managed by the Chico Mendes Institute for Conservation of Biodiversity (ICMBio).

Anavilhanas National Park has an area of some 350,000 ha, which includes the archipelago within Rio Negro itself, and an extensive and continuous area of upland forest on the river’s left banks that covers an area around 250,000 ha. There are some 430 islands in the archipelago (Scabin *et al*. 2011), with a total area of 100,000 ha. Within this, coverage is dominated by forest seasonally flooded by nutrient-poor blackwater (Sioli 1985; Melack and Hess 2010; Cintra 2012). Within the islands, there are approximately 70 lakes (Fig. 1).

At Anavilhanas the average annual temperature varies between 24-26^0 C, and the average annual rainfall varies between 1750-2500 mm (Scabin *et al*. 2011). The rainy season is from November-May and the dry season from June-October (Cintra 2012). The formation of the Anavilhanas Archipelago is related to the large sediment load carried by the Rio Branco into the Rio Negro (Sioli 2006). The resulting islands have elongated, narrow shapes (Sioli 2006; Scabin *et al*. 2011), with sedimentation from the current occuring on one side and erosion on the other. The appearance of the vegetation on the islands changes with their size (Scabin *et al*. 2011). Generally, on larger islands there is a predominance of tall trees (up to 25 meters in height), though up to three vegetation strata may be observed. Smaller islands may be totally submerged during the flooding period and on these lower growth predominates (Scabin *et al*. 2011).

Sampling was carried out in 45 lakes within the archipelago, with each being marked with numbers on the map and then selected via a random draw. Some lakes were difficult to access, so we conducted a second draw to replace these lakes with more accessible ones (Fig. 1).

Data Collection

Data collection was performed on 45 lakes in the archipelago, between 14 November and 17 December 2007, using visual surveys between 06:00 and 18:00 hr.

Bird Species Surveys

Bird species surveys were conducted via two visits to each lake, one in the morning (06:00-10:00 hr), and another in the afternoon (14:00-18:00 hr), so maximizing sampling effort while minimizing the possibility that species most active only during one part of the day would be missed. Bird species included in this study are those that spend the majority of their time on the margins of lakes and rivers, have medium to large bodies, and easy detection and identification, thus minimizing the possibility of false absences (Mackenzie and Royle 2005).

In addition to the first bird species survey, water sample collection, habitat quantification and recording lake physical parameters were recorded. In both morning and afternoon survey periods, each lake was completely circumnavigated with an aluminum boat with a 15 HP engine, travelling approximately 20 m from the lake shore at a speed of 15-20 km/h (with boat speed controlled using a Garmin GPS-etrex). The birds were identified in the field, through direct observation with binoculars, and field guides when necessary. In the analyses we used values from whichever survey (morning or afternoon) gave the greatest number of individuals for each species.

Sampling Protocol

To record the data for each sampled lake, field records were made in a form containing: a) a list, in alphabetical order, of the bird species that could be present; b) habitat types; c) cells in which to record key parameters (lake name, geographical coordinates, water depth and transparency). For data relating to the shape of the lake, the area, distances to the river margins and to the nearest neighboring lake, use of computer programs was needed (see below), so these data were subsequently recorded along with the field data directly into Excel spreadsheets. To this were added the concentrations of nitrogen and phosphorus from laboratory analyses.

During the surveys both species and numbers of individuals were recorded, plus nature of lakeshore and lake margin habitats (see below). Birds were recorded if on the shoreline. Birds fliying high or passing over the lakes were not recorded. Habitat types were recorded through direct observation, by a field assistant biologist experienced in habitat classification. With the boat moving, the field assistant looked at the shore of the lake every 10 seconds and recorded the type of habitat (vegetation type) on the field sheet (see above). While the bird species surveys were of short duration, this allowed the majority (64%) of the lakes in the archipelago to be sampled, and over a short time-frame that minimized seasonal variation, all of which enhanced sample representiveness and comparability. This field methodology minimizes duplication of records and consequente count overestimation and so is recommended for studies where capture and marking of birds is not possible. It also gives a snapshot of the system and can be compared with similar community-level studies conducted elsewhere in Amazonia.

After each morning bird survey, the team headed for the center of the lake, where geographic coordinates, lake depth and water transparency were recorded. A 50 ml sample of lake water was also made, from 10-20 cm below the surface, each lake sample stored in a unique sterile plastic bottle. Water samples were later sent for laboratory testing, to determine nitrogen and phosphorus concentrations.

Recording Habitat Types

The marginal vegetation and those located near the water were the only ones included because they are those most used by waterbirds (RC, unpublished data). Habitat types were named based on vegetation physiognomy and presence of dominant plant species, identified and described in previous studies in flooded areas of Amazonin flooded forests and also in the Anavilhanas Archipelago (Junk and Piedade 1997; Worbes 1997; Piedade *et al.* 2005; Cintra 2012). Habitat types were divided into the following categories: 1) Banks of wild rice (*Oryza perennis,* Poaceae); 2) Stands of igapó araçá bushes (*Eugenia inundata,* Myrtaceae); 3) Stands of carauaçu bushes (*Symmeria paniculata,* Polygonaceae); 4) Prevalence of macacarecuia (*Eschweilera tenuifolia,* Lecythidaceae); 5) Presence of fallen dead trunks; 6) Presence of standing dead trunks; 7) Secondary forest dominated by cecropia (*Cecropia* spp., Urticaceae); 8) secondary forest dominated by jauari palms (*Astrocaryum jauari*); 9) Sand Beach; 10) Stands of Solanaceous shrubs; 11) Igapó forest, dominated by arapari (*Macrolobium acaciifolium*), igapó macucu (*Aldina latifolia*), ipê (*Handroanthus barbatus* [=*Tabebuia barbata*]) and other species adapted to annual flooding; 12) clay beach lacking vegetation; 13) clay beach with with wild rice and Cyperaceae cover.

Collection of Physical and Chemical Data and Geographical Parameters

Depth. This was measured in the lake center, using a 20m nylon cord, marked at half meter intervals, positioned perpendicularly to the lake surface, with a 5 kg weight attached to the lower end. Depth values were recorded when the weight touched the lake bottom.

Transparency. This was also measured at the lake center using a Secchi Disk, perforated in the center and attached to a 5 kg weight on the same cord used to measure depth. The transparency value was recorded when the disk could no longer be seen.

Nitrogen and Phosphorus. Total Nitrogen (TN) and Total Phosphorus (TP) concentrations were used as proxy indices for lake productivity (Trevisan and Forsberg 2007). Water samples collected from each lake (See Sampling Protocol section) were sent for analysis in the INPA (National Institute for Amazonian Research) Geosciences Laboratory, where TN and TP values were calculated by simultaneous analysis (Valderrama 1981).

The variable "productivity" was evaluated since there is a strong correlation between nitrogen (N) and phosphorus (P) and aquatic ecosystems primary productivity (Araripe *et al.* 2006). Phosphorous is considered the limiting factor for fertility in most lakes (Araripe *et al.* 2006; Ricklefs 2009), but in Central Amazonian lakes, productivity is mainly controlled by nitrogen (Trevisan and Forsberg 2007). Trevisan and Forsberg (2007) found significant relationships between concentrations of nitrogen and phosphorus and α-chlorophyll. Consequently, the total concentrations of nitrogen and phosphorus in the lakes of Anavilhanas, were used as productivity ratios for this study.

Lake area and shape, distance to river margins, distance to nearest lake. The area and the perimeter length of the lakes were estimated using Global Mapper software 8.00 and georeferenced satellite images of the study area. The distance from the center of each lake to the nearest portion of river margins of the Rio Negro, and the distances from the center of each lake to its nearest neighboring lake were also estimated using this program. Lake shape was calculated using the Patton Shape Index (SI) (Patton 1975), adapted to metric units using the following formula:

$SI = Q / 200 (\pi A)^{0.5}$

Where SI = Lake Shape Index; P = lake perimeter in kilometers; π = 3.14; A = Lake area in square kilometers. According to this formula, for lakes whose shape is circular SI = 1; lakes with other formats have the SI with values >1, reaching SI values to 6, depending on the complexity of the shape of the lake.

Statistical Analysis

Statistical analyzes were made in Systat Program-12 (Wilkinson 2007). Initially, a Pearson correlation analysis with independent variables was made to check which variables were significantly correlated (see Appendix 1 for results). The following variables were then used in the analysis: habitat richness, water transparency, water depth, lake area and shape, distance from lake to the nearest river margins, distance from current to nearest neighboring lake, nitrogen (N) and phosphorus (P) levels. The results of the Pearson correlation analysis showed strong correlation between the following variables: distance to the nearest neighboring lake and lake area; lake depth and habitat richness; lake shape and phosphorus concentration (P); habitat richness and lake area. To avoid the use of significantly correlated variables in the same statistical model, two models were used, with five variables used in the first and four variables used in the second. These were:

Model 1

bird species abundance x = constant + distance from closest river margins + lake depth + lake area + water transparency + lake form

Model 2

bird species abundance x = constant + habitat richness + distance to nearest neighboring lake + nitrogen concentration + phosphorus concentration

Multiple linear models were used to evaluate the effects of lake characteristics on the abundance (dependent variable) of each bird species. The multiple linear model is analytical technique that uses a single continuous relationship between the dependent variable (dependent variable), and two or more independent variables (predictors) that are also continuous (Hair Jr. *et al*. 2005; Gotelli and Ellison 2011).

Multiple logistic models (using the same two models above) were used to assess the effects of the lake characteristics (independent variables) on the occurrence (presence or absence) of bird species. This type of analysis is recommended in cases where the variable Y (dependent) is categorical (bird presence at lake = 1, absence = 0) (Hair Jr. *et al*. 2005; Gotelli and Ellison 2011).

RESULTS

Characteristics of Lakes

Lake areas ranged from 0.29 km^2 (Lake 26) to 60.64 km^2 (Lake 31). Lake shapes ranged from 1.183 (circular) to 2.749 (elliptical). Distances from the lake to the nearest river margins ranged from 0.306 kilometers (Lake 40) to 10.4 km (Lakes 5, 6), and distance to the nearest neighboring lake ranged from 0.688 km (Lakes 25, 26) to 6.3 km (Lakes 42, 43). Lake depths varied from 0.88 m (Lake 12) to 7.0 m (Lake 42), and water transparencies ranged from 0.47 m (Lake 25) to 1.1 m (Lakes 42, 46). For lake productivity, nitrogen concentration ranged from 0.18 (Lakes 21, 22) to 0.81 µmol l^{-1} (Lake 16), while phosphorus concentration ranged from 0.020 (Lakes 6, 18) to 0.060 µmol l^{-1} (Lake 25). Habitat richness of lake margin vegetation ranged from 3 (Lake 12) to 11 habitats (Lake 31).

Bird Surveys

We recorded 17 bird species with predominantly piscivorous diets, distributed in seven families, in the Anavilhanas Archipelago. However, only 12 of these formed part of the analysis of this study. These were: Anhinga (*Anhinga anhinga*), Great Egret (*Ardea alba*), Cocoi Heron (*Ardea cocoi*), Striated Heron (*Butorides striata*), Amazon Kingfisher (*Chloroceryle amazona*), Green Kingfisher (*Chloroceryle americana*), Snowy Egret (*Egretta thula*), Ringed Kingfisher (*Megaceryle torquata*), Osprey (*Pandion haliaetus*), Large-billed Tern (*Phaetusa simplex*), Neotropic Cormorant (*Phalacrocorax brasilianus*) and Yellow-billed Tern (*Sternula superciliaris*).

Abundances of individuals per species ranged from 0-24 individuals (Anhinga), 0-89 individuals (Great Egret), 0-23 (Cocoi Heron), 0-7 (Striated Heron), 0-11 (Amazon Kingfisher), 0-2 (Green Kingfisher), 0-4 (Snowy Egret), 0-6 (Ringed Kingfisher), 0-54 (Large-billed Tern), 0-8 (Osprey), 0-76 (Neotropic Cormorant) and 0-29 (Yellow-billed Tern).

There were five species which were not used in the analysis, their records was too low, and they were the following: Agami Heron (*Agamia agami*), Black-collared Hawk (*Busarellus nigricollis*), American Pygmy Kingfisher (*Chloroceryle aenea*), Green-and-rufous Kingfisher (*Chloroceryle inda*) and Rufescent Tiger Heron (*Tigrisoma lineatum*).

Effects of Lakes Features on the Abundance of Species of Fish-eating Birds

The abundances of Cocoi Heron, Ringed Kingfisher and Osprey were influenced by lake depth, being greater in deeper lakes, while Snowy Egret was more abundant in shallower lakes (Table 1, Fig. 2). Lake area influenced the abundance of Anhinga, Great Egret, Cocoi Heron, Snowy Egret, Ringed Kingfisher, Osprey, Large-billed Tern and Neotropic Cormorant. For all of these species, abundances values increased with larger lake area (Table 1, Fig. 3).

Ringed Kingfisher had an inverse relationship with water transparency, as abundance decreased as water transparency increased, indicating a preference of the species for lakes with more turbid water (Table 1, Fig. 4). The abundance of Ringed Kingfisher was also influenced by the shape of the lake, with a marked preference for lakes with more complex shapes (Table 1, Fig. 5).

Lakeshore habitat richness influenced the abundance of Anhinga, Great Egret, Cocoi Heron, Ringed Kingfisher, Osprey and Neotropic Cormorant, indicating that these species prefer lakes with rich marginal habitats (Table 1, Fig. 6). The distance to nearest neighboring lake influenced the abundance of Cocoi Heron and Osprey, which were more abundant in more isolated lakes (Table 1, Fig. 7). Osprey was also influenced by lake productivity (phosphorus concentration), indicating that this species prefers more productive lakes (Table 1, Fig. 8).

Effects of Lake Characteristics on the Occurrence of Species of Fish-eating Birds

Level of lake isolation, as represented by the distance of the lake to the nearest river margins, influenced the occurrence of Anhinga and Yellow-billed Tern, indicating that these species preferred lakes on islands closer to river margins. In constrast, Striated Heron appeared to prefer lakes more distant from the river margins (Table 2, Fig. 9). Lake depth was negatively correlated with the occurrence of Snowy Egret, indicating that this species prefers shallower lakes (Table 2, Fig. 10).

Lake area influenced the occurrence of Snowy Egret, indicating that this species prefers larger lakes (Table 2, Fig. 11). The incidence of Great Egret was correlated with lake shape, indicating that this species prefers lakes with more complex shaped (Table 2, Fig. 12).

Habitat richness influenced the occurrence of Yellow-billed Tern, indicating a preference for lakes with higher habitat richness along their shore (Table 2, Fig. 13). Anhinga occurrence was related to the isolation of the lake, indicating the preference of this species for more isolated lakes (Table 2, Fig. 14). With lake productivity (as measured by phosphorus concentrations) influenced the occurrence of Striated Heron, indicating a preference by this species for more productive lakes (Table 2, Fig. 15).

DISCUSSION

The results of this study show that populations of picivorous bird species can respond to habitat characteristics in ways that are different to species assemblies (Cintra 2012). This agrees with a recent general world-wide topical review for a variety vertebrates taxa (Supp and Ernest 2014). The current study also provides clear evidence that natural limnological heterogeneity of blackwater lakes in the Amazon can influence the occurrence, abundance and spatial distribution of species of fish-eating birds, at least in black-water-lakes in igapo black-water systems on the Rio Negro.

The Anavilhanas Archipelago provides a complex mosaic of lacustrine environments to study how blackwater lake characteristics influence Amazonian fish-eating bird populations. The current study has shown that in such systems physico-chemical, biological and geographical features of blackwater lakes influence the occurrence and abundance of fish-eating birds at both local and regional scale within the archipelago. Most of the assessed limnological variables influenced significantly the abundance or occurrence of species (or both). The results confirm most of our predictions, and indicate that species of waterbirds, although general and widely distributed in the Amazon basin are tracking the ecological characteristics of blackwater lakes, with individuals using areas according to their preferences, based on the biological needs of each species.

Lake depth positively influenced the abundance Cocoi Heron, Ringed Kingfisher and Osprey, and negatively that of Snowy Egret. Herons are known to catch their prey near the surface of the water (Sick 1997), and prefer shallow waters (Gawlik and Crozier 2007; Lantz *et al.* 2011), thus increasing the depth of the lake could impede foraging and negatively affect the abundance of relatively shorter-legged species in deeper lakes, as is the case of Snowy Egret, when compared to larger egretts. The pattern of Cocoi Heron showing higher abundance in deeper lakes, is probably explained by the fact that this heron has much longer legs than that of Snowy Egret. Therefore, Cocoi Heron can forage in deeper lakes and explore places that other heron species cannot reach. However, there is clearly a leg-limited depth limit for wading species such as herons, beyond which the abundance of such species begins to decline (Bancroft *et al.* 2002). In a study conducted in northern Florida Everglades, it was found that the largest species heron, Great Blue Heron (*Ardea herodias*), could forage in deeper areas than the smallest species, Great Egret (*Ardea alba*). However, when each reached its particular depth threshold, its abundance began to decline (Bancroft *et al.* 2002). In Anavilhanas Archipelago, Cocoi Heron was the largest species of heron recorded, and its water-depth threshold was higher than those of the other three heron species, giving a plausible explanation for the positive link between its abundance and increasing depth.

Kingfishers always capture prey close to the water surface (Remsen 1991), therefore, they should not be influenced by the depth of the water body. Nevertheless, in this study, Ringed Kingfisher abundance was greater in deeper lakes. A study of the habitat preference of four kingfisher species in southern Tanzania, found they captured prey from perches of different heights. Those using tallest perches were more abundant on the deeper sections of river as this prevented damage to the bird as it plunged after fish (Bonnington *et al.* 2007). Ringed Kingfisher is the largest species of kingfisher occurring in Brazil and usually forages from tall trees (> ten meters high). Although Ringed Kingfisher does not submerge completely, it submerges by a few centimeters to capture prey (Sick 1997). Thus, the increase in local abundance of this species in deeper lakes may be explained by the increased physical protection they provid time to striking birds. However, there is also a possibility that the deeper lakes have different fish species and the young of these are present in the shallower fringing waters in which kingfishers normally operate. Osprey abundance was also positively correlated with lake depth. The increase in local abundance of this species in deeper lakes is probably due to the fact that the species tends to concentrate fishing in open water and in the center of medium to large lakes, where the depth is greatest (Sick 1997; Washburn *et al.* 2014).

In a study conducted in eight wetlands in Chile, González-Gajardo *et al*. (2009) found that the area of wetland and fluctuations in water level were the most important variables in determining the abundance of birds, with waterbird diversity being highest in the largest and structurally most complex wetlands. Larger wetlands generally have higher habitat diversity, also increasing bird species richness (Paracuellos and Tellería 2004). These relationships were also found at Anavilhanas where lake area positively influenced the abundance of most species of fish-eating birds recorded in Archipelago: Anhinga, Great Egret, Cocoi Heron, Snowy Egret, Ringed Kingfisher, Osprey, Large-billed Tern and Neotropic Cormorant. On larger lakes, it is possible that inter- and intra-specific competition is reduced because of (i) the greater dispersion of individuals that increased bank length allows, and (ii) reduced overall competition that increased resource abundance species allows. Both would favor an increase in the local abundance of species. However, at least for our study area there are no studies showing some evidence that resources (food or fish) are also disproportionately more abundant in larger lakes. Although wetland size does correlate with avian species richness (Paracuellos and Tellería 2004; González-Gajardo *et al.* 2009), some species show preferences for smaller water bodies, while others prefer larger ones (Pescador and Peris 2009). In the current study, abundance of Osprey and Large-billed Tern was linked to an increase in lake area, and this probably occurred because the fishing style of both species is facilitated by larger lakes, as these birds usually fish across extensive spaces of open water (Remsen 1991). The species that were not influenced by lake area, Striated Heron, Amazon Kingfisher, Green Kingfisher and Yellow-billed Tern, are much smaller species than Osprey and Large-billed Tern. This, and their foraging ecologies, means they are unlikely to be influenced by the extent of open water. In summary, it seems that the relationships between lake area and bird abundance is species dependent.

Water transparency negatively influenced Ringed Kingfisher abundance. This corroborates with the findings of Remsen (1991), who reported that turbid waters reduce surface fish capture, due to reduced visability imparing capture success. However, the converse is also possible and in water with high transparency the predator is more visible to the prey. Under such circumstances Ringed Kingfisher prey-fish might avoid places where they would be easily caught. Such places would then be unattractive for the bird because of the difficulty of obtaining food there, thus reducing its local abundance. It is also possible that kingfishers use movements in the water, as well as images of fish, to locate their prey. If this is so, then success in feeding on shallow-swimming fish, may be little influenced by water turbidity.

Ringed Kingfisher abundance was also influenced by lake shape, with abundance increasing on lakes with more complex shapes (dendritic). The occurence of Great Egret was also positively correlated with this variable. These results contrast with the results obtained by Cintra *et al.* (2007) and Cintra (2012) in white-water and black-water lakes of, respectively, the Amanã/Mamirauá sustainable use areas and Anavilhanas. In the Amanã/Mamirauá study, fish-eating bird richness was lower in lakes with more complex (elongated and dendritic) forms, and species abundance was not influenced this variable (Cintra *et al.* 2007). In an earlier study at Anavilhanas, lake shape had no influence on waterbirds community composition, probably because there was little variation, with most lakes tending to be elliptical (Cintra 2012). Lakes with more complex shapes have more extensive banks and so more linear space on or from which birds can forage: either by virtue of more bankside vegetation (which would provide perches for such species as Ringed Kingfisher), or the presence of shallow water areas (which would serve as foraging sites for such species as Great Egret). Thus, it seems that, when biological resources are similar, the provision of more feeding sites are certainly the main factor for the increase in abundance of species of fish-eating birds.

Lake productivity, as measured by phosphorus concentration, was positively related to Osprey abundance and the occurrence of Striated Heron. These results contrasted with the study results at the level of communities in Anavilhanas (Cintra 2012), where the of lake-based waterbird assemblages was not influenced by system productivity. Such results confirm recent obervations that communities and populations can be affected differently by the same ecological factors (Supp and Ernest 2014). Other studies corroborate the results of this study, showing that the productivity of lakes positively influences the abundance of waterbirds (Josens *et al.* 2009; Epners *et al.* 2010; Cintra 2015). In the Everglades, a positive relationship has been demonstrated between nutrient concentration and availability of food for waterbirds (Crozier and Gawlik 2002). In Anavilhanas the most productive lakes may also have followed this pattern, harboring more fish and so favoring increased local abundance of fish-eating birds. Unfortunately, however, there are currently no studies at Anavilhanas that have investigated whether variations in the community composition, species richness and individual abundance of waterbirds populations are influenced by concomitant changes in fish communities.

In contrast to phosphorous, the other proxy variable for lake productivity, nitrogen concentrations, appeared not influence any of the species. Two species of kingfisher, Amazon Kingfisher and Green Kingfisher, were not influenced by any of the variables. Both phosphorous and nitrogen are limiting nutrients and known to control productivity of the Central Amazonian lakes (Trevisan and Forsberg 2007), but phosphorus is usually the key limiting factor for fertility in most lakes (Araripe *et al*. 2006). It is possible that, during the period of our study, productivity of lakes of Anavilhanas, was being controlled by phosphorus and not nitrogen. Further studies are needed to evaluate the direct and indirect effects of other limnological variables on kingfishers species, and how these are related to the occurrence and abundance of these birds.

One of the variables used to investigate the effect of lake distance from the nearest neighboring lake, correlated with the occurrence of Anhinga. It also positively influenced Cocoi Heron and Osprey abundance. The collection of data from this study was conducted at the end of low water season, when water level was at its lowest. However, such residual waterbodies are less scattered and more concentrated in more isolated perennial wetlands, as demonstrated in a study of the upper Rio Paraná floodplain (Gimenes and Anjos 2007). The same pattern may have occurred in Anavilhanas lakes in the lowest-water period, leaving the prey most concentrated in the most isolated and perennial lakes. Osprey, Cocoi Heron and Anhinga all fly strongly, and conduct and intercontinental and regional migrations (Sick 1997), and consequently could easily colonize the more isolated lakes and exploit their rich resources. In addition to functioning as alternative sites for food, such isolated lakes may be more inaccessible to predators and so may be favoured sites for breeding waterbirds (Sebastián-González and Green 2014).

The other variable used to investigate the effect of lake isolation, lake distance to nearest river margins, was related to the occurrence of Anhinga, Striated Heron and Yellow-billed Tern. Studies have shown that Striated Heron is negatively affected by human disturbance (Martínez-Vilalta *et al.* 2014a). The more frequent occurrence of Striated Heron on lakes furthest from the river is probably due to the fact that there are many human riverside communities in the Anavilhanas region and, so that human disturbance levels are potentially higher on the margins of some lakes close to them. Such activities include intense fishing (RC, personnel observation). However, there are no studies evaluating the impact of these activities on waterbird abundance at Anavilhanas. During the reproductive period Yellow-billed Tern nests on beaches that are [i] far from the the river margins, and [ii] closer to other colonies of the species (Krannitz 1989; Zarza *et al.* 2013). However, in the current study, Yellow-billed Tern was encontered more often on those lakes near to the Rio Negro margins. Yellow-billed Tern seems to prefer less isolated areas to forage, probably due the benefit of intra and inter-específic associations to other terns, reducing predation risk and favouring the species envolved (Groom 1992). Anhinga occurred at greater frequency on more isolated lakes (see above), but also closer to the river. Although the species may make local and nomadic movements in Amazonia (Sick 1997), possibly the proximity to a source of colonizing individuals favored the occupation of lakes nearest the river banks.

Lake bank habitat richness positively influenced abundance of Anhinga, Great Egret, Cocoi Heron, Ringed Kingfisher, Osprey, Neotropic Cormorant and Yellow-billed Tern. With the exception of Yellow-billed Tern, all of these species spend much of their time perched on vegetation at the water's edge and depending on the availability of perches for hunting, resting and/or drying plumage (Sick 1997). Consequently, lakes with greater habitat richness favor higher abundances of these species. This variable also influenced local waterbird community through the increasing in bird species richness (Cintra 2012). Great Egret and Cocoi Heron as well as other species of Ardeidae, rest during the day and/or form colonies in the marginal vegetation of water bodies in which they sleep and reproduce (Sick 1997; Martínez-Vilalta *et al*. 2013; Martínez-Vilalta *et al.* 2014a; Martínez-Vilalta *et al.* 2014b). Consequently, lake margins vegetation is very important for these birds. Neotropic Cormorant and Anhinga rest for long periods on vegetation at the water’s edge, to drying out their feathers after diving, as well as using vegetation adjacent to water for reproduction (Sick 1997). Ringed Kingfisher fish from high perches on the edge of the water (Willard 1985; Remsen 1991; Sick 1997), and Osprey often perches before fishing and eat the prey in waterside trees after capture. Our results corroborate data from southeastern Brazil, where Osprey density was higher on rivers with forested margins (Silva and Olmos 2002). Yellow-billed Tern does not have the habit of perching, resting instead on sandbars along with other species such as Large-billed Tern and Black Skimmers (*Rynchops niger)* (Gochfeld and Burguer 1996). However, the species may still be benefiting from structurally heterogeneous habitats and so increasing its abundance (González-Gajardo *et al.* 2009). At Anavilhanas the increasing in the vegetation heterogeneity along lake margins may favor local increasing in food availabilty (i.e. fruits and leafs falling into water surface) attracting more fishes to the margins, this may consequently increase the abundance piscivorous birds.

Earlier, the richness and abundance of bird aquatic community in Anavilhanas were found not to be related to lake shape nor productivity, but influenced by hydrological period, water transparency, lake margins habitat richness, lake depth and lake isolation (Cintra 2012). In the current study, analyzes were performed at the species population level and obtained results which sometimes have corroborated and sometimes contrasted with the results of community dynamics in the same area (Cintra 2012). Here lake shape and lake productivity influenced the abundance and occurrence of some fish-eating birds, a relationship not found at community level, although other species were included in the analysis at community level and were influenced by limnological variables (Cintra 2012). Nevertheless, in the presente study we found them to be associated to none of the variables investigated (i.e. the kingfishers Amazon Kingfisher and Green Kingfisher). Our study provides clear evidence that the natural limnological heterogeneity of blackwater lakes in the Amazonia can affect the occurrence and abundance of species of fish-eating birds. Further studies are needed to better understand the relationships between characteristics of black-water lakes and fish-eating bird populations in Amazonia, for example local variations in abundance of fish stocks and the impact of fishing by human populations.

Our study provides information to guide management actions and policies for conservation of freshwater systems in Amazonia. The Brazilian Amazon has an urgent need for reform of policies relating to the management of wetland natural areas. Throughout the Amazon Basin the freshwater ecosystems are threatened by a variety of human activities, including increased deforestation, construction of dams and waterways, over-exploitation of natural resources and pollution. Connectivity between these ecosystems makes them even more prone to degradation and loss of ecological functions and environmental services. Current conservation policies are insuficient for the protection of these ecosystems, requiring more scientific information about them so that new, and more appropriate, policies can be adopted (Castello *et al*. 2013).

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Table 1. Results of multiple linear models, of the relations between the abundance of fish-eating birds species and lake depth (m), lake water transparency (m), lake shape, lake área (km^2), lake productivity - expressed in phosphorus concentration ($\mu mol\ l^{-1}$), distance from the lake to the nearest neighboring lake (km) and habitat richness of lake margins. Only results for those variables showing significant effects are presented (see also Appendix 2 for results with the complete models). For some species the number of lakes "*n*" were less than 45, because there were outliers in some relationships, however, they did not desestabilize the models (see also Figs. 2-8).

Species	Variables	R^2	*t*	*P* <
Anhinga	*Model 1*	0,545		
n = 44	Lake area		3,392	0,002
n = 44	*Model 2*	0,470		
	Habitat richness		2,706	0,010
Great Egret	*Model 1*	0,691		
n = 43	Lake area		5,322	0,000
n = 43	*Model 2*	0,564		
	Habitat richness		2,703	0,010

Cocoi Heron	*Model 1*	0,857		
n = 45	Lake depth		2,793	0,008
	Lake area		8,628	0,000
n = 44	*Model 2*	0,775		
	Habitat richness		5,792	0,000
	Distance to the nearest lake		2,059	0,046
Snowy Egret	*Model 1*	0,842		
n = 44	Lake depth		-4,420	0,000
	Lake area		8,802	0,000
Ringed Kingfisher	*Model 1*	0,771		
n = 44	Lake depth		3,933	0,000
	Lake area		3,390	0,002
	Water transparency		-2,768	0,009
	Lake shape		2,883	0,006
n = 45	*Model 2*	0,555		
	Habitat richness		2,966	0,005

Large-billed Tern	*Model 1*	0,660		
n = 45	Lake area		4,916	0,000
Osprey	*Model 1*	0,811		
n = 45	Lake depth		2,614	0,013
	Lake area		6,912	0,000
n = 44	*Model 2*	0,799		
	Habitat richness		5,273	0,000
	Distance to the nearest lake		3,475	0,001
	Lake productivity		2,533	0,015
Neotropic Cormorant	*Model 1*	0,817		
n = 44	Lake area		8,585	0,000
n = 44	*Model 2*	0,529		
	Habitat richness		3,330	0,002

Table 2. Results of multiple logistic models, of the relations between the occurrences of the of fish-eating birds species and variables lake area (km^2), lake shape, habitat richness of lake margins, lake depth (m), lake productivity - expressed in phosphorus concentration (µmol l^{-1}), distance from study lake to nearest neighboring lake (km) and distance from lake to nearest river margins (km). Only results for the variables with significant effects are shown (see Appendix 3 for results with complete models; see also Figs. 9-15).

Species	Variables	ρ	Z	*P* <
Anhinga	*Model 1*	0,326		
n = 45	Distance to river margins		-2,313	0,021
n = 45	*Model 2*	0,188		
	Distance to the nearest lake		1,934	0,053
Great Egret	*Model 1*	0,284		
n = 45	Lake shape		-2,075	0,038
Striated Heron	*Model 1*	0,187		
n = 45	Distance to river margins		1,976	0,048
n = 45	*Model 2*	0,150		
	Lake productivity		2,226	0,026

Snowy Egret	*Model 1*	0,456		
n = 45	Lake depth		-2,434	0,015
	Lake area		2,058	0,040
Yellow-billed Tern	*Model 1*	0,198		
n = 45	Distance to river margins		-2,099	0,036
n = 45	*Model 2*	0,202		
	Habitat richness		2,079	0,038

Figure 1: Location of the study area in the Brazilian Amazon, showing the Anavilhanas Archipelago and the 45 black-water lakes where bird surveys were conducted (Scale 2 cm = 20 km).

Figure 2: Relations (partials) between the abundances of Cocoi Heron (*Ardea cocoi*), Snowy Egret (*Egretta thula*), Ringed Kingfisher (*Megaceryle torquata*) and Osprey (*Pandion haliaetus*), and lake depth (m), in the Anavilhanas Archipelago, Central Amazon. Only significant relationships are shown ($p < 0.05$) (see Appendix 2 for the results with full multiple linear models, including the other variables). Some numbers on the axes are negative because the partial multiple models represent deviations from expected results if all other independent variables are held within the observed means.

Figure 3: Relations (partials) between the abundances of Anhinga (*Anhinga anhinga*), Great Egret (*Ardea alba*), Cocoi Heron (*Ardea cocoi*), Snowy Egret (*Egretta thula*), Ringed Kingfisher (*Megaceryle torquata*), Large-billed Tern (*Phaetusa simplex*), Osprey (*Pandion haliaetus*) and Neotropic Cormorant (*Phalacrocorax brasilianus*), and lake area (km2) in the Anavilhanas Archipelago, Central Amazon (see Appendix 2 for the results with full multiple linear models).

Figure 4: Relation (partial) between Ringed Kingfisher (*Megaceryle torquata*) abundance and water transparency (m), in the Anavilhanas Archipelago, Central Amazon (see Appendix 2 for the results with full multiple linear models).

Figure 5: Relation (partial) between Ringed Kingfisher (*Megaceryle torquata*) abundance and the shape of the lake at Anavilhanas Archipelago, Central Amazon (see Appendix 2 for the results with full multiple linear models).

Figure 6: Relations (partial) between the abundances of Anhinga (*Anhinga anhinga*), Great Egret (*Ardea alba*), Cocoi Heron (*Ardea cocoi*), Ringed Kingfisher (*Megaceryle torquata*), Osprey (*Pandion haliaetus*) and Neotropic Cormorant (*Phalacrocorax brasilianus*), and habitat richness of lake margins, at Anavilhanas Archipelago, Central Amazon (see Appendix 2 for the results with full multiple linear models).

Figure 7: Relations (partials) between the abundances of Cocoi Heron (*Ardea cocoi*) and Osprey (*Pandion haliaetus*), and the degree of lake isolation (distance from the nearest neighboring lake in km), at Anavilhanas Archipelago, Central Amazon (see Appendix 2 for the results with full multiple linear models).

Figure 8: Relation (partial) between Osprey (*Pandion haliaetus*) abundance and lake productivity (phosphorus concentration in µmol l^{-1}), at Anavilhanas Archipelago, Central Amazon (see Appendix 2 for the results with full multiple linear models).

Figure 9: Relations between the occurrences of Anhinga (*Anhinga anhinga*), Striated Heron (*Butorides striata*) and Yellow-billed Tern (*Sternula superciliaris*), and the degree of lake isolation (distance to river margins in km), at Anavilhanas Archipelago, Central Amazon (see Appendix 3 for the results with full multiple logistic models).

Figure 10: Relation between Snowy Egret (*Egretta thula*) occurrence and lake depth (m), at Anavilhanas Archipelago, Central Amazon (see Appendix 3 for the results with full multiple logistic models).

Figure 11: Relation between Snowy Egret (*Egretta thula*) occurrence and the lake area (km^2), at Anavilhanas Archipelago, Central Amazon (see Appendix 3 for the results with full multiple logistic models).

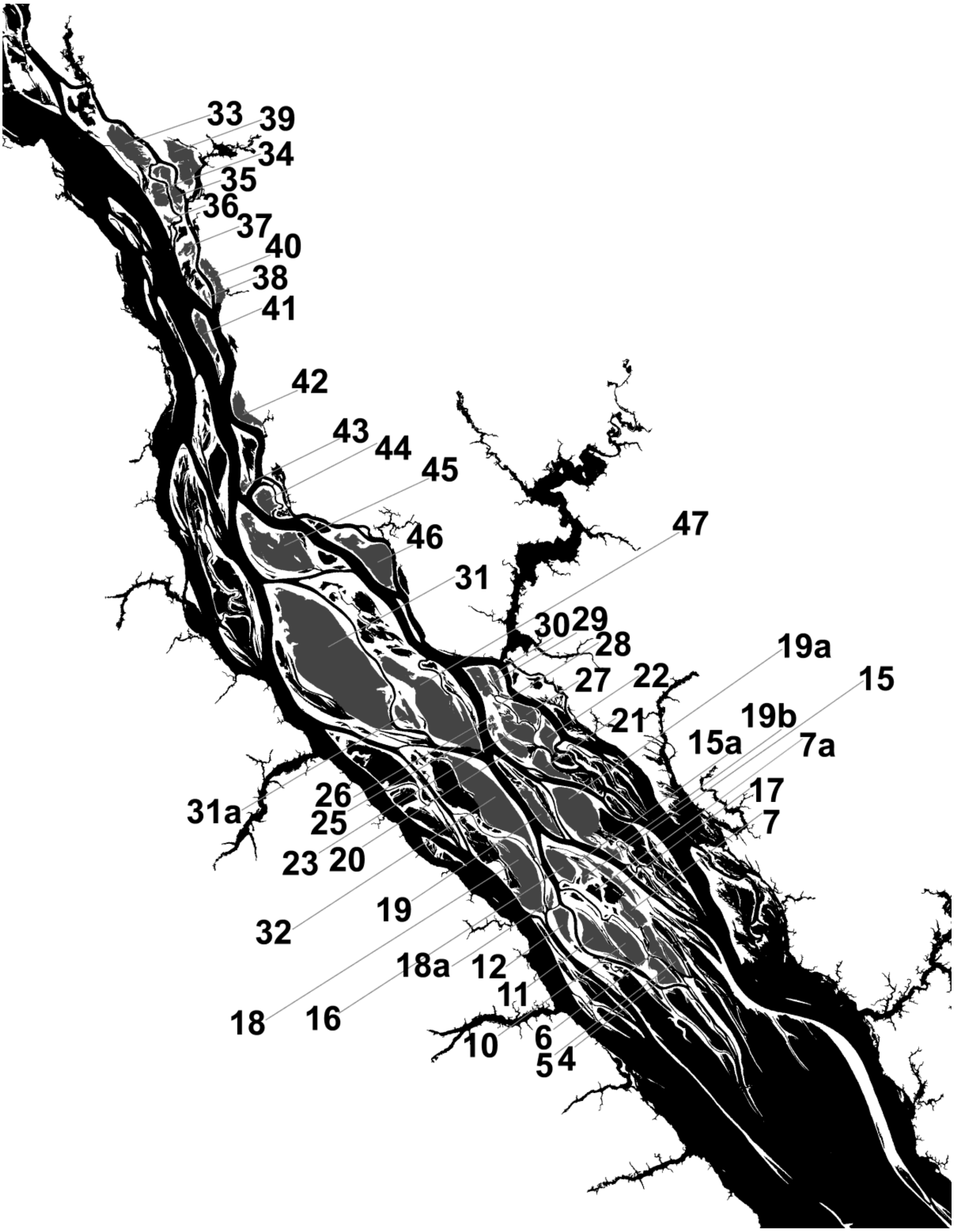
Figure 12: Relation between Great egret (*Ardea alba*) occurrence and lake shape, at Anavilhanas Archipelago, Central Amazon (see Appendix 3 for the results with full multiple logistic models).

Figure 13: Relation between Yellow-billed Tern (*Sternula superciliaris*) occurrence and habitat richness of lake margins, at Anavilhanas Archipelago, Central Amazon (see Appendix 3 for the results with full multiple logistic models).

Figure 14: Relation between Anhinga (*Anhinga anhinga*) occurrence and degree of lake isolation (distance from the nearest neighboring lake in km), at Anavilhanas Archipelago, Central Amazon (see Appendix 3 for the results with full multiple logistic models).

Figure 15: Relation between Striated Heron (*Butorides striata*) occurrence and lake productivity (phosphorus concentration $\mu mol\ l^{-1}$), at Anavilhanas Archipelago, Central Amazon (see Appendix 3 for the results with full multiple logistic models).

Figure 1:


33
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22
15
21
19b
15a
7a
17
7
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32
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18a
12
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6
10
5
4

Figure 2

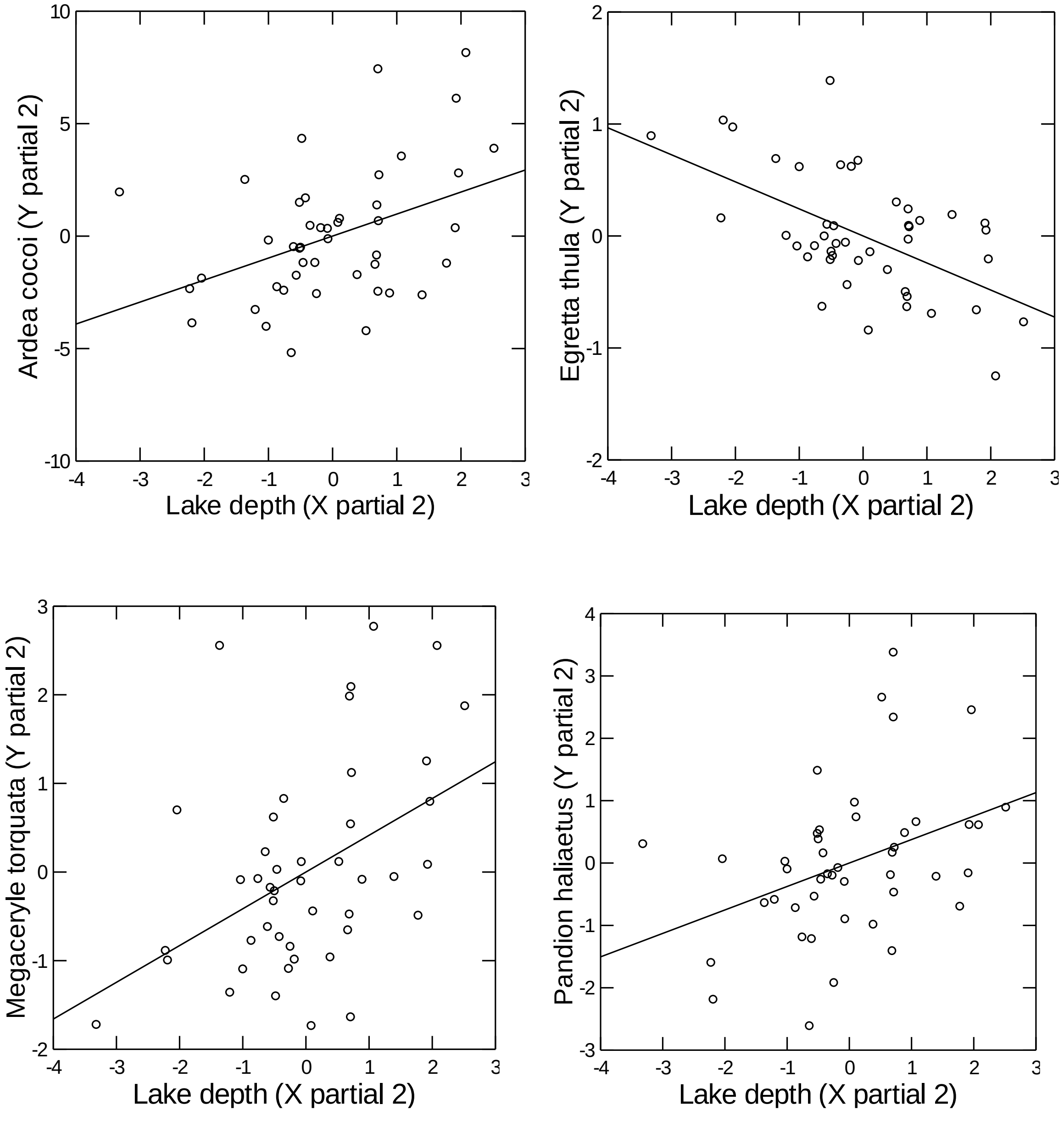
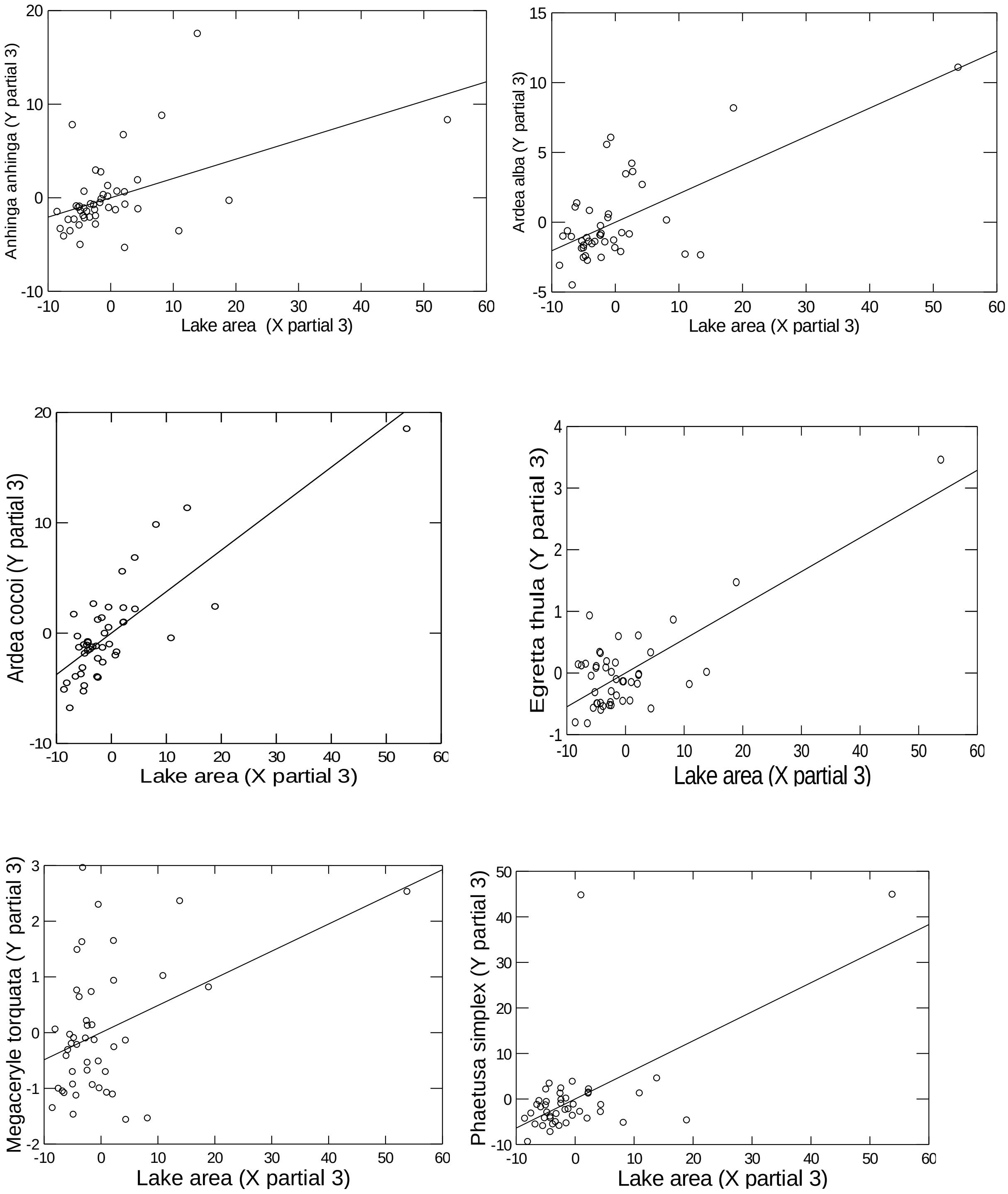
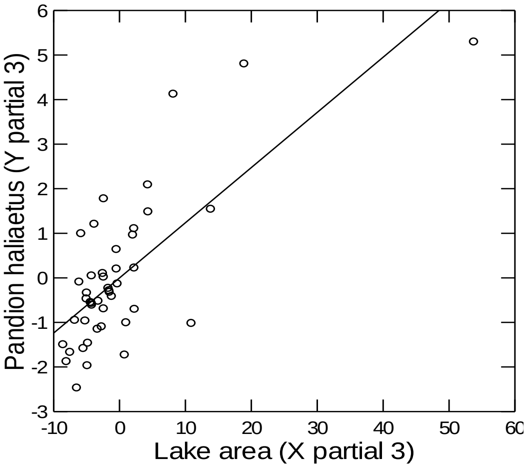

Ardea cocoi (Y partial 2)
10
5
0
-5
-10
-4
-3
-2
-1
0
1
2
3
Lake depth (X partial 2)
Egretta thula (Y partial 2)
2
1
0
-1
-2
-4
-3
-2
-1
0
1
2
3
Lake depth (X partial 2)
Megaceryle torquata (Y partial 2)
3
2
1
0
-1
-2
-4
-3
-2
-1
0
1
2
3
Lake depth (X partial 2)
Pandion haliaetus (Y partial 2)
4
3
2
1
0
-1
-2
-3
-4
-3
-2
-1
0
1
2
3
Lake depth (X partial 2)

Figure 3


Anhinga anhinga (Y partial 3)
Lake area (X partial 3)
20
10
0
-10
-10
0
10
20
30
40
50
60
Ardea alba (Y partial 3)
Lake area (X partial 3)
15
10
5
0
-5
Ardea cocoi (Y partial 3)
Lake area (X partial 3)
Egretta thula (Y partial 3)
Lake area (X partial 3)
4
3
2
1
0
-1
Megaceryle torquata (Y partial 3)
Lake area (X partial 3)
3
2
1
0
-1
-2
Phaetusa simplex (Y partial 3)
Lake area (X partial 3)
50
40
30
20
10
0
-10


Pandion haliaetus (Y partial 3)
6
5
4
3
2
1
0
-1
-2
-3
-10
0
10
20
30
40
50
60
Lake area (X partial 3)

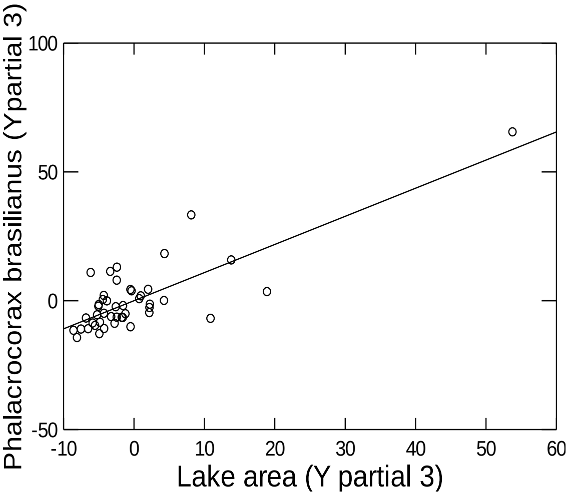

Phalacrocorax brasilianus (Ypartial 3)
100
50
0
-50
-10
0
10
20
30
40
50
60
Lake area (Y partial 3)

Figure 4

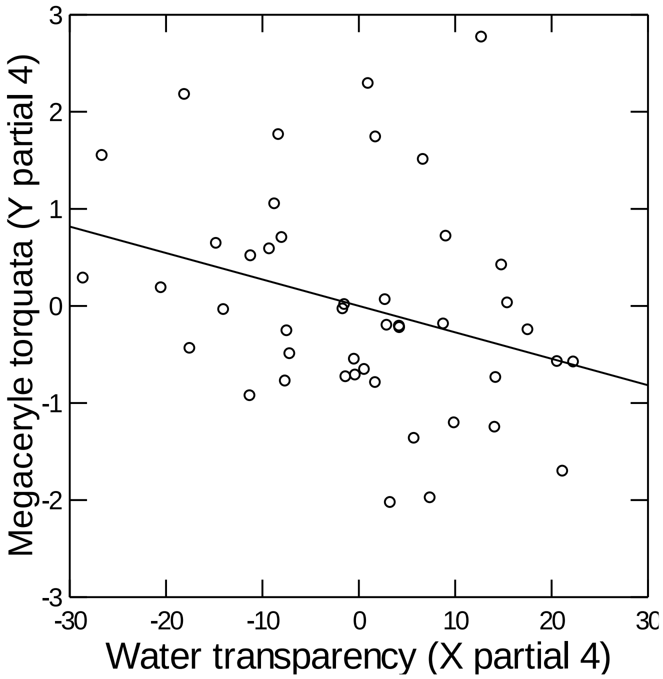

Megaceryle torquata (Y partial 4)
3
2
1
0
-1
-2
-3
-30
-20
-10
0
10
20
30
Water transparency (X partial 4)

Figure 5

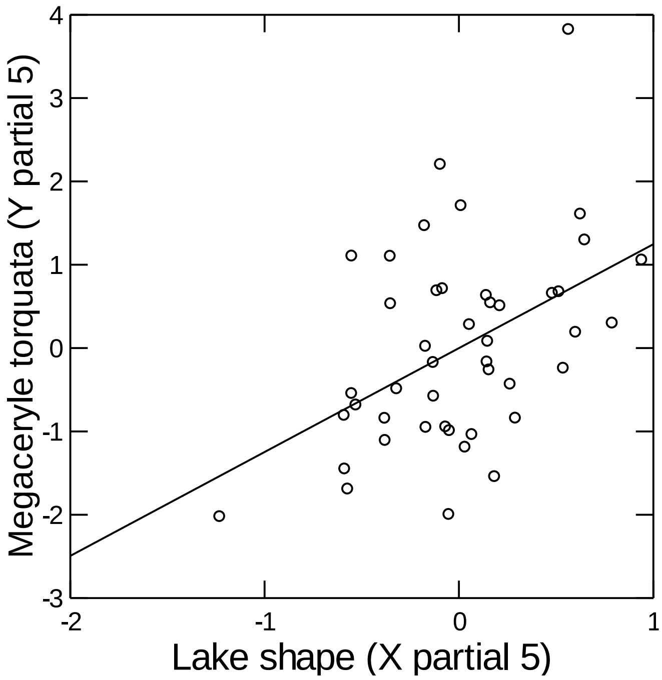
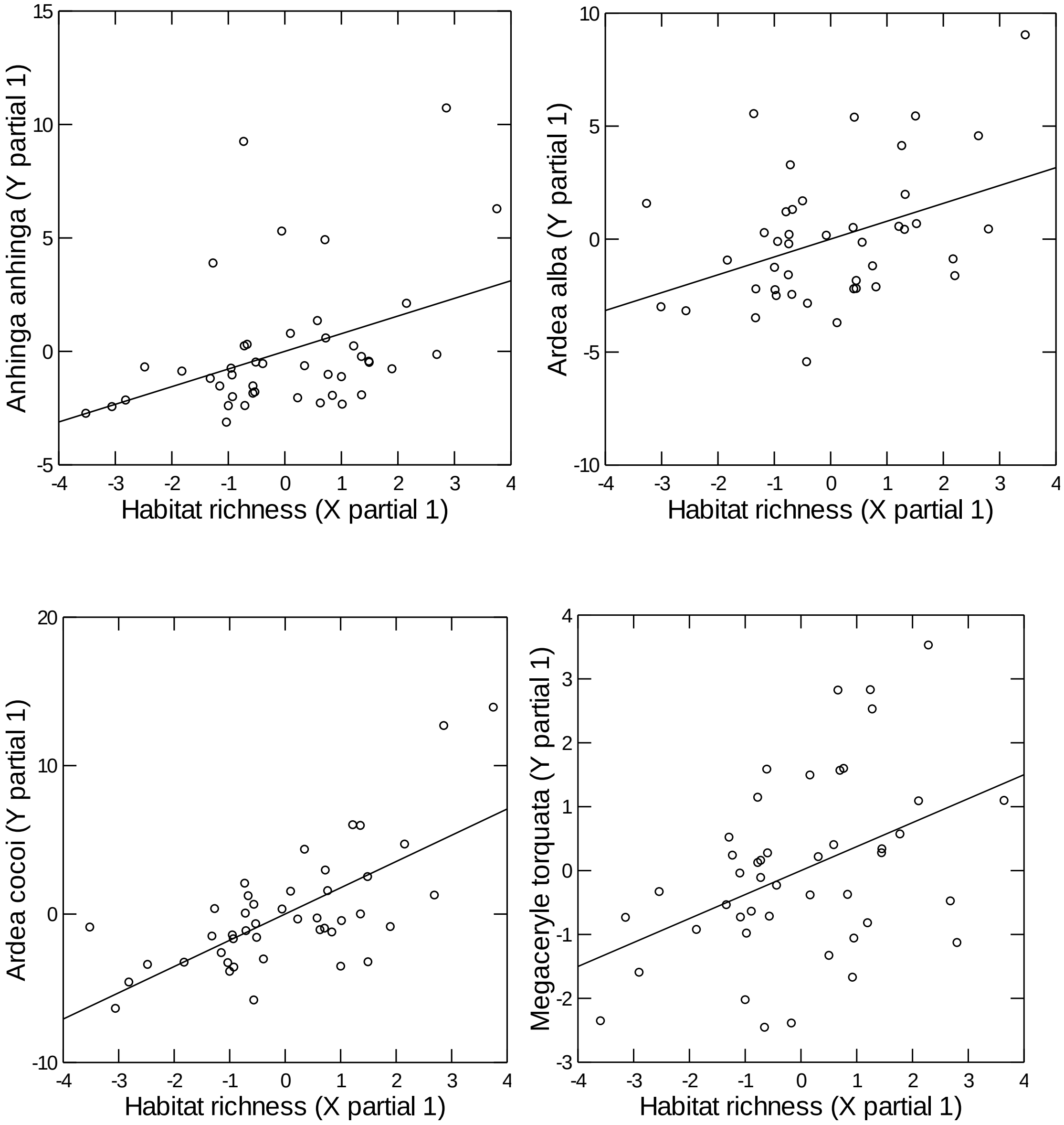
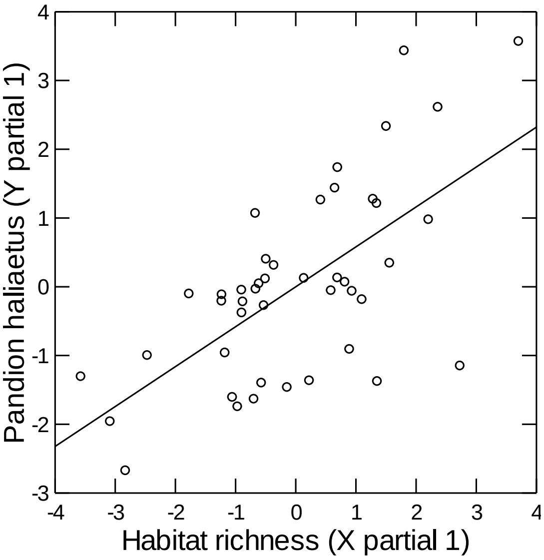

Megaceryle torquata (Y partial 5)
Lake shape (X partial 5)
4
3
2
1
0
-1
-2
-3
-2
-1
0
1

Figure 6


Anhinga anhinga (Y partial 1)
15
10
5
0
-5
-4 -3 -2 -1 0 1 2 3 4
Habitat richness (X partial 1)
Ardea alba (Y partial 1)
10
5
0
-5
-10
-4 -3 -2 -1 0 1 2 3 4
Habitat richness (X partial 1)
Ardea cocoi (Y partial 1)
20
10
0
-10
-4 -3 -2 -1 0 1 2 3 4
Habitat richness (X partial 1)
Megaceryle torquata (Y partial 1)
4
3
2
1
0
-1
-2
-3
-4 -3 -2 -1 0 1 2 3 4
Habitat richness (X partial 1)


Pandion haliaetus (Y partial 1)
Habitat richness (X partial 1)
4
3
2
1
0
-1
-2
-3
-4
-3
-2
-1
0
1
2
3
4

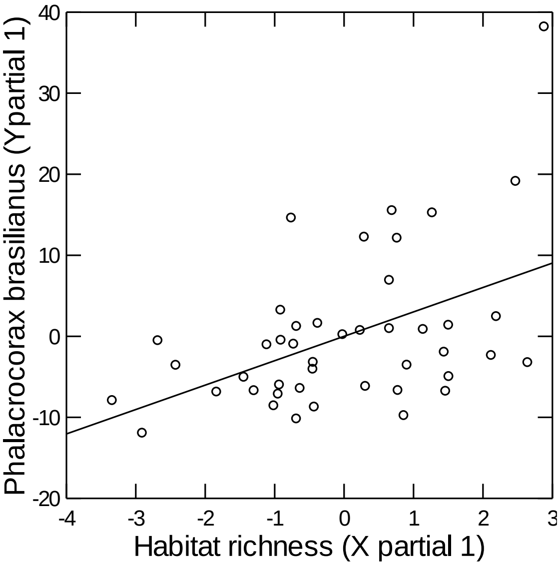

Phalacrocorax brasilianus (Ypartial 1)
Habitat richness (X partial 1)
40
30
20
10
0
-10
-20
-4
-3
-2
-1
0
1
2
3

Figure 7

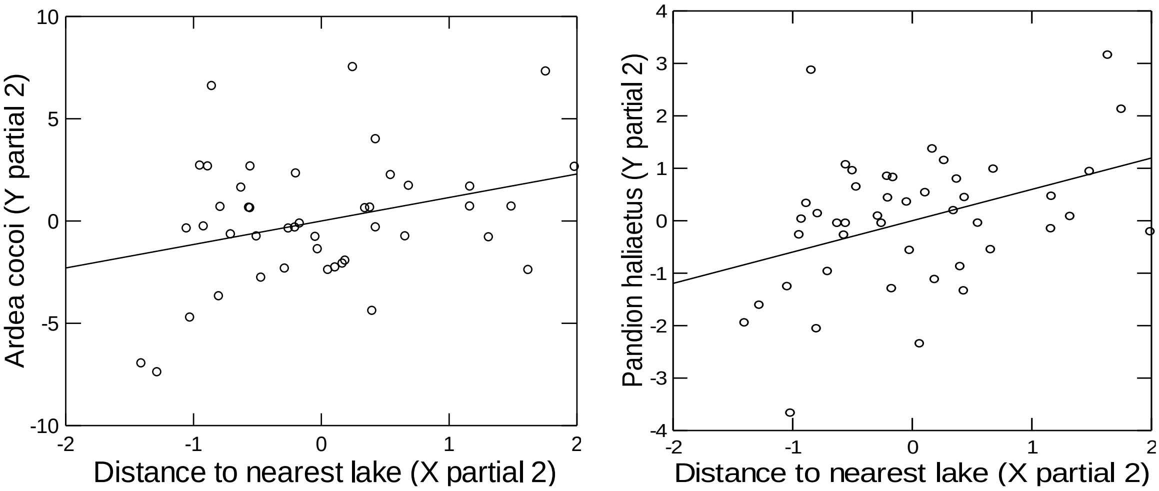

10
5
0
-5
-10
Ardea cocoi (Y partial 2)
-2
-1
0
1
2
Distance to nearest lake (X partial 2)
4
3
2
1
0
-1
-2
-3
-4
Pandion haliaetus (Y partial 2)
-2
-1
0
1
2
Distance to nearest lake (X partial 2)

Figure 8

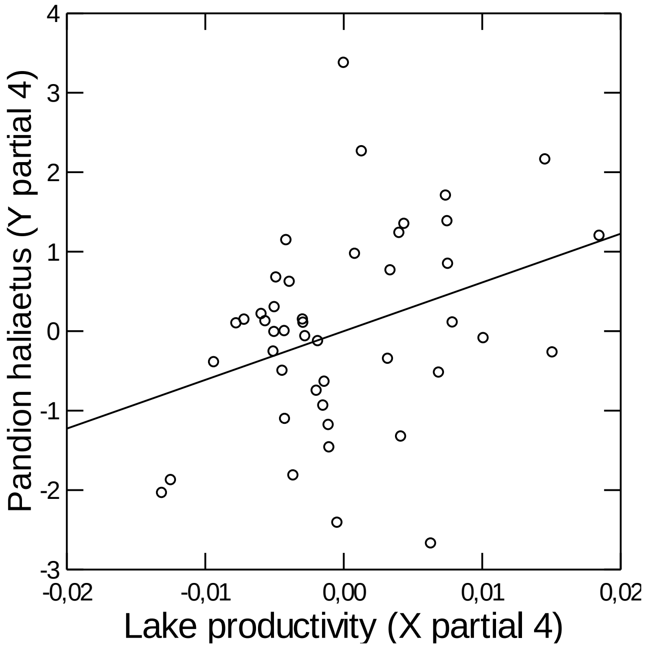

4
3
2
1
0
-1
-2
-3
-0,02
-0,01
0,00
0,01
0,02
Pandion haliaetus (Y partial 4)
Lake productivity (X partial 4)

Figure 9

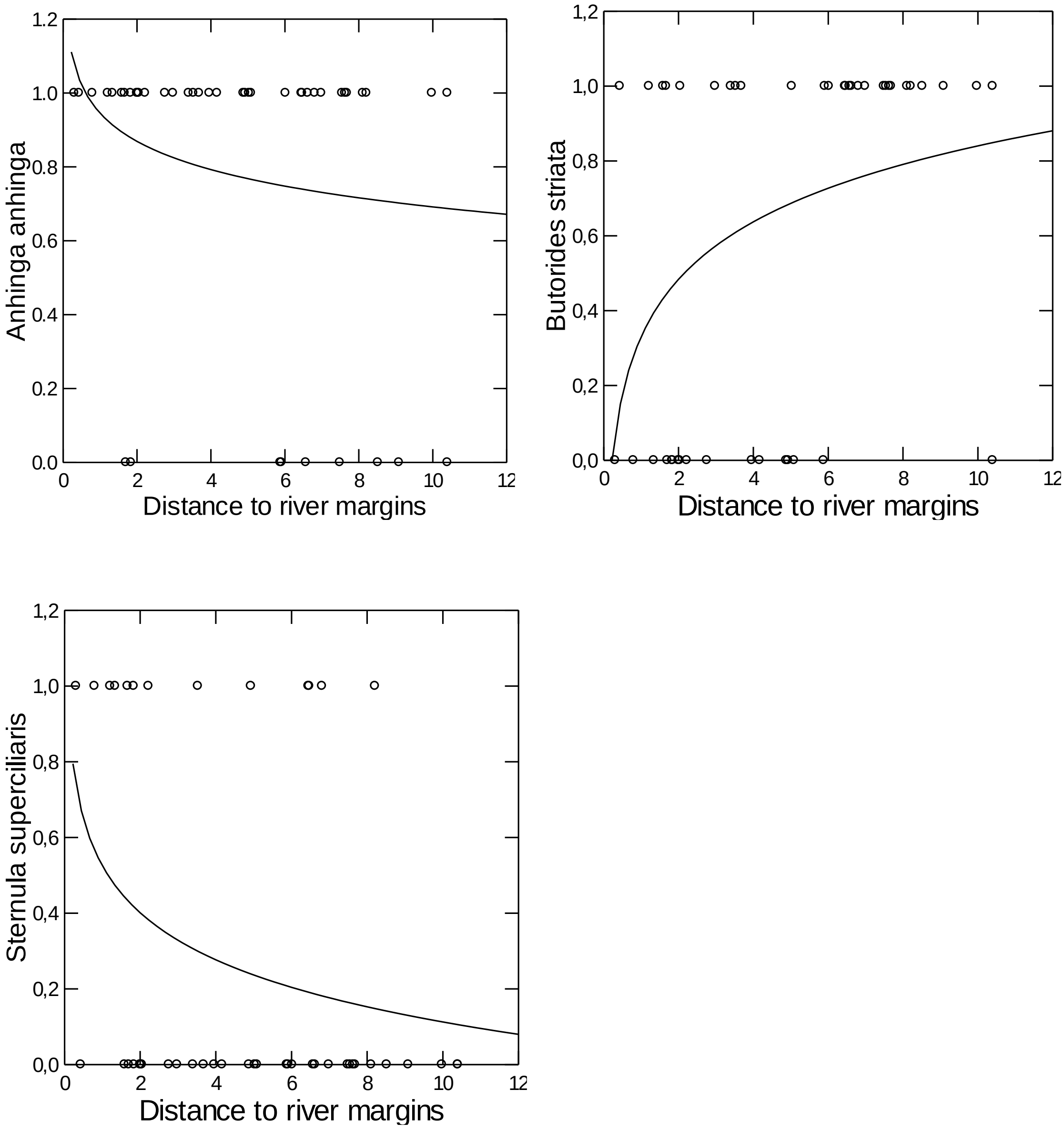

1.2
1.0
0.8
0.6
0.4
0.2
0.0
Anhinga anhinga
0
2
4
6
8
10
12
Distance to river margins
1,2
1,0
0,8
0,6
0,4
0,2
0,0
Butorides striata
0
2
4
6
8
10
12
Distance to river margins
1,2
1,0
0,8
0,6
0,4
0,2
0,0
Sternula superciliaris
0
2
4
6
8
10
12
Distance to river margins

Figure 10

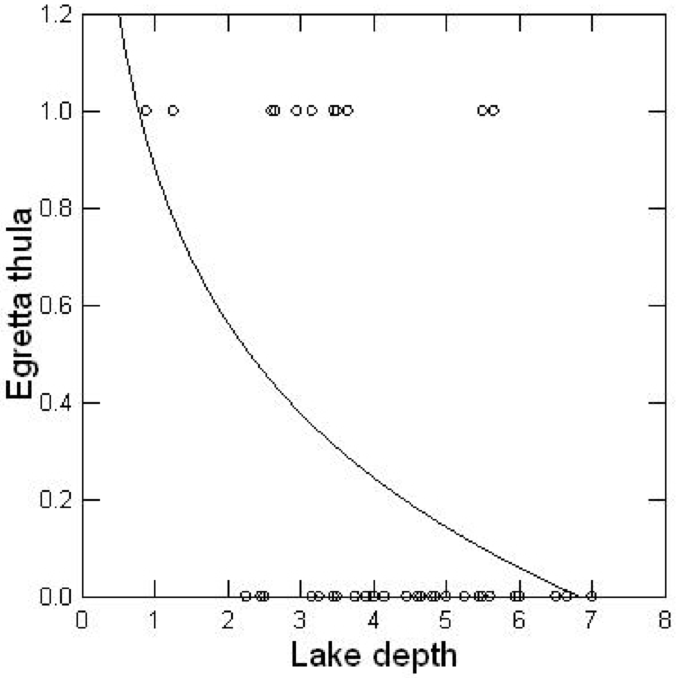


Figure 11

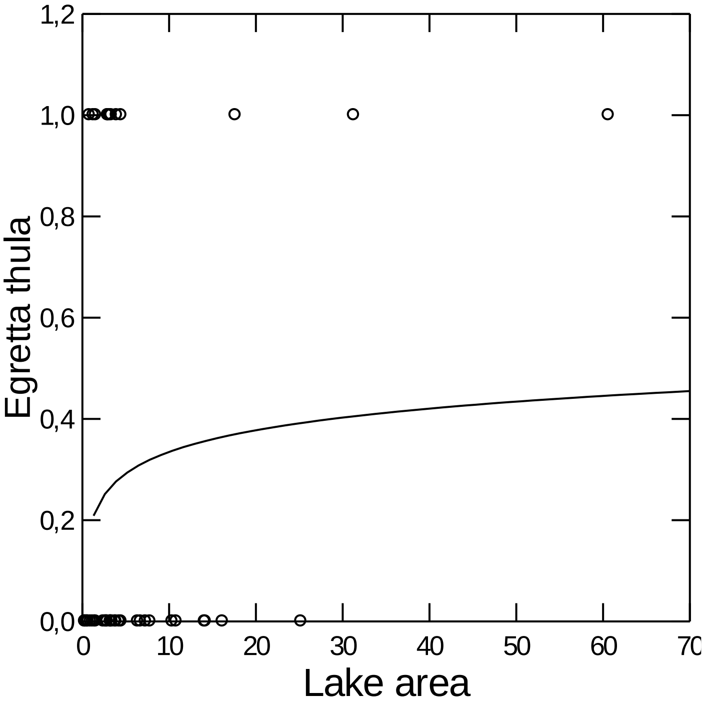


Figure 12

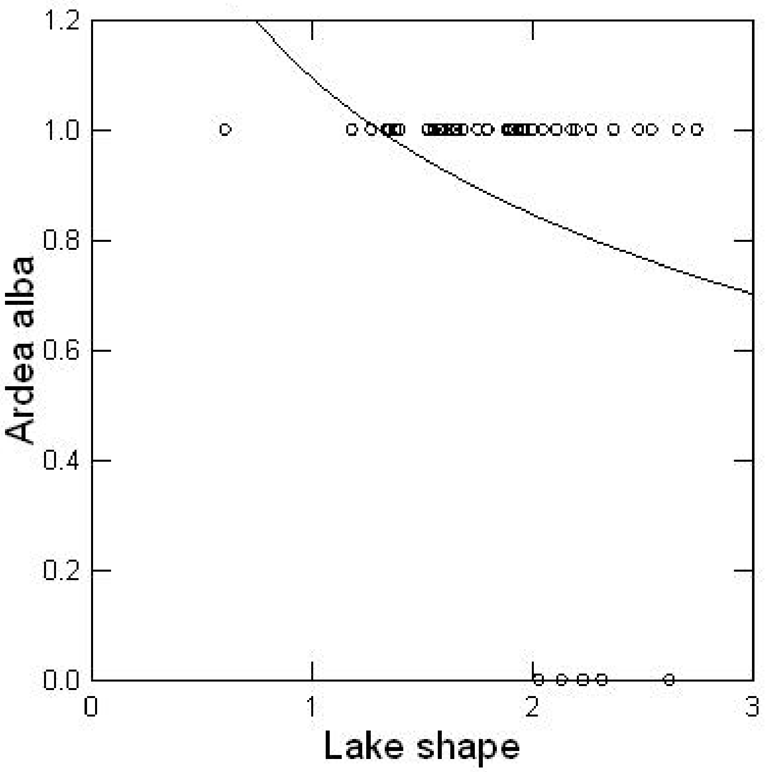
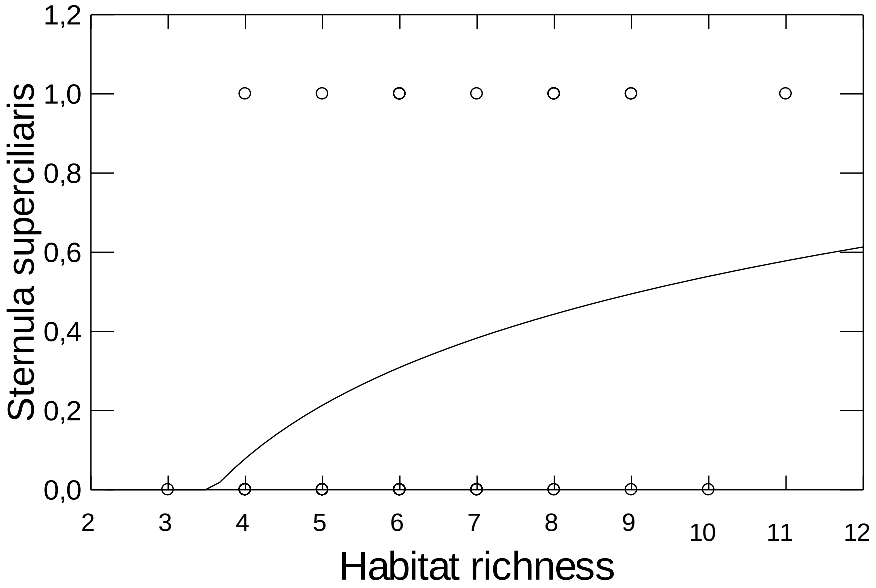


Figure 13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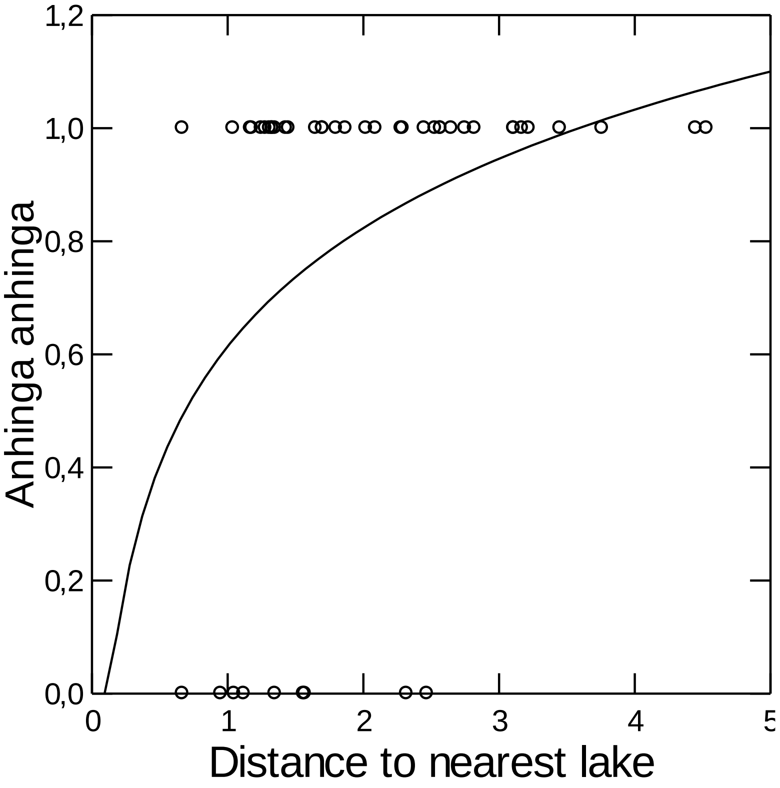
1,0
0,8
0,6
0,4
0,2
0,0
Sternula superciliaris
2
3
4
5
6
7
8
9
10
11
12
Habitat richness

Figure 14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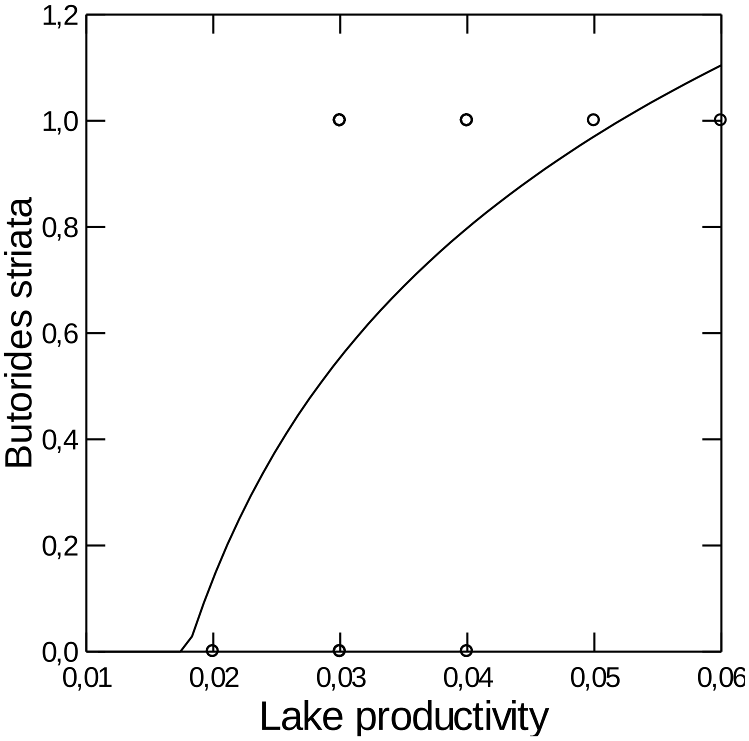
0,6
0,4
0,2
0,0
Anhinga anhinga
0
1
2
3
4
Distance to nearest lake

Figure 15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0,8
0,6
0,4
0,2
0,0
Butorides striata
0,01
0,02
0,03
0,04
0,05
0,06
Lake productivity

APPENDIX

Appendix 1: Results of Pearson correlation analyses for the lake limnological and geographical variables of 45 lakes from Anavilhanas Archipelago, Central Amazonia Central.

	Distance to river margins (km)	Distance to the nearest lake (km)	Lake depth (m)	Water transparency (m)	Lake shape	Productivity (Nitrogen µmol l^{-1})	Productivity (Phosphorus µmol l^{-1})	Habitat richness	Lake area (km^2)
Distance to river margins (km)	-								
Distance to the nearest lake (km)	-0,051	-							
Lake depth (m)	-0,113	0,232	-						
Water transparency (m)	-0,353	0,286	0,337	-					
Lake shape	-0,123	0,245	0,164	-0,025	-				
Productivity (Nitrogen									

µmol l^{-1})	-0,163	-0,152	-0,014	-0,114	-0,279	-			
Productivity (Phosphorus µmol l^{-1})	-0,034	-0,211	-0,251	-0,104	-0,487*	0,355	-		
Habitat Richness	-0,129	0,436	0,476*	0,180	0,238	-0,106	-0,300	-	
Lake area (km^2)	0,111	0,543*	0,282	0,098	0,084	-0,134	-0,172	0,707	-

* $P < 0.05$

Appendix 2. Results of full multiple linear models, of the relations between the abundance of fish-eating birds species and lake depth (m), lake water transparency (m), lake shape, lake área (km^2), lake productivity - expressed in phosphorus and nitrogen concentrations ($\mu mol\ l^{-1}$), distance from the lake to the nearest neighboring lake (km), distance from the lake to river margins (km) and habitat richness of lake margins. For some species the number of lakes "*n*" were less than 45, because there were outliers in some relationships, however, they did not desestabilize the models. Because *Chloroceryle amazona* and *Chloroceryle americana* had too low records they were not considerd in the analyses using multiple linear.

Species	Variables	R^2	*t*	*P* <
Anhinga	*Model 1*	0,545		
n = 44	Distance to river margins		-1,193	0,240
	Lake depth		0,476	0,637
	Lake area		3,392	0,002
	Water transparency		-0,804	0,426
	Lake shape		1,138	0,262
n = 44	*Model 2*	0,470		
	Habitat richness		2,706	0,010
	Distance to the nearest lake		0,693	0,492
	Nitrogen concentration		-0,013	0,990
	Phosphorus concentration		1,110	0,274

Great Egret	*Model 1*	0,691		
n = 43	Distance to river margins		0,290	0,774
	Lake depth		-0,137	0,892
	Lake area		5,322	0,000
	Water transparency		-1,653	0,107
	Lake shape		-0,619	0,540
n = 43	*Model 2*	0,564		
	Habitat richness		2,703	0,010
	Distance to the nearest lake		1,543	0,131
	Nitrogen concentration		-0,131	0,896
	Phosphorus concentration		1,657	0,106
Cocoi Heron	*Model 1*	0,857		
n = 45	Distance to river margins		-1,875	0,068
	Lake depth		2,793	0,008
	Lake area		8,628	0,000
	Water transparency		-1,757	0,087
	Lake shape		0,959	0,344

n = 44	*Model 2*	0,775		
	Habitat richness		5,792	0,000
	Distance to the nearest lake		2,059	0,046
	Nitrogen concentration		0,056	0,956
	Phosphorus concentration		0,707	0,484
Striated Heron	*Model 1*	0,372		
n = 45	Distance to river margins		1,338	0,189
	Lake depth		-0,503	0,618
	Lake area		-0,237	0,814
	Water transparency		-1,109	0,274
	Lake shape		-0,164	0,870
n = 44	*Model 2*	0,272		
	Habitat richness		0,237	0,814
	Distance to the nearest lake		-0,368	0,715
	Nitrogen concentration		-1,208	0,234
	Phosphorus concentration		1,584	0,121
Amazon Kingfisher	*Model I*	-		

	Distance to river margins		-	-
	Lake depth		-	-
	Lake area		-	-
	Water transparency		-	-
	Lake shape		-	-
	Model 2	-		
	Habitat richness		-	-
	Distance to the nearest lake		-	-
	Nitrogen concentration		-	-
	Phosphorus concentration		-	-
Green Kingfisher	*Model 1*	-		
	Distance to river margins		-	-
	Lake depth		-	-
	Lake area		-	-
	Water transparency		-	-
	Lake shape		-	-
	Model 2	-		

	Habitat richness		-	-
	Distance to the nearest lake		-	-
	Nitrogen concentration		-	-
	Phosphorus concentration		-	-
Snowy Egret	*Model 1*	0,842		
n = 44	Distance to river margins		1,462	0,152
	Lake depth		-4,420	0,000
	Lake area		8,802	0,000
	Water transparency		0,898	0,375
	Lake shape		0,089	0,930
n = 45	*Model 2*	0,372		
	Habitat richness		1,345	0,186
	Distance to the nearest lake		1,320	0,194
	Nitrogen concentration		-0,040	0,968
	Phosphorus concentration		0,084	0,934
Ringed Kingfisher	*Model 1*	0,771		
n = 44	Distance to river margins		-0,059	0,953

	Lake depth		3,933	0,000
	Lake area		3,390	0,002
	Water transparency		-2,768	0,009
	Lake shape		2,883	0,006
n = 45	*Model 2*	0,555		
	Habitat richness		2,966	0,005
	Distance to the nearest lake		0,878	0,385
	Nitrogen concentration		-0,135	0,893
	Phosphorus concentration		-0,622	0,537
Large-billed Tern	*Model I*	0,660		
n = 45	Distance to river margins		-0,532	0,598
	Lake depth		-0,927	0,360
	Lake area		4,916	0,000
	Water transparency		1,747	0,089
	Lake shape		-0,513	0,611
n = 44	*Model 2*	0,155		
	Habitat richness		0,694	0,492
	Distance to the nearest lake		0,029	0,977

	Nitrogen concentration		-0,452	0,654
	Phosphorus concentration		-0,051	0,959
Osprey	*Model 1*	0,811		
n = 45	Distance to river margins		-0,463	0,646
	Lake depth		2,614	0,013
	Lake area		6,912	0,000
	Water transparency		-0,042	0,967
	Lake shape		0,494	0,624
n = 44	*Model 2*	0,799		
	Habitat richness		5,273	0,000
	Distance to the nearest lake		3,475	0,001
	Nitrogen concentration		-0,900	0,374
	Phosphorus concentration		2,533	0,015
Neotropic Cormorant	*Model 1*	0,817		
n = 44	Distance to river margins		-0,998	0,324
	Lake depth		-0,920	0,363
	Lake area		8,585	0,000

	Water transparency		-0,002	0,999
	Lake shape		-0,051	0,959
n = 44	*Model 2*	0,529		
	Habitat richness		3,330	0,002
	Distance to the nearest lake		0,517	0,608
	Nitrogen concentration		-0,895	0,376
	Phosphorus concentration		1,776	0,083
Yellow-billed Tern	*Model 1*	0,424		
n = 45	Distance to river margins		-1,009	0,319
	Lake depth		1,741	0,090
	Lake area		1,646	0,108
	Water transparency		-1,532	0,134
	Lake shape		-0,256	0,799
n = 45	*Model 2*	0,292		
	Habitat richness		1,768	0,085
	Distance to the nearest lake		-0,231	0,819
	Nitrogen concentration		0,094	0,925

	Phosphorus concentration		-0,037	0,970

Appendix 3. Results of full multiple logistic models, of the relations between the occurrences of the of fish-eating birds species and lake depth (m), lake water transparency (m), lake shape, lake área (km^2), lake productivity - expressed in phosphorus and nitrogen concentrations (µmol l^{-1}), distance from the lake to the nearest neighboring lake (km), distance from the lake to river margins (km) and habitat richness of lake margins.

Species	Variables	ρ	Z	*P* <
Anhinga	*Model 1*	0,326		
n = 45	Distance to river margins		-2,313	0,021
	Lake depth		-0,445	0,656
	Lake area		1,813	0,070
	Water transparency		-1,661	0,097
	Lake shape		0,836	0,403
n = 45	*Model 2*	0,188		
	Habitat richness		1,031	0,303

	Distance to the nearest lake		1,934	0,053
	Nitrogen concentration		0,745	0,456
	Phosphorus concentration		0,420	0,675
Great Egret	*Model 1*	0,284		
n = 45	Distance to river margins		0,733	0,464
	Lake depth		0,482	0,630
	Lake area		0,549	0,583
	Water transparency		-0,808	0,419
	Lake shape		-2,075	0,038
n = 45	*Model 2*	0,129		
	Habitat richness		0,916	0,360
	Distance to the nearest lake		-0,353	0,724
	Nitrogen concentration		-1,414	0,157
	Phosphorus concentration		1,504	0,133
Cocoi Heron	*Model 1*	0,575		
n = 45	Distance to river margins		-1,173	0,241
	Lake depth		0,196	0,845

	Lake area		1,084	0,278
	Water transparency		-1,291	0,197
	Lake shape		0,258	0,796
n = 45	*Model 2*	1,000		
	Habitat richness		0,000	1,000
	Distance to the nearest lake		0,000	1,000
	Nitrogen concentration		0,000	1,000
	Phosphorus concentration		0,000	1,000
Striated Heron	*Model 1*	0,187		
n = 45	Distance to river margins		1,976	0,048
	Lake depth		-1,031	0,303
	Lake area		0,999	0,318
	Water transparency		-0,466	0,641
	Lake shape		-0,650	0,516
n = 45	*Model 2*	0,150		
	Habitat richness		-0,647	0,518
	Distance to the nearest lake		0,978	0,328

	Nitrogen concentration		-0,860	0,390
	Phosphorus concentration		2,226	0,026
Amazon Kingfisher	*Model 1*	0,059		
n = 45	Distance to river margins		0,613	0,540
	Lake depth		-0,292	0,770
	Lake area		-0,864	0,388
	Water transparency		-0,109	0,914
	Lake shape		0,997	0,319
n = 45	*Model 2*	0,092		
	Habitat richness		-1,385	0,166
	Distance to the nearest lake		0,345	0,730
	Nitrogen concentration		-0,871	0,384
	Phosphorus concentration		1,066	0,287
Green Kingfisher	*Model 1*	0,018		
n = 45	Distance to river margins		-0,726	0,468
	Lake depth		0,244	0,807
	Lake area		0,321	0,748

	Water transparency		-0,606	0,544
	Lake shape		-0,702	0,483
n = 45	*Model 2*	0,016		
	Habitat richness		-0,253	0,800
	Distance to the nearest lake		-0,464	0,643
	Nitrogen concentration		-0,504	0,614
	Phosphorus concentration		0,483	0,629
Snowy Egret	*Model 1*	0,456		
n = 45	Distance to river margins		1,908	0,056
	Lake depth		-2,434	0,015
	Lake area		2,058	0,040
	Water transparency		0,153	0,879
	Lake shape		0,727	0,467
n = 45	*Model 2*	0,038		
	Habitat richness		0,277	0,782
	Distance to the nearest lake		1,036	0,300
	Nitrogen concentration		0,631	0,528

	Phosphorus concentration		0,011	0,991
Ringed Kingfisher	*Model 1*	0,661		
n = 45	Distance to river margins		1,526	0,127
	Lake depth		1,372	0,170
	Lake area		-0,382	0,703
	Water transparency		-1,080	0,280
	Lake shape		1,264	0,206
n = 45	*Model 2*	0,253		
	Habitat richness		1,572	0,116
	Distance to the nearest lake		-0,583	0,560
	Nitrogen concentration		0,497	0,619
	Phosphorus concentration		-1,245	0,213
Large-billed Tern	*Model 1*	0,284		
n = 45	Distance to river margins		-1,491	0,136
	Lake depth		1,116	0,264
	Lake area		1,884	0,060
	Water transparency		0,153	0,879
	Lake shape		0,108	0,914

n = 45	*Model 2*	0,108		
	Habitat richness		1,724	0,085
	Distance to the nearest lake		-0,049	0,961
	Nitrogen concentration		-0,341	0,733
	Phosphorus concentration		0,165	0,869
Osprey	*Model 1*	0,161		
n = 45	Distance to river margins		-1,034	0,301
	Lake depth		1,174	0,241
	Lake area		0,722	0,470
	Water transparency		-0,643	0,520
	Lake shape		0,618	0,537
n = 45	*Model 2*	0,107		
	Habitat richness		0,567	0,571
	Distance to the nearest lake		1,502	0,133
	Nitrogen concentration		-0,049	0,961
	Phosphorus concentration		0,708	0,479

Neotropic Cormorant	*Model 1*	0,272		
n = 45	Distance to river margins		-0,633	0,527
	Lake depth		0,591	0,555
	Lake area		0,050	0,960
	Water transparency		1,260	0,208
	Lake shape		0,319	0,750
n = 45	*Model 2*	0,456		
	Habitat richness		1,816	0,069
	Distance to the nearest lake		0,957	0,339
	Nitrogen concentration		-0,900	0,368
	Phosphorus concentration		1,397	0,162
Yellow-billed Tern	*Model 1*	0,198		
n = 45	Distance to river margins		-2,099	0,036
	Lake depth		-0,140	0,889
	Lake area		1,759	0,079
	Water transparency		-0,539	0,590
	Lake shape		0,256	0,798

n = 45	*Model 2*	0,202		
	Habitat richness		2,079	0,038
	Distance to the nearest lake		-0,302	0,763
	Nitrogen concentration		1,665	0,096
	Phosphorus concentration		-0,811	0,417

CONCLUSÕES

Com base no exposto acima, concluímos que populações podem responder diferentemente de assembleias de espécies às características do habitat, por serem mais sensíveis às mudanças no meio, como mostrado por Supp & Ernest (2014). A heterogeneidade limnológica natural de lagos de água preta na Amazônia influencia a ocorrência e abundância das espécies de aves piscívoras.

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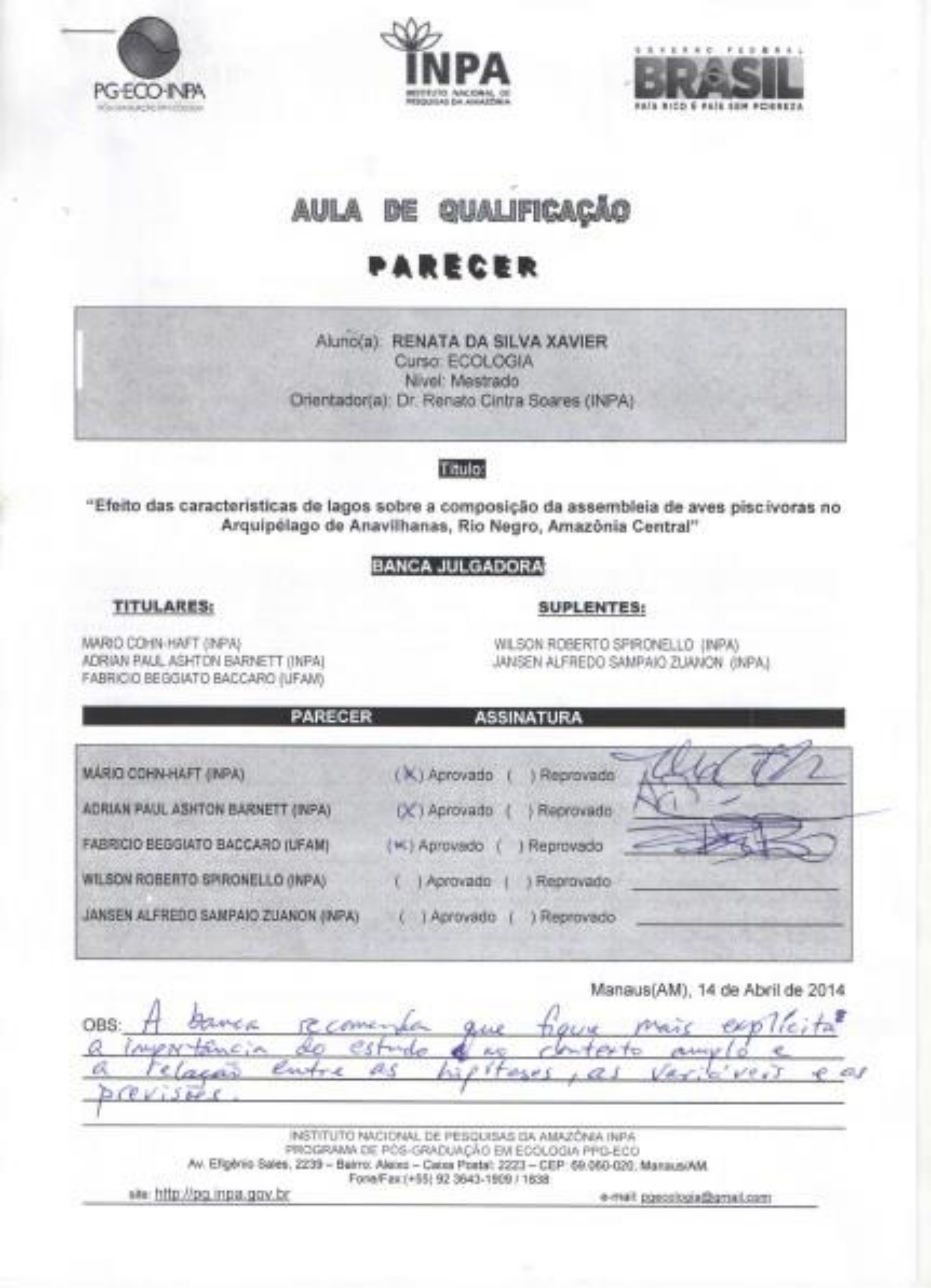
ANEXO 1 (Ata da Aula de Qualificação)



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AULA DE QUALIFICAÇÃO

PARECER

Aluno(a): RENATA DA SILVA XAVIER
Curso: ECOLOGIA
Nível: Mestrado
Orientador(a): Dr. Renato Cintra Soares (INPA)

Título:

"Efeito das características de lagos sobre a composição da assembleia de aves piscívoras no Arquipélago de Anavilhanas, Rio Negro, Amazônia Central"

BANCA JULGADORA:

TITULARES:	**SUPLENTES:**
MARIO COHN-HAFT (INPA) ADRIAN PAUL ASHTON BARNETT (INPA) FABRICIO BEGGIATO BACCARO (UFAM)	WILSON ROBERTO SPIRONELLO (INPA) JANSEN ALFREDO SAMPAIO ZUANON (INPA)

	PARECER		ASSINATURA
MÁRIO COHN-HAFT (INPA)	(X) Aprovado	( ) Reprovado	
ADRIAN PAUL ASHTON BARNETT (INPA)	(X) Aprovado	( ) Reprovado	
FABRICIO BEGGIATO BACCARO (UFAM)	(X) Aprovado	( ) Reprovado	
WILSON ROBERTO SPIRONELLO (INPA)	( ) Aprovado	( ) Reprovado	
JANSEN ALFREDO SAMPAIO ZUANON (INPA)	( ) Aprovado	( ) Reprovado	

Manaus(AM), 14 de Abril de 2014

OBS: A banca recomenda que fique mais explícita a importância do estudo no contexto amplo e a relação entre as hipóteses, as variáveis e as previsões.

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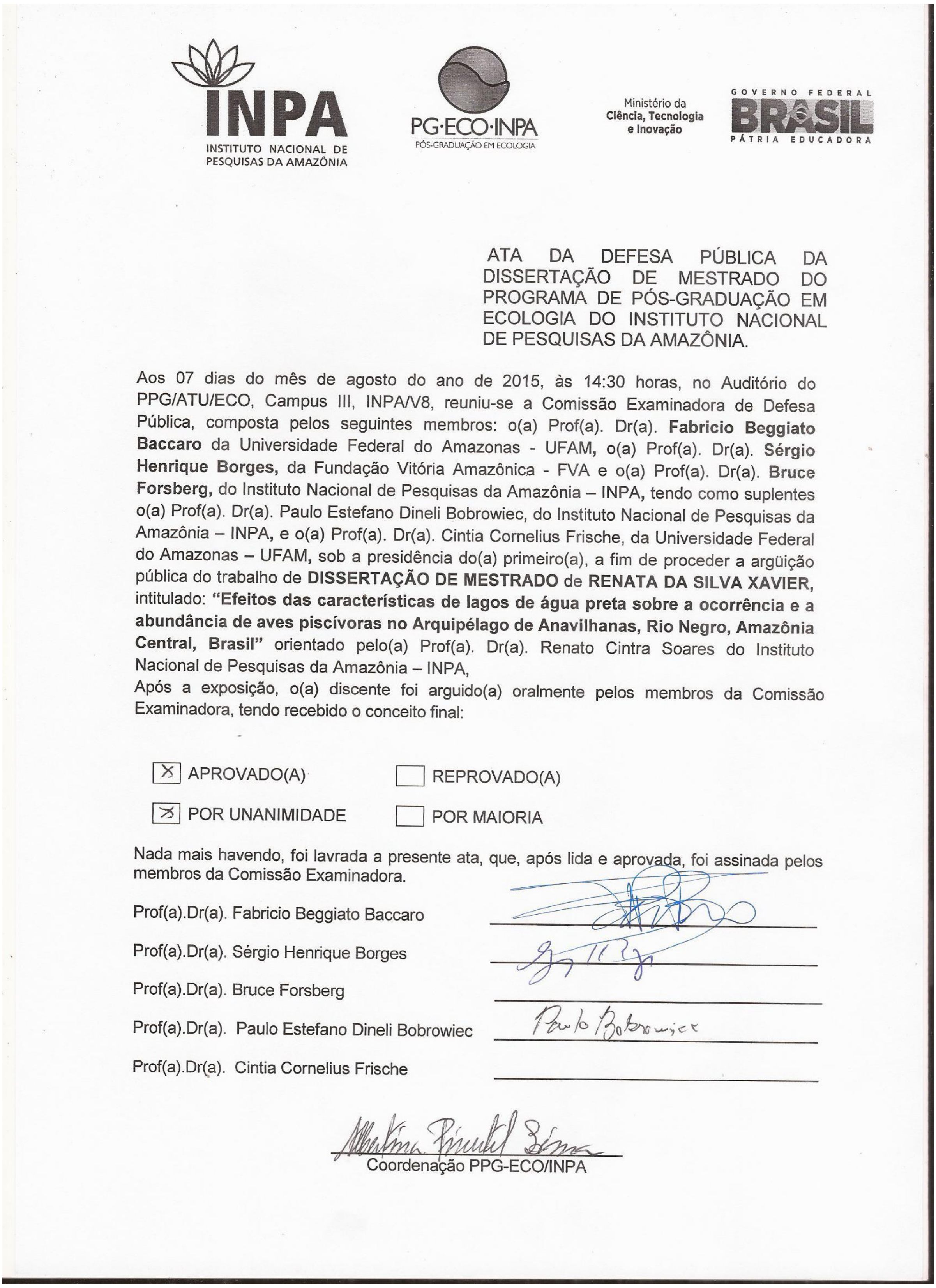
ANEXO 2 (Ata da Defesa Oral Pública)



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ATA DA DEFESA PÚBLICA DA DISSERTAÇÃO DE MESTRADO DO PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA DO INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA.

Aos 07 dias do mês de agosto do ano de 2015, às 14:30 horas, no Auditório do PPG/ATU/ECO, Campus III, INPA/V8, reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: o(a) Prof(a). Dr(a). **Fabricio Beggiato Baccaro** da Universidade Federal do Amazonas - UFAM, o(a) Prof(a). Dr(a). **Sérgio Henrique Borges,** da Fundação Vitória Amazônica - FVA e o(a) Prof(a). Dr(a). **Bruce Forsberg,** do Instituto Nacional de Pesquisas da Amazônia – INPA, tendo como suplentes o(a) Prof(a). Dr(a). Paulo Estefano Dineli Bobrowiec, do Instituto Nacional de Pesquisas da Amazônia – INPA, e o(a) Prof(a). Dr(a). Cintia Cornelius Frische, da Universidade Federal do Amazonas – UFAM, sob a presidência do(a) primeiro(a), a fim de proceder a argüição pública do trabalho de **DISSERTAÇÃO DE MESTRADO** de **RENATA DA SILVA XAVIER,** intitulado: **"Efeitos das características de lagos de água preta sobre a ocorrência e a abundância de aves piscívoras no Arquipélago de Anavilhanas, Rio Negro, Amazônia Central, Brasil"** orientado pelo(a) Prof(a). Dr(a). Renato Cintra Soares do Instituto Nacional de Pesquisas da Amazônia – INPA,

Após a exposição, o(a) discente foi arguido(a) oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

☒ APROVADO(A)   ☐ REPROVADO(A)

☒ POR UNANIMIDADE   ☐ POR MAIORIA

Nada mais havendo, foi lavrada a presente ata, que, após lida e aprovada, foi assinada pelos membros da Comissão Examinadora.

Prof(a).Dr(a). Fabricio Beggiato Baccaro ____________________

Prof(a).Dr(a). Sérgio Henrique Borges ____________________

Prof(a).Dr(a). Bruce Forsberg ____________________

Prof(a).Dr(a). Paulo Estefano Dineli Bobrowiec Paulo Bobrowiec

Prof(a).Dr(a). Cintia Cornelius Frische ____________________

Coordenação PPG-ECO/INPA