
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E BIODIVERSIDADE

A acústica como dimensão de comunidades
ecológicas e instrumento para o
monitoramento da biodiversidade

Larissa Sayuri Moreira Sugai

Tese apresentada ao Instituto de Biociências do Câmpus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de Doutor em Ecologia e Biodiversidade.

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LARISSA SAYURI MOREIRA SUGAI

Orientador: **Prof. Dr. Tadeu de Siqueira Barros**

Co-orientador: **Prof. Dr. Thiago Sanna Freire Silva**

Co-orientador: **Prof. Dr. Diego Llusia**

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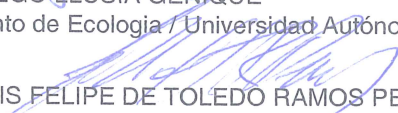
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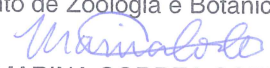
AUTORA: LARISSA SAYURI MOREIRA SUGAI
ORIENTADOR: TADEU DE SIQUEIRA BARROS
COORDINADOR: THIAGO SANNA FREIRE SILVA
COORDINADOR: DIEGO LLUSIA GENIQUE

Aprovada como parte das exigências para obtenção do Título de Doutora em ECOLOGIA E BIODIVERSIDADE, área: Biodiversidade pela Comissão Examinadora:


Prof. Dr. DIEGO LLUSIA GENIQUE
Departamento de Ecologia / Universidad Autónoma de Madrid


Prof. Dr. LUIS FELIPE DE TOLEDO RAMOS PEREIRA
Departamento de Biologia / Universidade Estadual de Campinas

Profa. Dra. DENISE DE CERQUEIRA ROSSA FERES
Departamento de Zoologia e Botânica / UNESP/Câmpus de São José do Rio Preto


Profa. Dra. MARINA CORREA CORTES
Departamento de Ecologia / UNESP - Instituto de Biociências de Rio Claro - SP

Prof. Dr. VICTOR SATORU SAITO
Centro de Ciências Biológicas e da Saúde / Universidade Federal de São Carlos

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APRESENTAÇÃO

Após muito refletir sobre uma transversal retórica que pudesse amarrar os marcos no trajeto que culmina no desfecho desta tese, largo a partir de um dos raros momentos de grandes certezas na vida, quando muito pequena, decidi me tornar “roqueira”. Notavelmente, este desejo foi reprogramado ao longo da vida. Aos 17 e sob inescapáveis efeitos da idade, iniciei a faculdade de Ciências Biológicas motivada pelo abstrato ímpeto de entender a natureza. Motivada a despertar interesse por alguma linha de pesquisa, busquei diversificar em estágios e iniciações científicas, começando por parasitologia de jacarés, invertebrados cavernícolas, dispersão de sementes por bugios, polinização de ipês e genética da mosca da fruta. Também me voluntariei a auxiliar levantamentos florísticos, coletas de aranhas, morcegos, anuros, invertebrados herbívoros, abelhas e fungos endofíticos. Acreditava que, ao diversificar as práticas, em algum momento atingiria um nirvana e então saberia o que seguir na vida. Mas faltou noradrenalina, e isso nunca aconteceu.

Decidi mudar a escala e explorar o sensoriamento remoto como proposta de mestrado. Utilizei medidas de heterogeneidade da vegetação em veredas/brejos no Cerrado e as relatei a comunidades de anuros que meu irmão Massao havia coletado em seu mestrado. *“Interessante o projeto, existe todo um nicho de mercado para monitorar a Amazônia com satélites”*, me saudou um parente, sumariamente ignorando minha explicação sobre o mestrado. Ironicamente, me aproximei de um professor recentemente ingressado no departamento de Geografia da UNESP de Rio Claro que utilizava sensoriamento remoto para monitorar aspectos da vegetação da Amazônia (Thiago!). Essa ponte ocorreu pela minha prima Lelê, que me sugeriu a disciplina de ecologia de paisagem ministrada pelo Milton César Ribeiro, que por sua vez, me sugeriu trocar uma ideia sobre o doutorado com o Thiago Silva.

Nas entranhas destes acontecimentos, ainda não havia desistido de ser roqueira. Participava de uma banda com crescente espaço no cenário alternativo de Campo Grande na época. Quando gravamos uma faixa musical em um estúdio pela primeira vez, fiquei obstinada com o abismo que separava o som que tocávamos ao vivo e som gravado profissionalmente. Era literalmente o oposto de conhecer uma faixa de um álbum e a escutar ao vivo. Durante as gravações, me perguntaram se eu colocaria elementos que não estariam presentes ao vivo. Por um lado, era interessante

explorar novas possibilidades sonoras, e por outro, seria injusto se não fosse capaz de apresentá-las ao vivo. Esse impasse me motivou a utilizar pedais de efeito e a prezar pela qualidade do som, de forma a minimizar potenciais fenômenos acústicos (como a famosa microfonia) a partir de equalizadores e de configurações em mesas de som. Paralelamente, comecei a ter contato com trabalhos propondo o conceito de paisagens sonoras (sons ambientais) e de investigações sobre as dinâmicas dessas paisagens sonoras. Foi então que me convenci a aproximar a acústica à ecologia como uma linha investigativa, o que me induziu a buscar visões integrativas de áreas como comunicação animal, ecologia comportamental, ecologia de comunidades e sensoriamento remoto.

Dessa forma, eu e Thiago concebemos o projeto de doutorado propondo abordar o papel de interações acústicas na organização das comunidades. Além do sensoriamento remoto a partir de ondas eletromagnéticas, estávamos adentrando ao monitoramento de ondas sonoras produzidas por animais. Essa é uma tendência relativamente nova em ecologia, onde espécies que usam comunicação acústica podem ser registradas e associadas a uma coordenada geográfica. Entramos em contato com um pesquisador influente na área (Jêrome Sueur) para apresentar nossas ideias, que por sua vez, sugeriu que procurássemos o Diego Llusia, que passava uma temporada em Goiânia em função de seu projeto financiado pela *Marie Skłodowska-Curie Actions* (União Europeia). Trocamos alguns e-mails sobre o projeto que foram essenciais para consolidar as ideias propostas à Fapesp (Fundação de amparo à pesquisa do estado de São Paulo), que por fim aceitou financiar minha bolsa de doutorado.

Ao decorrer do projeto, identificamos a necessidade de sintetizar os muitos trabalhos que lançavam mão desta abordagem. Realizamos um levantamento sistematizado da literatura e revisamos as tendências dos estudos utilizando monitoramento acústico em ambientes terrestres (*capítulo I*), e uma síntese sobre os desenhos amostrais utilizados nesta literatura (*capítulo II*). O momento foi bastante oportuno para lançar esses trabalhos, que foram aceitos para publicação em revistas científicas (*BioScience* e *Remote Sensing in Ecology and Conservation*). Ainda, durante meu estágio na *Universidad Autónoma de Madrid* sob a supervisão do Dr. Diego Llusia, escrevemos uma opinião sobre o valor futuro das gravações ambientais que estão sendo realizadas atualmente, como um paralelo às cápsulas do tempo (*prólogo*), que também foi publicado (*Ecological Indicators*).

Os seguintes capítulos são frutos do nosso projeto de monitoramento acústico de anuros no Pantanal (figuras 1 e 2) e são aqui apresentados como manuscritos a serem submetidos. No *capítulo III*, utilizamos as características acústicas e as relações evolutivas entre as espécies para caracterizar as comunidades. Seleccionamos comunidades que representassem locais abrangendo um gradiente desde lagoas em um contexto florestal até lagoas em paisagens dominadas por gramíneas, as quais representam feições do mosaico de vegetações existentes no Pantanal. Geramos expectativas teóricas baseadas em hipóteses que previam um determinado arranjo do perfil acústico das comunidades de acordo com pressões seletivas ou interações sociais, e contrastamos essas expectativas com nossas observações. Já no *capítulo IV*, investigamos como a composição das espécies nas comunidades variam durante o período de atividade diária das espécies (ao decorrer da noite). Essa abordagem considera que as espécies apresentam diferentes padrões de atividade em seus turnos de vocalização. Dessa forma, investigamos se essas diferenças são detectáveis a partir da perspectiva de comunidades e se as características ambientais experimentadas por estas influenciam em maior ou menor grau as diferenças de composição em curto prazo.



Figura 1. Lagoas e formações vegetacionais típicas da região sul do Pantanal (Nhicolândia), localizadas na fazenda Barranco Alto, município de Aquidauana, Mato Grosso do Sul, Brasil. Dispomos gravadores autônomos acústicos para gravar a atividade de espécies de anuros em 39 lagoas.

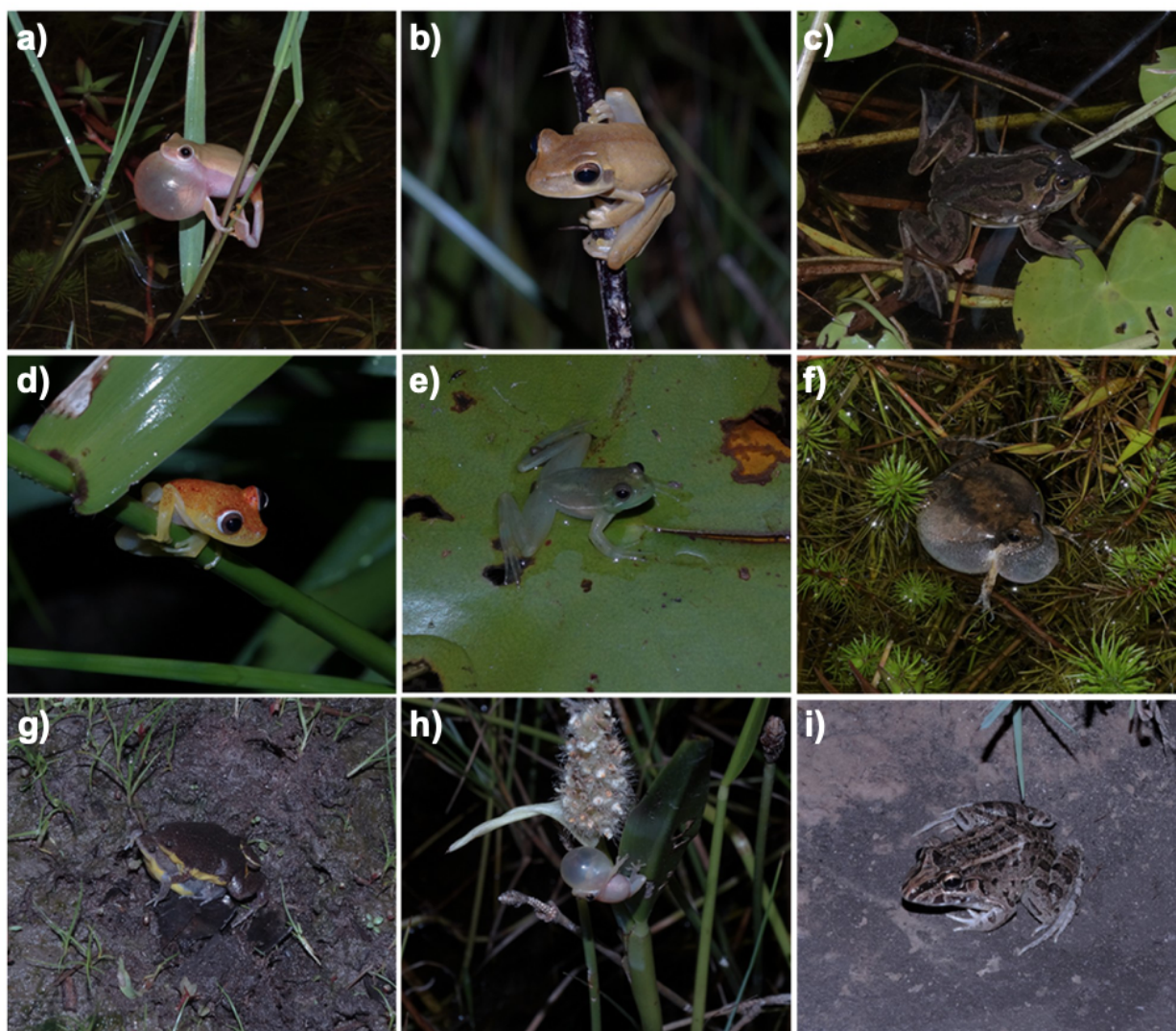


Figura 2. Algumas das espécies registradas durante o monitoramento acústico de anuros em lagoas localizadas na região sul do Pantanal: a) *Dendropsophus elianeae*, b) *Hypsiboas raniceps*, c) *Pseudis paradoxa*, d) *H. punctatus*, e) *Lysapsus limellum*, f) *Physalaemus albonotatus*, g) *Elachistocleis matogrosso*, h) *Scinax fuscomarginatus*, i) *Leptodactylus chaquensis*.

Para apresentar o conteúdo relacionado a este projeto, apresento uma introdução geral composta por três seções, onde discorro os alicerces teóricos respaldados nos capítulos (figura 3). Na seção I, convido o leitor a uma introspecção acerca de aspectos filosóficos sobre construção do conhecimento na ciência e na ecologia. Na seção II, apresento bases conceituais sobre os principais temas subjacentes aos capítulos III e IV: ecologia de comunidades, ecologia da informação e comunicação acústica. Finalmente, na seção III discuto sobre aspectos relacionados a amostragem (escala e período de observação) e como novas tecnologias podem auxiliar a preencher lacunas de conhecimento em ecologia. Busco ser sintética nestas

seções introdutórias, conduzindo a narrativa para desembocar o referencial argumentado nos quatro capítulos aqui apresentados.

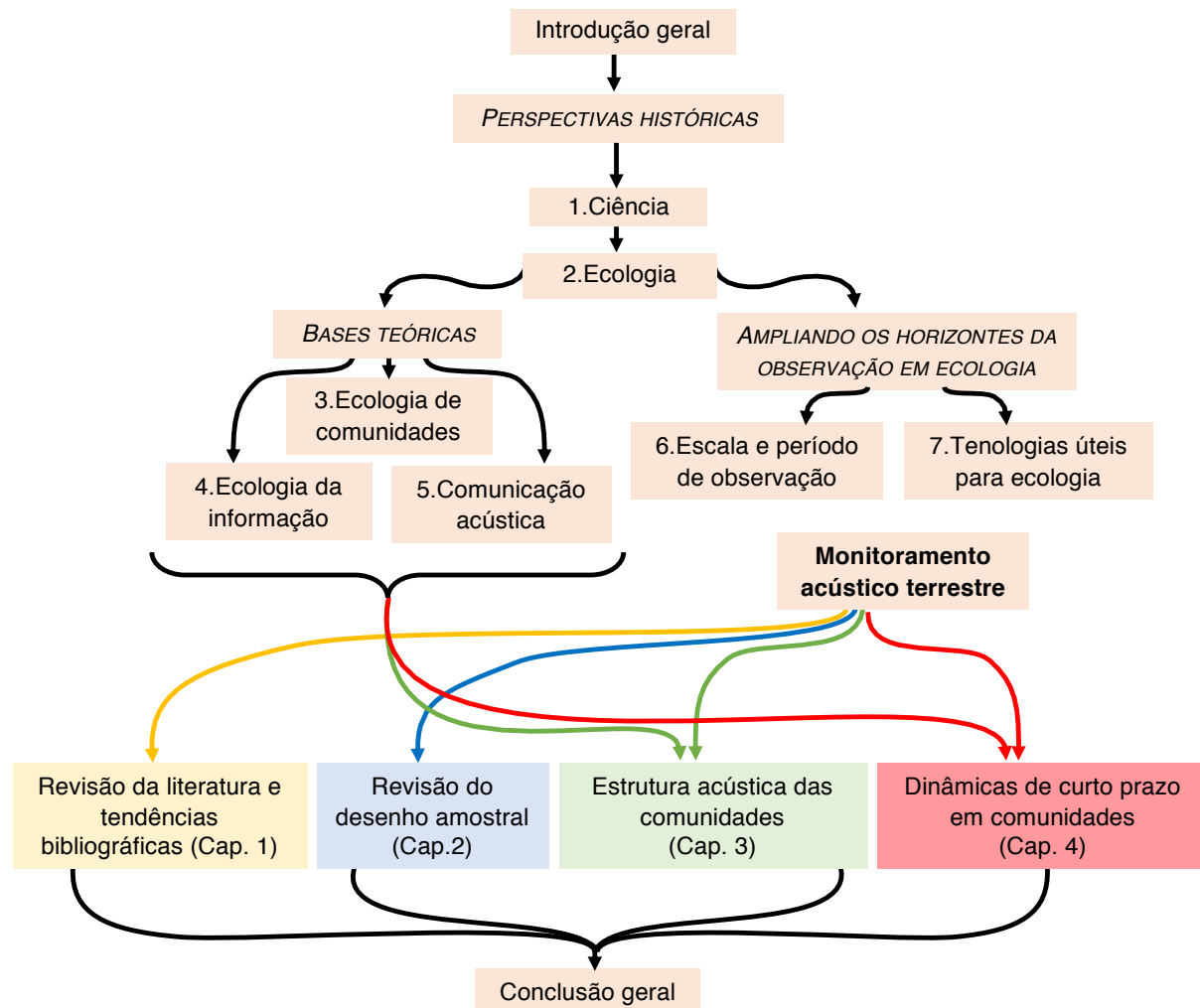


Figura 3. Estrutura desta tese de doutorado, com uma introdução geral composta por três seções, as quais apresentam os tópicos abordados nos quatro capítulos (caixas coloridas).

RESUMO

A natureza é ruidosa. Passarinhos gorjeiam enquanto o vento silva ao pentear os campos com abelhas e seus zunzuns rondando flores. Desatentos, deixamos de notar uma incrível quantidade de elementos retumbando em nosso entorno. No entanto, cada som parte de uma fonte, deixando uma pista sobre a situação na qual foi produzido. Podemos identificar a espécie de passarinho pelo seu canto, e, quem sabe, revelar a passagem de uma espécie migratória. A imagem de um campo nos é desperta ao escutar o vento soprando por gramíneas, que ressoaria diferente se soprasse por uma floresta. Por conseguinte, podemos registrar a atividade acústica dos organismos e descrever as dinâmicas de ecossistemas através de um conjunto de técnicas oferecidas pelo *monitoramento acústico passivo*. Além disto, os diversos sons emitidos por animais são produzidos sobretudo para fins reprodutivos e territoriais. Sua produção possui elevado custo energético e influencia se a performance de um organismo resultará em saldo positivo para a perpetuação de seus descendentes. Diante disso, alguns percalços no caminho entre a emissão e a recepção desses sons podem adulterar suas características e inviabilizar seu reconhecimento. Por serem ondas mecânicas, a vegetação pode refratar e absorver elementos dos sons emitidos por animais. Ou ainda, em grandes agregações, como os coros por aves no amanhecer e por anuros e invertebrados ao ocaso, os diversos sons podem gerar interferências. Em ambos os casos, a degradação sonora pode comprometer o sucesso reprodutivo das espécies. Contrariamente, uma outra perspectiva prevê que esses percalços não seriam tão custosos assim, e que na verdade os sons emitidos intermediam interações entre diferentes espécies podendo influenciar a distribuição dos organismos. Isto posto, tive como objetivos nesta tese i) sumarizar aplicações do monitoramento acústico em ecologia e conservação e ii) investigar a organização de comunidades de anuros no Pantanal sul-matogrossense a partir de seus aspectos acústicos e de uma alta precisão temporal para representar as comunidades. Para tal, começo com um *prólogo* que traça um paralelo entre o conjunto de gravações acústicas obtidos atualmente à “cápsulas do tempo” que no futuro, podem se tornar registros únicos do passado dos ecossistemas. Em sequência, os dois primeiros capítulos buscam sintetizar aplicações e tendências bibliográficas sobre monitoramento acústico passivo em ambientes terrestres, sendo o *primeiro capítulo* uma revisão sistemática da literatura. No *segundo capítulo*, resumo os desenhos amostrais utilizados e apresento diretrizes para otimizar a amostragem. A segunda parte da tese é destinada a investigação da organização de comunidades de anuros através de monitoramento acústico. No *capítulo 3*, caracterizo as comunidades a partir de atributos das vocalizações dos anuros e investigo se o espaço acústico estaria arranjado de forma a minimizar potenciais interferências na comunicação. Em geral, as comunidades foram constituídas por espécies acusticamente similares, e aquelas comunidades contendo espécies mais distintas filogeneticamente apresentaram maior similaridade acústica. Esses resultados sugerem que, sob uma perspectiva acústica, as comunidades podem estar organizadas em função do uso de informação a partir dos sinais acústicos umas das outras. No *capítulo 4*, analiso as comunidades de anuros a partir de um recorte temporal bastante preciso, onde variações dentro do período de atividade diária das espécies são consideradas. As

comunidades apresentaram a maior parte das espécies ativas no começo do período noturno, com conseguinte decaimento ao longo da noite. Essa variação em curto prazo é maior em locais cujo ambiente é estruturalmente mais complexo, sugerindo contundentes dinâmicas temporais de curto prazo associadas a periodicidade e ao ambiente. Isso implica que essas dinâmicas podem modular interações entre espécies e, por consequência, refletir na estruturação das comunidades. Por fim, espero que essa tese possa estimular o uso do monitoramento acústico em pesquisas ecológicas, e apresentar novas perspectivas, a partir da acústica, sobre o funcionamento de comunidade ecológicas.

Palavras-chave: montagem de comunidades, comunicação acústica, anuros, Pantanal, ecologia da informação

ABSTRACT

Nature is noisy. Birds chirps while the wind whistle when brushing the fields, with bees buzzing around flowers. Meanwhile, our absence of mind prevents us to notice many elements rumbling on our surroundings. However, each sound has a source that leaves clues about the situation in which it was produced. The songbird can be identified by its song and eventually reveal the passage of a migratory species. The wind blowing through the grass quickly resemble the image of a field that would otherwise sound different if it blew through a forest. Therefore, such acoustic activity of the organisms can be recorded and used to describe ecosystems dynamics through a set of techniques included in *passive acoustic monitoring*. In addition, sounds emitted by animals are produced mainly for reproductive and territorial purpose. Its production is costly and influences whether the performance of an organisms will lead a positive balance for the perpetuation of its descendants. As such, obstacles on the path between sound emission and reception may distort its characteristics and impair sound recognition. As sound are mechanical waves, vegetation can refract and absorb elements on the acoustic signal, or in large aggregations, such as dawn bird chorus and dusk anuran and invertebrate choruses, an abundance of animal sounds can generate interferences. In both cases, sound degradation may compromise species' reproductive success. On the contrary, another perspective predicts that such obstacles are not that hard, and that in fact, animals use sounds to mediate interactions between species, even influencing the distribution of those relying in such interactions. Hence, my goals with this thesis were i) to summarize applications of acoustic monitoring in ecology and conservation, and ii) to investigate the structuring of anuran communities in the southwest Pantanal in Brazil using acoustic characteristics and a high temporal precision perspective to determine communities. Thereby, I begin this thesis with a *prologue* that parallels the set of acoustic recordings being acquired currently to "time capsules" for the humanity. Following up, I devote two chapters to synthesize applications and bibliographic tendencies about passive acoustic monitoring in terrestrial environments. The *first chapter* is a systematic review of the literature and the *second* is a synthesis of survey designs used in the reviewed bibliography, with guidelines to optimize acoustic sampling. The next chapters are dedicated to investigating the organization of anuran communities in the Pantanal wetlands, acoustic monitoring was employed. In *chapter 3*, I address the acoustic dimension to characterize communities, described by anurans' advertisement calls. We

explore the arrangement of such acoustic space and whether its structure may reflect strategies to minimize interference in animal communication. In general, communities were composed by species with similar acoustic characteristics, where those communities composed by more distantly related species showed greater acoustic similarities. These findings suggest that communities may reflect strategies for information use through the acoustic signals of heterospecifics. In *chapter 4*, I use a fine temporal resolution scale to address species' diel activity and investigate its consistency within and between communities. Communities had most species are active in early periods of nocturnal activity and short-term species composition decay along the night. Such nocturnal decay in species composition was also associated with communities located at more structurally complex habitats. These findings suggest widespread short-term dynamics across communities associated to diel cycle and environmental structure, which may influence species interaction potential and consequently, the structure of communities. Finally, I hope that this thesis can stimulate ecological research with acoustic monitoring and to open new perspectives with acoustics on the dynamics of ecological communities.

Keywords: community assembly, acoustic communication, anura, Pantanal, ecology of information

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1. INTRODUÇÃO

1.1 Seção I – Perspectivas epistemológicas

1.1.1 A CONSTRUÇÃO DO CONHECIMENTO CIENTÍFICO

“For myself, I am interested in science and in philosophy only because I want to learn something about the riddle of the world in which we live, and the riddle of man's knowledge of that world. And I believe that only a revival of interest in these riddles can save the sciences and philosophy from an obscurantist faith in the expert's special skill and in his personal knowledge and authority” – Karl Popper

Na quinta-feira de 11 de abril deste ano (2019), as capas dos jornais ao redor do mundo destacavam a imagem de um dos fenômenos mais intrigantes do imaginário humano: o buraco negro (figura 4). Há cem anos, o físico Albert Einstein consolidava a teoria da relatividade geral, a qual postulava o efeito da gravidade sobre a luz, sendo capaz de gerar distorções no espaço-tempo. A fascinante imagem de um anel luminoso no espaço, mesmo que borrada, é a mais forte evidência que reitera a importância da teoria da relatividade no entendimento do universo e, consequentemente, na nossa existência.

Esse marco histórico não seria possível sem o amplo e recorrente uso de uma metodologia científica tanto por precursores quanto por sucessores a Einstein. De maneira simplificada, a lógica aplicada utilizou 1) *uma teoria subjacente* – teoria da relatividade, 2) *o levantamento de uma hipótese* – o buraco negro, 3) *teste/coleta de observações* – obtenção de medidas a partir de uma rede de oito radiotelescópios espalhados pelo mundo e 4) *análise* – processamento de quatro milhões de gigabytes em um supercomputador ao longo de dois anos. Este exemplo foi deliberadamente escolhido para ilustrar que a partir de então, quaisquer outras hipóteses prevendo uma conformação do buraco negro distinta daquela divulgada nos jornais pelo mundo será dificilmente aceita pois um novo paradigma foi estabelecido e servirá de base para a formulação e teste de novas hipóteses (Kuhn 1962).

A assertiva de que algo foi “cientificamente provado” já é parte de nosso cotidiano. Mas já se perguntou como é possível provar (cientificamente) algo? Imagine

que a imagem obtida do buraco negro resultasse em algo incompatível com o esperado pela teoria. Claro, isto poderia decorrer de falhas nos algoritmos usados para gerar a imagem, ou nas engrenagens dos telescópios, ou nas práticas adotadas por aqueles que operaram os telescópios, e por aí vai. Mas se essas instâncias todas estiverem em perfeita sintonia e livre de erros, é provável que a inconsistência esteja na hipótese sobre o buraco negro, o que levantaria sérias dúvidas sobre a teoria da relatividade. Ou seja, a credibilidade é dependente de um julgamento das hipóteses levantadas a partir da teoria, mediante testes e critérios genuinamente apropriados. Esta base filosófica é atribuída a *Karl Popper*, que propôs traçar uma clara distinção entre o *que é ciência* e o *que não é ciência*. Um breve retrospecto histórico nos permite ambientar o surgimento deste princípio: à época em que *Popper* propôs o princípio de falseabilidade, o mundo era inundado por inéditas teorias em história, psicologia e física (*Marx*, *Freud*, *Adler* e *Einstein*), e nas palavras do autor: “*There was a lot of popular nonsense talked about these theories*” (Havia um monte de besteiras populares faladas sobre essas teorias)¹ (*Popper* 1963). A atmosfera na década de 20 era tomada por verdades absolutas à luz dessas teorias, onde praticamente tudo podia ser explicado por elas. *Popper* cita uma passagem na qual apresenta um estudo de caso a *Adler* que, sem examinar o caso e nem ao menos ver o paciente, rapidamente apresenta uma explicação segundo sua teoria. Sua justificativa quanto a certeza do diagnóstico foi: “*Because of my thousandfold experience*” (algo como: Devido a minha imensa experiência). Naquele momento, *Popper* percebeu que, na realidade, *Adler* não havia conseguido confirmar nada a não ser o fato de que aquele caso poderia ser interpretado de acordo com sua teoria.

O que veio a seguir foi a proposta que rompeu definitivamente o científico do não-científico: não é possível fazer ciência a partir de uma proposição que não é testável/falseável². E como a ciência avança com este princípio? Com um pouco de abstração, podemos traçar um paralelo com o processo de separar grãos de feijão de um conjunto de grãos duvidosos. Só prossegue para o cozido aqueles grãos que sejam constatados sadios mediante um critério (no meu caso, atendendo ao crivo de minha mãe, que foi aperfeiçoado conforme sua experiência com minha avó). Grãos defeituosos, pedrinhas e até milho vindos do mesmo saco são descartados do conjunto. Imagine que, através do método científico, aquelas conjecturas improváveis sobre o funcionamento de determinado fenômeno são como os grãos de feijão

desprezados. Cada vez que abrimos um saco de conjecturas e descartamos aquelas menos consistentes, aprimoramos a receita e avançamos no conhecimento científico.



Figura 4. Capas de jornais impressos ao redor do mundo no dia 11 de abril de 2019. Em destaque, a imagem do fenômeno do buraco negro.

Em geral, há uma expectativa de que investigações científicas resultem em leis generalizáveis que expliquem um fenômeno. Contudo, esta é apenas uma das abordagens existentes que permitem a construção do conhecimento – a abordagem *nomotética*. Charles Darwin, acreditando equivocadamente empregar um raciocínio indutivo, realizou experimentações de cunho hipotético-dedutivo sobre sua então hipótese sobre a seleção natural, pelas quais levantou evidências sobre o processo adaptativo de seres vivos e da diversificação de espécies ao longo do tempo (Ayala 2009). A seleção natural, também concebida independentemente pelo impetuoso naturalista e precursor da biogeografia Alfred Russel Wallace, se tornou uma peça chave na biologia e é tido como o mecanismo central no processo evolutivo das espécies. Sua formulação possui tamanho poder de generalização que pode inclusive transcender aplicações em ciências naturais e contribuir teoricamente a distintas áreas de estudo, como a evolução da própria cultura humana (Mesoudi 2011).

“When radium was discovered, no one knew that it would prove useful in hospitals. The work was one of pure science. And this is a proof that scientific work must not be considered from the point of view of the direct usefulness of it” – Marie Curie

Em contraste a essa abordagem que objetiva leis e princípios gerais, a abordagem *ideográfica* tem um enfoque na particularidade dos estudos de caso. Na

abrangente área de ciências da vida, a história natural é a área dedicada ao descobrimento, descrição e classificação dos aspectos singulares da biodiversidade (tanto a atual quanto a extinta) (Cotterill & Foissner 2009). Praticamente todos os aspectos biológicos de um organismo foram (ou serão) descritos através de sistemáticas observações de suas características diagnósticas, dos locais onde se abriga e se reproduz, da estrutura social, entre outras características. De maneira irônica, a prática da história natural é atualmente vista como retrógrada por alguns ecólogos, quando seu papel é imprescindível para embasar estudos orientados a outros níveis de organização, como populações e comunidades. Além disso, o conjunto de observações sobre a performance dos organismos é fundamental para persuadir suposições gerais, que por sua vez, é um aspecto nomotético (Bartholomew 1986). *Edward Osborne Wilson* sugere a pesquisadores incipientes que o processo iterativo de observação/experimentação ante um objeto de estudo é fundamental para levantar hipóteses que posteriormente possam ser formalmente testadas (Wilson 2014).

Portanto, é notável que há diversas formas de se construir o conhecimento nas áreas científicas, seja pela busca de leis gerais, seja por exaustiva descrição de fenômenos particulares, contanto que uma conduta legítima seja transversal a ambas as práticas. Ao final, esses dois extremos (nomotético-ideográfico) acabam sendo retroalimentados quando o objetivo em comum é a busca do conhecimento.

¹ *Popper* pôde ver o “ovo da serpente” se formando, e conseguiu lançar sua perspicaz forma de discernir as fake-news da época. “[...] qualquer um que fizer o mínimo esforço poderá ver o que nos espera no futuro. É como um ovo de serpente. Através das membranas finas pode-se distinguir o réptil já perfeitamente formado.” Hans Vergerus em O ovo da Serpente, de Ingmar Bergman.

² Uma consequência desta revolução entre científico e não científico foi o descrédito às teorias propostas por Freud sobre os sonhos e sobre o nosso subconsciente, uma vez que elas não eram testáveis, especialmente pelas limitações metodológicas da época. Atualmente, neurocientistas conseguem traçar impressionantes semelhanças entre mecanismos cerebrais e as ideias psicanalíticas propostas por Freud.

1.1.2 A ECOLOGIA COMO ELA É...

"Generalizations in biology are almost invariably of a probabilistic nature. As one wit has formulated it, there is only one universal law in biology: 'All biological laws have exceptions.' This probabilistic conceptualization contrasts strikingly with the view during the early period of the scientific revolution that causation in nature is regulated by laws that can be stated in mathematical terms. Actually, this idea occurred apparently first to Pythagoras. It has remained a dominant idea, particularly in the physical sciences, up to the present day. Again and again it was made the basis of some comprehensive philosophy, but taking very different forms in the hands of various authors. With Plato it gave rise to essentialism, with Galileo to a mechanistic world picture, and with Descartes to the deductive method. All three philosophies had a fundamental impact on biology."- Ernst Mayr

Na ecologia, buscamos entender as interações entre diferentes organismos e suas relações com o meio em que vivem, de forma a revelar os motivos que levam as espécies a atingir determinadas abundâncias e a possuir suas respectivas distribuições no espaço e no tempo (*adaptado de Begon et al. 2006*). Para tanto, os elementos fundamentais de estudo são particularmente complexos: indivíduos pertencentes a diferentes espécies, em variados estágios de desenvolvimento, em um dentre muitos estados comportamentais determinado tanto pelo ambiente quanto por outros organismos em seu entorno, os quais igualmente estão sujeitos aos mesmos fatores.

O ambiente físico no qual os organismos se encontram pode ser delimitado por diversos recortes espaciais, desde escalas extremamente locais, até escalas de amplo alcance geográfico, como por exemplo, i) um espaço de 30 x 30 cm em uma área de floresta de terra firme na Amazônia, ii) uma faixa de 1 km em uma floresta de várzea à beira do Rio Amazonas e iii) toda a floresta de várzea da bacia do rio Amazonas (dentro de 7 milhões de km²). Podemos esperar que, em cada uma dessas escalas, diferentes fatores estejam associados a ocorrência de diferentes espécies. Imagine a organização populacional na escala do seu bairro, do seu estado e do nosso país. Sabemos que houve no Brasil um processo histórico envolvendo o fluxo de europeus para o interior do país, estabelecendo colônias com mão de obra escravizada africana e acompanhado da dizimação de populações nativas indígenas. Isso reflete hoje em um país amplamente estratificado, onde classes desfavorecidas são predominantemente

constituídas por negros e indígenas. No período de República, o país foi arbitrariamente esquadrihado em diferentes unidades administrativas que passaram por profundas alterações até a determinação de unidades federativas, que hoje confluem em determinados aspectos culturais (como festividades e culinária em comum). Finalmente, a organização territorial urbana pode ocorrer de forma planejada ou de maneira desordenada e que, por influência da especulação imobiliária, especulação imobiliária, gentrificação, renda e recursos econômico financeiro dos habitantes, determina os padrões e qualidade de vida dos bairros.³

Já sob uma perspectiva ecológica, os diferentes fatores relacionados a organização dos organismos no espaço e no tempo operam em função da escala em questão. Em uma escala temporal retrospectiva, houve eventos históricos determinantes no caminho da evolução das espécies, como processos geológicos, climáticos ou eventos imprevisíveis, como o asteroide que se chocou ao nosso planeta há 66.038 milhões de anos atrás e levou os dinossauros à extinção⁴. Em escalas mais regionais, fatores associados a diferentes tipos de vegetação condicionados a diferentes altitudes, ou arranjos de forma mais ou menos conectada (como exemplo, áreas de floresta contíguas em biomas distintos como Mata Atlântica e Cerrado) resultam em diferentes padrões de diversidade das espécies, por exemplo. Já em escalas mais próximas à nossa percepção, os principais fatores ecológicos são mais pontuais aos locais de observação, como o ambiente de entorno e a presença de competidores e de predadores. Portanto, a complexidade de elementos envolvidos na ecologia é descomunal em seus pormenores.

"The problem of relating phenomena across scales is the central problem in biology and in all of science" – Simon Levin

Devido a tamanha quantidade de fatores associados aos padrões observados na natureza, há em geral poucas generalizações em forma de leis universais em ecologia se comparado às leis da termodinâmica na física, por exemplo. Por esta razão, a ecologia começou a ser criticada como uma ciência "fraca" (Lawton 1999). Particularmente, é comum encontrar discrepâncias entre estudos sobre o mesmo objeto, especialmente devido a dificuldade em controlar todas propriedades capazes de interferir nos estudos: variação entre indivíduos, dificuldade em identificar atributos fenotípicos com causalidade ecológica, dificuldade em classificar e medir o ambiente de maneira adequada, relações não-lineares, um número alto de variáveis que podem interagir entre si, falta de correspondência entre experimentos

laboratoriais e de campo e inconsistência de resultados entre laboratórios (Pigliucci 2002). Em geral, essas são as mesmas críticas destinadas a caracterizar a psicologia como ciência “fraca”. No entanto, com respaldo na seção anterior, estaria correto julgar a importância de uma área científica pela sua falta de generalizações ou leis universais?

Como vimos anteriormente, não existe apenas uma forma categórica de se construir o conhecimento. O conjunto de estudos de casos (abordagem ideográfica) pode permitir estabelecer generalizações e criar hipóteses plausíveis a serem testadas. Daniel Simberloff argumenta que, sob a ótica de problemas ambientais, em muitas situações é mais conveniente analisar e entender o aspecto idiossincrático das comunidades ecológicas do que derivar leis gerais sobre seu funcionamento. Logo, um rol de “estudos de caso” pode ajudar a resolver problemas de maneira eficiente e pragmática e levantar potenciais generalizações que possam guiar futuros estudos (Simberloff 2004).

³ Há ainda a escala de seu próprio quarteirão ou rua e todos os potenciais conflitos entre vizinhos, cenário cotidiano retratado com primazia em “O som ao redor”, de Kleber Mendonça Filho.

⁴ Evento simbolicamente representado no desconcertante ato ao som de *Le Sacre du printemps* de Stravinsky no filme Fantasia).

1.2 Seção II – Bases teóricas

1.2.1 ADENTRANDO ÀS COMUNIDADES ECOLÓGICAS

“Actually, the entire ascent of life can be presented as an adaptive radiation in the time dimension. From the beginning of replicating molecules to the formation of membrane-bounded cells, the formation of chromosomes, the origin of nucleated eukaryotes, the formation of multicellular organisms, the rise of endothermy, and the evolution of a large and highly complex central nervous system, each of these steps permitted the utilization of a different set of environmental resources, that is, the occupation of a different adaptive zone.” – Ernst Mayr

Por que encontramos diferentes tipos e número de espécies em locais diferentes? Esta pergunta cose a malha que veste as investigações de comunidades ecológicas. Para tal, uma comunidade, em sentido amplo, corresponde ao conjunto completo de todos os organismos atribuídos a um determinado local e período. Em termos práticos, esta definição é impraticável nos moldes tradicionais de investigação (digo isso porque atualmente já existem métodos como o DNA *metabarcoding*, que permite avaliar o material genético de múltiplas espécies a partir de amostras do ambiente). Portanto, a “identidade” das comunidades é geralmente determinada por semelhanças taxonômicas, hábitos alimentares ou interações entre os organismos, como polinização e dispersão de sementes. Uma vez determinado este conjunto, é necessário lhe atribuir um recorte no espaço e no tempo que formam a unidade utilizada para caracterizar esse conjunto de espécies. Tradicionalmente, a escala de observação das comunidades ecológicas foi comumente determinada a partir de uma perspectiva antropocêntrica, uma vez que os fenômenos mais familiares eram frequentemente o objeto de estudo de naturalistas e ecólogos (Wiens 1989). Pelo foco nesta escala local, investigações precursoras sobre as engrenagens que geram e mantêm a diversidade de espécies realçaram os componentes locais às áreas nas quais as comunidades eram localizadas.

Por muito tempo, a dependência de uma espécie ao seu ambiente e o papel da competição entre espécies foram as principais retóricas nas abordagens sobre diversidade de espécies, aspectos esses que remetem ao nicho de uma espécie. Em arquitetura, o nicho pode ser uma reentrância na parede que permite a colocação de

móveis ou eletrodomésticos de forma embutida, ou que pode ocupar um local simbólico em uma igreja para abrigar uma estátua. Em ecologia, o nicho de uma espécie pode ser imaginado como um espaço de características ecológicas que representam os requerimentos de uma espécie para sobreviver e se reproduzir. Este espaço possui inúmeras dimensões, cada uma representando um componente ecológico da espécie, como disponibilidade de alimentos ou de espaço adequado para a manutenção da população (Hutchinson 1957).

Os recursos presentes na natureza são finitos e frequentemente comuns a diferentes espécies, o que porventura gera conflito pela sua aquisição. Darwin mesmo ponderou que espécies com maior grau de parentesco possuíam requerimentos ecológicos mais similares, o que o levou a conjectura de que deveriam competir mais intensamente entre si. Formalmente proposta como o princípio da exclusão competitiva pelo biólogo evolutivo Georgii Gause (Gause 1932) e apresentada como um modelo teórico da similaridade limitante por Robert MacArthur & Richard Levins (MacArthur & Levins 1967), o papel da competição por trás dos padrões de diversidade se tornou um dos pilares da ecologia. No entanto, uma consequência ecológica da competição seria encontrar comunidades compostas por espécies com lugares delimitados e segregados no espaço ecológico devido a seus nichos. Diversos trabalhos buscaram encontrar essas regularidades nas comunidades e não tiveram sucesso, o que pôs em xeque o papel central da competição.

O “paradigma da competição” começou a se romper, com especial destaque a crítica feita por Edward Connor & Daniel Simberloff (Connor & Simberloff 1979) em resposta ao trabalho de Jared Diamond (Diamond 1975), no qual um compêndio sobre o papel de forças competitivas na determinação das comunidades biológicas foi apresentado. Os autores mostraram que Diamond se baseou em hipóteses não falseáveis e sujeitas a testes não genuínos (lembre-se de Popper!). Com o acúmulo de evidências refutando o determinismo das comunidades, os ecólogos começaram a adotar propostas que iam além da dependência local do nicho das espécies (Ricklefs 1987). Assim, processos que ocorrem em escalas mais amplas espacial e temporalmente, como a imigração de espécies e o próprio processo evolutivo, começaram a ter mais destaque nas investigações dos padrões locais de diversidade. Houve ainda críticas que convocaram o abandono de estudos com enfoque local devido a falta de generalizações ou leis quanto aos determinantes das comunidades. “[...] community ecology is a mess, with so much contingency that useful generalisations are hard to find” (A ecologia de

comunidades é uma bagunça, com tanta contingência que generalizações úteis são difíceis de se encontrar) – a frase provocativa de *John Lawton* (Lawton 1999) resume a crítica a ecologia de comunidades, onde o autor argumenta que deveríamos lançar mão de abordagens em escalas geográficas mais amplas e buscar perspectivas macroecológicas para o entendimento da diversidade de espécies.

A julgar pelo histórico, torna-se claro o aspecto chave da escala na conciliação da ecologia de comunidades. Todo padrão biológico é dependente da escala de observação (Levin 1992), logo, os padrões de diversidade de espécie dependem da escala na qual uma comunidade é delimitada. Por exemplo, é provável que, em uma mancha de habitat, os aspectos locais influenciem a composição das comunidades ali presentes. Não obstante, essa mancha tanto aporta indivíduos vindo de outras manchas de habitat quanto pode contribuir como fonte de indivíduos para outros habitats. Ou seja, fatores não necessariamente associados à escala local influenciam os padrões observados localmente.

Um marco histórico nesta linha de pensamento foi o trabalho de *Robert MacArthur & Edward Wilson* (MacArthur & Wilson 1967), o qual mostrava a importância da distância entre ilhas oceânicas e de seu tamanho para a movimentação de indivíduos, o que resultava em mais ou menos espécies em diferentes ilhas. Em ambientes terrestres, essas ideias foram incorporadas ao entendimento de dinâmicas das espécies em manchas de vegetação natural que foram descontinuadas por alteração do uso do solo para, por exemplo, atividades agrícolas ou áreas residenciais. Além de que, o fluxo de indivíduos também está relacionado a quantidade de indivíduos presentes em diferentes manchas, a capacidade inerente da espécie em se locomover em diferentes ambientes (p. ex. diferentes padrões de deslocamento em áreas de eucalipto e de plantação de soja) e aos tipos de ambiente disponíveis: aspectos que dependem de uma perspectiva em extensão regional. Por conseguinte, o papel do arranjo espacial dos ambientes foi incorporado ao entendimento dos padrões de diversidade e são fundamentais para entender e solucionar problemas contemporâneos sobre a perda e a fragmentação de ambientes naturais.

A ruptura do “paradigma da competição” foi especialmente promovida com a síntese sobre as dinâmicas de fluxo de indivíduos entre comunidades (Etienne & Alonso 2007). Este fluxo está sujeito a flutuações imprevisíveis, onde uma espécie não possui vantagem alguma sobre a outra. Essa proposta paralela à *deriva genética*, na qual alelos que não estão sujeitos a seleção (ou seja, neutros) são passados para próximas gerações

seguindo um critério aleatório de amostragem, como uma roda da fortuna. Essa intervenção do acaso pode gerar flutuações que levam alguns alelos a se fixar, sem a necessidade de gerar vantagem adaptativa. A ideia da neutralidade foi aplicada a espécies ao invés de alelos, e constitui o cerne do arcabouço de teorias neutras da biodiversidade promovidas por *Stephen Hubbell* (Hubbell 2001). Consequentemente, ao reconhecer que comunidades locais estão inescapavelmente associadas a dinâmicas de dispersão e do componente estocástico, foi possível estabelecer novos paradigmas na investigação de comunidades.

Especificamente ao conjunto de comunidades locais que compartilham indivíduos entre si (metacomunidades), algumas propostas gerais foram sintetizadas para explicar as dinâmicas entre comunidades (Leibold *et al.* 2004). Além disso, a teoria neutra também considera o balanço entre extinção e especiação na manutenção das espécies nas metacomunidades. Sabemos que as populações de diferentes espécies estiveram sujeitas a pressões seletivas distintas ao longo da história de vida (Ricklefs 1987), como pelo rompimento de habitats, pela quebra de fluxo por modificação do relevo, ou até mesmo por interações com outros conjuntos de espécies anteriores às contemporâneas. Entender como diferentes fatores históricos influenciaram os caminhos da evolução e que hoje interagem com fatores ecológicos e moldam as comunidades é reconhecidamente um importante passo para ampliar nosso conhecimento sobre a diversidade de espécies (Ricklefs 2008).

As visões dicotômicas entre nicho *versus* neutro (local *versus* regional, determinístico *versus* estocástico) movimentaram esforços para, a princípio, validar a predominância de uma perspectiva sobre a outra. Por um lado, a evidência resultante, tanto em prol quanto contra cada perspectiva, nos permite avançar o entendimento sobre esses dois abrangentes processos na natureza. Por outro lado, esses embates nos distanciam de atingir uma concordância em como esses processos podem operar no mundo de fato (Leibold & McPeck 2006; Adler *et al.* 2007). Por exemplo, os mecanismos derivados da teoria neutra da biodiversidade podem ser associados a modelos prevendo a coexistência entre espécies mediada por diferenças de nicho. Novos esforços propõem que essas dicotomias refletem nada mais do que extremos de um *continuum* de processos ecológicos mediados pelas características das espécies e por dinâmicas demográficas em diferentes escalas. A julgar por modelos que representam os mecanismos de coexistência entre espécies baseados em diferenças competitivas e de nicho, onde *trade-offs* na performance de uma função ecológica possui um custo

em outra função (p.ex., especialização em um tipo de recurso em detrimento de outros recursos), e que podem ser promovidos por fatores associados a diferentes escalas temporais e espaciais (Kneitel & Chase 2004; HilleRisLambers et al. 2012; Vellend 2016).

Felizmente o cenário futuro para ecologia de comunidades é empolgante. Abordagens utilizando medidas diretamente associada a performance das espécies (atributos funcionais) permitiram atualizar as expectativas sobre interações entre espécies ao longo de gradientes ambientais. Nessa ótica, as comunidades são descritas a partir da distribuição dos atributos das espécies ao invés de suas identidades (McGill et al. 2006). Ainda, a popularização dos métodos de sequenciamento genético e de reconstrução da história evolutiva de diversos grupos biológicos promoveu a inclusão de uma perspectiva filogenética nas comunidades, permitindo cada vez mais relacionar o papel da evolução nos padrões atuais de diversidade (Webb et al. 2002). A interface integrativa entre ecologia-evolução de comunidades é uma fronteira que promete trazer novos panoramas, como a quebra de barreiras entre abordagens baseadas em clados e em comunidades (Weber et al. 2017).

Finalmente, a consolidação dos arcabouços teóricos em ecologia nos permite realizar observações mediante expectativas e predições que, respeitando o método científico, fazem com que avancemos no entendimento dessa complexa entidade que é a comunidade ecológica. No entanto, vale recordar como a observação da natureza era o principal instrumento dos naturalistas para testar predições intuitivas e inspirar novas ideias. Atualmente, nos distanciamos tanto dessa essência naturalista que a falta de “ligação” ou curiosidade sobre o objeto de estudo pode deixar escapar importantes nuances da natureza. Considerando a tamanha complexidade das comunidades ecológicas, é possível que ainda seja necessário balancear nossas ideias com observações diretas na natureza para criar novas perspectivas de investigação (Ricklefs 2012).

1.2.2 A ECOLOGIA DA INFORMAÇÃO

“Se podes olhar, vê. Se podes ver, repara” – Jose Saramago

“We find animals doing things that we, in our arrogance, used to think was “just human” – Jane Goodall

Enquanto o “paradigma da competição” foi prevalente nas discussões sobre a manutenção da diversidade de espécies, apenas o lado negativo das interações biológicas foi enfatizado, manifestado na *luta pela sobrevivência*. O papel de interações positivas foi amplamente ofuscado, apesar de sua reconhecida existência mesmo em comunidades com diversos competidores, como a partir de facilitação por meio da supressão de competidores de maneira indireta (Bruno *et al.* 2003). Interações positivas englobam relações entre uma ou mais espécies que afetam positivamente ao menos uma espécie envolvida. É comumente investigada em interações em redes mutualísticas, como as bactérias fixadoras de nitrogênio existentes nas raízes de plantas leguminosas. Contudo, interações positivas podem ocorrer de forma direta ou indireta entre organismos que compartilham recursos similares em um mesmo nível trófico em comunidades ecológicas (Bertness & Callaway 1994).

Estudos em ecologia comportamental e sensorial têm contribuído para elucidar como os animais detectam, processam e respondem ao seu ambiente (tanto biótico quanto abiótico). Qualquer organismo incapaz de possuir total ciência do estado atual de seu entorno ou de prever condições futuras acaba utilizando estratégias que diminuam essas incertezas. Essas estratégias são mediadas pelo uso de uma informação, que pode ser obtida das mais diversas formas. Por exemplo, quando escutamos barulho de passos em um corredor, sabemos que alguém se aproxima a um determinado ritmo e distância. A partir de uma conversa entre duas pessoas que chegue a outros ouvidos, podemos inadvertidamente saber quem matou *Odete Roitman* (vilã da telenovela *Vale Tudo*). Se você está no Pantanal e escuta o esturro de uma onça próximo a si, provavelmente entrará em estado de alerta pela iminência do encontro com o felino.

De maneira similar, os organismos produzem informações tanto de forma ativa, como a partir da emissão de sons que mediam diretamente a comunicação entre organismos, quanto de forma indireta, como a partir da interceptação de informações

de forma inadvertida para seu próprio benefício (p. ex., para encontrar um determinado recurso), ou com sons irrompidos não intencionalmente, como o barulho causado pela fuga de uma presa em meio a uma mata ao fugir de um predador. Esses sinais produzidos por animais podem ser emitidos por diferentes modalidades sensoriais e configuram *informações sociais*, em função de aspectos comportamentais dos organismos. Essas informações ficam disponíveis no ambiente e podem ser utilizadas por outros indivíduos, sejam eles conspecíficos ou de outras espécies (Schmidt et al. 2010). Como exemplo, um recente estudo mostrou que sons de polinizadores provocam respostas em flores, que instantaneamente aumentam a concentração de açúcar no néctar (Veits et al. 2019), elucidando uma inesperada forma de uso de informação social. Esse ilustre exemplo certamente se utilizou da mescla de cuidadosas observações em campo e ponderações hipotéticas, o que reitera o grande potencial de afiar nossa capacidade de observação da natureza para explicar os mais diversos fenômenos.

Além de influenciar o comportamento de um indivíduo, o uso de uma informação social pode promover a correlação entre comportamentos e distribuição dos organismos. Essas correlações podem ser exemplificadas por fortes padrões de agregação espacial, como um grupo de aves migrando em conjunto, ou padrões menos óbvios, como o cessar comunitário de atividade a partir da exposição de um sinal de um predador. Além disso, as decisões tomadas por indivíduos influenciam sua performance em diferentes atividades, como a busca por recursos alimentares e a dispersão para novos habitats. Indivíduos informados possuem mais vantagens do que indivíduos não informados, como para encontrar locais mais adequados para reprodução ou diminuir sua chance de ser predado.

O acesso à informação pode conferir vantagem competitiva, e caso reflitam em maior sucesso reprodutivo, a interação entre espécies a partir do uso de informações sociais promove efeitos positivos no crescimento populacional e, consequentemente, acabam por influenciar os mecanismos de coexistência entre espécies (Gil et al. 2019). Além do mais, quando o benefício é maior com o aumento da abundância das fontes produtoras de informação, o crescimento populacional pode ser *dependente de densidade positiva* (também conhecido como efeito *Allee*), ou seja, o crescimento da população informada é positivamente relacionado a densidade de informantes. No entanto, para competidores em mesmo nível trófico ou com alta sobreposição de requerimentos ecológicos, o uso da informação só é benéfico se o potencial de

competição por recursos em comum é compensado (Gil *et al.* 2018). Essas predições possuem implicações na estruturação de comunidades, que investigadas sob a ótica de interações positivas, como aquelas mediadas a partir dos sistemas sensoriais dos animais, pode ser útil para compreender os mecanismos responsáveis pela organização das comunidades ecológicas (Parejo & Avilés 2016).

1.2.3 COMUNICAÇÃO ACÚSTICA EM ANUROS

"I like the look of frogs, and their outlook, and especially the way they get together in wet places on warm nights and sing about sex"- Archie Carr

A comunicação, de maneira geral, é caracterizada pela transmissão de um sinal contendo uma informação codificada, que parte de um emissor e é destinada a um receptor específico. Estes sinais podem ser codificados a partir de elementos visuais, químicos e/ou acústicos. A partir de interações sociais, a troca de informações é um aspecto fundamental no comportamento dos organismos. Assim sendo, estudos sobre o fenômeno da comunicação possuem interface com diversas áreas do conhecimento, como evolução, ecologia, comportamento animal, genética de populações, neurobiologia e fisiologia (Bradbury & Vehrencamp 2011).

Durantes as estações mais quentes na região temperada e as mais úmidas na região tropical, o espetáculo noturno da natureza se destaca por uma característica trilha sonora: coros compostos por anuros (sapos, pererecas e rãs). Machos das mais diversas espécies de anuros possuem adaptações fisiológicas e morfoanatômicas especialmente úteis para ampla produção de sinais acústicos, como fibras musculares com alta concentração de mitocôndrias e de atividade enzimática aeróbica. Os músculos do tronco são repetidamente contraídos, expelindo o ar que é moldado nas cordas vocais e gera ondas sonoras, as quais são amplificadas no saco vocal, este, um adereço morfológico inflável que permite a irradiação do som para o ambiente exterior. Essas vocalizações são utilizadas para atrair fêmeas e para defender territórios contra outros machos. Os *sinais acústicos* (Caixa 1) apresentam variações entre indivíduos de uma mesma população, sendo que algumas características parecem ser preferidas no processo de escolha de machos pelas fêmeas, o que sujeita os sinais acústicos a pressões seletivas que conferem maior vantagem reprodutiva (seleção sexual). O sistema de reconhecimento de sinais reprodutivos evoluiu de tal forma que as vocalizações sejam espécie-específicas, assim, uma fêmea exposta a um sinal acústico pode reconhecê-lo como proveniente de um macho da mesma espécie (Wells 2007).

Por outro lado, a efetividade da comunicação depende da correta detecção, interpretação e posterior localização da fonte emissora pela fêmea. No entanto, o sinal acústico está sujeito a diversas barreiras durante sua transmissão que podem interferir na estrutura do sinal e inviabilizar sua correta decodificação pelo receptor. Em geral, ondas sonoras perdem intensidade e se degradam em função da distância que percorrem. Em experimentos laboratoriais, fêmeas não apresentam respostas a sinais conspecíficos de machos quando emitidos a partir de longas distâncias, apesar das respostas variarem entre diferentes espécies (Gerhardt & Huber 2002). A estrutura física do ambiente também pode afetar a propagação de ondas sonoras. Alguns habitats com contínua presença de ruídos, como cachoeiras, podem oferecer condições adversas a comunicação por sobreposição aos sons produzidos por anuros. Este mesmo fenômeno tem sido descrito devido a ruídos de origem antrópica, como aqueles provenientes de estradas e de atividade de mineração. Finalmente, as vocalizações produzidas por outras espécies, especialmente em grandes adensamentos em forma de coro, criam um ruído de fundo que pode causar o mascaramento dos sinais acústicos, aumentando assim a chance de confusão do sinal por fêmeas de outras espécies (Brumm 2013; Schwartz & Bee 2013).

Ao longo de décadas, alguns eminentes pesquisadores se dedicaram a entender como anuros conseguem se comunicar nessas diversas condições, como Robert Capranica, H. Carl Gerhardt, Peter Narins, Michael Ryan, Joshua Schwartz e Kentwood Wells. Foram descobertas alterações comportamentais e fisiológicas que permitem a melhor discriminação do sinal: alternância da emissão de sinais nos intervalos de vocalização de indivíduos, aumento da intensidade do sinal acústico (como aumentar o volume), aumento da frequência de sinalização (também conhecido como redundância do sinal), entre muitos outros (Ryan 1988). Apesar disso, a julgar que a emissão de sinais acústicos é extremamente custosa aos organismos e que sua efetividade é prejudicada diante das situações apresentadas, há ainda a possibilidade de que as fontes de ruído e de degradação dos sinais possam atuar como pressões seletivas na estrutura das vocalizações.

Caixa 1. Caracterizando um sinal acústico

Uma onda sonora é causada por uma variação na pressão do ar que gera um distúrbio nas moléculas que o constitui (figura Ia-b). Essa variação de pressão é transmitida a partir da expansão e contração do espaçamento das moléculas, que podem ser caracterizados como uma onda, e a distância entre os picos da onda determina seu comprimento (figura Ic). Uma vez que período está inversamente relacionado à frequência, ondas de *comprimento maior* possuem *frequências mais baixas* (percebidas como mais graves), e ondas de *menor comprimento* possuem *maior frequência* (percebidas como mais agudas). A quantidade de energia aplicada a onda nos remete a um aumento ou diminuição do volume, e não possui implicações na frequência do som.

Sons produzidos por animais são complexos, sendo compostos por diversas frequências que variam em sua energia. Com a finalidade de analisar essas ondas sonoras, utilizamos um método de decomposição de sinais complexos (a transformada de Fourier), que permite “separar” as frequências e suas variações de energia e ser representado por um gráfico de frequência e energia em função do tempo (espectograma, figura II). A partir disto, podemos extrair uma série de medidas que caracterizam a vocalização dos animais, como por exemplo, em qual frequência há maior concentração de energia e qual é a amplitude de frequências utilizadas.

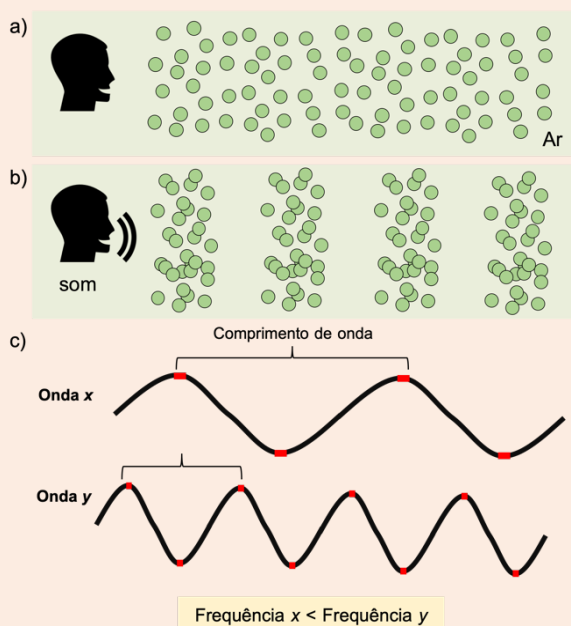


Figura I. Onda sonora e propagação do som. O ar é composto por moléculas (a), que quando sofrem um distúrbio causado por variação da pressão do ar (uma vibração), se expandem e contraem no espaço (b) de maneira que pode ser caracterizada com uma onda senoidal (c). A distância entre dois picos da variação da onda representa seu comprimento, sendo que ondas maiores possuem menor frequência, e ondas menores, maior frequência.

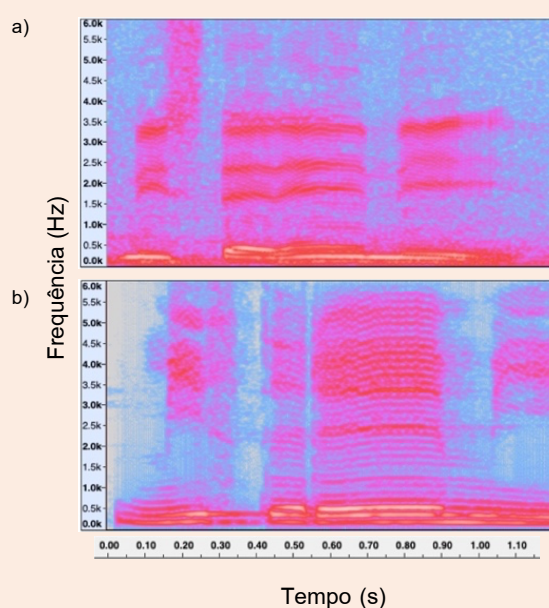


Figura II. Espectogramas representando onda sonoras complexas em frequência e energia ao longo do tempo. Ambos representam a mesma frase, típica de um programa televisivo onde o locutor profere a frase “Mister M”, sendo que em (a) é emitido por Cid Moreira e em (b) por Larissa Sugai. Note que as frequências com mais energia são mais baixas (graves) para Cid Moreira, e a frequência máxima alcançada pelos harmônicos não ultrapassa 3.5 kHz. Essas características, a partir de análises do espectograma, permitem discernir um discurso emitido por Cid Moreira e Larissa Sugai.

Estudos pioneiros com aves sugeriram que seus sinais acústicos refletem adaptações para reduzir atenuação (afeta a intensidade do som) e degradação (afeta a fidelidade do sinal) em comunicação à longas distâncias (Morton 1975). Frequências altas (agudas) se degradam mais rapidamente do que as frequências mais baixas (graves) com o aumento da distância de propagação. Além disso, a estrutura do ambiente pode obstruir fisicamente as ondas sonoras, pois o solo consegue absorver as ondas, enquanto folhas e troncos refletem, refratam e difratam diferentes comprimentos de onda. Dessa forma, em ambientes estruturalmente mais complexos, seria esperado que anuros vocalizassem a partir de locais mais elevados e com frequências mais baixas para otimizar a comunicação à longa distância. Adicionalmente, aspectos temporais da vocalização também podem ser afetados. Com a reflexão das ondas sonoras no ambiente, o som pode atingir um receptor a partir de diferentes fontes, algo similar a uma casa de espelhos, onde é possível se ver em vários espelhos ao mesmo tempo. Assim sendo, vocalizações que possuem abruptas variações de intensidade, com curtas e repetitivas emissões, podem acabar sendo percebidas como um som contínuo devido a reflexão no ambiente. Apesar de alguns testes empíricos de propagação do som e de resposta de fêmeas parecerem corroborar com essas previsões (Ey & Fischer 2009), uma melhor compreensão deste fenômeno deve surgir com abordagens incorporando o potencial de adaptações nas estruturas do sinal acústico sob uma perspectiva filogenética (Goutte *et al.* 2018).

Dentre os elementos dos sinais acústicos de anuros, aqueles relacionados à frequência sonora são responsáveis pela discriminação de espécies. Algumas observações pioneiras de comunidades de anuros na Amazônia sugeriram que as espécies ali presentes possuíam diferenças notáveis na frequência de suas vocalizações, levantando a hipótese de um tipo de segregação das frequências utilizadas pelas espécies, ideia análoga àquelas previstas para o nicho ecológico (Hödl 1977; Duellman & Pyles 1983). Outra possibilidade é de que a diferenciação das frequências sonoras entre diferentes espécies possa ter ocorrido ao longo de um processo evolutivo, como resultado de divergência destas características para evitar hibridização entre espécies que ocorrem em uma mesma área geográfica (simpátricas) (Schwartz & Bee 2013). Nesse cenário, seria esperado que um par de espécies simpátricas apresente maior diferença nas características dos sinais acústicos do que o mesmo par em locais cuja distribuição geográfica não se sobreponha (alopátricas) (Gerhardt 1994). No entanto, uma crítica pertinente a estes estudos é a ausência de um modelo nulo que

permita contrastar os resultados observados com aqueles esperados pelo acaso (se isso lhe despertar a memória sobre o debate entre *Diamond vs. Simberloff*, você fez meu dia feliz). Ao comparar os padrões de segregação acústica com cenários de comunidades sorteadas aleatoriamente, um estudo constatou que apenas algumas comunidades parecem apresentar tendência a segregação acústica, com aparente relação ao número de espécies presentes (*Chek et al. 2003*). Dessa forma, ainda é necessário explorar diferentes condições ecológicas das comunidades para entender o potencial papel desta competição pelo espaço acústico.

Além do relevante papel da comunicação acústica nas interações entre indivíduos da mesma espécie, ainda existe uma fronteira a ser investigada sobre as potenciais interações entre espécies. Durante a transmissão do sinal acústico, a informação pode ser interceptada por outros ouvintes. A recepção inadvertida de um sinal acústico permite ao interceptor, no mínimo, obter uma localização referente ao emissor. Esta informação pode ser utilizada por predadores para localizar presas, como morcegos e mosquitos fazem com algumas espécies de anuros (*Tuttle & Ryan 1981; Bernal et al. 2006*). Sem embargo, outras espécies em um mesmo nível trófico podem interceptar a informação para seu próprio benefício. Por exemplo, indivíduos podem tanto aumentar quanto diminuir a atividade de vocalização quando expostos a estímulos vindo de outras espécies de anuros (*Phelps et al. 2006*). Importante, não se trata necessariamente de sinais acústicos utilizados em situações de alarme, mas também daqueles comumente utilizados para atrair fêmeas (canto de anúncio). Esse tipo de interação indireta entre espécies pode aumentar a eficiência de forrageio decorrente de menor investimento em vigilância. Essas ideias estão alinhadas com as bases teóricas da ecologia da informação, que lança perspectivas sobre o valor da informação em coros de anuros, em contraste a abordagem na qual coros são vistos como ruído de fundo, como proposto pela hipótese de segregação de frequências acústicas.

Apesar do maior foco até então ter sido nos mecanismos de produção do som, há ainda um universo de outros mecanismos sensoriais atuando nos enigmas da comunicação acústica de anuros. Por exemplo, os mecanismos de recepção de sinais por fêmeas e machos podem estar muito bem calibrados aos elementos acústicos de sua espécie (*Gerhardt 2001*). Outras modalidades de comunicação podem emergir a partir da produção do som, como a propagação de ondas pelo solo, estabelecendo um canal de comunicação sísmica onde a recepção pode ocorrer em outros órgãos além do tímpano (*Narins 1990*). Estímulos visuais também são utilizados para informar decisões,

como por estímulos provocados pelo saco vocal ou por rituais envolvendo o movimento de membros, do corpo de forma estacionária, e movimentação do indivíduo (Hödl W & A 2001). Ainda assim, o uso de mais de uma modalidade de comunicação pode beneficiar a recepção da informação (Taylor & Ryan 2013), da mesma forma que utilizamos uma combinação de estímulos visuais, sons, e expressões corporais em uma apresentação.

1.3 Seção III – Ampliando os horizontes de observação em ecologia

1.3.1 PONTOS CEGOS: ESCALA E PERÍODO DE OBSERVAÇÃO

*“What man sees depends both upon what he looks at and also upon what his previous visual-conception experience has taught him to see”-
Thomas Kuhn*

“One way to open your eyes is to ask yourself, What if I had never seen this before? What if I knew I would never see it again? - Rachel Carson

Vimos que alguns aspectos metodológicos na ecologia resultam da familiaridade dos pesquisadores com seus objetos de estudo, o que muitas vezes acaba se perpetuando como uma forma tradicional de estudar determinados organismos (Wiens 1989; Levin 1992). No entanto, a perspectiva antropocêntrica possui limitações pela nossa própria maneira de perceber a natureza e suas nuances. Vimos que o uso de diferentes escalas pode levar a observação de padrões distintos, o que acaba promovendo diferentes “escolas” de descrição da biodiversidade que eventualmente se confrontam (McGill *et al.* 2015). Por exemplo, resultados contraditórios sobre o declínio da biodiversidade abrandam as críticas sobre os impactos antropogênicos na biodiversidade, sendo que essas diferenças podem estar associadas a divergências de escala. Portanto, a escala tem um papel central na unificação das abordagens em ecologia.

A escala de observação pode variar amplamente no espaço e no tempo. Uma recente análise sobre as escalas utilizadas em estudos ecológicos mostrou que, entre 2004-2014, a maior parte dos estudos utilizou escalas espaciais com menos de 1 m² (67%) ou exatos 1 m² (24%) como unidades de observação. Quanto a dimensão temporal, 37% dos estudos tiveram apenas uma observação temporal, enquanto 20% utilizaram réplicas diárias ou mensais, e 17% utilizaram réplicas em períodos curtos (menos de um dia) (Estes *et al.* 2018). Em síntese, os estudos utilizaram uma resolução espacial de até 1m² para amostrar extensões espaciais de até 10.000 hectares, com observações únicas ou com intervalos maiores de um mês, e com duração total de até um ano. Essas tendências atuais, comparadas a estudos pioneiros reportando o uso da escala em ecologia, mostram que a extensão espacial e a frequência de observação têm

aumentado, mas que a duração e a resolução espacial são ainda muito similares às utilizadas há 30 anos. Dessa forma, ainda há uma gama de escalas operacionais que podem ser exploradas para buscar assinaturas de diferentes processos ecológicos.

Dentre questões fundamentais para o avanço da ecologia identificadas nesta década, determinar a importância relativa de efeitos determinísticos (relacionadas ao nicho das espécies) e estocásticos figuram em destaque no tópico de comunidades ecológicas (Sutherland et al. 2013). Contudo, é cada vez mais reconhecido que os padrões de diversidade são moldados por processos que atuam em escalas distintas daquelas observadas (Wiens 1989; Levin 1992). Assim, a importância de considerar as escalas no entendimento das comunidades locais é crescente (Rahbek 2005). Em uma recente síntese sobre as mais diversas proposições teóricas em ecologia de comunidades, Mark Vellend mostra que a escala é uma entidade representada tradicionalmente por livros-texto como uma “*thing to think about*” – uma coisa a se pensar (pág. 47, Figura 4.4) (Vellend 2016). Talvez, mais do que apenas pensar, devêssemos começar a incorporar explicitamente a escala, ou melhor, as diferentes escalas, como componentes indispensáveis nos estudos (Viana & Chase 2019).

Outro aspecto pouco explorado é a precisão temporal em que as observações são tomadas. Geralmente associamos variações temporais a efeitos sazonais ou mesmo anuais (p. ex., El Niño), mas um mesmo ambiente possui marcadas diferenças ao longo de 24 horas. Por exemplo, diferenças entre dia e noite vão além da óbvia variação da luminosidade: temperatura, velocidade do vento e umidade interagem com a estrutura da vegetação e criam variações temporais e espaciais diferentes daquelas encontradas durante o dia. O ambiente da noite oferece “o palco ecológico para o ato noturno” (Hutchinson 1965 apud Gaston 2019). Em relação ao período diurno, essas variações noturnas nas condições dos ambientes influenciam gastos energéticos dos animais e, logo, sua performance em atividades como dispersão e capacidades de interação com outros indivíduos. Todavia, é intrigante que a menor proporção de artigos nos principais jornais em ecologia esteja tratando de fenômenos associados a essas variações, batizadas como o “problema noturno”. Ainda mais quando uma alta proporção de animais possui hábitos noturnos (30% dos vertebrados e 60% dos invertebrados) (Gaston 2019). Dentre os potenciais motivos pela desatenção ao problema noturno, figuram o fato de ecólogos serem predominantemente pertencentes a uma espécie diurna e por isso se encontram mais confortáveis investigando fenômenos

diurnos, e uma duradoura crença de que a maior parte das espécies são diurnas e que o funcionamento do ecossistema ocorre predominante de dia (Gaston 2019).

"It is usual to speak of an animal as living in a certain physical and chemical environment, but it should always be remembered that strictly speaking we cannot say exactly where the animal ends and the environment begins – unless it is dead, in which case it has ceased to be a proper animal at all..." – Charles Elton

Finalmente, a necessidade de ampliar as abordagens nas diversas escalas, tanto espaciais quanto temporais, ainda é uma lacuna persistente para entender o papel simultâneo de diferentes processos ecológicos nos padrões de diversidade. Felizmente, conforme a tecnologia tem avançado e se tornado acessível para pesquisadores em sua limitada passagem pelo planeta, ecólogos tem cada vez mais contado com novas ferramentas que permitem vencer limitações na coleta e análise de dados. Esses novos métodos permitem amostrar ambientes com alta resolução, tanto espacial quanto temporal, em extensões espaciais largas e durante longos períodos, características que permitem estabelecer relações entre escalas e que possivelmente permitirá ampliar nossas perspectivas em ecologia e conservação.

1.3.2 COMO A TECNOLOGIA AUXILIA A ECOLOGIA?

"I saw with regret, (and all scientific men have shared this feeling) that whilst the number of accurate instruments was daily increasing, we were still ignorant" - Alexander Von Humboldt

Não fosse o fato de Von Humboldt escrever tais palavras no início do século XIX, sua reflexão é, em aspectos gerais, metaforicamente contemporânea. No entanto, diferentemente dos equipamentos de alta precisão da época, como termômetros, barômetros, telescópios e sextantes⁵, hoje temos à disposição um arsenal de equipamentos sofisticados. Quando eu ou minhas irmãs pegamos um Uber, costumamos compartilhar o trajeto entre nós para acessar o percurso estimado até o ponto de chegada e acompanhar em tempo real a movimentação do carro, como medida de segurança. Costumo refletir se eu conseguiria imaginar essa realidade há pelo menos 20 anos atrás, quando me considerava imersa em tecnologias por cuidar de um bichinho virtual (*tamagotchi*) e almejar um *pager*. O fato é o aprimoramento da tecnologia segue um ritmo incessante, de forma que hoje, previsões futuras do que esperamos vivenciar podem ficar muito aquém do que pode vir a se concretizar.

"Vivemos num futuro imaginado, imaginando outros futuros. O futuro imaginado em que vivemos nunca coincide com o futuro imaginado que imaginámos ou que outros imaginaram para nós."- Manuel Portela, prefácio de Admirável mundo novo (Aldous Huxley)

Felizmente, muitos ecólogos são extrovertidos e capazes de absorver tecnologias emergentes e incorporá-las ao seu ferramental de pesquisa. Nas últimas décadas, vivemos uma verdadeira revolução tecnológica nos métodos utilizados em ecologia. Supercomputadores chegaram aos laboratórios, técnicas para extração e amplificação de DNA foram otimizadas, poderosos métodos estatísticos se popularizaram (como modelos mistos e estatística bayesiana) e dispositivos de monitoramento por sensoriamento remoto se tornaram mais acessíveis e pequeninos (Sutherland et al. 2013). Com o advento na tecnologia de sensores, foi possível ampliar espacial e temporalmente a forma de observar fenômenos ecológicos e lançar mão de

alta precisão na tomada de dados a partir de “olhos” e “ouvidos” mais eficientes que os nossos (Porter *et al.* 2009; Pimm *et al.* 2015). Por exemplo, atualmente é possível caracterizar relações evolutivas dentro e entre espécies e revelar características dos hábitos alimentares de indivíduos a partir de análises genéticas e de isótopos estáveis. Os padrões de movimentação individual podem ser rastreados por meio de equipamentos emissores de radiofrequência ou por meio de localização via satélite, de forma que diversos indivíduos podem ser monitorados simultaneamente.

Determinados sensores podem capturar informações de maneira completamente remota, como é o caso das imagens a partir de sensores acoplados a satélite artificiais lançados à órbita do planeta (cuja forma é de fato similar a uma esfera). Alguns sensores podem registrar diferentes faixas no espectro eletromagnético da luz do sol (imagem ótica, como os sensores TM e OLI nos satélites da série LANDSAT), enquanto outros podem ser acoplados a aeronaves e capturar pulsos emitidos de uma antena acoplada a nave (radar de abertura sintética, como o PALSAR do satélite ALOS). Existem outros sensores com variados mecanismos de funcionamento, como imagens produzidas por veículos aéreos não tripulados e LIDAR, e sensíveis a diferentes faixas eletromagnéticas, como sensores multiespectrais, cada qual capaz de gerar imagens com maior ou menor resolução espacial e sensibilidade a diferentes características dos objetos na superfície do planeta (Marvin *et al.* 2016). O monitoramento a partir de sensores remotos em satélites permitiu que pudéssemos acessar características físicas do relevo, bem como fatores abióticos, como precipitação e temperatura. Além disso, os mais variados tipos de ambientes podem ser discernidos em categorias de formações vegetacionais a partir de mapeamentos ou da própria heterogeneidade dos valores de pixel das imagens. Esta fonte de informação tem sido amplamente utilizada para caracterizar habitats nas paisagens em estudos ecológicos (Pettorelli *et al.* 2014).

Sem embargo, alguns sensores mais comuns, como os presentes em câmera fotográfica e gravadores de som, foram otimizados para registrar informações em campo. Por exemplo, armadilhas fotográficas permitem registrar os organismos que porventura atravessam a área onde uma câmera automatizada está instalada (Pimm *et al.* 2015). Nessa linha, gravadores acústicos com funções pré-programáveis foram idealizados para registrar, por um longo período, o som de qualquer animal dentro da área de detecção do gravador. As ondas sonoras produzidas pelos animais são registradas por microfones e convertidas em sinais digitais, os quais são

posteriormente analisados para caracterizar os sons animais (Caixa 1). Com isso, é possível ampliar a quantidade de locais monitorados ao mesmo tempo, o que diminui intrusões de variações temporais entre localidades, além de minimizar intervenções causadas pela presença do observador no comportamento dos animais. As linhas investigativas as quais o monitoramento acústico pode ser útil são diversas e crescentes. Diversos taxa emitem sinais acústicos que podem ser detectados por sensores acústicos: invertebrados (como grilos, gafanhotos e invertebrados aquáticos), peixes, mamíferos aquáticos, aves, mamíferos terrestres (lobos, elefantes, primatas), morcegos e anuros (Browning *et al.* 2017). Distintos níveis de organização podem ser investigados sob novas perspectivas temporais, como aspectos comportamentais, estrutura populacional e de comunidades. Essa técnica também tem sido útil a aspectos práticos voltados a conservação da biodiversidade, como o monitoramento de caça ilegal a elefantes e a detecção de atividade de exploração madeireira ilegal (Gibb *et al.* 2019).

Por meio de novos sensores com precisa capacidade de amostragem e ampla cobertura espacial e temporal, podemos complementar as lacunas de informação a respeito de como diferentes escalas em ecologia regem os padrões da biodiversidade, o que potencialmente pode ajudar a sintetizar nosso entendimento sobre processos ecológicos. Também podemos reinventar as possibilidades de caracterizar as espécies, o amplia nossa capacidade de compreender aspectos básicos de sua história de vida e aperfeiçoa o monitoramento da biodiversidade. Novas tecnologias nos abrem oportunidades tanto para descrever aspectos ideográficos a partir de diferentes escalas e dimensões da diversidade (como diferentes aspectos ecológicos) como para levantar abordagens abrangentes com fins nomotéticos. Ambos eixos são perfeitamente justificáveis e complementares quando o objetivo é edificar o conhecimento sobre os determinantes dos padrões ecológicos.

⁵ Outros instrumentos utilizados por A. Von Humboldt :
https://www2.humboldt.edu/scimus/AvH_HSU_Centennial%20Exhibit/AvH_Dis.htm

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2. PRÓLOGO

Bioacoustic time capsules: using acoustic monitoring to document biodiversity

Larissa Sayuri Moreira Sugai^{*1,2,4}, Diego Llusia^{3,4}

¹ Universidade Estadual Paulista (Unesp), Instituto de Biociências, Rio Claro, 13506–900, São Paulo, Brazil.

² Universidade Estadual Paulista (Unesp), Instituto de Geociências e Ciências Exatas, Ecosystem Dynamics Observatory, Rio Claro, 13506–900, São Paulo, Brazil.

³ Laboratório de Herpetologia e Comportamento Animal, Departamento de Ecologia, Instituto de Ciências Biológicas, Universidade Federal de Goiás, Campus Samambaia, CEP 74001–970, Goiânia, Goiás, Brazil.

⁴ Terrestrial Ecology Group (TEG), Departamento de Ecología, Universidad Autónoma de Madrid, C/ Darwin, 2, 28049, Ciudad Universitaria de Cantoblanco, Facultad de Ciencias, Edificio de Biología, C-211, Madrid, Spain.

*corresponding author: lariagus@gmail.com

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2.1 Abstract

In the current extinction crisis, emerging technologies can support the urgent need to document biodiversity worldwide. Automated acoustic recorders are increasingly being used to remotely monitor species and soundscapes across the planet, generating a growing and valuable sound collection from present ecosystems. Such a collection can become a benchmark for future ecological research and shed light on our understanding of global change. Here we discuss the challenges and potential of acoustic monitoring to compose bioacoustic time capsules, environmental recordings capable to document, for future generations, how the planet's acoustic communities were in the past. For the present, acoustic monitoring can assist in ecological research and increase the chances of a species being detected, described, and hence protected. For the future, the collected time-series of audio recordings will compose bioacoustic time capsules, providing singular historical information on the structure and dynamics of past ecosystems and the activity of extinct fauna (acoustic fossils). Thus, we claim that acoustic monitoring should be included in biologist's toolbox to optimize the diligent task of documenting and protecting biodiversity.

Keywords: Conservation, Biodiversity loss, Soundscape, Audio recorder, Bioacoustics

2.2 Main text

Human activities are prompting alarming rates of species loss and natural population declines worldwide, pushing biodiversity into a new extinction crisis (Barnosky et al., 2011; Johnson et al., 2017). Such a global process exceeds the capacity of biologists to properly document, understand, and protect the planet's life (Wilson, 2017), and many species may likely undergo extinction even before being described (Costello et al., 2013). Facing this urgent challenge, we do need more “boots on the ground” to document biodiversity (Wilson, 2017), and novel emerging technologies can be invaluable tools for this task.

Automated audio recorders enable systematic and unattended recordings of environmental sounds and have recently opened new opportunities for ecological research and conservation practices (Wrege et al., 2017; Sugai et al., 2018). A myriad of organisms, including crustaceans, arachnids, insects, fish, amphibians, reptiles, birds, and mammals produces species-specific acoustic cues during their daily activity (Bradbury and Vehrencamp, 1998; Gerhardt and Huber, 2002), leaving a highly-informative trace that can be registered and further examined to reveal the presence

of species and multiple aspects of their ecology and behavior (Blumstein et al., 2011; Obrist et al., 2010). Thus, the passive acoustic monitoring (PAM) of biological sounds can provide, in a non-invasive manner, long-term and standardized data of the composition and dynamics of animal communities.

Ecological research using PAM is increasingly being employed both in terrestrial and aquatic ecosystems (Linke et al., 2018; Sugai et al., 2018). Among a wide range of applications, PAM has been used to support rapid acoustic inventories on priority conservation areas, to detect the presence of cryptic species, and to unveil changes in species' abundance, phenology and distribution patterns (Laiolo, 2010; Sueur and Farina, 2015). Particularly, PAM recordings can broaden the possibilities to monitor populations and communities over time (Farina et al., 2011; Deichmann et al., 2017) and space (Llusia et al., 2013; Lomolino et al. 2015), improving our capacity to assess large-scale ecological processes.

In addition to its current use, acoustic monitoring may have an important role in future research. PAM and directional recordings reserve valuable information about our current biodiversity and can work as a bioacoustic time capsules, i.e., audio records that are capable to document, for future generations, how the planet's acoustic communities were in the past. Once ecosystems' integrity is approaching unsafe boundaries for biodiversity persistence (Newbold et al., 2016), the recordings being currently collected worldwide can become a benchmark for upcoming research and perhaps help to understand the magnitude and direction of global change in the future.

Recordings containing sounds of probably extinct species can already be found in biological collections, such as the Ivory-billed woodpecker (*Campephilus principalis*), the Bachman's warbler (*Vermivora bachmanii*), or the Chile Darwin's frog (*Rhinoderma rufum*). Following the paleontological terminology, these recordings resemble trace fossils, i.e. records of past biological activity, like animal's footprints or burrows (Seilacher, 2007). Thus, we can refer them to acoustic fossils. Given the current scenario of mass extinction, it is expected that many of the collected audio recordings will likely become evidence of extinct fauna in a near future, adding to the records of acoustic fossils.

Beyond the importance of audio recordings to document biodiversity patterns, they can also help to piece together aspects of species' natural history. Paleontologists

have tried to reconstruct sounds of extinct species based on their morphological characters and sound production structures, including those produced by crickets (Gu et al., 2012), dinosaurs (Diegert and Williamson, 1998), and hominids (Barney et al., 2012). For instance, the finding of an exceptionally preserved stridulatory apparatus of the 165 million-year-old extinct bush-cricket *Archaboilus musicus* unveiled that the species likely produced radiated songs at 6.4 kHz, and together with paleobotanical reconstructions of the Jurassic forest where this bush-cricket inhabited, suggested a communication system well adapted to long-distance signaling close to the ground (Gu et al., 2012). However, this is rather a rare example, and for most of the extinct species, we probably will never be able to hear their vocalizations, even for those recently extinct but unrecorded, such as the Dodo (*Raphus cucullatus*), the Steller's sea cow (*Hydrodamalis gigas*), or the Madagascan sloth lemurs (*Palaeopro pithecius* spp.). Thus, the collection of audio recordings nowadays helps to preserve evidence of our current and ephemeral environment and will possibly have an inestimable value in the future.

To build bioacoustics time capsules, audio recordings at any temporal scope must be stored, curated and preserved for the long term. Museums and biological collections can assist in such purpose as they preserve types, specimens, and other biological material that are used as a baseline to investigate changes in biodiversity, playing an important role in our understanding of nature (Suarez and Tsutsui, 2004; Pyke and Ehrlich, 2010). For instance, directional recordings of animal vocalizations have long been deposited in museums and sound libraries. The British Library provides a section of digitalized biological sounds, with early bird recordings made by Ludwig Koch (1881–1974) and Carl Weismann (1906–1999) since the 1930's. The Macaulay Library, maintained by the Cornell Lab of Ornithology, includes more than 367 thousand audio files, mostly focused on birds, while FonoZoo sound library at the Spanish National Museum of Natural Sciences house recordings of more than one thousand frog species. These sound repositories have supported research in multiple areas, such as taxonomy (Köhler et al., 2017), conservation (Laiolo, 2010), evolution (Goicoechea et al., 2010), and behavior (Guerra et al., 2018).

With the widespread adoption of automated audio recorders by biologists for PAM-based research (Linke et al., 2018; Sugai et al., 2018), the diverse and huge collection of environmental recordings being collected can be important assets for bioacoustics time capsules. Yet, to take advantage of such opportunity, present

constraints in data preservation and open access should be overcome. Differently from manual recordings, automated recordings are considerably larger and commonly gathered in time-series, generating enormous amounts of data. Thus, PAM data currently challenge the capacities of sound libraries and audio repositories. To accommodate these datasets as bioacoustic time capsules, biological collections should be supplied with cutting-edge digital infrastructure to allow big data management and online deposit of PAM datasets. First steps on this direction have started to be developed, with pioneering platforms specifically designed to deal with passive audio recordings, such as ARBIMON (Aide et al., 2013), REAL (Kasten et al., 2012), and Ecosounds, which can guide forthcoming PAM-oriented public libraries. Additionally, some initiatives to collect long-term audio recordings from environments undergoing human-impacts have been promoted so far and, in some cases, at the interface between science, art, and citizen-science (e.g., Wild Sanctuary, 2018, Fragments of Extinction, Center for Global Soundscapes). For instance, the Wild Sanctuary, led by Bernie Krause, contains over 4500h of environmental sounds, with a remarkable portion recorded before human-induced habitat alterations.

Besides the aim of having suitable collections for long-term storage of large volume of recordings, the availability of PAM datasets for a future use also requires a more active role from researchers, who are responsible for the data deposit (Riede, 2018). Toledo et al. (2015) have recently emphasized the scant application of this practice among scientists and called for journals to demand authors to provide their recordings along with publications. The worldwide collected audio recordings from PAM are mostly scattered over individual projects, preventing them from being properly safeguarded and shared. This common practice increases the potential risk of loss or damage of valuable audiovisual records, as for what has dramatically happened in recent dates (Dena et al. 2018) and hampers the collective effort of documenting the current biodiversity crisis.

To contribute to the need of registering biodiversity for present and future research, many options of commercial and customized audio recorders developed for PAM are currently available: (i) programmable devices with scheduling functions for terrestrial (e.g. SM4, ~\$850, 219 × 186 × 78 mm, Wildlife Acoustics®; BAR, ~\$600, 110 × 130 × 70 mm, Frontier Labs®; SWIFT, ~\$300, 119 × 129 × 61 mm, 119 × 129 × 61 mm, 1.1kg, Cornell Lab of Ornithology, BRP®) and marine environments (e.g. SM4MDEEP, ~9.000, 1.480 × 165 mm, 32.2 kg, Wildlife Acoustics®), (ii) permanent cellular-based

recording stations (ARBIMON Permanent Station, ~\$4000, $174 \times 116 \times 48$ mm plus solar panel, 1.2 kg, Sieve Analytics®), (iii) low-cost programmable recorders (AudioMoth, ~\$40, $58 \times 48 \times 18$ mm, 80 g, Open Acoustic Devices; Hill et al., 2017), (iv) low-cost non-programmable USB flash drive audio recorders (e.g., UR09, ~\$10, $64 \times 22 \times 10$ mm, 14 g, HNSAT, Farina et al., 2014), or (v) open-source customizable devices (AURITA, ~\$450, $350 \times 230 \times 86$ mm, with hard case Beason et al., 2018; SOLO, ~\$110, Whytock and Christie, 2017).

Moreover, straightforward and best practices guides for field recording provide researchers the fundamentals of acoustics, equipment, and recording methods (Obrist et al., 2010; Llusia et al., 2011; Browning et al., 2017; Gibb et al., 2018). Despite its underlying complexity, analytical solutions to extract and synthesize biological information from passive audio recordings are also growing and moving from manual procedures to automated frameworks employing machine learning algorithms (e.g. Kholghi et al., 2018; Sueur, 2018; Ulloa et al., 2018). These new methods offer options to discriminate singular elements contained in audio recordings, hence decreasing the time devoted in identifying species-specific acoustic signals over long time-series datasets. Paired with big data analysis in ecology (Marvin et al., 2016; Farley et al., 2018), advances toward automated analyses offer new perspectives on the use of PAM within the ecologist's toolbox (Gibb et al., 2018). The growing use of PAM for a variety of taxa, subjects, and locations across the planet offers an excellent framework to build bioacoustic time capsules. Thus, we encourage scientists to intensify the use of passive acoustic monitoring with the aim of documenting biodiversity patterns worldwide. Basic information on natural history, species distribution, and ecology is still lacking to effectively protect species and their habitats (Whittaker et al., 2005; Brito, 2010), and acoustic monitoring can help researchers in this diligent task. For the present, PAM can assist in biodiversity inventories, field surveys, and monitoring programs (Laiolo, 2010; Obrist et al., 2010; Sueur and Farina, 2015) and increase the chances of a species being detected, described, and hence protected. For the future, the collected time-series of environmental recordings will compose *bioacoustic time capsules*, providing singular historical information on the structure and dynamics of past ecosystems. In this last perspective, we will all have failed to protect biodiversity if these recordings soon become acoustic fossils of extinct species or communities, but at least we would provide future generations historical registers of extinct fauna and how our ecosystems once sounded.

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3. CAPÍTULO 1

Terrestrial Passive Acoustic Monitoring: Review and Perspectives

Larissa Sayuri Moreira Sugai^{*1,2,4}, Thiago Sanna Freire Silva², José Wagner Ribeiro Jr.¹,
Diego Llusia^{3,4}

¹ Universidade Estadual Paulista (Unesp), Instituto de Biociências, Rio Claro, 13506–900, São Paulo, Brazil.

² Universidade Estadual Paulista (Unesp), Instituto de Geociências e Ciências Exatas, Ecosystem Dynamics Observatory, Rio Claro, 13506–900, São Paulo, Brazil.

³ Laboratório de Herpetologia e Comportamento Animal, Departamento de Ecologia, Instituto de Ciências Biológicas, Universidade Federal de Goiás, Campus Samambaia, CEP 74001–970, Goiânia, Goiás, Brazil.

⁴ Terrestrial Ecology Group (TEG), Departamento de Ecología, Universidad Autónoma de Madrid, C/ Darwin, 2, 28049, Ciudad Universitaria de Cantoblanco, Facultad de Ciencias, Edificio de Biología, C-211, Madrid, Spain.

*corresponding author: lariagus@gmail.com

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3.1 Abstract

Passive acoustic monitoring (PAM) is quickly gaining ground in ecological research, following global trends toward automated data collection and big data. Using unattended sound recording, PAM provides tools for long-term and cost-effective biodiversity monitoring. Still, the extent of the potential of this emerging method in terrestrial ecology is unknown. To quantify its application and guide future studies, we conducted a systematic review of terrestrial PAM, covering 460 articles published in 122 journals (1992–2018). During this period, PAM-related studies showed above a fifteenfold rise in publication and covered three developing phases: establishment, expansion, and consolidation. Overall, the research was mostly focused on bats (50%), occurred in northern temperate regions (65%), addressed activity patterns (25%), recorded at night (37%), used nonprogrammable recorders (61%), and performed manual acoustic analysis (58%), although their applications continue to diversify. The future agenda should include addressing the development of standardized procedures, automated analysis, and global initiatives to expand PAM to multiple taxa and regions.

Keywords: audio recorders, auditory monitoring, automated data collection, bioacoustics, ecoacoustics, faunal survey, soundscapes

3.2 Introduction

Wildlife monitoring has undergone a remarkable transformation in the twenty-first century, with the development and introduction of technologies that greatly expand the possibilities for biodiversity assessment and ecological research (e.g., remote sensing, camera trapping, DNA barcoding; Pimm et al. 2015). These methods have allowed us to better track the effects of a rapidly changing environment on biodiversity, including the impacts of habitat loss, species introductions, and climate change (Llusia et al. 2013, Schmeller et al. 2017). Among these cutting-edge technologies, automated audio recorders have recently revolutionized traditional faunal survey methods based on auditory detection (Obrist et al. 2010, Blumstein et al. 2011).

Terrestrial environments are typically replete with sounds from multiple sources, particularly from animals (McGregor 2005). Animal sounds are highly informative. In addition to their use as characteristics for species identification, they also convey cues about abundance, position, body size, and motivation of emitters (Bradbury and Vehrencamp 1998, Wilkins et al. 2013). Additionally, sounds can

propagate in multiple directions, through physical obstacles, and over relatively long distances; therefore, vocal animals are generally more easily detectable by hearing than by seeing (Rosenthal and Ryan 2000, Heinicke et al. 2015). For this reason, auditory surveys have become the basis for many biodiversity assessment programs, such as the North American Amphibian Monitoring Program (Weir and Mossman 2005) and several terrestrial bird survey initiatives (Rosenstock et al. 2002).

In addition to these properties, sounds can be reliably recorded by analog or digital devices. Historically, the development of portable tape recorders enabled researchers to record animal sounds in the field, providing new opportunities for faunal surveys (Parker 1991, Vielliard 1993, Haselmayer and Quinn 2000). A subsequent milestone was the release of digital audio recorders, which supplied researchers with affordable and smaller devices, maintaining high fidelity to analog signals and optimizing auditory surveys (Obrist et al. 2010). More recently, early autonomous recorders provided additional innovations by allowing unattended recording over long periods, with longer battery life and programmable recording schedules (Sueur et al. 2012, Digby et al. 2013). These advances translate into several advantages for species surveys, including broader temporal and spatial sampling, reduced observer bias, and long-term storage of field recordings, which can later be digitally analyzed and checked for dubious vocalizations. Therefore, passive acoustic monitoring (PAM) now stands as a powerful tool for biodiversity monitoring, supporting a variety of ecological, behavioral, and conservation applications (Farina and Gage 2017, Wrege et al. 2017, Linke et al. 2018).

Wildlife surveys based on passive acoustics have been widely applied in marine environments to detect species presence, estimate population dynamics, measure home ranges, and determine activity patterns and movement routes (Mellinger et al. 2007). Similarly, this technique offers ample possibilities for faunal surveys in terrestrial environments, because acoustic sensors allow noninvasive data collection for a wide range of animals emitting detectable acoustic signals (Browning et al. 2017). Moreover, PAM can increase the temporal and spatial coverage of monitoring programs while providing favorable cost-benefit trade-offs for wildlife surveys in relation to traditional survey methods (Ribeiro et al. 2017, Wrege et al. 2017). Nevertheless, the use of PAM in terrestrial-monitoring programs is still relatively incipient when compared with its use for marine fauna, and it has only recently gathered significant attention (Servick 2014). By understanding the current trends,

limitations, and challenges of terrestrial PAM, we can better guide future applications and the progress of this emergent method in ecological research.

In the present article, we provide a comprehensive review and synthesis of the use of passive acoustic monitoring for terrestrial wildlife survey. First, we characterize the historical evolution and expansion of PAM-based studies across research topics, focal organisms, geographical locations, and methodological procedures. Second, we synthesize current applications, trends, key shortfalls, and future challenges, drawing attention to the potential of PAM to support of global initiatives and citizen science projects, through the adoption of standardized procedures and coordinated monitoring of multiple taxa and regions using common monitoring stations.

3.3 Reviewing the literature of terrestrial passive acoustic monitoring

We conducted a systematic review of passive acoustic monitoring on terrestrial ecosystems using complementary literature searches in the Thomson Reuters Web of Science (WoS) platform, spanning all years on record (1900–2018). The first search was performed on 24 August 2017, with the following keywords: (((sound* OR acoustic* OR call* OR song* OR sing* OR vocal*) AND (monito* OR passive OR record* OR survey OR sampl* OR automat* OR activit*)) AND (wildlife OR biodiversit* OR animal* OR soundscape* OR ecoacoustic* OR vertebrate* OR mammal* OR bird* OR avian* OR anura* OR amphibia* OR frog* OR toad* OR insect* OR artropod* OR orthoptera OR cricket* OR cicada*)). A second search was performed on 9 September 2017, using ((call* OR acoustic*) AND (survey OR activit*)). To update our database, the two previous literature searches were repeated on 27 September 2018. These searches were restricted to 13 WoS subject areas: biology, biodiversity conservation, environmental sciences, remote sensing, ecology, entomology, acoustic, behavioral sciences, zoology, ornithology, and evolutionary biology. In addition, to include potentially meaningful articles absent from the reviews in WoS, complementary searches were performed using Google Scholar on 15 September 2017 and 27 September 2018, using the keyword combination ((wildlife acoustic) AND (passive acoustic monitoring)).

The literature search procedure resulted in more than 10,000 articles. From this initial list, we excluded those unrelated to this review (false positives)—that is, articles that did not employ PAM to survey biological aspects of terrestrial fauna, such as underwater environments (for a review, see Mellinger et al. 2007); environmental

sound pressure level assessments (see Lynch et al. 2011, Shannon et al. 2016); and the use of acoustic lures, playbacks, and call-broadcast surveys without joint use of passive acoustics (see McGregor 2000, Suraci et al. 2017). Articles aimed at estimating species density and movement by acoustic location systems using microphone arrays were also excluded, because several comprehensive reviews have been published on these methods (see Marques et al. 2013, Stevenson et al. 2015, Measey et al. 2017). This filtering finally led to a final data set of 460 selected articles (see the supplemental information).

From each article found in this literature search, we extracted key information to characterize PAM-based research: publication year, monitoring year, journal of publication, research topic, monitored taxa, geographical coordinates of the recorded sites, recording settings (type of recorder and daily recording period), and acoustic analysis applied to derive biological information from the passive recordings (table 1).

3.4 Overview of *passive acoustic monitoring in terrestrial ecosystems*

Studies using PAM in terrestrial ecosystems started in the 1990s and have exponentially increased in the last decades, at an average rate of 2.8 articles per year in the 1990s (from 0 to 11 per year), 10.8 in the 2000s (from 3 to 19 per year), and 42.5 in the 2010s (from 28 to 62 per year; figure 1a). Noticeably, the number of articles increased more than fifteenfold during this period, with the peak in 2017 (i.e., the last complete year spanned by this review). The actual monitoring reported in these articles has a similar pattern to the publication trend, with a 3–4-year lag between monitoring and publication; the peak was in 2012, and 50% of the recordings were made after 2008 (figure 1b). This prominent rise in PAM-based research has mostly resulted from the increased availability of automated audio recorders, whose use has risen from 2 to 48 articles per year since their commercial release in 2007. So far, this type of recorder represents 39% of all published articles, whereas nonprogrammable audio recorders represent 61% (figure 1a).

Table 1. Description of items compiled in this review and used to characterize publication and research trends in passive acoustic monitoring in terrestrial ecosystems from 1992–2018.

Items	Classes	Categories	Description
Publication	Publication year Journal of publication		
Data collection	Monitoring year Study sites		Years when the acoustic monitoring was conducted Geographical coordinates of the sites at which the acoustic monitoring was conducted
Research area	Research topics	Activity patterns	Studies assessing seasonal and diel activity levels of populations and communities
		Behavior	Studies focused on aspects of animal behavioral biology
		Community Ecology	Studies addressing the determinants of species diversity, community structure, and assembly
		Conservation Biology	Studies concerned with the conservation of species, habitats, and ecosystems
		Ecoacoustics	Investigations of soundscape patterns and dynamics
		Habitat use	Studies addressing species preference and selection over distinct environmental conditions
		Signal processing	Automated methods for detecting and classifying species in acoustic recordings
		Species assessment	Faunal inventories and surveys aiming to document biodiversity
		Species distribution/Occupancy	Estimates of distribution patterns of species over multiple scales; imperfect species detectability
		Survey technique	Protocols, data collection procedures, or comparisons with other survey methods
		Urban Ecology	Ecological studies that include urban context
	Monitored taxa	Bats	
		Nonflying mammals	
		Birds	
		Anurans	
		Invertebrates	
		Soundscapes	Environmental sounds as a whole that emerge from the landscape
Recording settings	Recording system	Automated recorder	Audio recorders with scheduled recording options
		Nonprogrammable recorder	
	Recording period	Continuous	Recordings obtained continuously across the day
		Dawn	Recordings obtained exclusively at dawn
		Morning	
		Afternoon	
		Dusk	
		Night	
Acoustic analysis		Manual	Extraction of biological information mostly relied on human effort (e.g., manual measurement of acoustic parameters, visual or aural inspection of spectrograms)
		Semiautomated	Combination of manual and automated methods
		Automated	Extraction of biological information mostly relied on computing effort (e.g., built-in software recognizers, ad hoc discriminant function analyses)
		Acoustic indices	Estimation of α or β acoustics-based ecological indices (which is a particular automated method)

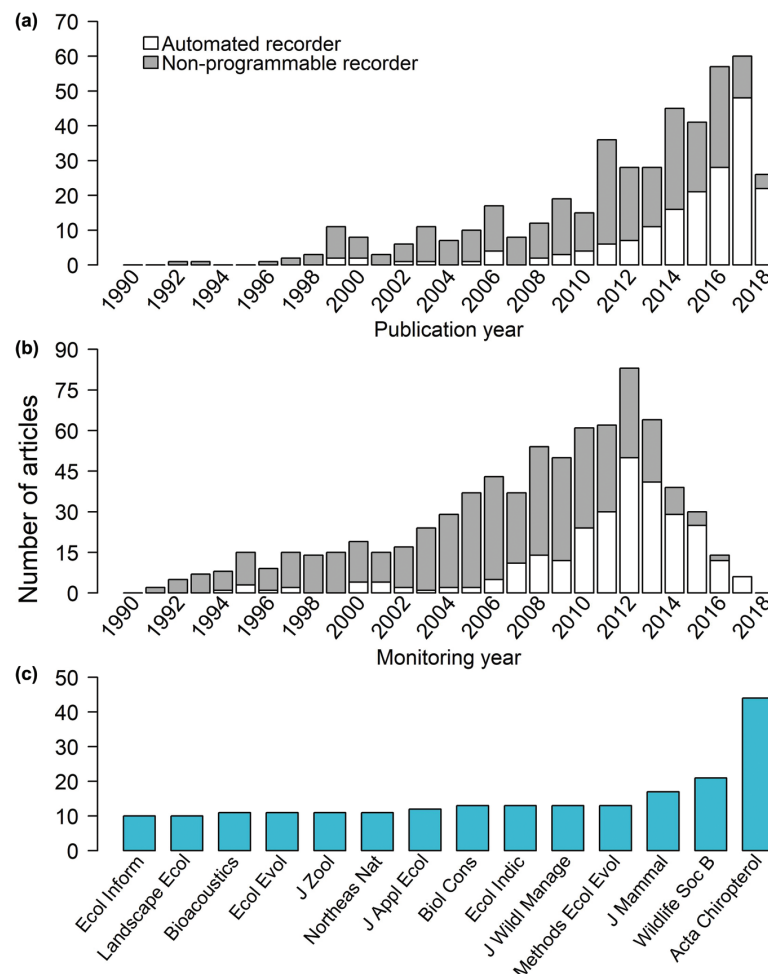


Figure 1. The publication rates of studies using passive acoustic monitoring in terrestrial ecosystems (1992–2018) across (a) years, (b) monitoring periods, and (c) journals. Only journals with the most number of articles are shown. In the upper panels (a) and (b), the colors represent the recording system employed: automated audio recorders (white) and nonprogrammable recorders (gray).

Overall, we could delimit three general developing phases of terrestrial PAM: establishment, during which the first studies using ad hoc acoustic methods to assist faunal inventories and investigate species activity and habitat use were published (before 2000); expansion, which is represented by a visible increase in the number of studies focusing on the same earlier topics, followed by an initial diversification of research areas (conservation biology, community ecology, and ecoacoustics, between 2000–2010); and consolidation, which is the exponential growth of studies covering multiple research topics and reaching the highest publication rates in recent years (after 2010; figure 2).

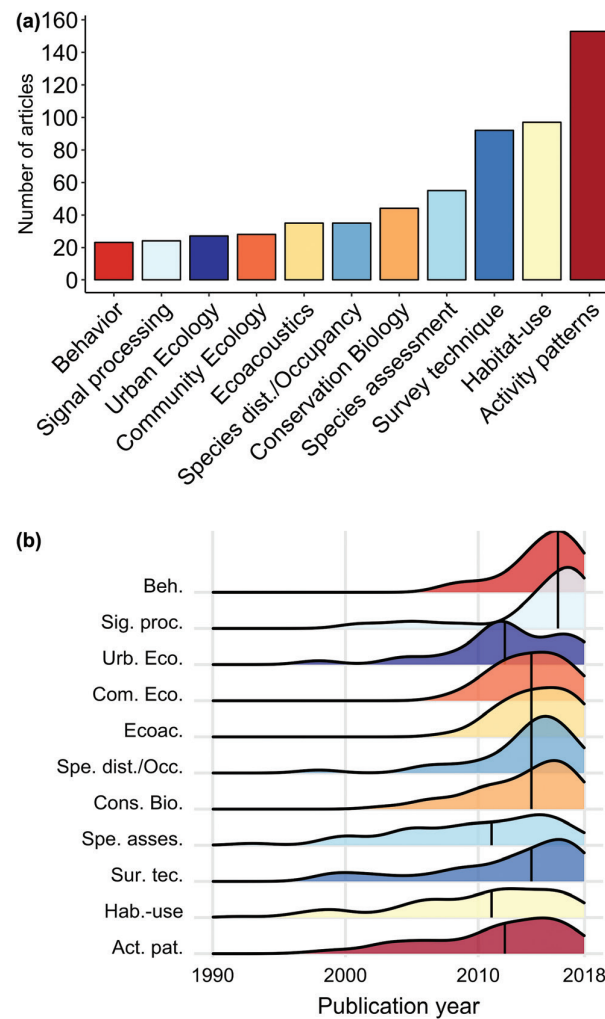


Figure 2. The research topics of studies using passive acoustic monitoring in terrestrial ecosystems (1992–2018): (a) number of published articles per topic, and (b) density plots of articles over time. Vertical black lines represent the median number of published articles for each topic.

Presently, studies using terrestrial PAM cover a wide range of research areas, studied organisms, surveyed locations, and methodological approaches. The 460 articles identified in our search were published in 122 journals, with 14 journals concentrating 46% (210) of all of the articles (figure 1c). Across these journals, the main research subjects were divided among taxonomy-oriented studies, applied ecology and conservation biology, and methodological studies. Among the research topics investigated so far, reports on species activity patterns were the most frequent (25%), followed by habitat use (16%), survey technique (15%), and species assessment (9%; figure 2).

Terrestrial PAM has become as useful as other well-established survey techniques (e.g., camera traps) to assess and monitor species, either as a standalone method or as a complementary approach (Browning et al. 2017). For example, Llusia

and colleagues (2013) used anuran phenological patterns to estimate thermal tolerances of calling behavior, with further implications for the assessment of climate change impacts. Cryptic, rare, and endangered species, such as koalas (Ellis et al. 2011) and elephants (Wrege et al. 2017), have been monitored to reveal behavioral and ecological aspects. Applied conservation programs have also benefited from PAM, through monitoring of hunting activities (Astaras et al. 2017), studies of species responses to anthropogenic impacts (Gil et al. 2014), and multitaxa assessments (Deichmann et al. 2017). Together, these successful applications reinforce the ample potential of passive acoustics for practical applications in terrestrial ecosystems, contributing to the toolbox of conservation practitioners and researchers (Ribeiro et al. 2017).

3.4.1 MONITORED TAXA. Over the focal organisms investigated with terrestrial PAM, bats were, by far, the biological group most studied (50% of the articles; figure 3a). Likewise, the journal with the most articles on terrestrial PAM is fully devoted to this group (9%, *Acta Chiropterologica*; figure 1c). However, most of the articles within this taxon were based on nonprogrammable audio recorders (89%), with automated devices only recently appearing (figure 3b). The trajectory of PAM applications for bat surveys clearly exemplifies the three distinct developing phases of PAM for terrestrial application: first, focusing on methodological issues regarding the use of ultrasound detectors and early applications for species assessment (Rachwald 1992, Kuenzi and Morrison 1998), followed by an increase in applications and diversification of investigated topics, and, finally, consolidating as a robust method to support a variety of goals including species inventory, population/community assessment, and species conservation (Russo and Jones 2003, Froidevaux et al. 2014).

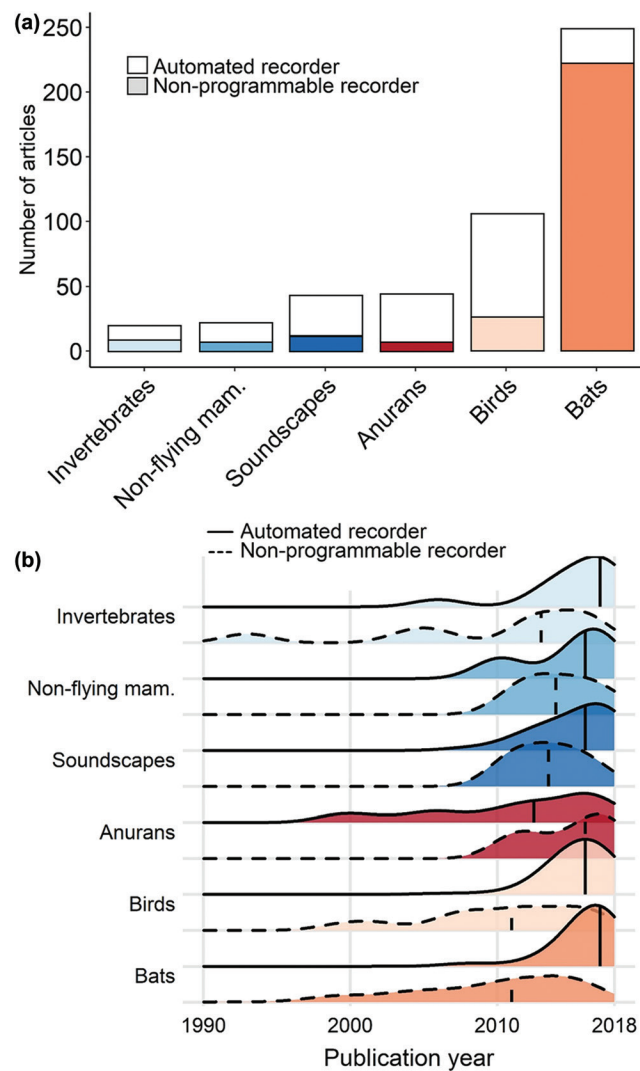


Figure 3. The taxa studied in articles using passive acoustic monitoring in terrestrial ecosystems (1992–2018): (a) the number of published articles per focal organism and (b) density plots of the articles over time. The colors and line types represent the recording system employed: automated audio recorders (the white boxes and solid lines), and nonprogrammable recorders (the color boxes and dashed lines). The vertical black lines represent the median number of published articles for each taxon.

After bats, birds were the most researched terrestrial group (20%), followed by anurans (12%), nonflying mammals (6%), and invertebrates (5%). Automated recording systems were more frequently used than nonprogrammable ones for all of these groups, except invertebrates (figure 3a). Pioneer contributions between 1990 and 2000 mostly reported the efficiency of acoustic methods, discussed the optimization of sampling procedures (e.g., Mohr and Dorcas 1999, Bridges and Dorcas 2000), and addressed general activity patterns, such as for tropical cricket assemblages (Riede 1993) and birds (Evans and Mellinger 1999).

Soundscapes (i.e., environmental sounds as a whole that emerge from the landscape) were examined in 7% of the studies. This recent approach has been fostered by the challenge of extracting biological information from the large volumes of acoustic data obtained through PAM, using acoustic indices to synthesize patterns made by vocal organisms, irrespective of species identity (Sueur et al. 2008). Consequently, a new research area was created, first formalized as soundscape ecology and posteriorly as ecoacoustics (Pijanowski et al. 2011, Sueur and Farina 2015). Soundscape dynamics have shown promise to represent overall animal activity patterns, and this new research program has been garnering increasing significance in ecological research (Servick 2014, Gasc et al. 2015, Farina and Gage 2017).

3.4.2 GEOGRAPHICAL DISTRIBUTION. PAM-based studies have been mostly concentrated in the northern temperate zone (65%), primarily in North America and Europe, whereas a markedly smaller number of studies occurred in tropical (25%) and southern temperate zones (10%). To our knowledge, large areas of the globe still have no recorded sites with this technique to date, with regions of Asia, western Oceania, northern Africa, and southern South America standing as the main gaps (figure 4). Passive recordings of bats, birds, and anurans were more widely distributed than other biological groups. PAM of nonflying mammals was concentrated on a few focal taxa, such as elephants in Africa, whereas invertebrate and soundscape studies likely reflect the geographical location of the main research groups in Europe and the United States.

3.4.3 RECORDING PERIODS. Although 19% of the studies using PAM recorded audio samples throughout the entire day, the majority of studies recorded only during specific periods (figure 5a). Among these, sampling effort was mostly concentrated at night (37%) and dusk (32%), when nonprogrammable recorders were primarily used (72% and 74%, respectively). This temporal asymmetry was due to the larger contribution of studies focusing on nocturnal species—namely, bats and anurans (figure 5b). The recordings at dawn represented 21% of the recording periods and were conducted with both types of recorders in a similar proportion (56% with nonprogrammable). Morning and afternoon were the least frequent recording periods (figure 5a), with a higher proportion of automated recorders being used (68% and 74%, respectively).

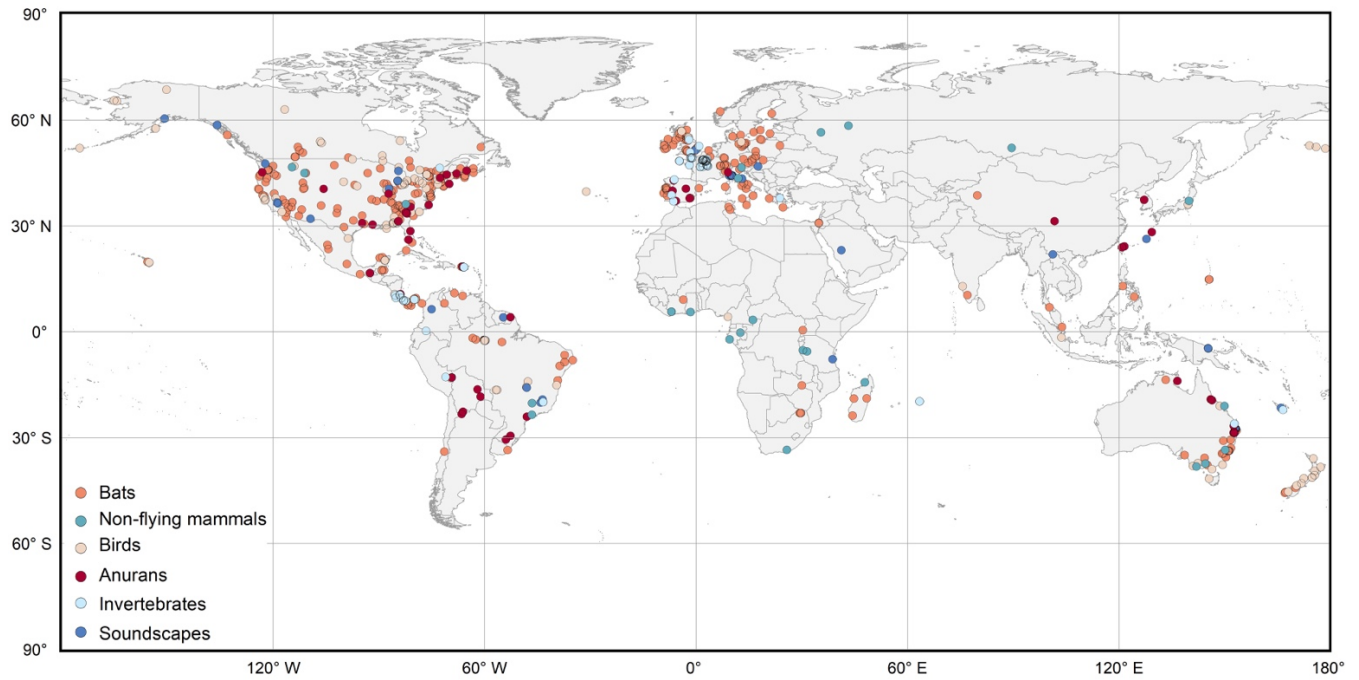


Figure 4. The geographic distribution of the study sites in articles using passive acoustic monitoring in terrestrial ecosystems (1992–2018) included in this review. The colors represent the focal taxa of each article.

As was expected, researchers generally prioritized acoustic monitoring on periods coinciding with the highest activity levels of the species of interest (figure 5b). Therefore, bats and anurans were investigated at more restricted daily periods, mainly at night (43% and 51%) and dusk (38% and 30%, respectively), whereas birds and soundscapes were investigated over wider periods and mainly at dawn (34% and 37%). During the morning and afternoon, recordings were collected only in studies focused in nonflying mammals, birds, invertebrates, and soundscapes (figure 5b).

3.4.4 ACOUSTIC ANALYSIS. The main procedure used to extract biological information from PAM recordings has been manual analysis, which mostly relies on human effort (e.g., manual measurement of acoustic parameters, visual or aural inspection of spectrograms) and corresponded to 58% of the studies (figure 6a). Fully automated analyses were applied in only 19% of the studies, with relatively more frequent use for bat signals (32% of the articles within the group), because several software packages contain built-in classification algorithms and libraries for automated recognition of bat species (e.g., Analook and Batsound). For other biological groups, fully automated methods are still being developed and tested (e.g., Digby et al. 2013, Astaras et al. 2017, Ulloa et al. 2018), and there are still relatively few alternatives to manual or semiautomated PAM data analysis (Kasten et al. 2012, Llusia et al. 2013).

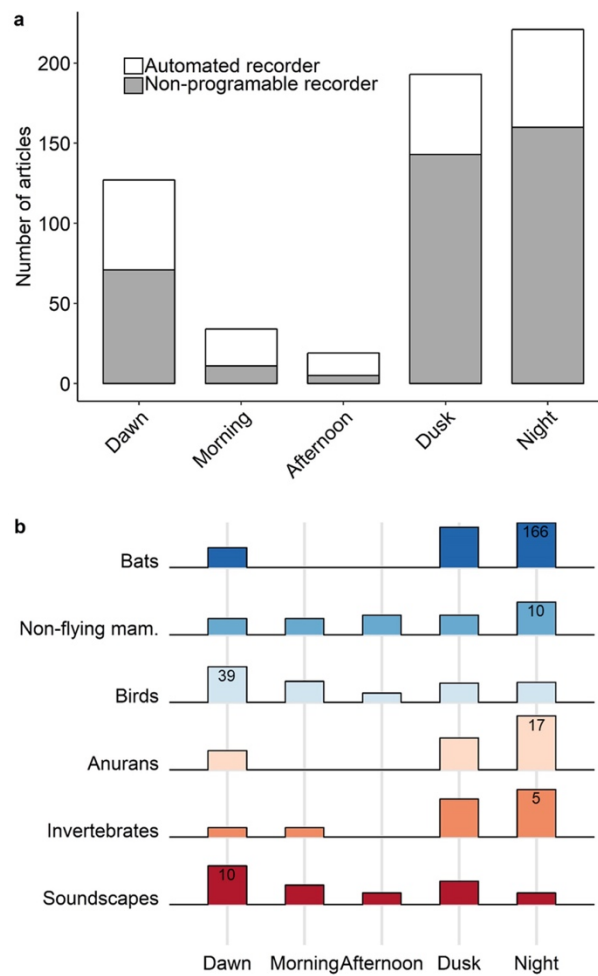


Figure 5. The daily recording periods applied in studies using passive acoustic monitoring in terrestrial ecosystems (1992–2018): (a) the number of published articles per period (excluding those performed throughout the entire day) and (b) the number of articles per period for each taxon. In the upper panel (a), the colors represent the recording system employed: automated audio recorders (white) and nonprogrammable recorders (gray).

Semiautomated procedures (i.e., combining both manual and automated analyses) were applied in 15% of the studies, with more applications than fully automated procedures for anurans, birds, and nonflying mammals (figure 6). Acoustic indices (10.5%) were applied mostly for soundscape studies, which, by definition, rely exclusively on the automated extraction of these indices to represent overall patterns of acoustic communities. Interestingly, acoustic indices were also used as proxies for species diversity by a few studies (figure 6).

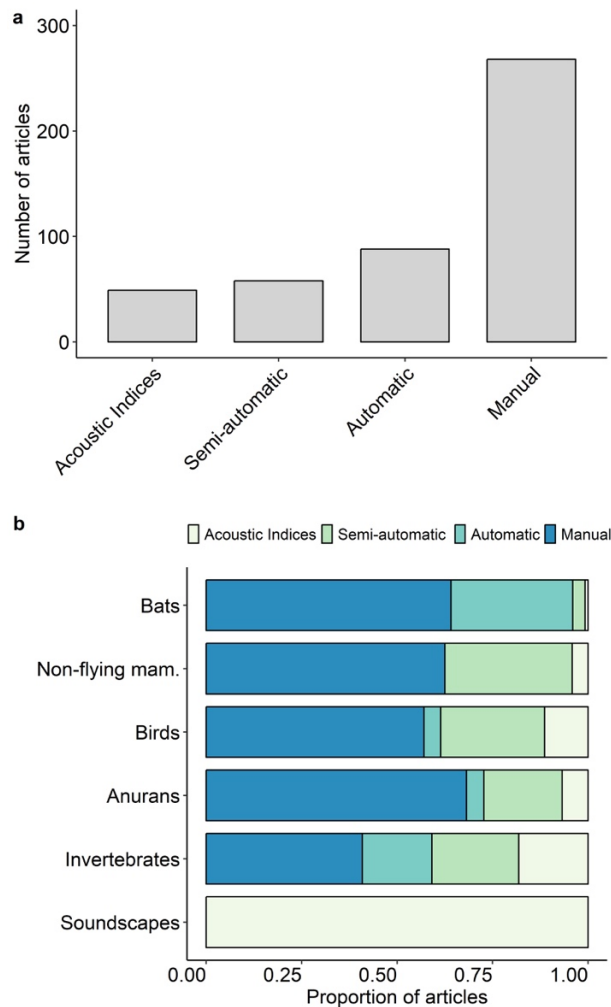


Figure 6. The analysis approach applied to acoustic data in studies using passive acoustic monitoring in terrestrial ecosystems (1992–2018): (a) the number of published articles per type of acoustic analysis and (b) the proportion of articles per type for each taxon.

3.5 Challenges and future directions for terrestrial PAM

We identified three main challenges for a further expansion of PAM-based research in terrestrial ecosystems. These shortfalls, which can likely be extended to the application of PAM in other environments, are non-standardized monitoring procedures, time-consuming acoustic analysis, and limited data curation and data sharing resources.

Research focused on methodological approaches and the limitations of PAM only substantially appeared during the consolidation phase identified in this review (2010–2018), although some custom passive audio recorders capable of monitoring the vocal activity of terrestrial fauna were proposed early in the literature (Peterson and Dorcas 1994). Examples of methodological developments include studies providing

field recording protocols (Obrist et al. 2010), designing methods for estimating the detection space of PAM stations (Llusia et al. 2011), comparing detection accuracy in relation to human observers (Digby et al. 2013, Wimmer et al. 2013) and to other survey techniques (Horton et al. 2015, Enari et al. 2017), and evaluations of changes in detectability given different recording schedules (La and Nudds 2016, Madalozzo et al. 2017). In addition, recent efforts to promote ecoacoustics as a new discipline have also generated contributions to PAM through both semiotic and theoretical unifying proposals (Farina 2014, Sueur and Farina 2015, Farina and Gage 2017). However, despite these efforts, further formalization of general methods for designing and employing PAM programs remain a challenging objective for future research. Such a methodological framework should include, for instance, generalized procedures to estimate species detectability, protocols for determining adequate recording schedules and sampling efforts, and guidelines to optimize the set of audio settings and autonomy in PAM stations. These accomplishments would benefit forthcoming studies by guiding decision-making in PAM planning and standardizing sampling protocols (Brandes 2008, Roch et al. 2016).

A critical challenge in PAM studies is still the analysis and handling of very large amounts of acoustic data, especially for programs spanning wide temporal or spatial extents (Browning et al. 2017). As the data volumes resulting from PAM programs often approach the scale of big data, automation of essential procedures such as species detection and recognition are desirable. There are currently several research areas devoted to developing automated methods to meet this pressing demand (e.g., signal processing and pattern recognition; Xie et al. 2017, Ulloa et al. 2018). However, current solutions often require professional experience and time-consuming supervision. An open avenue is the development of analytical solutions that are transferable among multiple species and acoustic conditions, thus facilitating management and data mining of PAM recordings for wildlife monitoring. Although fully automated solutions are progressing, PAM users and researchers should consider the best balance between research goals, measurement accuracy, and time allocated to analysis of the time series of recordings, with semiautomated procedures currently being the preferred solution (Kasten et al. 2012, Llusia et al. 2013).

The challenge of extracting biological information is larger for noisy and complex environments. Manual scanning may be valuable when automated procedures show poor performance, such as recordings containing overlapping

vocalizations or a low signal-to-noise ratio (Hugel 2012, Browning et al. 2017). Still, manual approaches are labor intensive and can be unattainable for large amounts of recordings. These challenges have favored the development and use of acoustic diversity indices to characterize overall acoustic communities, although their biological meaning is arguable (Servick 2014). Acoustic indices are more reliable in representing general patterns of species vocal activity instead of diversity (Gasc et al. 2017) and offer singular opportunities to track global change impacts on biodiversity (Krause and Farina 2016, Sueur and Farina 2015). More research focused on identifying and understanding the facets of biodiversity provided by acoustic indices are highly encouraged, because the acoustic component expressed by these indices can be related to other biodiversity aspects, such as phylogenetic and functional diversity (Gasc et al. 2015).

Another necessary step forward for increasing the applicability of PAM is the development and improvement of widely available sound repositories for curation, management, and sharing of temporal acoustic data sets, facilitating the access and preservation of these sizeable data sets. Existing public sound libraries and repositories are mostly focused on storing conventional manual audio recordings (i.e., directional recordings), and their infrastructure is often not suitable for transferring and storing the raw time series of recordings produced by PAM. To fill this gap, new repository initiatives have been appearing for managing PAM data, such as ARBIMON (Aide et al. 2013), Pumilio (Villanueva-Rivera and Pijanowski 2012), and REAL (Kasten et al. 2012). Ideally, researchers should archive audio recordings in sound repositories, similar to what is done for museum specimens and DNA sequences, although this practice is still not ubiquitous (Toledo et al. 2015). Because bandwidth and storage capabilities have been increasing exponentially, we expect the rapid proliferation of acoustic repositories in the next decade, with new opportunities for collective efforts on managing and analyzing terrestrial PAM data.

3.6 Integrating PAM to global monitoring networks

Methods to capture multiple taxa information over broad spatial and temporal scales have been a central issue for improving global biodiversity monitoring in the face of human-driven changes (Schmeller et al. 2017). Worldwide long-term ecological research and monitoring networks have often been supported by methods that enable coordinated, standardized, and scalable projects (Pimm et al. 2015). In this context, we

strongly advocate the use of PAM as a suitable and standardized method for measuring essential biodiversity variables using sensor networks (Kissling et al. 2017), thus increasing our ability to monitor and preserve global biological diversity.

PAM stations can easily be added to existing monitoring sites and can provide data from vocal animals. Affordable commercial or custom-built recorders have become increasingly available, making acoustic monitoring more accessible (e.g., Mennill et al. 2012, Farina et al. 2014, Whytock and Christie 2017). Moreover, individual research teams should pool resources and combine efforts to overcome logistical limitations and financial costs, benefiting collectively from extended data collection and improved knowledge of species natural history, site selection, and signal identification. Coordinated PAM stations may also inspire the development of more customizable or accessible recording systems adaptable for different research purposes.

Such advances could favor the implementation of PAM in remote and currently unmonitored areas, meeting the urgent need for tracking unprotected areas at risk (Watson et al. 2016), located mostly in the same regions in which spatial gaps in acoustic monitoring have been identified by our review. PAM is suitable for surveying threatened fauna and monitoring their responses to environmental change, contributing to the development of wildlife protection strategies under the current global biodiversity crisis. In addition, a wide variety of taxa can be simultaneously monitored with audio recordings. Therefore, worldwide efforts to commit to a set of standardized procedures can be facilitated by the availability of programmable recording schedules that allow the recording of multiple species in PAM (e.g., static ultrasonic detectors for monitoring high-frequency animal sounds as bats and orthopteran species; Newson et al. 2017).

The increasing role of citizen science in providing large-scale ecological data also has a large potential to support the widespread adoption of PAM. The French national acoustic biodiversity monitoring gathers acoustic data from orthopteran communities over a large extent of France, using passive audio recorders that have been supervised by volunteers since 2006 (see Jeliaskov et al. 2016). In another citizen-based program, a long-term integrated system of audiovisual recordings from Japan provides live streaming from remote areas to online users; participants can identify bird species and discuss their identification through social media, improving the efficiency of bird inventories (Saito et al. 2015). Ritts and colleagues (2016) worked with

First Nations in Canada to deploy automated sound sensors and interpret sounds along a potential shipping corridor and to determine its impacts on the population. Even before the expansion of passive acoustics, the volunteer-based wildlife acoustic survey proposed by the North American Amphibian Monitoring Program had already demonstrated the synergistic potential between citizen science and acoustic monitoring (Cosentino et al. 2014).

3.7 Conclusions

Our review traces the emergence and progress of terrestrial PAM, a burgeoning toolbox for animal surveys. The use of PAM in terrestrial ecology has been growing exponentially since the 1990s, reaching widespread adoption and a wide range of applications, with unprecedented publication rates. Bats have been the most researched group until now, mainly supported by nonprogrammable audio recorders. Nevertheless, new technologies for the automated recording of animal sounds have fostered the consolidation of this emerging method, especially since the 2010s, expanding applications to a large variety of ecological and conservation studies focused on several terrestrial organisms and surpassing the use of nonprogrammable recorders. The development of innovative analytic tools for automated signal detection and the computation of acoustic diversity indices have opened new avenues for PAM applications in community ecology and other scientific areas. However, our review also unveiled important gaps in terms of both geographical coverage and temporal design of PAM programs. Monitored areas have been mostly concentrated in a few regions of the northern temperate zone, whereas recording efforts mainly focused at dusk and night, because of the larger contribution of studies on nocturnal species.

The main barriers for the expansion of terrestrial PAM remain in establishing baselines for standardizing acoustic sampling, and in developing efficient solutions for automated signal analysis of long-term acoustic data sets. Another step forward is the improvement of PAM-oriented sound repositories for data management and sharing. Global monitoring and citizen science initiatives can find in PAM flexible options to coordinate multitaxa assessments over varying ecological conditions, providing new procedures for data collection over large spatial and temporal extents.

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4. CAPÍTULO 2

A roadmap for survey designs in terrestrial acoustic monitoring

Larissa Sayuri Moreira Sugai^{*1}, Camille Desjonquères², Thiago Sanna Freire Silva^{1,3},
Diego Llusia^{2,4,5}

1 Universidade Estadual Paulista (Unesp), Instituto de Biociências, Rio Claro, 13506-900, São Paulo, Brazil.

2 Departamento de Ecología, Terrestrial Ecology Group, Universidad Autónoma de Madrid (UAM), C/ Darwin 2, E-28049, Ciudad Universitaria de Cantoblanco, Madrid, Spain

3 Biological and Environmental Sciences, Faculty of Natural Sciences, University of Stirling, Stirling, UK, FK9 4LA.

4 Centro de Investigación en Biodiversidad y Cambio Global (CIBC-UAM), Universidad Autónoma de Madrid, C/ Darwin 2, E-28049, Ciudad Universitaria de Cantoblanco, Madrid, Spain

5 Departamento de Ecología, Laboratório de Herpetologia e Comportamento Animal, Instituto de Ciências Biológicas, Universidade Federal de Goiás (UFG), Campus Samambaia, Avenida Esperança, 74001-970, Goiânia, GO, Brazil

*corresponding author: lariagus@gmail.com

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4.1 Abstract

Passive acoustic monitoring (PAM) is increasingly popular in ecological research and conservation programs, with high-volume and long-term data collection provided by automatized acoustic sensors offering unprecedented opportunities for faunal and ecosystem surveys. Practitioners and newcomers interested in PAM can easily find technical specifications for acoustic sensors and microphones, but guidelines on how to plan survey designs are largely scattered over the literature. Here, we (i) review spatial and temporal sampling designs used in passive acoustic monitoring, (ii) provide a synthesis of the crucial aspects of PAM survey design and (iii) propose a workflow to optimize recording autonomy and recording schedules. From 1992 to 2018, most of the 460 studies applying PAM in terrestrial environments have used a single recorder per site, covered broad spatial scales and rotated recorders between sites to optimize sampling effort. Continuous recording of specific diel periods was the main recording procedure used. When recording schedules were applied, a larger number of recordings per hour was generally associated with a smaller recording length. For PAM survey design, we proposed to (i) estimate memory/battery autonomy and associated costs, (ii) assess signal detectability to optimize recording schedules in order to recover maximum biological information and (iii) evaluate cost-benefit scenarios between sampling effort and budget to address potential biases from a given PAM survey design. Establishing standards for PAM data collection will improve the quality of inferences over the broad scope of PAM research and promote essential standardization for cross-scale research to understand long-term biodiversity trends in a changing world.

Keywords: acoustic recorders, recording settings, wildlife survey, recording schedules, temporal sampling, acoustic monitoring

4.2 Introduction

Passive acoustic monitoring (PAM) is a trending method for biological data collection and has been increasingly employed on diverse lines of ecological research worldwide (Deichmann et al. 2018; Gibb et al. 2019; Sugai et al. 2019). Innovative audio devices capable of unattended recording allow acoustic surveys over a wide range of environmental conditions, thereby broadening the capabilities for long-term and large-scale monitoring (Ribeiro et al. 2017; Wrege et al. 2017). PAM brings together distinct scientific areas, such as animal behavior, ecology and acoustics, meaning that

the design of sampling protocols for data acquisition has to be based on multidisciplinary aspects of species, environments and sound (Laiolo 2010; Obrist et al. 2010; Blumstein et al. 2011; Sueur et al. 2012). Although an underlying knowledge on these areas is desirable to properly conduct PAM surveys, practitioners and newcomers to PAM may lack such in-depth training (Browning et al. 2017). Thus, researchers using PAM would benefit from methodological frameworks for survey design.

PAM provides systematic data collection that allows cross-scale and long-term comparative research (Browning et al. 2017; Shonfield and Bayne 2017). Collections of PAM time-series can also be considered as historical records of ecosystem acoustic dynamics worldwide, holding a special value for areas undergoing intense changes in land use and/or climate (Krause and Farina 2016; Dena et al. 2019; Sugai and Llusia 2019). Still, these datasets require detailed recording protocols to promote repeatable surveys and research synthesis (Cassey and Blackburn 2006; Gibb et al. 2019). Sampling design in PAM surveys is influenced by the researchers' knowledge and experience on target species (Gibb et al. 2019), resulting in a variety of recording protocols, not necessarily transferrable between biological groups and research goals (Darras et al. 2018a; Pérez-Granados et al. 2019).

Sampling effort in acoustic monitoring can be optimized through spatial distribution of acoustic sensors (Fig. 1) and recording schedules that determines the continuity and resolution of temporal sampling (Fig. 2). Since continuous 24-h monitoring quickly decreases the autonomy of acoustic sensors, built-in functions to pre-program recording schedules allow for longer monitoring periods and decrease maintenance requirements. Increased autonomy also promotes the investigation of biological groups that are inactive during typical temporal sampling windows for human observers (Gaston 2019, Laiolo 2010; Shonfield and Bayne 2017).

While primers on the use of microphones and recording systems are available (see Obrist et al. 2010; Blumstein et al. 2011; Browning et al. 2017), no current literature synthesizes the different practices employed in survey designs for acoustic monitoring, especially regarding automated acoustic recorders. Here, we (i) review spatial and temporal sampling designs used in terrestrial passive acoustic monitoring, (ii) provide a synthesis of the crucial aspects of PAM survey design and (iii) propose a workflow to optimize recording autonomy and recording schedules.

4.3 Literature review

We extracted information about spatial and temporal sampling from 460 research articles addressing passive acoustic monitoring in terrestrial environments compiled through a systematic literature review (Sugai et al. 2019). These articles were filtered from more than 10 000 articles returned by searches on Thomson Reuters Web of Science and Google Scholar from 1900–2018, using distinct combinations of 35 keywords (Sugai et al. 2019). We screened articles for information describing the spatial sampling, including (i) spatial scale (maximum distance between monitored sites), (ii) total number of recorders used, (iii) spatial distribution of recorders per site (single or multiple –distributed randomly, over transects or over grids–), (iv) use of between-site recorder displacement (i.e. if recorders were rotated over distinct sites) and (v) use of within-site recorder displacement during the recording sessions (e.g. mobile transects; Fig. 1). To describe temporal sampling, we compiled (i) if recording schedules covered the entire 24-h day or specific diel periods, (ii) if recordings were continuous or discontinuous (e.g. starting at regular intervals), (iii) the length of each recording and (iv) the number of recordings taken per hour (Fig. 2).

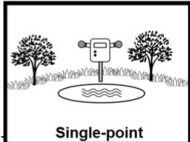
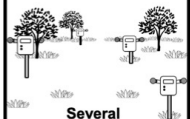
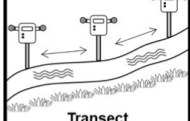
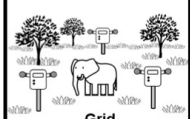
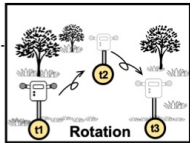
Item	Definition	Categories	Examples
Spatial scale	Maximum distance between two monitored sites	Micro: < 1 km and single-site studies Meso: 1 – 20 km Macro: > 20 km	Towsey <i>et al.</i> , 2019 Piel, 2018 Torrent <i>et al.</i> , 2018
Total number of recorders		Low: < 2 Medium: 3 – 10 High: > 10	Priyadarshani <i>et al.</i> , 2018 Oliver <i>et al.</i> , 2018 Ribeiro <i>et al.</i> , 2018
Spatial distribution of recorders	Arrangement of the acoustic sensors in each study site	Single: one recorder per site Several: random distribution of recorders Transect: recorders distributed along a path Grid: regular distribution of recorders Single and transect (si. & tr.): recorders distributed as single or along transects in different locations Single and several (si. & se.): recorders distributed as single or multiple (randomly) in different locations	 Single-point  Several  Transect  Grid Bridges and Dorcas, 2000 Munro <i>et al.</i> , 2018 Estrada-Villegas <i>et al.</i> , 2018 Deichman <i>et al.</i> , 2017 Abrahams and Deny, 2018
Between-site recorders displacement	Whether acoustic sensors are displaced between the monitored sites	Fixed: recorders remains in a single site throughout the monitoring period Rotating: recorders are rotated between different sites	 Rotation Phillips <i>et al.</i> , 2018 Ross <i>et al.</i> , 2018
Within-site recorders displacement	Whether acoustic sensors are displaced within a monitored sites	Static: recorders are static during a recording session Traveling: recorders are moved by an operator during recording session Static and traveling (st. & tr.): use of static and traveling recorders in different sites	 Traveling McCracken <i>et al.</i> , 2018 D'Accunto <i>et al.</i> , 2018 Winter <i>et al.</i> , 2017

Figure 1. Spatial sampling components extracted from articles using passive acoustic monitoring. Items are described with respective categories and examples for its use.

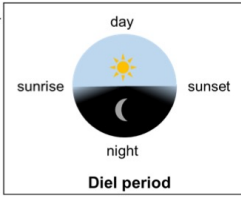
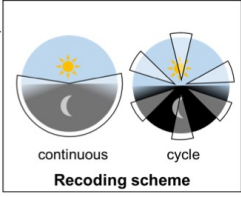
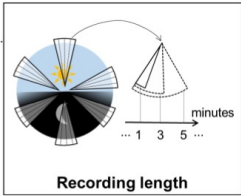
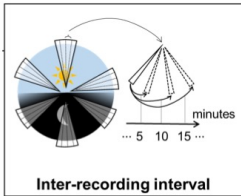
Item	Definition	Examples
Diel period	Specific periods of the day which acoustic monitoring takes place. Usually associated with the highest activity levels of the studied organism	 24 hours (Astaras <i>et al.</i>, 2017), Dawn (Buxton <i>et al.</i>, 2016)
Recording scheme	Whether the onset and end of a recording session is continuous or scheduled to distinct periods	 Continuous through the night (Torrent <i>et al.</i>, 2018), regular samples through the day (Campos-Cerqueira and Aide, 2016)
Recording length	Whitin a recording session, the amount of minutes of each single recording event	 One minute (Schalk and Saenz, 2016), 30 minutes (Burivalova <i>et al.</i>, 2018)
Inter-recording interval	Whitin a recording session, the interval separating single recording events	 One recording each 10 minutes (Aide <i>et al.</i>, 2017)

Figure 2. Temporal sampling components from articles using passive acoustic monitoring. Items are described with respective examples for its use.

4.4 Spatial sampling

4.4.1 SPATIAL SAMPLING IN THE LITERATURE

Over three decades of research using PAM in terrestrial environments (1992–2018), studies have been mostly focused on macro spatial scales (64%), followed by meso (22.1%) and micro (14%) scales (Figs. 1 and 3A), with some investigations spanning entire countries (e.g. Frey-Ehrenbold *et al.*, 2013). Most studies used between one and three acoustic recorders (50.1%), with only 13.5% using more than 10 recorders (Fig. 3B). The main spatial distribution of devices was a single recorder per site (70.8%), with

less studies using a random assignment (15.5%) and a minority using transects, grids, or a mix of both (9.6%, 2.5% and 1.6% respectively, Fig. 3C).

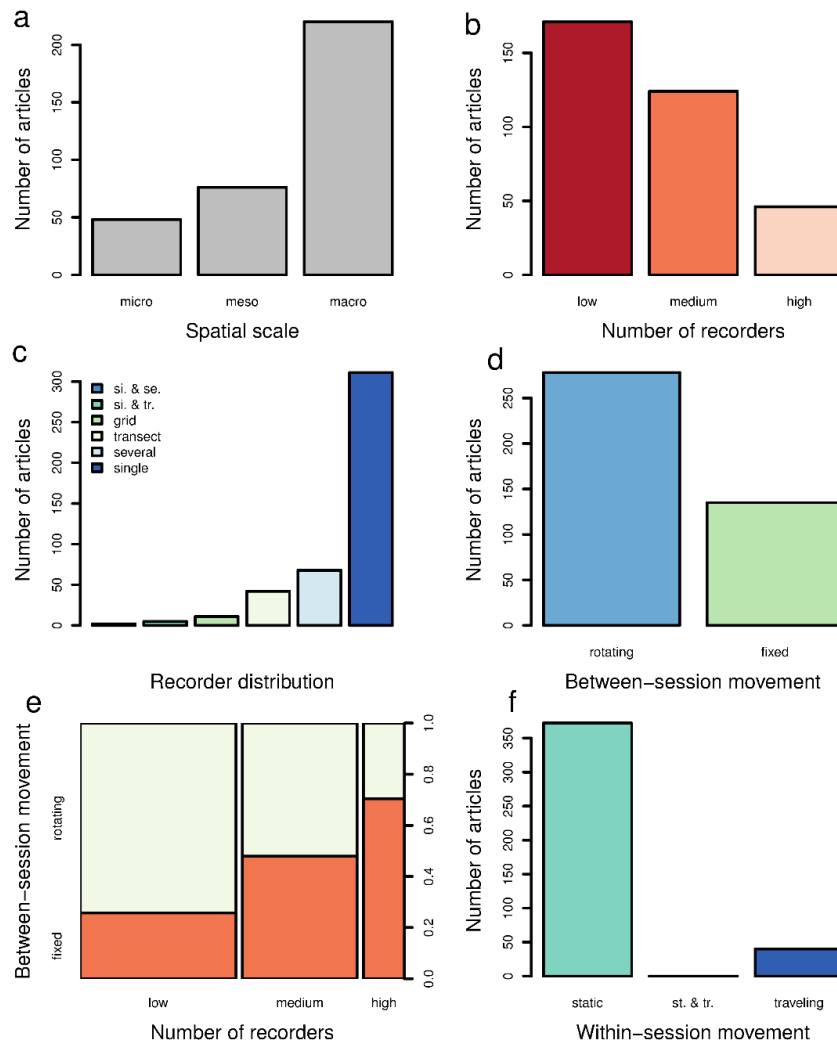


Figure 3. Spatial characteristics in articles employing passive acoustic monitoring in terrestrial environments (1992–2018): (A) spatial scale of published studies based on passive acoustic monitoring (micro: <1 km; meso: 1–20 km; macro: >20 km); (B) number of recorders per study (low: <3; medium: 3–10; high: >10); (C) recorder distribution within each study site (“si. & tr.”: both single point and transect; “si. & se.”: both single point and several); (D) between-site recorder displacement; (E) between-site recorder displacement in function of the number of recorders; (F) within-session recorder displacement (“st. & tr.”: both static and traveling recorders).

Between-site recorder displacement prevailed among the studies (67%; Fig. 3D), especially when few recorders were used (75%; Fig. 1; Fig. 3E). Within-site recorder displacement was reported for only 9.3% of the studies, whereas the vast majority used static recorders during the recording sessions (85.6%; Fig. 3F). Only 53.7% of all studies described their sampling designs with all five reviewed features of

spatial sampling, characterizing an important shortfall in current practices for documenting protocols.

4.4.2 OVERVIEW OF SPATIAL SAMPLING IN PAM

Passive acoustics use sound recordings from multiple sources at a given time and place through automated acoustic sensors, in contrast with traditional targeted recording techniques used in bioacoustic surveys (e.g. Laiolo 2010). When focused on particular species, spatial sampling relies on the home range, habitat use and calling behavior of focal taxa. Nonetheless, research on soundscapes often deploy recorders according to the spatial configuration of environmental factors (e.g. landscape structure and urbanization level; Depraetere et al. 2012; Fuller et al., 2015). Generally, single recording stations are broadly used to monitor populations and communities with clumped distribution patterns, such as lekking and chorusing species (Bridges and Dorcas 2000; Oseen and Wassersug 2002; Frommolt 2017). Long-term acoustic monitoring allows the investigation of broad aspects of seasonal activity and population dynamics (Sugai et al. 2019). A standalone recorder per site along an ecological gradient or over different habitat types can be employed to account for environmental heterogeneity (Wrege et al. 2010; Llusia et al. 2013a; Figueira et al. 2015), for instance, to determine the influence of spatially structured environmental factors on soundscapes, diversity patterns, occupancy models, or behavioral changes across species ranges (Campos-Cerqueira et al. 2019; Depraetere et al. 2012; Llusia et al. 2013b; Gil et al. 2015). However, more than a single recorder within a site may be required to properly detect a target species or to characterize spatial variation in soundscapes. For example, several recorders may be desirable to study populations with low densities (Haselmayer and Quinn 2000; Pérez-Granados et al. 2018). Additionally, the physical nature of each habitat alters species detectability, with increased detection reported for non-forested areas (Enari et al. 2017) and flat riparian habitats (Ribeiro et al. 2018). Therefore, specific spatial arrangements with multiple recorders as random assignments of recorders (Munro et al. 2018) or replicates along horizontal or vertical transects and grids (Rodriguez et al. 2014; Kalan et al. 2015) can be used to increase spatial replicates and species detectability (Pollock et al. 2002). These spatial sampling designs are particularly suitable to monitor species with less predictable distribution patterns, such as highly mobile species, solitary animals, moving flocks, species with explosive activity patterns and low-density populations (e.g. Brooke et al. 2000; Pieretti et al. 2011; Hagens et al. 2018).

Although sampling over multiple locations is often essential to increase sound detection and to address the effect of environmental factors on biodiversity (Skalak et al. 2012; Wood et al. 2019), animal behavior (Gil et al. 2015; Ulloa et al. 2019), or soundscape dynamics (Fuller et al., 2015), it requires a higher number of automated recorders, which may be a limiting factor for researchers. As an alternative, protocols based on recorders rotation can be used to cover a higher number of sampling sites (Gil et al. 2015; Machado et al. 2017). However, this method has two main drawbacks: (i) rotation procedures precludes simultaneous recording across sampling sites, potentially introducing bias from seasonal or weather changes, which must be accounted for; (ii) the number of monitoring days before rotating will influence species detectability, especially for rare species. Monitoring for more than a single day per site is thus recommended to ensure adequate detectability (Skalak et al. 2012; Ribeiro et al. 2017; Pérez-Granados et al. 2019). Additionally, recent development of low cost and versatile acoustic devices as alternatives to costly commercial automated units (Farina et al. 2014; Whytock and Christie 2017; Hill et al. 2018) may allow researchers to employ at least one stationary acoustic sensor at each monitoring site (Whytock and Christie 2017).

Within-site recorder displacement is usually performed by an operator walking, riding a bike or driving a car along a transect or road and aims to increase spatial coverage (Schmidt et al. 2013; Mendes et al. 2017; D'Acunto et al. 2018). As it requires an operator, long-term data collection is challenging (but see citizen science-based approaches and car-based techniques; Newson et al. 2015; Whitby et al. 2014). Although this practice is usual for surveys of bat activity, its efficiency to capture activity patterns is lower when compared with designs using several stationary automated sensors (Stahlschmidt and Brühl 2012, Braun de Torrez et al. 2017).

4.4.3 CONSIDERATIONS ABOUT DETECTION SPACE

The area within which a particular signal is detected by an acoustic sensor (i.e. the detection space) strongly influences species detectability and is key to standardize sampling efforts in PAM (Darras et al., 2016, Llusia et al. 2011). Thus, measurement of detection space should be required to define the number of recorders per site or to estimate population densities, but it is often absent from studies as it is a labor-intensive task under field conditions (Merchant et al., 2015, Obrist et al. 2010). Estimates of detection areas can be achieved using focal signals played back at varying

distances and directions from the recorder (Llusia et al. 2011; Hagens et al. 2018), allowing standardization of detectability among recorders (Yip et al. 2017; Hagens et al. 2018) and leading to better detection rates than point-count methods (Darras et al. 2018b). Recent efforts in combining playback tests and models of sound transmission provide robust estimates of species-specific detection distances (Sebastián-González et al. 2018; Yip et al. 2019), and together with models of sound attenuation over heterogeneous environments (Royle 2018), they should support the standardizing of spatial sampling efforts in PAM.

4.5 Temporal sampling

4.5.1 TEMPORAL SAMPLING IN THE LITERATURE

Our review unveiled that 76.9% of the studies on terrestrial passive acoustic monitoring used continuous recordings, whereas 69.5% monitored specific diel periods (Figs. 2 and 4). Discontinuous recordings (i.e. regular sampling) were used in only 23.1% of the studies, within which monitoring of specific diel periods or 24 h occurred in similar proportions (52.4% and 47.6%, respectively; Fig. 4A). Recording schedules were highly diverse across studies, although a larger number of recordings per hour were generally associated with a smaller recording length (Fig. 4B–C). Moreover, studies tended to either use a few recordings per hour with small recording lengths when recorded 24 h, or larger recording lengths for monitoring specific diel periods (Fig. 4B–C). Particularly, most studies using discontinuous recordings over 24 h (Fig. 4B) used a single recording per hour (46.9%), either up to 3 min length (59%) or between 3 and 10 min (31.8%). The remaining studies used 2, 4, or 6 recordings per hour. Among this type of studies targeting specific diel periods (Fig. 4C), 51% had a single recording per hour of 10 to 30 min length (48%), or 2.5 min or less (32%).

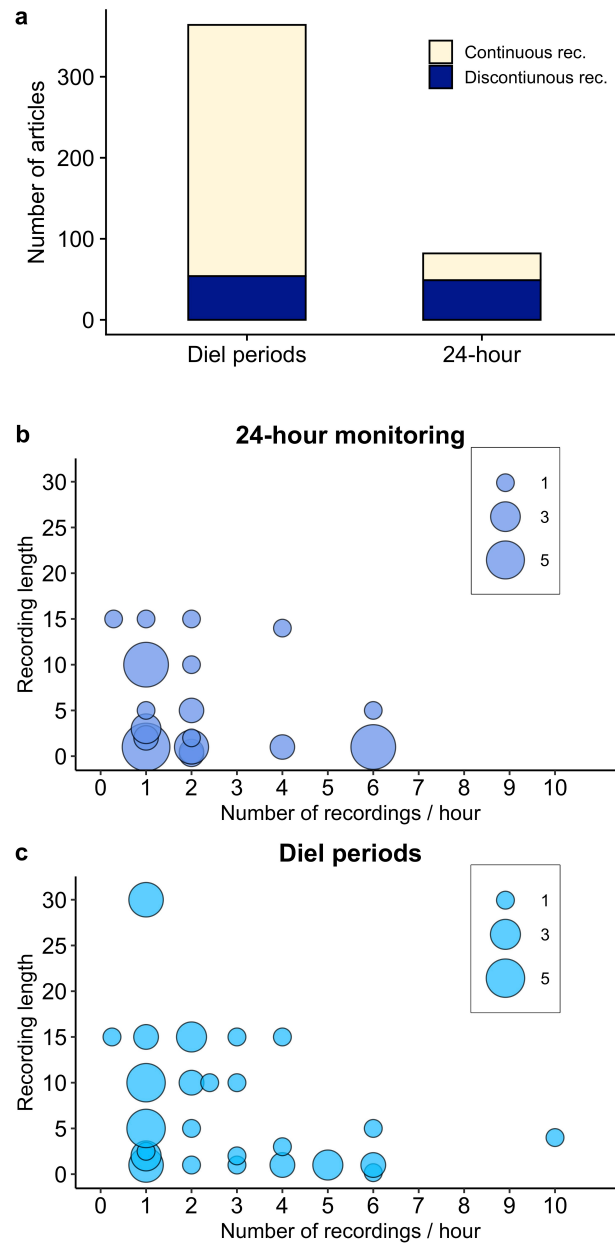


Figure 4. Recording schedules used in articles employing passive acoustic monitoring in terrestrial environments (1992-2018): (a) number of articles that used 24-hour or diel monitoring periods and employed continuous (white) or discontinuous recordings (blue); and (b) recording lengths (vertical axis) in relation to number of recording events per hour (horizontal axis) used in articles that employed discontinuous recordings over 24-hour or (c) at a specific diel period.

4.5.2 OVERVIEW OF TEMPORAL SAMPLING IN PAM

PAM offers a wide variety of temporal sampling protocols that can be selected according research goals, study groups and equipment. Continuous monitoring over 24 h and over large periods are preferable to increase the likelihood of recording sounds within a site, and is especially necessary to investigate the temporal activity of rare or cryptic species (Astaras et al. 2017; Wrege et al. 2017). However, it requires larger

storage space and power supply. Equipment autonomy can be increased by powering the system with solar panels and by using wireless networks for data transfer (Aide et al. 2013; Kasnesis et al. 2019), which can be added to the motherboard of customizable acoustic sensors (Whytock and Christie 2017). Additionally, data storage can also be reduced with recordings set to be triggered only when sound level reaches a certain threshold (usually employed for bats and katydids, Andreassen et al. 2014; Jeliaskov et al. 2016). This, however, can result in missed detection of signals emitted at low levels, from long distances, or in noisy environments.

Conversely, the autonomy of acoustic sensors is often optimized by scheduling recordings within specific diel periods coinciding with high activity levels of the target species (Gibb et al. 2019). Thus, continuous recording at specific periods is the most common monitoring practice found in the literature, with night, dusk and dawn being the most investigated diel periods for bats, birds and anurans (Sugai et al. 2019). Focusing on continuous diel periods can provide higher estimates of species diversity when compared with discontinuous 24-h monitoring (Wimmer et al. 2013; La and Nudds 2016; Pérez-Granados et al. 2018), as detection probabilities usually decrease after the daily activity peak (e.g. sunset for bats, Skalak et al. 2012). Furthermore, extending monitoring periods on long-term studies is required to properly capture seasonal variations in species activity (Shearin et al. 2012; Hagens et al. 2018), as for species influenced by light intensity and lunar phases (e.g. bats and katydids, Lang et al. 2006; e.g. anurans, Onorati and Vignoli 2017; Underhill and Höbel 2018), or species with variable activity associated with seasonal phenology, such as the bimodal daily activity peak during summer reported for bats (Skalak et al. 2012).

Additionally, a greater autonomy can also be achieved by scheduling recordings at regular intervals (Browning et al. 2017). As a starting point, protocols of point counts and other traditional acoustic surveys can offer guidance to determine recording lengths for PAM, as they can provide comparable biological data with PAM methods to estimate alpha and gamma diversity (Darras et al. 2018a), community composition (Alquezar and Machado 2015), population trends of cryptic species (Digby et al. 2013; Hagens et al. 2018), and to discriminate individual calls (Ehnes and Foote 2015). Point counts surveys have been widely used in avian (Rosenstock et al. 2002; Matsuoka et al. 2014) and amphibian research (Pierce and Gutzwiller 2004; Dorcas et al. 2009). For long-term monitoring of amphibian population trends, call surveys with three to 5-min lengths per hour have shown to be adequate for most species (Shirose et al. 1997;

Dorcas et al. 2009), whereas for birds shorter lengths may increase false negatives, and studies have often used lengths of five to 20 min (Bonthoux and Balent 2012, Table 1). Overall, longer surveys increase detection probabilities and produce better estimates of species diversity, but still acceptable levels of accuracy can be obtained for the same metrics by using shorter time windows (Table 1), without affecting the overall scientific conclusions (Hagens et al. 2018).

Sound-producing invertebrates (e.g. crickets and katydids) have been less studied using PAM, but still produce species-specific signals (Riede 2018) that can be reliably monitored by acoustic sensors (Diwakar et al. 2007). Low temporal partitioning among sound-producing insects seems to be pervasive across communities (Schmidt et al. 2013), allowing acoustic monitoring to rely on fewer short-length recordings per night (e.g. 3-min recordings every 30 min, Thompson et al. 2019). Remarkably, orthopterans are one of the most targeted group for large-scale citizen science PAM studies, where recordings are taken continuously along a circuit and standardized based on speed instead of time (Penone et al. 2013; Jeliazkov et al. 2016).

The frequency of recordings taken during monitoring determines the temporal data resolution and also influences target species detection. Shorter inter-recording intervals from 24-h monitoring provide better estimates of temporal acoustic dynamics than larger intervals (Bradfer-Lawrence et al. 2019), although the performance varies over habitat types (Pieretti et al. 2015). Additionally, extending the number of monitored days leads to higher detection probabilities (Pérez-Granados et al. 2019; Skalak et al. 2012, but see Thompson et al. 2019), and may also increase the statistical power for detecting meaningful effects over temporal trends (Wood et al. 2019). As distinct combinations of recording length and number of scheduled recordings influence how well total acoustic activity is captured, a critical appraisal of the sampling effort is required to set appropriate temporal PAM designs. In this sense, pilot studies can provide initial estimates of the efficiency of distinct recording schedules for a given goal (Wimmer et al. 2013; Hagens et al. 2018; Bradfer-Lawrence et al. 2019).

4.5.3 CONSIDERATIONS ABOUT AUDIO SETTINGS

The selection of audio settings on acoustic sensors determines the quality of the recordings of PAM programs (Obrist et al. 2010; Villanueva-Rivera et al., 2011). Here, we

highlight here essential audio settings that must be considered, and common standards used in PAM.

Table 1. Examples of recommendations of calling survey length (also point counts or other acoustic surveys) from literature that addressed the effect of distinct survey techniques on diversity patterns.

Biological group	Duration	Reasoning	Reference
Anurans	3	Adequate to sample species occurrence and calling intensity for most species. In most cases, all species were identified in the first minute of survey.	Shirose et al. (1997)
	5	Sufficient to detect 94% of all species	Gooch et al. (2006)
	5 to 15	Higher detection probability on 5-minute calling survey for large populations during peak breeding	Williams et al. (2013)
	10	Higher detection probability to detect all species	Crouch & Paton (2002)
	15	Sufficient to detect 90% of all species	Pierce and Gutzwiller (2004)
Birds	5	Other lengths (10, 15 and 20) improve moderately explanation of community structure and prediction of species distribution	Bonthoux
	5	Detection increase with larger survey duration only for few species	Thompson et al. (2002)
	5 to 10	Better performance of species-habitat models	Detmers et al. (1999)
	10	Larger duration did not produced better richness estimates	(Gutzwiller et al. 1991)
	2 to 10	Density estimates from 2 minutes are only 13% lower than 10-min count	Lee & Marsden (2008)
		Suggestion of group-specific count period:	
		4 min for omnivores	
		6 min for nectarivores and upperstorey gelaning insectivores	
		8 min for understorey insectivores and canopy frugivores	
		10 min for sallying insectivores, ground-dwellers, carnivores and coucals/koels	

Sampling rate is the number of sound amplitude measures captured per second by a microphone (in Hz). The sampling rate must be at least twice the maximum intended frequency to be recorded (Nyquist–Shannon sampling theorem) to ensure a proper recording of the signal. A broad range of vocalizations from most terrestrial vertebrates and some invertebrates can be recorded with standard microphones sensible to the human-ear frequency range (20 Hz–20 kHz) using 44.1 or 48 kHz sampling rates. Conversely, bats, some mammals (e.g. rodents) and most invertebrates demand ultrasonic microphones recording at higher sampling rates (e.g. 96–192 kHz).

As larger sampling rates produce larger file sizes, an alternative to enhance sensor autonomy is to identify the frequency of the highest-pitched sound of the target species (e.g. 7 kHz), double it ($2 \times 7 = 14$ kHz) and set the sampling rate a few kHz higher to avoid missing signals at slightly higher frequencies. In the example of a 7 kHz signal, a sampling rate of 20 kHz would be high enough to capture the intended signal and would produce files that are about 50% smaller than files produced from sampling rates of 48 or 44.1 kHz.

Audio gain modulates the sound amplitude of the recorded signal by amplifying or attenuating it by a constant rate. Higher gain increases the likelihood of recording a distant or weak sound and consequently the detection space. However, it also amplifies background noise and increases the chance of audio clipping (i.e. amplitudes that exceed the maximum range of the device), resulting in distortions that can compromise further analysis (Obrist et al. 2010). In most automated recording units, gain is pre-set and remains fixed within the temporal extent of monitoring, unlike manual focal recording where gain can be adjusted by the operator according to acoustic conditions. Undertaking pilot tests over varying conditions can thus help optimize this parameter. Alternatively, stereo recordings with distinct gains for each channel can be used for long-term acoustic monitoring where changing sound levels are expected. However, while different gain levels have negligible impacts on sensor autonomy, stereo recordings double the amount of collected data and increase power consumption for high sampling rates (above 44.1 kHz).

When more than one microphone is available, stereo/multichannel mode can be used to place microphones in different locations with extension cables to monitor different habitats or strata using a single acoustic device, or to guarantee a suitable record (from at least one channel) in case of microphone malfunction (Digby et al. 2013; Rodriguez et al. 2014). Other common standards in audio settings are (i) a minimum of 16-bit audio bit depths and (ii) the use of uncompressed (WAVE or AIFF) or lossless compressed audio formats. Lossy compression formats such as MP3 or AAC can alter the acoustic parameters in recordings and decrease the performance of automated analysis of acoustic data (Araya-Salas et al., 2019). Still, compressed audio recordings have proven useful for analyses based on aural recognition (Villanueva-Rivera et al., 2011) and can yield similar estimates of acoustic diversity provided by uncompressed files, with the benefit of optimizing memory usage (Linke & Deretic, 2019).

4.6 Autonomy estimation

The autonomy of acoustic sensors is determined by (i) memory usage, considering audio settings and the capacity of storage units (e.g. memory cards) and (ii) battery usage, considering the electrical aspects of battery cells and acoustic sensors (Fig. 5). To illustrate how different recording schedules and audio settings can influence sensor autonomy, we explore memory and battery usage using a SM4 (Wildlife Acoustics Inc.) with default settings (stereo recording powered by size 4D alkaline batteries and stored in .WAV format) for recording (i) continuous 24-h, 5 h per day (e.g. dawn and dusk), and 2 h per day (e.g. only dawn or dusk); (ii) recording lengths of 1, 3 and 5 min; (iii) regular recording intervals from one to six recordings per hour and (iv) sampling rates of 24 and 48 kHz (Fig. 6).

As expected, memory and battery autonomy decrease with longer monitoring periods, recording lengths and sampling rate. For schedules containing a higher number of recordings per hour, memory consumption sharply increases with larger sampling rates and recording lengths (Fig. 6). For instance, negligible differences in memory consumption are observed for one and two recordings per hour, whereas memory consumption changes considerably among five and six recordings per hour.

Overall, short recording lengths provide greater autonomy for schedules of discontinuous recordings through the day. Conversely, monitoring specific diel periods allows increased recording lengths and/or number of recordings per hour with less impact on autonomy when compared with the minimum scheduling settings for 24-h monitoring (Fig. 6).

Estimating sensor autonomy	
Memory	Battery
Memory usage (MU) of one recording event (Gb): $(1) MU = (RL * SR * C * B) / 10^9$ <u>RL</u>: recording length (s), <u>SR</u>: sample rate (Hz) <u>C</u>: number of recording channels (1 = mono, 2 = stereo, etc.) <u>B</u>: number of bytes related to the audio bit-depth (2 = 16-bit, 4 = 32-bit, etc.). Memory usage per day (MUd), according to the recording schedule: $(2) MUd = RE * H * MU$ <u>RE</u>: number of recording events per hour <u>H</u>: number of monitored hours per day <u>MU</u>: is the memory usage of one recording event (see 1). Number of memory cards required for the total monitoring period: $(3) n. \text{ memory cards} = (MUd * D * AD) / MS$ <u>MUd</u>: memory usage of a given recording schedule per day (see 2) <u>D</u>: number of days of the monitoring period <u>AD</u>: number of acoustic devices, <u>MS</u>: storage capacity of each memory unit card Memory autonomy per acoustic recorder (days): $(4) \text{Mem. autonomy} = (n. \text{ memory slots} * MS) / MUd$	The capacity of small batteries is usually rated in milliampere-hours (mAh), and power usage for small electronics is normally given in milliwatts (mW). Audio recorder power draw can be converted to current draw (CD) with: $(i) CD = \text{Power usage} / (\text{voltage} * n. \text{ batteries})$ Consider an audio recorder that draws 200 mW when recording (rec) and 2 mW when in standby (st) and requires four D alkaline batteries (a typical D-size alkaline battery has a capacity of 15000 mAh and delivers 1.5 volts). CD is obtained with: $CD_{rec} = 200 \text{ mW} / (1.5 \text{ V} * 4) = 33.3 \text{ mAh}$ $CD_{st} = 2 \text{ mW} / (1.5 \text{ V} * 4) = 0.33 \text{ mAh}$ Active operation hours (AP) is obtained with: $(ii) AP_h = \text{battery capacity} / CD \text{ (see i)}$ In practice, battery autonomy will be lower given climatic conditions, and a safer estimate would be thus to reduce AP by ~25%. Thus, according to the recording schedule (total hours in standby (ST) and recording (RT)), overall battery autonomy (days) can be estimated as: $(iii) \text{Battery autonomy} = 0.75 * \text{battery capacity} / (ST * CD_{st}) + (RT * CD_{rt})$

Figure 5. Estimating sensor autonomy by calculating memory and battery usage given audio settings, recording schedule, and electrical calculations.

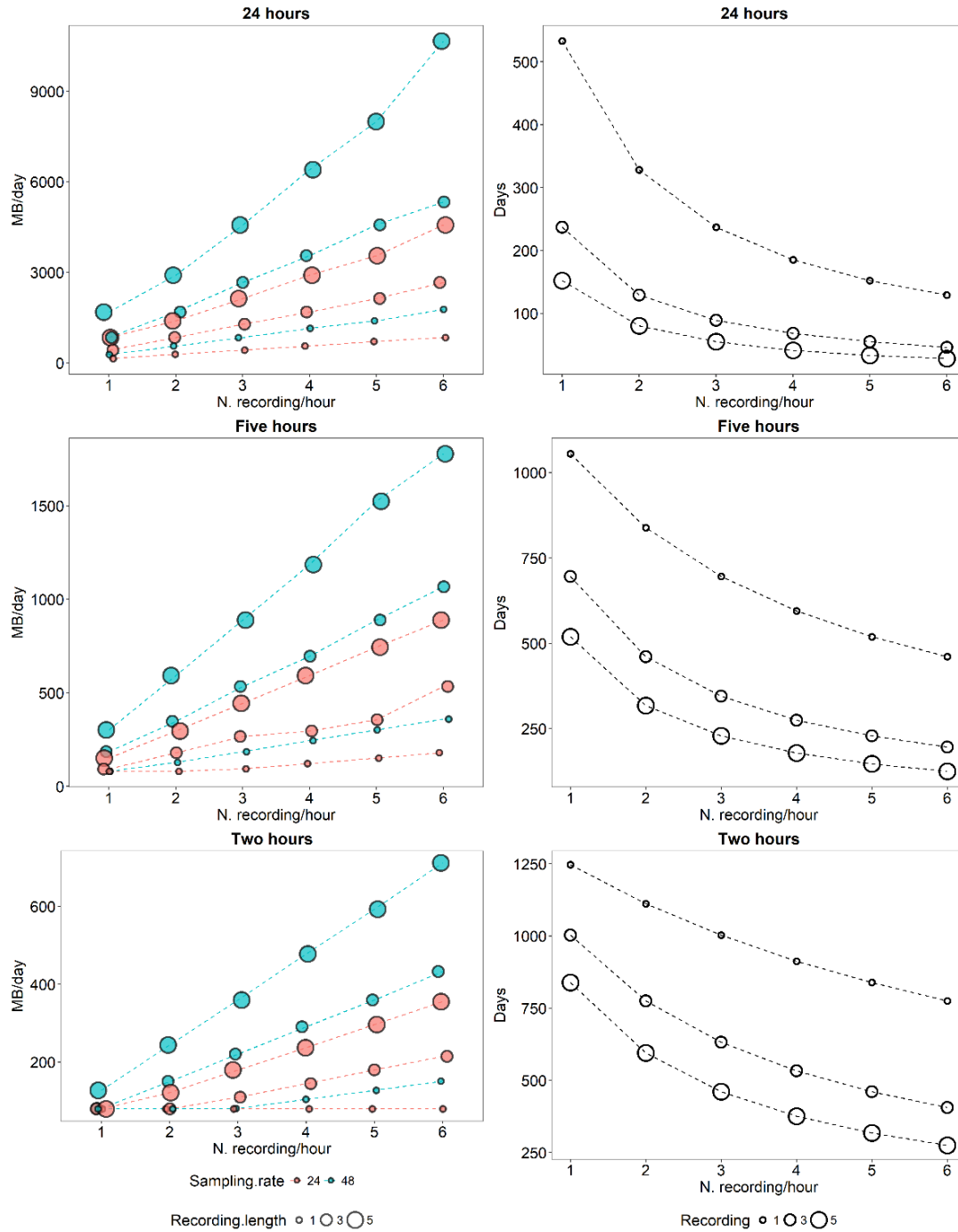


Figure 6. Memory (left) and battery (right) usages for a combination of recording schedules and audio settings based on distinct (i) recording periods (continuous 24-hour, five hours, and two hours), (ii) sample rates (24 and 48 kHz), (iii) recording lengths (one, three, and five minutes), and (iv) recording intervals (one to six recordings per hour).

4.7 Rewinding the tape: trade-offs between sampling efficiency and cost

Based on our assessment of the current literature, we suggest the following workflow to optimize spatial and temporal sampling designs for passive acoustic monitoring (Fig. 7):

- (i) Design spatial effort over the study area to properly address the extent of the spatial scale studied (Pollock et al. 2002; Wood et al. 2019). If the number of available recorders is low, consider employing rotation procedures, lower cost recorders or more microphones. Whenever possible, undertake pilot tests to estimate the detection space (or distance) of sensors over the range of monitoring habitats, while also optimizing gain levels (Llusia et al. 2011; Enari et al. 2017; Darras et al. 2018b; Pérez-Granados et al. 2019; Yip et al. 2019). Use this information to determine the appropriate distance among sampling sites.
- (ii) Make a list of potential recording schedules based on behavioral and ecological aspects of focal taxa and research goal. Prioritize larger diel periods and continuous recordings. When employing discontinuous recordings, include a wide range of distinct recording lengths, supported by previous recording protocols (Table 1), and number of recordings per hour (i.e. inter-recording interval).
- (iii) Conduct continuous 24-h audio recordings prior to start monitoring and estimate species detectability or other biological parameters of interest (e.g. species richness, community composition; Hagens et al. 2018) for the previously listed recording schedules (see point 2). Conversely, when monitoring is already on course and scheduled following given standards, consider conducting continuous recordings for a subset of sites during specific days. Evaluate the congruence of information obtained from the different recording schedules with the information obtained from 24-h recordings. For instance, use species accumulation or rarefaction curves and non-parametric estimates of species diversity (Gotelli and Colwell 2001; Brose et al. 2003), cumulative standard errors of mean estimates (Bradfer-Lawrence et al. 2019), coefficient of variance of acoustic activity indices (Pérez-Granados et al. 2019), or procrustes superimposition for compositional similarities (Saito et al. 2015). Alternatively, resort to modeling techniques to estimate species detection probabilities and occupancy rates that include imperfect detection when estimating biological parameters such as species richness (Dorazio et al. 2006; Celis-Murillo et al. 2012; Hagens et al. 2018; Ribeiro et al. 2018). This procedure can support choosing

among distinct recording schedules prior to start PAM. Additionally, for studies already on course, once the initial data are collected and analyzed, such estimates can assist in the interpretation of the results and provide a measure of data reliability. In cases when this procedure cannot be applied, such as in remote areas or on a limited budget, more intense schedules may be selected according to literature (Table 1).

(iv) Estimate sensor autonomy and associated costs for the distinct recording schedules. For each recording schedule, generate trade-off scenarios between autonomy and bias in biological estimates previously calculated. From the scenarios generated, define which design is suitable considering budget, sampling effort and autonomy (Wintle et al. 2011).

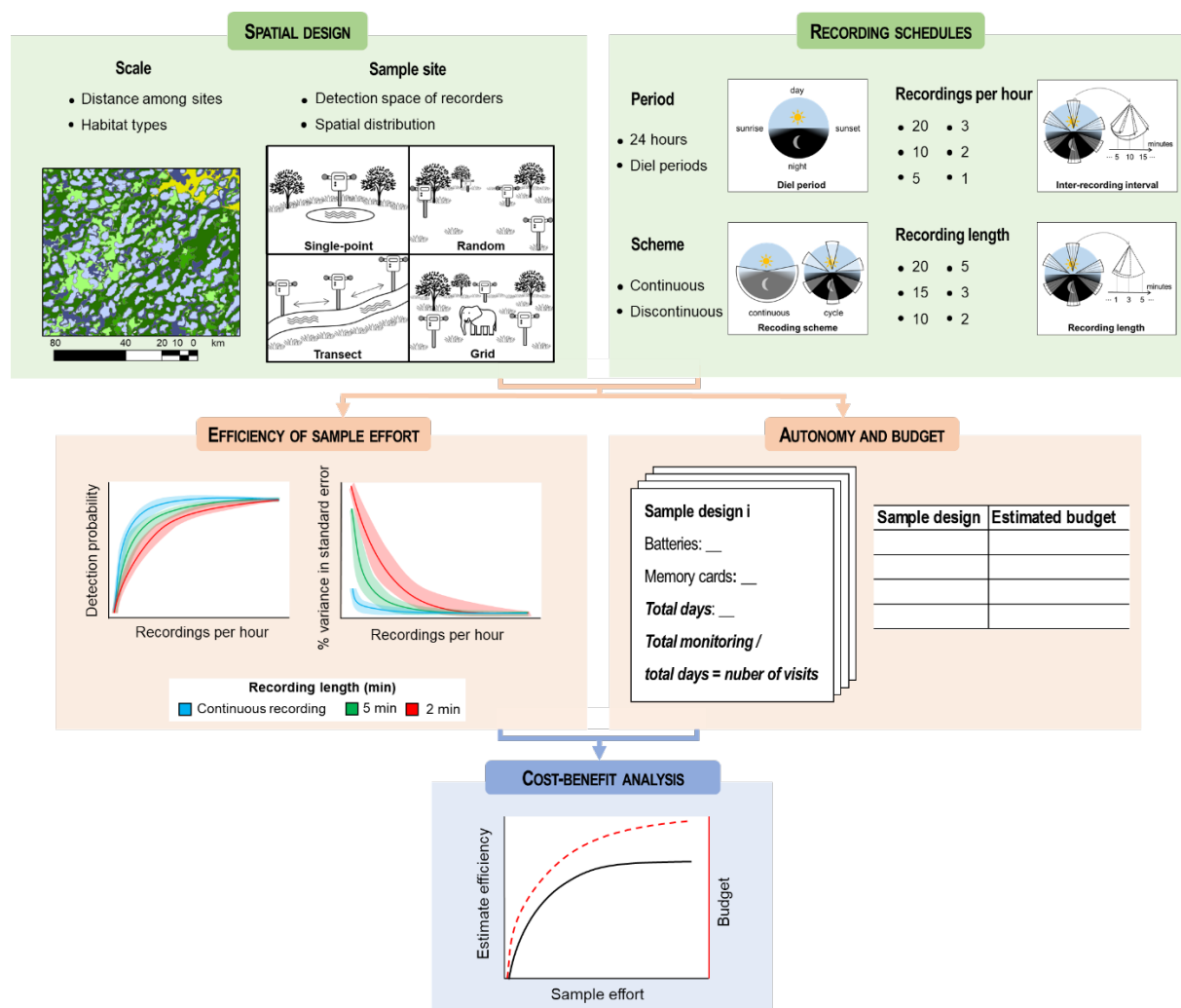


Figure 7. Workflow for planning and optimizing the design of spatial and temporal sampling in passive acoustic monitoring. Spatial design should consider aspects of spatial scale of inference and species detectability. Distinct recording schedules can be set according to specific monitoring period, continuous or discontinuous recordings, number of recordings per hours and the length of recordings. Whenever possible, 24-hour recordings can be employed prior or during monitoring to address whether

distinct recording schedules can retrieve the biological information obtained in 24-hour continuous monitoring. Estimate the autonomy of distinct survey designs and their respective costs, and evaluate their suitability according to sampling effort, estimate efficiency and budget.

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5. CAPÍTULO 3

A role for social information use on the structure of signaling communities

Larissa S. M. Sugai^{*1,2}, Diego Llusia^{2,3}, Tadeu Siqueira¹, Thiago S. F. Silva^{1,4}

¹Universidade Estadual Paulista (Unesp), Instituto de Biociências, Rio Claro, 13506–900, São Paulo, Brazil.

²Terrestrial Ecology Group (TEG), Departamento de Ecología, Universidad Autónoma de Madrid, C/ Darwin, 2, 28049, Ciudad Universitaria de Cantoblanco, Facultad de Ciencias, Edificio de Biología, C-211, Madrid, Spain.

³Laboratório de Herpetologia e Comportamento Animal, Departamento de Ecologia, Instituto de Ciências Biológicas, Universidade Federal de Goiás, Campus Samambaia, CEP 74001–970, Goiânia, Goiás, Brazil.

⁴University of Stirling, Department of Biological and Environmental Sciences.

*corresponding author: lariagus@gmail.com

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5.1 Abstract

1. The cacophony from signaling animals has long cast doubts on how acoustic signaling overcomes potential constraints in communication. Signaling properties have been traditionally considered to result from selection in predictable directions against signal degradation and masking interference. Such paradigm was challenged as the role of social interactions in natural communities started to be elucidated. However, social interactions are largely reliant on ecological contexts of communities, and a gap remains in addressing how acoustic signaling strategies are structured across communities experiencing distinct ecological conditions.
2. We investigated potential drivers of acoustic signaling strategies in animal communities across distinct ecological contexts. We analyzed tropical anuran communities in the south Pantanal wetlands of Brazil using acoustic monitoring and assessed the acoustic and phylogenetic dimensions of communities over a gradient of environmental heterogeneity.
3. Local communities were predominantly composed of sets of species with high acoustic similarities and phylogenetic relatedness. Nonetheless, the acoustic space tended toward a convergent structure across communities composed by more distantly related species. Such relationship was stronger in contexts of higher environmental heterogeneity. The assembly of closely related species was influenced by environmental heterogeneity, and these communities tended to diverge in acoustic structure.
4. In the light of social information use, the benefit of social information has to overcome competitive drawbacks, and our findings are consistent with strategies enhancing the net benefit of information use. The quality of information is higher either with more diverse emitters or when used in spatially heterogeneous environments. Thus, in addition to reduced interspecific competition, communities of ecologically different species produce high quality information, and similar signals among heterospecifics facilitate information access through a common communication channel. Conversely, the occurrence of closely related species upon environmental filtering can increase competition among heterospecifics. As such, differences in acoustic signals can promote conspecific interactions, especially because intraspecific information is more valuable in such contexts and decrease interspecific competition.

5. Our findings contrast classical predictions for signaling communities and instead suggest a role for social information use on the acoustic structure across communities, unfolding new perspectives for social interactions on the assembly of signaling animals.

Keywords: behavior, bioacoustics, community phylogenetics, sensory drive, habitat filtering, metacommunity

5.2 Introduction

How can information reliably achieve a receiver in acoustic communication is a long intriguing debate (Wilkins, Seddon & Safran 2013). Acoustic signals convey information aimed to an intended receiver and once emitted; signal transmission can be hindered by challenging environments. Background noise can induce signal confusion, while propagation through complex environments can degrade signals, thus hampering species recognition and increasing chances of heterospecific mismatches (Wells & Schwartz 2007). A number of hypotheses explaining how species cope with such challenges in communication have been proposed. The sensory-driven framework predicts sensory systems and signaling behavior to drive signal evolution (Endler 1992). Two remarkable hypotheses stem from this framework: i) selection against masking interference is proposed to drive signal divergence (acoustic partitioning hypothesis; Hoskin & Higgie 2010; Wilkins, Seddon & Safran 2013), and ii) selection for optimized transmission through the environment drive signal convergence (acoustic adaptation hypothesis; Morton 1975; Ey & Fischer 2009). Mixed empirical evidence for the acoustic partitioning and acoustic adaptation hypotheses started to question the prevalence of such processes acting on the acoustic signaling space of communities (Boncoraglio & Saino 2007; Wells & Schwartz 2007; Luther & Wiley 2009; Tobias et al. 2014). In contrast, such selective pressures may be weakly represented on community-wide acoustic structure, and the resulting acoustic space may instead represent signaling strategies that extend species-specific boundaries and mediates interspecific competitive interactions (communication network hypothesis; Tobias et al. 2014). However, none hypotheses addressed whether the observed patterns are consistent across communities and emerge, for instance, as a by-product of other ecological processes acting on community assembly (Chek, Bogart & Loughheed 2003).

Species interactions have traditionally been emphasized for negative effects on competitive outcomes (Roughgarden 1976; Schoener 1983), where a potential

influence of species' social behavior has been largely neglected (Parejo & Avilés 2016). Nonetheless, a simple behavioral display or even an unintended cue about an organisms' presence produce an information made publicly available as a social information (Seppänen et al. 2007). Mounting evidence suggest that such social information can be used by heterospecifics and generate positive effects on interacting species, which can theoretically alter the dynamics of ecological communities (Bertness & Callaway 1994; Parejo & Avilés 2016). Acoustic signals mediating intentional conspecific interactions compose a rich source of social information conveying hints from multiple emitters about their identity, location, and performance (Valone 2007; Goodale et al. 2010). In addition to influence individuals' behavior, social information can underly decision making to avoid predation, to forage, and to choose suitable breeding sites (Phelps, Rand & Ryan 2006; Slabbekoorn & Bouton 2008; Both & Grant 2012). Such potential for indirect positive interactions can induce positive density dependence, whereby enhanced survival and reproduction promotes growth in the informed population when the information-source population experiences large densities (Gil et al. 2018). However, negative competitive interactions for ecological resources can counteract the benefits of social information use, especially for those species with shared resources and predators (Gil, Baskett & Schreiber 2019). For instance, higher interspecific than intraspecific competition may not drive species exclusion if the value of heterospecific social information is higher than conspecific, which can be exemplified by the cohesion of mixed-bird flocks (Gil, Baskett & Schreiber 2019). Moreover, selection of breeding location is largely influenced by spatial and temporal habitat heterogeneity, and whether social information correlates with spatiotemporal variability of breeding environments and enhances heterospecific reproductive success, it can play a role in the assembly of communities (Fletcher Jr. 2008; Schmidt, Dall & Van Gils 2010; Schmidt & Massol 2019). Therefore, signaling strategies in communities can likely reflect a role of information use strategies among species (Bruno, Stachowicz & Bertness 2003; Parejo & Avilés 2016; Gil et al. 2018).

The structure of community-wide ecological attributes and phylogenetic relatedness has been incorporated in approaches of community ecology as complementary means to address the drivers of community assembly (Webb et al. 2002; HilleRisLambers et al. 2012). A legacy from such approaches is that there is no simplistic way to infer process from ecological pattern, since a similar phylogenetic

and trait community-wide pattern (e.g. both convergent) can be generated by distinct evolutionary and ecological processes (Gerhold et al. 2015; Saito et al. 2018). Hence, it is reasonable that the acoustic space can indirectly result from other ecological processes acting on communities, such as habitat filtering of species incapable to persist in all types of environments or dispersal dynamics mediating colonization/extinction and migration rates (Leibold & Chase 2017). Thus, addressing both acoustic and phylogenetic variation across communities experiencing distinct ecological contexts can provide a comprehensive understanding of the potential drivers of signaling strategies in animal communities.

Here, we investigated the acoustic structure of signaling anuran communities and assess the support of acoustic and phylogenetic components of communities for predictions of evolutionary outcomes on acoustic signals. Upon phylogenetic niche conservatism of acoustic signals on local communities, (i) a tendency toward dispersion on the acoustic space could be promoted by acoustic partitioning, whereas aggregation could emerge from acoustic adaptation to the environment or by an extended communication network. We further (ii) investigate how acoustic and phylogenetic structures vary over distinct ecological contexts to assess the consistency of the acoustic space across communities and to address potential roles of environmental selection acting on the assembly of communities.

Anurans rely heavily on acoustic communication for breeding and resource defense (Wells & Schwartz 2007) and are typically present in tropical choruses, characterized by abundant species emitting simultaneous acoustic signals and generating high levels of background noise (Gerhardt & Huber 2002; Berg, Brumfield & Apanius 2006; Ulloa et al. 2019). Thus, this is a suitable system to test the above hypothesis. Temporal and spectral call parameters are cues for conspecific recognition, and call structure is usually species-specific (Schwartz & Bee 2013). In this scenario, call characteristics would be under selection as predicted by the sensory drive and communication networks frameworks, and the acoustic dimension of communities would present predictable structural patterns.

5.3 Methods

5.3.1 STUDY AREA

We sampled anuran communities in an area of approximately 100 km² located in the Nhecolândia region (Fig. S1) of South Pantanal wetlands in Brazil (Silva & Abdon 1998). This semiarid region experiences a wet season from October to April and a dry season from May to September. Landscapes are characterized by permanent and seasonal ponds of fresh water (baías), brackish water (salinas), and brackish ponds that can seasonally mix with fresh water from overland flooding (salobras), all embedded within a natural mosaic of grassland savannas, woody savannas and forested areas (Evans & Costa 2013).

5.3.2 SAMPLING SITE SELECTION AND VEGETATION CHARACTERIZATION

We applied a sampling design that minimized spatial dependence among sampling sites and allowed site selection along a gradient of habitat heterogeneity, defined using satellite images (Text S1). We selected 39 permanent ponds that covered an environmental gradient from landscapes spanning forested to grassland savannas, with a minimum distance of 1 km among sites. Landscape heterogeneity was estimated by the Normalized Difference Vegetation Index - NDVI (Rouse et al. 1974) from RapidEye 3A images (5 m pixel size), a consolidated proxy of environmental structure (Pettorelli et al. 2011), extracted from a 200 m buffer around each sample site (Text S1, Fig. S1).

We also characterized local vegetation heterogeneity, since habitat features at distinct scales can affect the propagation of acoustic signals (Bosch & De la Riva 2004; Erdtmann & Amézquita 2009). Using measurements from wide-angle optical sensors and a model of radiative transfer (Text S1), we estimated the Leaf Area Index (LAI), a proxy of local vegetation structure (Bréda 2003).

5.3.3 ACOUSTIC MONITORING

To determine the composition of communities, we monitored the calling activity of anuran communities over the 39 selected sites using passive acoustic monitoring (Sugai et al. 2019a). During 10 consecutive days in the peak of the rainy season (January/17), we recorded each site for up to five consecutive days using a rotation of 22 automated acoustic recorders (Wildlife Acoustics®) among sites. We deployed the

automated recorders at 1.5 meters height on trees or wood stakes up to 10 meters from the ponds to record in stereo mode with 6 dB and 12 dB gain on each channel, at a 44.1 kHz sample rate and 16-bit WAV format. Our recording schedule was set to register two minutes every 20 minutes (i.e. three 2-min samples every hour), starting one hour before sunset and ending one hour after sunrise (approximately from 16:30 to 07:30, local time). Each recording was examined by the main author to detect and identify anuran species based on aural recognition of advertisement calls and visual spectrogram inspection (Fast Fourier Transform [FFT] = 512, Hamming window) using Audacity (Audacity Team 2018) and Raven 1.4 (Bioacoustics Research Program 2014). Since the first and last hours of the recordings were characterized by low anuran activity and overlapped with bird and invertebrate activity (e.g. cicadas and orthoptera), we excluded them and considered recordings from 19:00h to 04:00h for subsequent analyses. We considered all species that occurred over the three 2-min recordings from each hour as an acoustic signaling community.

5.3.4 ACOUSTIC TRAITS

To characterize the advertisement call of the detected species, we obtained high-quality directional audio recordings using “shotgun” directional microphones (Sennheiser ME66) and manual digital sound recorders (Tascam DR-40 and ZOOM H4n Pro). During the breeding season (03–07 Oct/16, 10–16 Dec/16, 22–29 Jan/17, 20–26 Feb/17), we searched for calling males at the sample sites and recorded a minimum of 2 minutes of audio from each individual at a distance about 1.5 meters. Recordings were registered at a 44.1 kHz sampling rate, .WAV format, using manual controls for gain levels to avoid clipping. We complemented this acoustic dataset with acoustic recordings from acoustic libraries and from personal researcher’s databases (Text S2, Table S1).

We obtained a total of 115 individual advertisement calls (Text S3, Table S2). From each advertisement call, we extracted six acoustic parameters over the temporal and frequency domains: call rate (number of calls per second), note duration (ms), inter-quartile range bandwidth (Hz), peak frequency (Hz), aggregate entropy, and average entropy (Charif, Strickman & Waack 2010; Köhler et al. 2017), and computed the mean value of each parameter for each species. Peak frequency is a parameter commonly correlated with body-size for anurans (Gingras & Fitch 2013; Rodríguez et al. 2014), and our data indicated a moderate correlation among these two

characteristics (Pearson correlation coefficient = - 0.6). Thus, we applied a phylogenetic generalized least squares regression (PGLS) between peak frequency and snout-to-vent length (SLV – see Text S1 and Table S2) and used the model residuals to represent peak frequency using the *ape* package (Paradis & Schliep 2018) of the R language (R Core Team 2018). This approach considers that residual errors are distributed according to a matrix of variance and covariance of phylogenetic relationships (Grafen & Hamilton 1989).

Finally, we performed a principal component analysis (PCA) on the log-transformed mean acoustic parameters using the *vegan* R package (Oksanen et al. 2018). The first three axes captured 92% of the variation in call parameters (Table S1, Figure S2–S4). The first axis showed a positive relationship with measures associated with the spectral dispersion of the call (aggregate entropy, average entropy, and inter-quartile range bandwidth) and represented calls with signals ranging from pure-tone-like to signals containing wide frequency ranges and many harmonics. The second axis showed a relationship with temporal parameters, being positively related to call rate and negatively related to note duration. The third axis had a positive relationship with peak frequency and represented calls according to characteristics of the dominant pitch. All axes were tested for phylogenetic signal (Text S1). We refer to these three PCA axes as acoustic traits in subsequent analyses, specifically: frequency distribution, call timing, and peak frequency.

5.3.5 SIGNALING AND PHYLOGENETIC STRUCTURE

To represent the structure of acoustic traits and phylogenetic relatedness of the studied communities, we calculated the mean nearest taxon distance among species (MNTD). MNTD averages the distances of attributes present in a community but only considers the distances from each species with its most similar species (Clarke & Warwick 1998; Webb et al. 2002). Because competitive outcomes are expected to be more intense among closely related species or species with similar traits, MNTD is recommended over metrics that average all species' distances (Tucker et al. 2017).

For each of the three acoustic traits (frequency distribution, call timing, and frequency peak), we calculated MNTD over pairwise Euclidean distances between species. For relatedness, we calculated MNTD over pairwise cophenetic distances between species, based on a time-calibrated tree (Pyron & Wiens 2011) pruned to represent the species observed in our study. We used *picante* (Kembel et al. 2010),

vegan (Oksanen et al. 2018), and adephylo (Jombart, Balloux & Dray 2010) R packages. To account for different phylogenetic scales that could be obscured by phylogenetic MNTD (e.g. random values that arise by a combination of closely related and distantly related species), we calculated the contribution of specific clades to the distribution of species in communities, the specific overrepresentation score (Borregaard et al. 2014; Text S1).

5.3.6 NULL MODELS

We generated null expectations of MNTD values to assess whether observed MNTD values were consistent with patterns found from chance alone. For each community, null models involved (i) randomizing species names in the dissimilarity matrices, (ii) calculating MNTD based on the randomized dissimilarity matrix, (iii) repeating the previous step 5000 times, (iv) averaging the mean value of all null MNTD values. We restricted the randomization of species names within each family, as the randomization between families could yield largely unrealistic acoustic traits.

We also computed the standardized effect size over MNTD (SES MNTD) for each acoustic trait and phylogenetic relatedness. SES MNTD was calculated by subtracting the observed and null MNTD values respectively and dividing the result by the standard deviation of null MNTD. Positive values of SES MNTD would represent greater phylogenetic distances between the closest relatives on communities than expected by chance (i.e., an overdispersed pattern), whereas negative values would represent smaller distances (i.e., an aggregated pattern; Webb et al. 2002). For these procedures, we used picante R package (Kembel et al. 2010).

5.3.7 STATISTICAL ANALYSES

To test (i) whether the acoustic space of local communities presented a structural pattern consistent with predictions from the acoustic niche, acoustic adaptation, and the communication network hypotheses, we first fitted four linear mixed models (LMM) on MNTD from each acoustic trait and on phylogenetic relatedness, using MNTD type (observed vs. null) as fixed terms.

To assess (ii) the consistence of acoustic space across communities we fitted three LMM for SES MNTD of each acoustic trait, with fixed terms describing different ecological contexts: phylogenetic structure (SES phylogenetic MNTD), habitat heterogeneity (landscape and local), species richness, and family dominance (SOS

values). To address the potential of environmental selection on the assembly of communities, we fitted a LMM for SES phylogenetic MNTD and the variables representing ecological contexts previously mentioned. For such LMM, we used as random factors recording date, site ID, and recording period: early (19:00h–22:00h), mid (22:00h–01:00h), and late (01:00h–04:00h). We included random intercepts and allowed random slopes to keep type I error at the nominal 5% level (Barr et al. 2013).

Normality and homoscedasticity were assessed through visual inspection of residuals and probability plots (Q-Q plots). We used a likelihood-ratio test to perform model inference over a null model with only random effects (Forstmeier & Schielzeth 2011). Likewise, we assessed the effect of individual predictors with iterative likelihood-ratio tests over reduced models using the function `drop1` in R package `lme4` (Bates et al. 2015). We also included interaction terms between phylogenetic SES MNTD and habitat heterogeneity variables when models were more plausible than a model with no interaction. Using 1,000 bootstrap iterations we estimated confidence intervals for model coefficients using the `bootMer` function in `lme4` (Bates et al. 2015).

5.4 Results

From a total of 5,916 2-min audio recordings (197.2 hours), we registered 25 species from four families, with Hylidae (12 species) and Leptodactylidae (9 species) being the most representative ones (Table S2). Species richness within each signaling community (all species registered in a given hour) varied from 1 to 12 species ($\bar{x}=5.5 \pm 2.07$ sd), and within local communities (i.e., considering all recordings from all sampled days for each site) varied from 6 to 19 ($\bar{x}=10.5 \pm 3.07$ sd).

Local communities showed (i) an aggregated acoustic space (represented by MNTD) for all acoustic traits (frequency parameters: $\beta=-0.2 \pm 0.02$ sd and $\beta=-0.4 \pm 0.03$ sd, both $p<0.001$; temporal parameter: $\beta=-0.1 \pm 0.03$ sd, $p=0.003$, Figure 1 and Table 1), consistent with predictions from the acoustic adaptation and communication network hypotheses. Likewise, a convergent phylogenetic structure indicated that local communities were mainly composed of closely related species when compared to null models ($\beta=-11.9 \pm 1.62$ sd, $p<0.001$, Figure 1, Table 1). Despite the pervasive aggregated acoustic and phylogenetic we found no clear evidence of a phylogenetic signal on acoustic signals using Blomberg's K (Table S4) or the Mantel test ($r=-0.07$, $p=0.664$; Figure S6), indicating that the overall acoustic aggregation observed is not necessarily a by-product of phylogenetic structure of communities.

Table 1. Coefficients of linear mixed models on mean nearest taxon distances (MNTD) for phylogenetic distances and acoustic similarities from observed and null model values (predictor) of anuran communities in South Pantanal wetlands.

	X ²	df	Estimate	Std. Error	t-value	p-value
<i>Phylogenetic relatedness</i>	16.3	1				
Intercept			126.1	1.05	120.5	
Type (obs. vs. null)			-11.9	1.62	-7.4	< 0.001
<i>Frequency distribution</i>	11.2	1				
Intercept			0.7	0.03	21.6	
Type (obs. vs. null)			-0.2	0.02	-7.5	< 0.001
<i>Call timing</i>	9.0	1				
Intercept			0.7	0.03	21.8	
Type (obs. vs. null)			-0.1	0.03	-3.3	0.003
<i>Peak frequency</i>	19.3	1				
Intercept			0.7	0.03	21.8	
Type (obs. vs. null)			-0.4	0.03	-10.4	< 0.001

When we evaluated communities over distinct ecological contexts (ii), we found the acoustic space to have no relationship with habitat heterogeneity or species richness, and the tendency toward a convergent acoustic space was not associated with a convergent phylogenetic structure or a larger presence of species within families, ruling out the predictions of acoustic partitioning and acoustic adaptation hypotheses (Figure 2, Table 2). Instead, we found an unexpected negative relationship between acoustic structure and phylogenetic relatedness across communities. Specifically, convergent acoustic spaces (lower acoustic SES MNTD) were associated with communities composed of distantly related species (higher phylogenetic SES MNTD), whereas relaxed acoustic convergent patterns were found on communities composed of closely related species ($\beta = -0.59$ and -0.99 , $p < 0.001$ only for signal frequency, Figure 2, Table 2). Moreover, an interaction of phylogenetic structure with vegetation heterogeneity resulted in a steeper negative relationship with acoustic structure, specifically in sites within landscapes with higher forest cover (Figure 2 a-c) and locally characterized by more heterogeneous vegetation (Figure 2-b).

Phylogenetic structure showed a tendency towards convergence on communities within landscapes with higher proportion of forest cover and low vegetation heterogeneity at local scale (high NDVI and low LAI values; Figure 2, Table 2), indicating that species sharing recent evolutionary histories are likely those that persist in such environmental conditions.

Table 2. Coefficients of linear mixed models on standardized mean nearest taxon distance (SES MNTD) of phylogenetic relatedness and acoustic similarities of anuran communities of South Pantanal wetlands. Habitat heterogeneity at landscape and local are represented by NDVI and LAI. Overrepresentation scores from node-based analysis are represented by code “SOS score”.

	X ²	df	Estimate	Std. Error	Upper CI	Lower CI	t-value	p-value
<i>Phylogenetic relatedness</i>	14.4	4						<0.001
Intercept			-0.48	0.07	-0.63	-0.35	-6.94	
LAI			0.04	0.05	-0.09	0.16	0.7	0.438
NDVI			-0.12	0.07	-0.22	0.02	-1.87	0.068
SOS score			0.03	0.04	-0.04	0.09	0.75	0.442
LAI*NDVI			-0.12	0.05	-0.26	-0.01	-2.28	0.035
<i>Frequency distribution</i>	30.2	7						<0.001
Intercept			-0.59	0.05	-0.71	-0.48	-11.26	
LAI			-0.04	0.05	-0.13	0.06	-0.78	0.456
NDVI			0.05	0.05	-0.04	0.15	1.08	0.197
Richness			-0.01	0.03	-0.06	0.04	-0.29	0.784
SOS score			0.05	0.04	-0.03	0.12	1.37	0.187
Phylogenetic relatedness			-0.36	0.07	-0.49	-0.22	-5.46	<0.001
Phylo rel*LAI			-0.13	0.05	-0.24	-0.02	-2.44	0.018
Phylo rel*NDVI			-0.16	0.05	-0.27	-0.05	-3	0.003
<i>Call timing</i>	1.92	5						0.859
Intercept			-0.14	0.05	-0.25	-0.03	-2.59	
LAI			-0.002	0.04	-0.09	0.09	-0.05	0.959
NDVI			0.02	0.05	-0.08	0.11	0.35	0.744
Richness			0.02	0.02	-0.02	0.06	1.11	0.292
SOS score			0	0.02	-0.04	0.05	0.17	0.866
Phylogenetic relatedness			-0.04	0.04	-0.12	0.05	-0.88	0.385
<i>Peak frequency</i>	21.2	7						0.003
Intercept			-0.99	0.04	-1.07	-0.9	-22.71	
LAI			-0.04	0.04	-0.12	0.04	-1.196	0.297
NDVI			0.05	0.04	-0.03	0.13	1.383	0.412
Richness			-0.01	0.02	-0.05	0.04	-0.28	1
SOS score			0.01	0.03	-0.05	0.06	0.272	1
Phylogenetic relatedness			-0.36	0.07	-1.07	-0.9	-5.29	<0.001
Phylo rel*LAI			-0.08	0.06	-0.2	0.04	-1.271	0.376
Phylo rel* NDVI			-0.15	0.06	-0.27	-0.03	-2.56	0.027

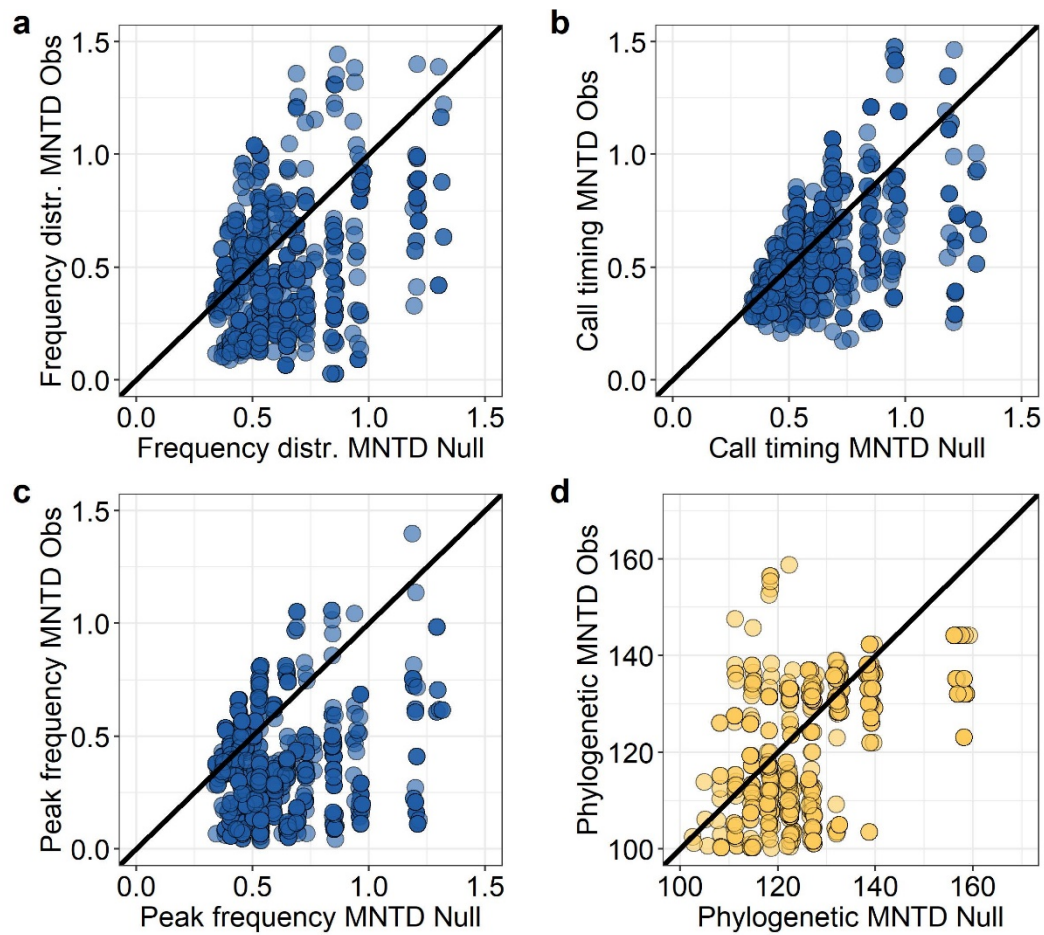


Figure 1. Observed and null values of mean nearest taxon distances (MNTD) from and acoustic traits (a–c: frequency distribution, call timing, and peak frequency) and phylogenetic relatedness (d) in anuran communities of South Pantanal wetlands. Equivalent values are represented by the solid line.

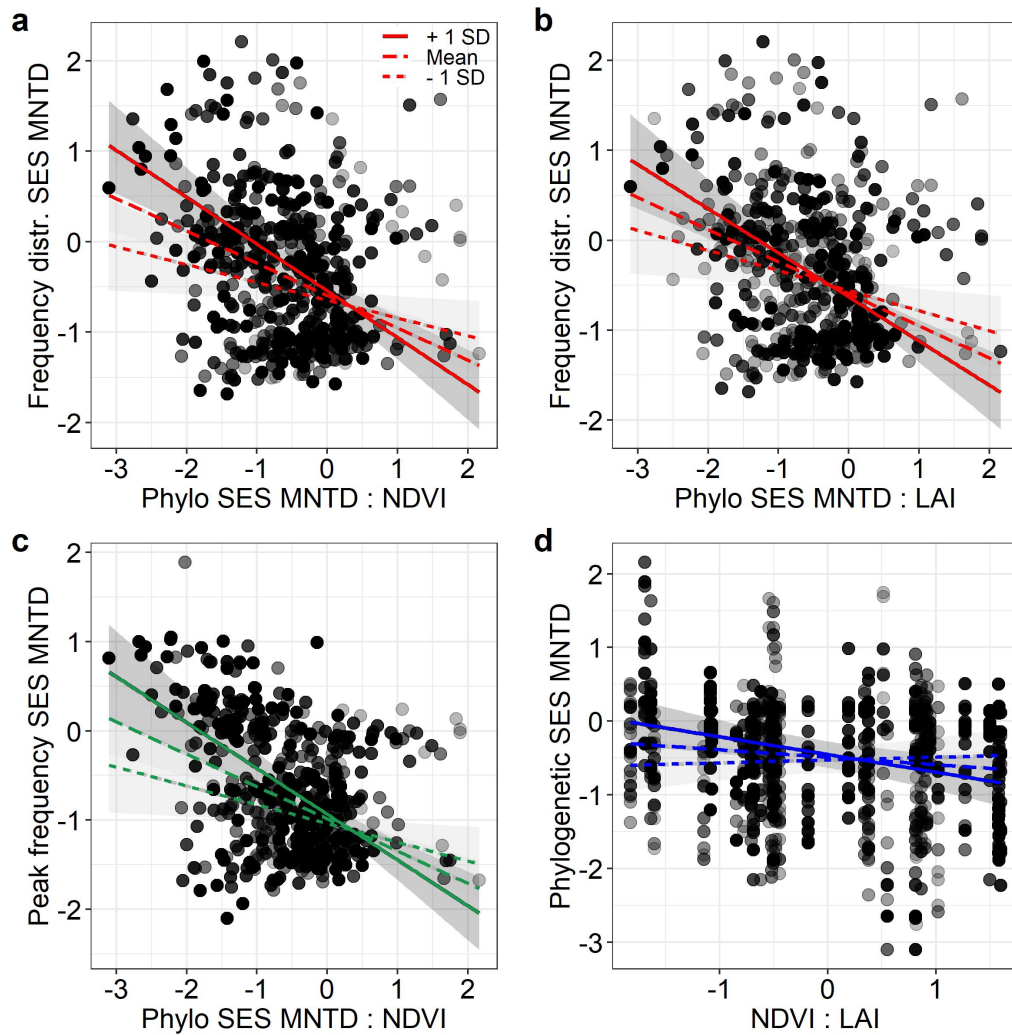


Figure 2. Results from linear mixed models with the standardized effect sizes of mean nearest taxon distances (SES MNTD) of acoustic traits (a–c) and phylogenetic relatedness (d) of anuran communities of South Pantanal wetlands. Frequency distribution was negatively related with phylogenetic structure (dashed line), and the interaction with larger values y (solid line: +1 sd) and lower value (dotted line: -1 sd) of habitat heterogeneity at landscape (represented by NDVI, panel a), and local (represented by LAI; panel b) resulted in a stronger or a weaker relationship, respectively. Phylogenetic structure was negatively influenced by the interaction of landscape and local habitat heterogeneity, with larger local values associated with mean local values of habitat heterogeneity (solid line) leading to negative effect on the phylogenetic relatedness of communities (d).

5.5 Discussion

Multisource background noise is traditionally associated with drawbacks in communication systems (Gerhardt & Huber 2002; Schwartz & Bee 2013). Several hypotheses postulate signals to be an adaptive solution to communication challenges (Wilkins, Seddon & Safran 2013) or to reflect interactions mediating communication networks (Tobias *et al.* 2014). By investigating tropical anuran choruses, we found low support for such hypotheses underlying the acoustic space of animal communities. We found no evidence for acoustic partitioning, as local communities showed a highly similar acoustic space. Partitioning on the acoustic space has been suggested to emerge in species-rich communities experiencing a highly packed acoustic space (Chek, Bogart & Loughheed 2003), but we found no tendency towards partitioning driven by species richness. Instead, the widespread convergent acoustic space could arise by acoustic adaptation to the environment, but we found no relationship between acoustic structure and environmental structure. An inadequate environmental characterization has been suggested to bias results when testing for the acoustic adaptation hypothesis (Bosch & De la Riva 2004; Ey & Fischer 2009), but we were unable to find any tendency on the acoustic space even with quantitative measures detailing landscape and local habitat. Instead environmental structure, it is likely that the most detrimental environmental constraint for anuran vocalization is the continuous background noise produced by running water in streams. Community-wide acoustic patterns suggest species' calls to be high-pitched, with large-bodied and low-frequency species absent in such communities (Vargas-Salinas & Amézquita 2014), and large-scale clade-based approaches suggest call evolution to be constrained by the “acoustic window” provided by torrent habitats (Goutte *et al.* 2016; Goutte *et al.* 2018). Although a convergent pattern is expected in competitive communities relying in social interactions, the communication network hypothesis relies in intentional interspecific communication, a phenomenon unlikely to be widespread in anurans.

In turn, anurans can rely in cues gathered inadvertently from heterospecifics to assess suitable breeding sites, ecological resources, or predation risk (Phelps, Rand & Ryan 2006; Slabbekoorn & Bouton 2008; Both & Grant 2012). Under strong reliance on social information, a correlation between individuals' behaviors and spatial distribution can potentially alter species interaction and community dynamics (Valone 2007; Gil *et al.* 2018). As such, our findings suggest the acoustic space to reflect strategies of information use across communities and argue for social information use

as the broad mechanism driving acoustic signaling strategies in animal communities (Goodale *et al.* 2010).

Advertisement calls primarily mediate communication among conspecifics, with heterospecific stimulus often disregarded when presented alongside conspecific calls (Gerhardt 2001; Gerhardt & Huber 2002). Therefore, an extended communication network mediating species interaction is unlikely to support a convergent acoustic space for the anuran communities studied. Conversely, individuals often rely in acoustic signals produced by the surrounding individuals. Eavesdropping on both conspecific and heterospecific signals is widespread over a variety of taxa (Simmons, Popper & Fay 2003) and characterized by the use of public social information (Grafe 2005; Magrath *et al.* 2015). Acoustic signals not only encode information important for conspecifics, but also announce the presence, location, and motivation of emitters, which can benefit heterospecifics (Grafe 2005; Wells & Schwartz 2007). Such source of information can increase individual awareness and enhance fitness by reducing costs to access environmental information (Valone 2007) as for prospecting suitable breeding sites (Buxton & Sperry 2016). Eavesdropping on species with similar acoustic signals can be especially common in anurans, as signal characteristics should approximate the tuning of the peripheral auditory system (Gerhardt 1994). Thereby, convergent acoustic signaling can be an efficient strategy for information access through a common communication channel in animal communities. For environments characterized by high predation pressure, amphibians tend to be more selective to habitat conditions and increase responsiveness to predation cues (Both & Grant 2012; Medeiros *et al.* 2017). Eavesdropping on public information can be especially important for the anurans surveyed in the Pantanal wetlands, where population dynamics are largely influenced by predation risk (Costa-Pereira *et al.* 2018).

While acoustic similarities may benefit species sharing a same habitat, a divergence in relatedness of such communities may decrease potential competitive interaction among species sharing similar ecological resources. Although social information is especially valuable for species within the same trophic level, increasing resource overlap among competing species may counteract the benefit of information (Seppänen *et al.* 2007; Gil *et al.* 2018). An increased net benefit is provided with higher quality of social information (Gil, Baskett & Schreiber 2019), which is largely reliant on how emitters respond to their environmental context (Goodale *et al.* 2010). For instance, social information from species under high predation pressure are reliable hints for predator avoidance (Schmidt, Dall & Van Gils 2010; Gil *et al.* 2018). Ecologically

similar species share analogous ways to explore their surroundings and thus provide redundant information about their environments for public information (Seppänen *et al.* 2007; Schmidt, Dall & Van Gils 2010). Through the assembly of differing species in the same guild, interspecific information can increase environmental awareness while decrease potential competition for similar resources (Goodale *et al.* 2010; Gil *et al.* 2018; Martínez *et al.* 2018). For species-rich anuran communities, we might expect lower resource overlap among distantly related species since habitat and reproductive requirements can be markedly different (Haddad & Prado 2005).

The structure of local anuran communities is largely influenced by deterministic processes regarding the identity of species (Hamer & Parris 2011), as for environmental differences affecting the persistence of species having certain ecological attributes (Signorelli *et al.* 2016; Sugai *et al.* 2019b). Our findings suggest that an increase in environmental heterogeneity influences the occurrence of species sharing similar reproductive and habitat requirements across communities. Specifically, a higher heterogeneity on the vegetation surrounding pond-breeding habitats provides more sites for species that vocalize perched on trees, trunks (e.g. *Boana* species), and leaves (e.g. *Scinax* and *Dendropsophus* species) and may unfit species that vocalize on bare ground (e.g. *Leptodactylus* species) or on temporary water (e.g. *Physalaemus* species; Prado, Uetanabaro & Haddad 2005).

Remarkably, for such communities composed by closely related species, the corresponding acoustic space tended to be less convergent. For communities influenced by environmental filtering and restricted to the co-occurrence of ecologically similar species, divergent acoustic signals can presumably hinder interspecific eavesdropping and decrease competition strength for shared resources. Increased signal divergence among species theoretically provides larger species-specific recognition spaces (Amézquita *et al.* 2011), which can alter the quality of intraspecific social information (Gil, Baskett & Schreiber 2019) and thus the net benefit of conspecific use on social information (Schmidt, Dall & Van Gils 2010). The value of conspecific social information can further increase upon higher spatial heterogeneity since informed individuals are able to make better decisions on the choice of breeding locations and enhance their fitness (Schmidt & Massol 2019). Interestingly, when communities composed by closely related species were located at more heterogeneous sites, there was a shift towards a more divergent acoustic space (Figure 2), which presumably increase the importance of intraspecific information. Therefore, increasing divergence in the acoustic space among competitive species both decrease

interspecific competition and increase the benefit of conspecific social information (Schmidt & Massol 2019). We suggest that in addition to environmental heterogeneity, ecological contexts of communities can alter the strategies for social information use. Additionally, the probability of crossbreeding and maladaptive hybridization is reduced on such communities, as closely related species with similar vocalization can confound heterospecific signals with their own (e.g. Célio, Pombal & Batistic 1994; Gerhardt 2001; Lipshutz 2018).

The legacy of selective pressures on signal design is weakly supported according to our findings on the acoustic signaling space of local communities. However, we acknowledge that addressing past evolutionary processes on present-day patterns require vanguard integrative research on eco-evolutionary dynamics of species interactions, phenotypic evolution, and diversification (Weber *et al.* 2017). For instance, although observed patterns of acoustic partitioning stand for competitive interactions or character displacement as main mechanisms driving acoustic signaling, acoustic traits may have evolved on past and distinct ecological contexts unrelated to competitive interactions (Hendry 2017). Additionally, the signature of acoustic adaptation may be unclear for site-based appraisals as the range of environmental conditions required for optimized signal transmission is unclear (Goutte *et al.* 2016; Graham, Storch & Machac 2018) and the timing for selection to drive signal evolution may fall short for the current environments. Thus, the role of acoustic competition and adaptation as evolutionary drivers of community-wide patterns can gain new insights as new techniques combines explicit evolutionary modelling of trait evolution (e.g. Drury *et al.* 2018; terHorst *et al.* 2018) and historical processes involved in community assembly (Pigot & Etienne 2015).

Our findings on the acoustic space of signaling communities fail to support the paradigms explaining the acoustic structure of animal communities, and instead suggest a potential role of social information use. Across communities, signaling similarities from ecologically different species can favor access to high-quality interspecific information through a common communication channel while decrease competition for shared resources. Conversely, when communities are composed by closely related species in heterogeneous environments, a lower similarity in acoustic signals can decrease interspecific competition and increase the value of intraspecific information, which is especially useful under higher spatial heterogeneity. Together, our findings open novel perspectives for the role of communication networks and

social interactions in species coexistence (Hofmann *et al.* 2014), being largely generalizable for multiple taxa that rely on public information.

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5.8 Supplementary Material

Text S1

Sampling site selection

We defined a sampling design that minimized spatial dependence among sampling sites, and that provided sample site selection along a gradient of habitat heterogeneity (Figure S1). To do that, we used the Normalized Difference Vegetation Index (NDVI, Rouse *et al.* 1974) as a proxy of environmental structure. This index is based on the diverging pattern of high photosynthetic absorption of red light and high degree of reflection of near-infrared light by healthy leaves and has good performance in representing the heterogeneity in plant communities, with higher values representing denser green vegetation. Here, we use it to represent habitat heterogeneity (Pettorelli *et al.* 2011). The index is given as:

$$(\rho_{\text{(NIR)}} - \rho_{\text{(red)}}) / (\rho_{\text{(NIR)}} + \rho_{\text{(red)}})$$

Equation 1.

where ρ is light reflectance at the different regions of the spectrum. The index varies between -1 and 1, with negative values corresponding to clouds and water bodies, values between 0 and 0.2 corresponding to bare ground, and values above 0.2 representing increasing amounts of photosynthetically active vegetation.

First, we manually mapped all ponds within the limits of Barranco Alto farm, at a scale of 1:15,000, using Google Earth PRO® and the provided “basemap imagery” from ArcGIS. The perimeter of the ponds differed among reference images as they were from different seasonal periods, so we included within the mapped limits of each pond the surrounding areas that get submerged during the wet season. These were visually characterized by grassy areas with browner color tones than its surrounding (Figure S1-a). We then excluded from the analysis all ponds with less than 0.5 km², because of the uncertainty on whether they were seasonal ponds in the reference images, as well as ponds that were too close to the main river, since access to these ponds during the rainy season would be difficult. We also opted to exclude *salinas* from our analysis, since this particular environment is not commonly occupied by anurans. To classify the potential *salinas* to be excluded from our analysis, we used object-based image analysis (OBIA) applied to RapidEye 3A satellite images acquired on 2014-07-29, by applying a multiresolution segmentation algorithm. This approach allows the analyst to consider both spectral and spatial information to segment a

remote sensing image into homogeneous objects (polygons), rather than focusing on single pixel information (Burnett & Blaschke 2003). For this, we used the five bands (channels) contained on RapidEye imagery (blue: 440–510 nm, green: 520–590 nm, red: 630–685 nm, red edge: 690–730 nm, and near infrared: 760–850 nm), and one layer containing the NDVI calculated from bands 5 and 3. For the segmentation algorithm, we used a scale parameter of 130, 0.1 for the shape/color parameter and 0.5 for the compactness/smoothness parameter. We then defined the following legend to be classified: “forests”, “open areas”, “*baías*”, “*salobras*”, and “*salinas*”. We trained the classification algorithm using samples selected by visual inspection of (i) Google Earth PRO and “basemap layer” from ArcGIS, (ii) a manual mapping of the ponds provided by the landowners (in .kmz format), and (iii) the type of pond from a visual inspection of the land use map from (Evans & Costa 2013) (Figure S1-a). After classification, we excluded the classified *salinas* from the manually mapped ponds.

Finally, to select our 39 intended sampling sites, we first created 500 points randomly distributed along the perimeter of the ponds, from which we selected those located at least 1 km distant from each other ($n=72$ points; Figure S1-b). The 1 km distance was adopted to minimize spatial dependence among sampling units, considering the low rates of anuran species dispersal and high site fidelity (Cushman 2006).

To assess habitat heterogeneity associated with each sampling point, we generated a 200 m radius buffer around each point and removed from the buffer areas occupied by open water (according to the manually mapped ponds). We then extracted the mean NDVI value for the remaining buffer area (Figure S1-c). From the distribution of mean NDVI values for all point buffers, we selected our final set of 39 sites according to the following criteria: (i) maximize a gradient from open to forested areas, (ii) be accessible by established ranching tracks within the farm (also manually mapped), and (iii) spaced at least 1km from each other Figure S1 d-e).

Local vegetation heterogeneity

In addition to a landscape measure of vegetation heterogeneity, we also characterized variation on local vegetation because habitat features at distinct scales can affect the propagation of call features (Bosch & De la Riva 2004; Erdtmann & Amézquita 2009). We measured the Leaf Area Index (LAI), which characterizes the canopy of a given area by estimating the projected area of leaves (Bréda 2003). Using the LAI-2200 Plant Canopy Analyzer, we indirectly measured LAI by registering solar radiation above and

below the highest vertical vegetation stratum at each sample, and thus estimating light interception under a model of radiative transfer (LI-COR Biosciences 1992).

For each sample site, we took 30 measurements along the target monitoring area by: i) we first estimated a point located at the minimum distance from the audio recorder and the edge of the pond (approximately 10 m), ii) from this point, we delimited a 15 meters trail for both sides along the edge of the pond (totalizing 30 m), iii) at each 3 meters on this trail, we established one intersection point, iv) at each intersection, we delimited a 3-meter perpendicular transect and took LAI measurements at each one meter. We then used the FV2200 software to estimate LAI used the mean to characterize each site.

Acoustic parameters

We adopted a call-centered terminological for measuring the acoustic parameters of species' advertisement call. In this view, a call is characterized by a coherent sound unit encoding an information. A call can be composed by sub-units, called notes, which are segregated by short silent periods (Köhler *et al.* 2017). We measured six acoustic parameters (Table S2) for each advertisement call registered in a directional recording (Charif, Strickman & Waack 2010). To characterize the acoustic parameter for each species, we averaged the mean within and among individuals' acoustic parameters.

Testing for phylogenetic signals

Species tend to retain ancestral traits, with closely related species often resembling each other (Wiens 2008; Münkemüller *et al.* 2015). To acknowledge the potential of phylogenetic signal on acoustic traits, we determined Blomberg's K value, which consists of a descriptive statistic under the Brownian model of trait evolution. A value of 1 represents that trait similarity is the same as expected under the Brownian model, whereas a value of 0 indicates independence of trait similarity and phylogeny. Thus, values above 1 indicate trait similarity greater than expected by a Brownian Model (Blomberg *et al.* 2003). We also assessed the correlation among the dissimilarity matrix of phylogenetic distances and acoustic variables with a Mantel test. We used phytools (Revell 2012) and vegan (Oksanen *et al.* 2018).

Body size

During our field recordings, whenever possible we measured the snouth-vent length (SNV) of the same individuals that were acoustically recorded (n=70, 13 species, table S2) and used mean values. To complement this information for those species that were

not found in the study area, we used literature information from the following references:

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<<http://amphibiaweb.org/species/1025>> University of California, Berkeley, CA, USA. Accessed May 7, 2018.
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Node-based phylogenetic patterns

To account for different phylogenetic scales that could be obscured by phylogenetic SES MNTD (e.g. random values that arise by a combination of closely related and distantly related species), we calculated the contribution of specific clades to the distribution of species in communities, the specific overrepresentation score (SOS), using the *nodiv* R package (Borregaard *et al.* 2014). First, we detected the pair of sister clades that had the largest contribution to the observed patterns, in this case, the one segregating the Hylidae and Leptodactylidae families (Figure S5). Thus, for each community, we calculated an SOS value (more negative values indicate a greater contribution of species from Leptodactylidae and positive values, species from Hylidae).

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Table S1. Descriptive summaries and correlation coefficients of variables of a principal component analysis (PCA) over six acoustic parameters that characterize the advertisement calls of anuran species in south Pantanal. The three axis captures 92% of the variation in acoustic parameters.

	PC1	PC2	PC3
<i>Descriptive summary</i>			
Eigenvalue	2.48	1.92	1.12
% variance captured	41.34	31.99	18.64
% cumulative variance	41.34	73.32	91.96
<i>Correlation coefficients</i>			
IQR BW	0.78	-0.02	-0.57
Peak frequency	0.37	0.32	0.84
Aggregate entropy	0.96	0.08	-0.03
Average entropy	0.86	0.21	0.11
Call per second	-0.2	0.92	-0.27
Note duration	0.19	-0.96	0.06

Table S2. List of species recorded in the studied anuran communities (South Pantanal wetlands). Number of individuals per species analyzed to characterize the acoustic traits of species and respective database sources. Tot. n. = Total number of individuals. N. source = number of individuals from respective source. N. CRC = number of individuals used to extract SVL measures.

Family	Species	Tot. n.	Source	N. source
Ceratophryidae	<i>Ceratophrys cranwelli</i> (Barrio, 1980)	1	SFTB	1
Hylidae	<i>Dendropsophus minutus</i> (Peters, 1872)	6	LS	
	<i>Dendropsophus nanus</i> (Boulenger, 1889)	6	LS	
	<i>Lysapsus limellum</i> (Cope, 1862)	5	LS, PAM	
	<i>Dendropsophus elianeae</i> (Napoli & Caramaschi, 2000)	6	LS	
	<i>Hypsiboas punctatus</i> (Schneider, 1799)	5	FNJV, ML, JS, TAFG	5
	<i>Hypsiboas raniceps</i> (Cope, 1862)	6	LS	
	<i>Phyllomedusa azurea</i> (Cope, 1862)	4	LS, PAM	
	<i>Pseudis paradoxa</i> (Linnaeus, 1758)	5	LS, PAM, TAFG	1
	<i>Scinax acuminatus</i> (Cope, 1862)	3	LS	
	<i>Scinax fuscomarginatus</i> (A. Lutz, 1925)	7	LS	
	<i>Scinax nasicus</i> (Cope, 1862)	7	LS	
	<i>Trachycephalus typhonius</i> (Linnaeus, 1758)	2	PAM, ML	2
Leptodactylidae	<i>Adenomera diptyx</i> (Boettger, 1885)	3	LS, PAM	
	<i>Leptodactylus elenae</i> (Heyer, 1978)	4	FNJV, ML, CCRP	4
	<i>Leptodactylus fuscus</i> (Schneider, 1799)	7	LS, PAM, FNJV	
	<i>Leptodactylus labyrinthicus</i> (Spix, 1824)	3	FNJV, SFTB	3
	<i>Leptodactylus mystacinus</i> (Burmeister, 1861)	3	FNJV, CCRP	3
	<i>Leptodactylus podicipinus</i> (Cope, 1862)	5	LS, PAM, JS	4
	<i>Physalaemus albonotatus</i> (Steindachner, 1864)	5	LS, JS	1
	<i>Physalaemus biligonigerus</i> (Cope, 1861)	5	LS, FNJV	3
	<i>Pseudopaludicola motorzinho</i> (Pansonato, 2016)	4	LS, AP	3
Microhylidae	<i>Chiasmocleis albopunctata</i> (Boettger, 1885)	3	FNJV, CCRP	3
	<i>Dermatonotu muelleri</i> (Boettger, 1885)	5	LS, FNJV	2
	<i>Elachistocleis matogrosso</i> (Caramaschi, 2010)	5	LS	

Codes:LS=xx, PAM=From the PAM recordings of the present study, JS=xx, FNJV= Fonoteca Neotropical Jacques Vierlard, SFTB=Sounds of Frogs and Toads of Bolivia, TAFG=Sound Guide To The Tailless Amphibians Of French Guiana, CCRP=Guia Interativo dos Anfíbios Anuros do Cerrado, Campo Rupestre e Pantanal, ML=Macaulay Library, AP=André Pansonato.

Table S3. Description of acoustic parameters used to describe advertisement calls of anuran species located in the South Pantanal wetlands.

	Description
Inter-quartile range bandwidth (IQR-BW)	Computes the difference between the first and third quartile frequencies
Peak frequency	The frequency containing the maximum power value
Aggregate entropy	Measures of disordeness of frequencies. Higher entropy indicates greater disorder while a pure tone would return zero entropy.
Average entropy	Calculates the entropy for single frames and use the average of all frames composing a given acoustic signal. Also returns a measure of disordeness.
Call rate	Number of calls emitted per second, where call is considered the unit of vocalization separated for long periods of silence. Calls can be composed by one note type or by more types.
Note duration	The amount of time for the complete emission of a single note, where note is the subunit of a call being often emitted in a stereotyped manner.

Table S4. Results of Blomberg's K test for phylogenetic signal of acoustic parameters and for principal component axes summarizing the set of acoustic parameters of the advertisement call of anuran species located in the South Pantanal wetlands.

	K	p-value
IQR BW	0.467	0.647
Peak frequency	0.445	0.703
Aggregate entropy	0.549	0.29
Average entropy	1.125	0.002
Call per second	0.454	0.657
Note duration	2.64	0.002
PC1 – Frequency distribution	0.688	0.072
PC2 – Call timing	0.819	0.014
PC3 – Peak frequency	0.394	0.894

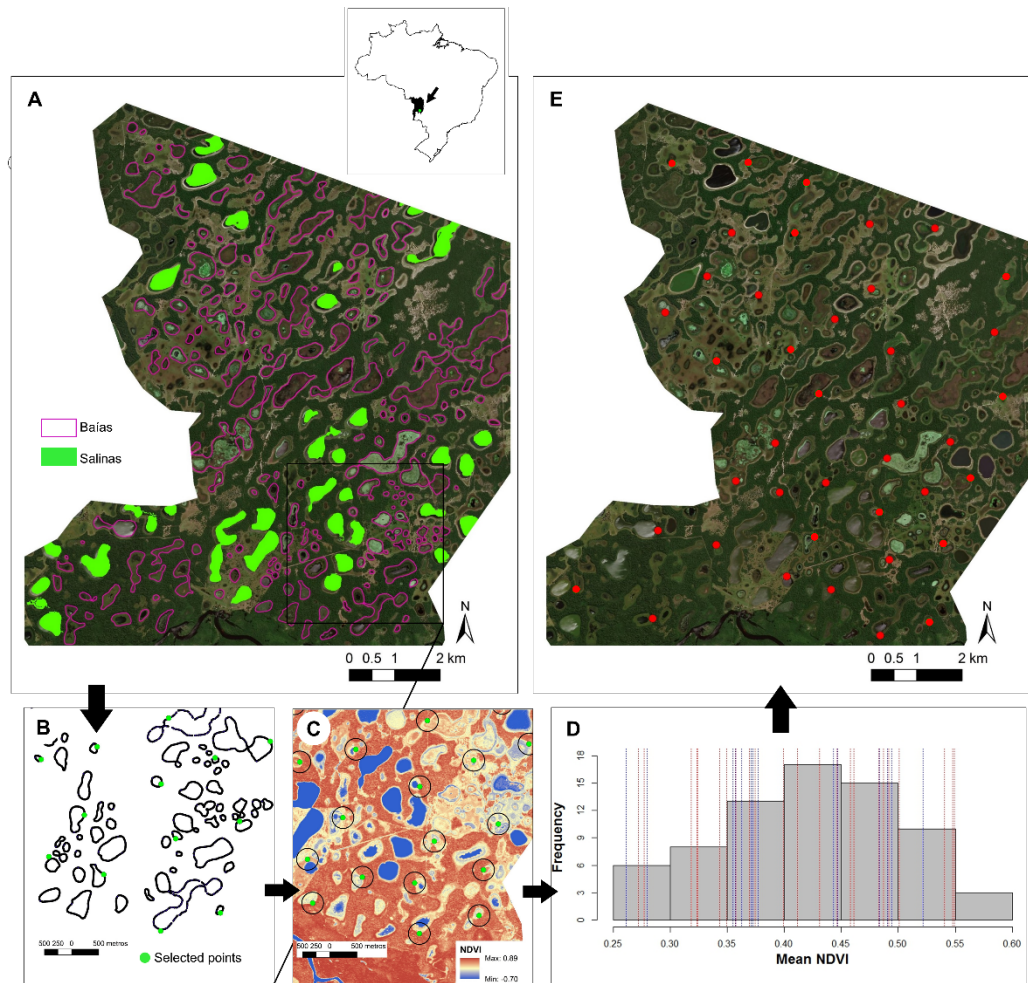


Figure S1. Experimental design for the selection of 39 sampling sites following spatial and environmental gradient criteria, on Barranco Alto farm, Mato Grosso do Sul state, Brazil. Approximate location of the study site within the Pantanal biome, and perimeter of the manually mapped ponds (Baías) and classified *salinas* that were not accounted for sampling (a). Detail of the random distribution of 500 points on the perimeter of all mapped ponds, and random selection of points spaced at a minimum of 800 m (b). Generation of 200-meter radius buffers around each selected point, from which the areas occupied by water was removed, and the mean NDVI value for each buffer was determined (c). Selection of points spaced >1km, accessible by ranching tracks, and that maximized the gradient of mean NDVI values (d).

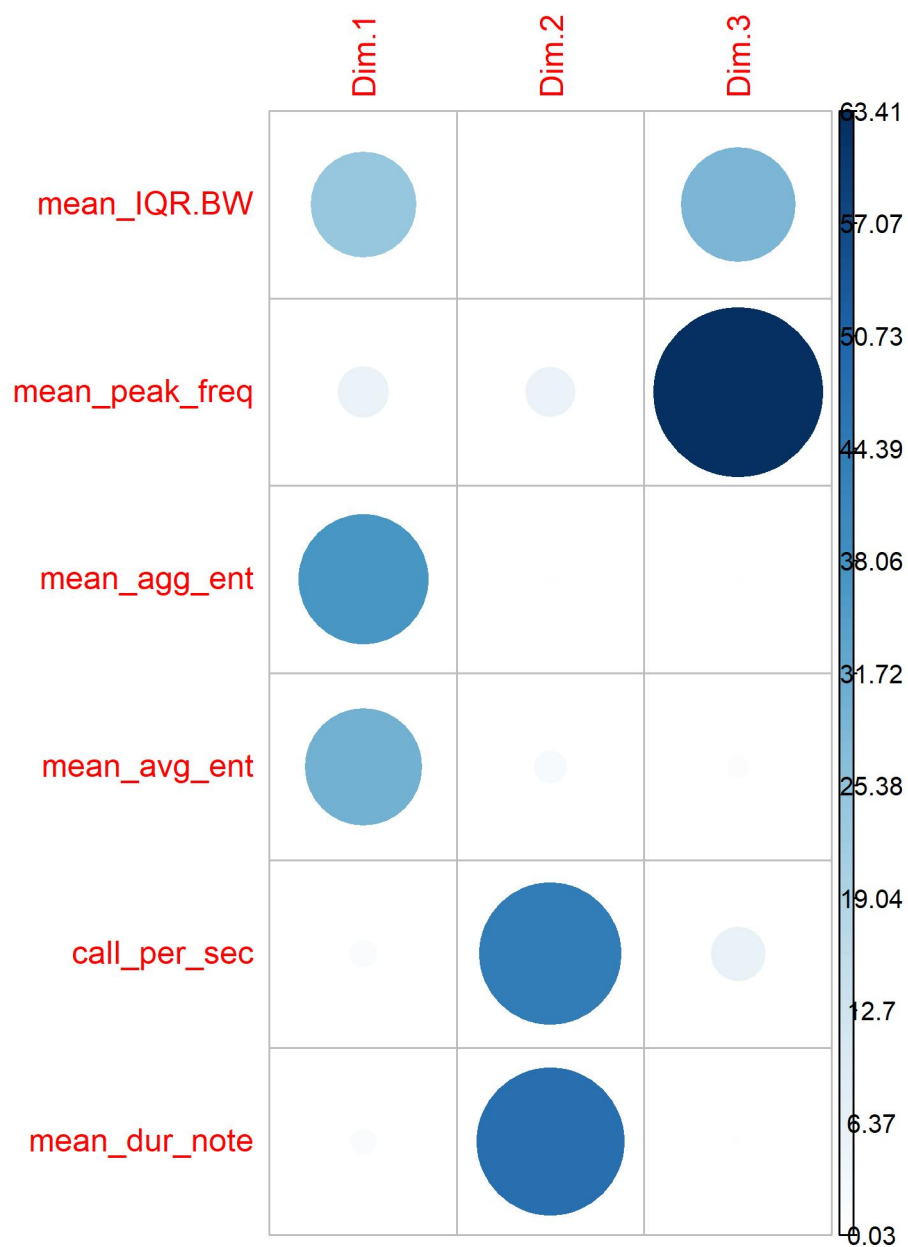


Figure S2. Correlation of acoustic variables and the acoustic traits (three first axes of a principal component analysis: frequency distribution, call timing, and peak frequency) on their log-transformed values.

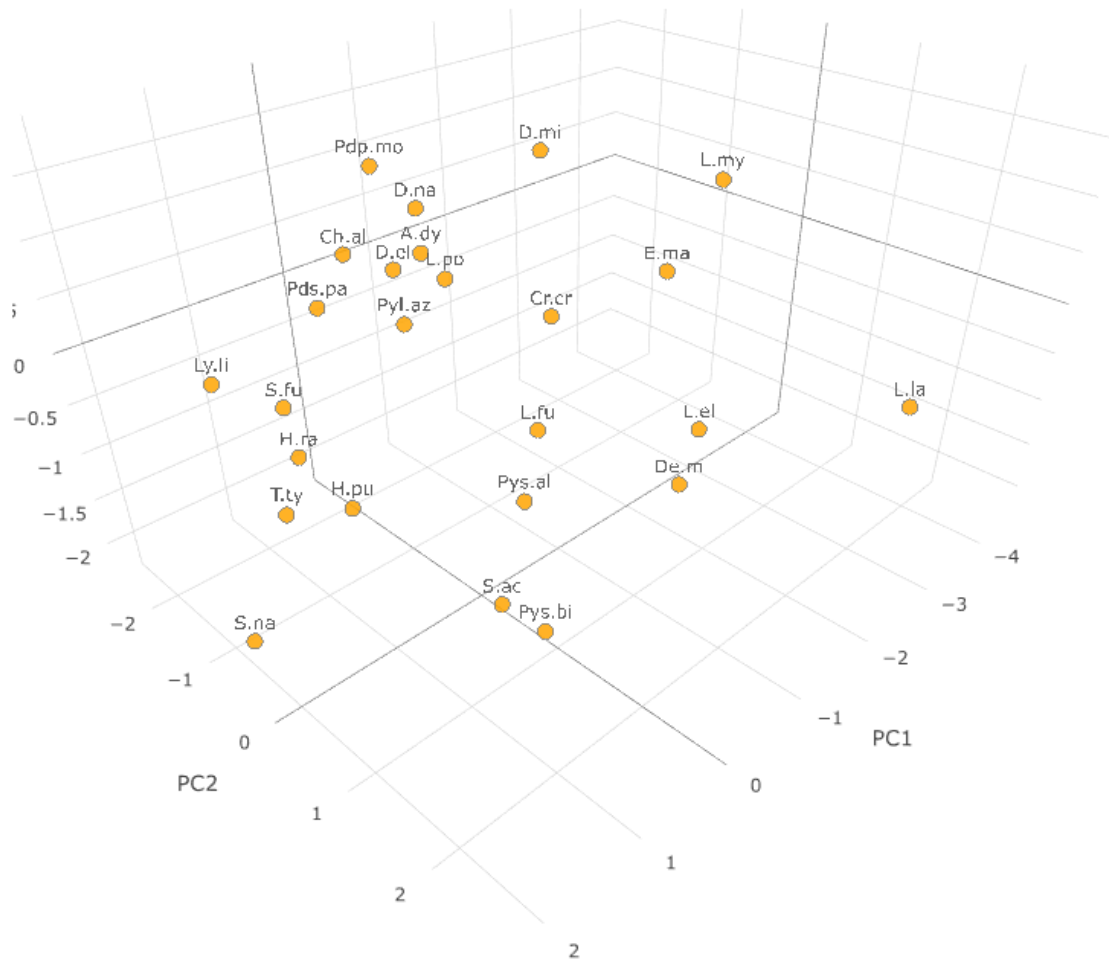


Figure S3. Acoustic space of the advertisement calls of anuran species from communities in the South Pantanal wetlands (species list in Table S1). The three axes of a principal component analyses are correlated with spectral distribution (aggregate entropy, average entropy, and IQR BW), temporal parameters (call rate and note duration), and peak frequency, respectively (see Table S2).

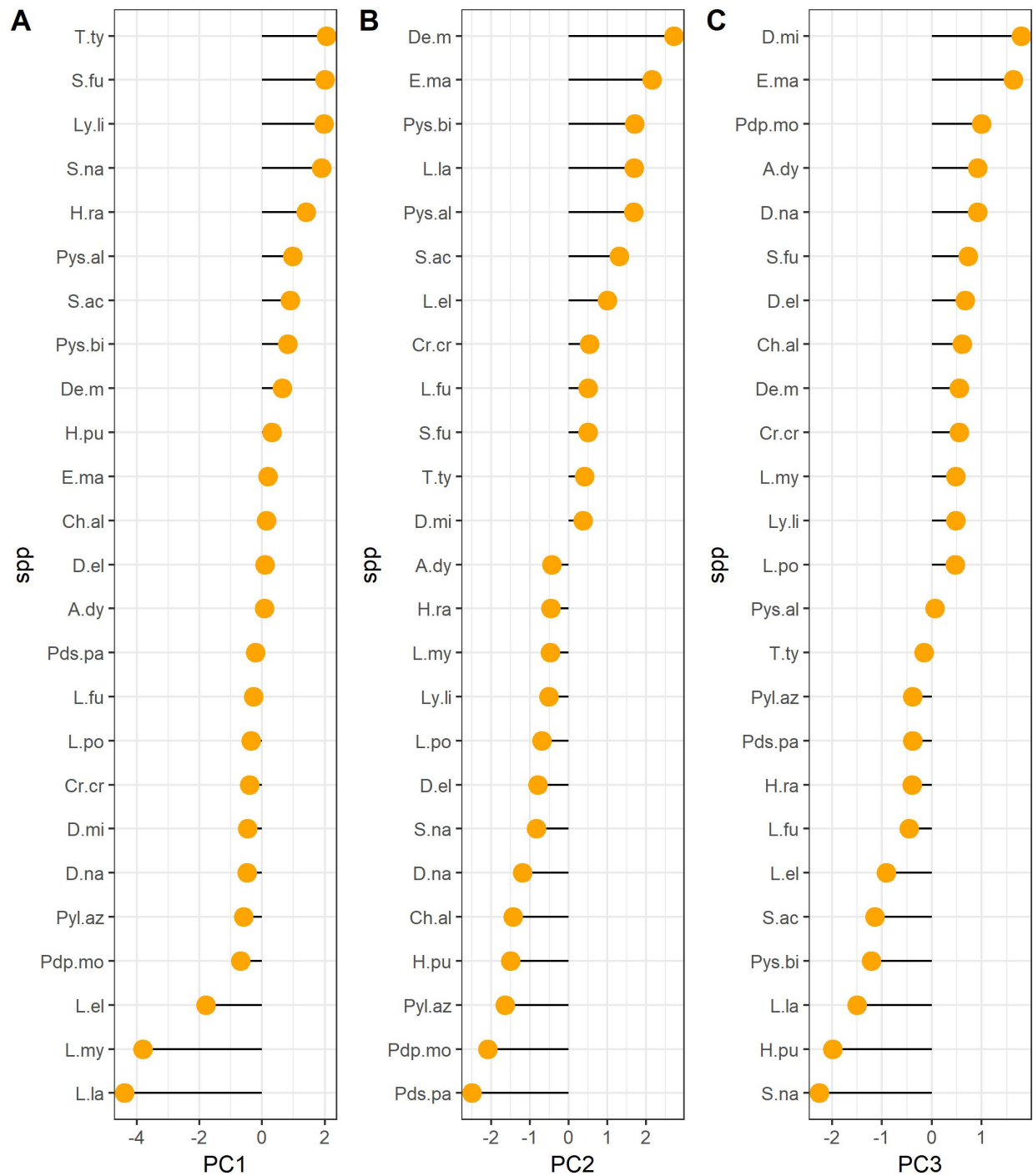


Figure S4. Anuran species found in South Pantanal wetlands (species list in Table S1) ordered by acoustic similarities in three axes from a principal component analysis that are correlated with spectral distribution (aggregate entropy, average entropy, and IQR BW), temporal parameters (call rate and note duration), and peak frequency, respectively (see Table S2).

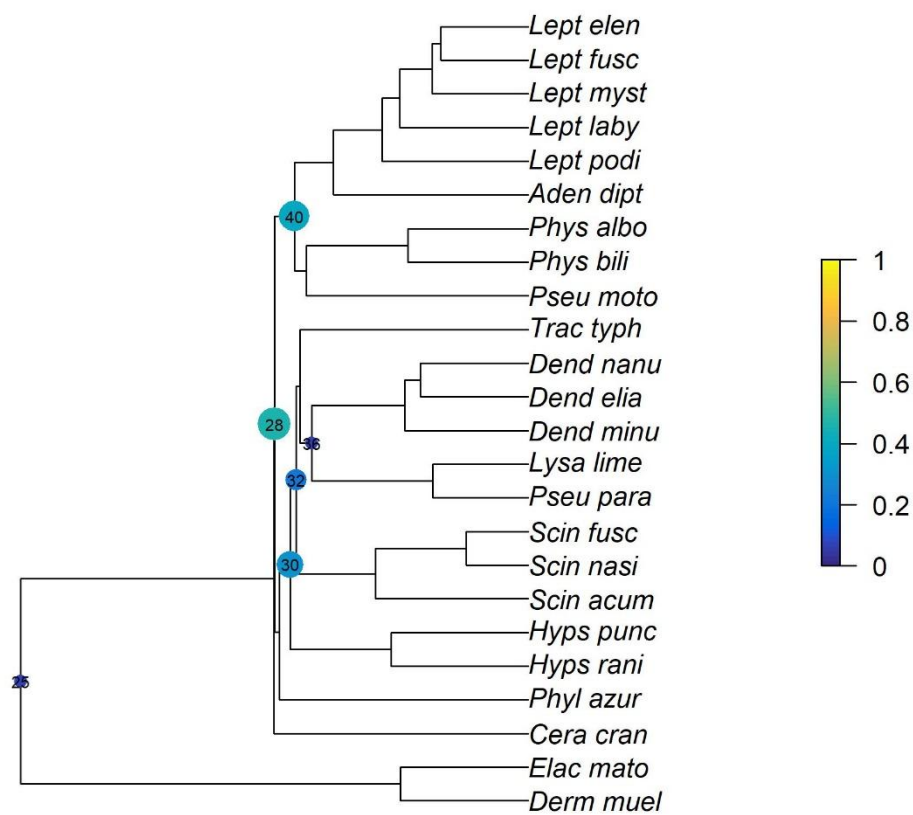


Figure S5. Phylogeny and resulting node-based analysis of anuran species found in the study site located in South Pantanal wetlands (species list in Table S1). Color nodes are represented by the value of geographic node divergence, being the greater values those representing the pair of sister clades that contributes more to the composition of communities.

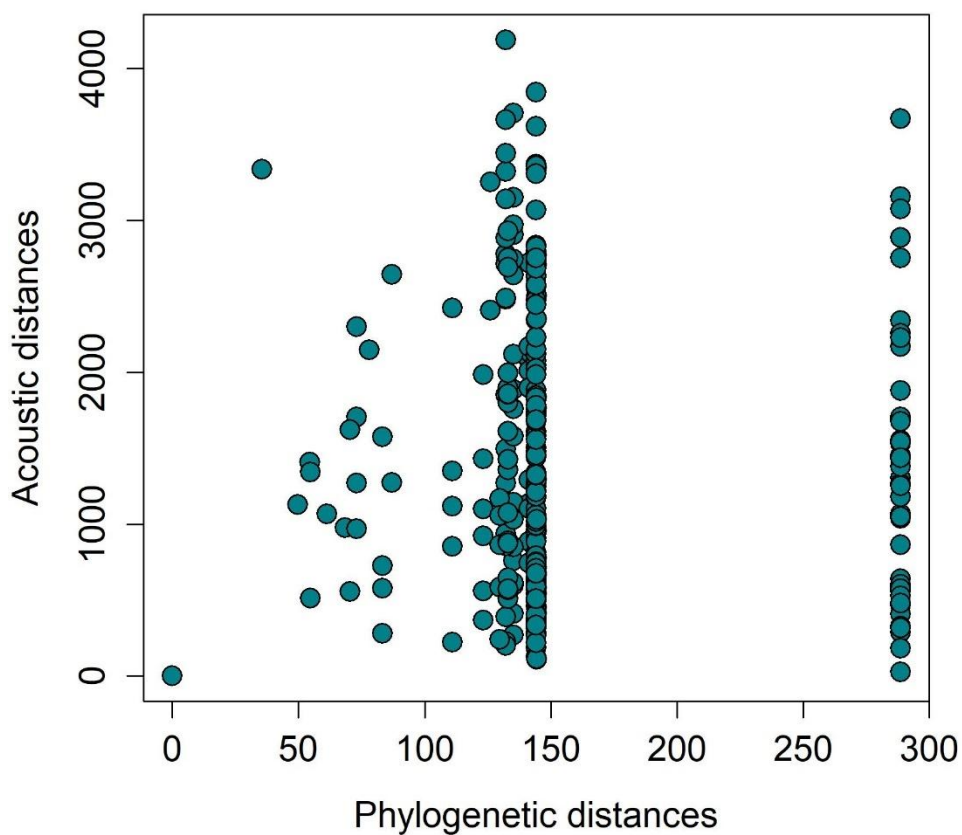


Figure S6. Relationship between phylogenetic distances and acoustic distances (all six variables) from anuran communities located in the South Pantanal wetlands.



6. CAPÍTULO 4

Widespread short-term dynamics in tropical anuran communities

Larissa S. M. Sugai^{*1,2}, Diego Llusia^{2,3}, Thiago S. F. Silva^{1,4}, Tadeu Siqueira¹

¹Universidade Estadual Paulista (Unesp), Instituto de Biociências, Rio Claro, 13506-900, São Paulo, Brazil.

²Terrestrial Ecology Group (TEG), Departamento de Ecología, Universidad Autónoma de Madrid, C/ Darwin, 2, 28049, Ciudad Universitaria de Cantoblanco, Facultad de Ciencias, Edificio de Biología, C-211, Madrid, Spain.

³Laboratório de Herpetologia e Comportamento Animal, Departamento de Ecologia, Instituto de Ciências Biológicas, Universidade Federal de Goiás, Campus Samambaia, CEP 74001-970, Goiânia, Goiás, Brazil.

⁴University of Stirling, Department of Biological and Environmental Sciences.

*corresponding author: lariagus@gmail.com

6.1 Abstract

Time is a fundamental ecological dimension influencing the dynamics of ecological communities, where temporal resolution determines the set of concurrent species. Temporal variation is usually associated with seasonal effects on animal communities, and within-season variation is seldom addressed. Although animal activity is largely acknowledged to vary over a diel cycle, diel community-wide activity patterns are still largely unexplored. Here we investigate short-term variation in anuran communities within diel cycles and address the effects of time and environment, at a local and a landscape context, on the diel variation of species composition. We monitored anuran communities in the Pantanal wetlands with automated audio recorders and compiled hourly composition of 39 local communities for up to five days during the peak of a reproductive season, where most species are likely to be active. Despite the anecdotal perspective of animal chorus as a disorganized cacophony of sounds, our findings indicate a coordinated decrease of species activity over nocturnal periods to be pervasive across communities and point to a role of environmental structure in influencing community-wide variation in diel species composition. We contend that such short-term differences might influence the potential of species interaction upon temporal partitioning of space and argue for the integration of space and temporally explicit approaches of ecological communities.

6.2 Introduction

Time is notably a fundamental dimension of ecological communities prone to scaling issues (Soininen 2010, Wolkovich et al. 2014), and addressing changes across timescales is an urgent, challenging task if we want to predict and mitigate biodiversity responses to global environmental changes (Dornelas et al. 2013, Sutherland et al. 2013). However, ecologists have largely overlooked fine-resolution timescales (Estes et al. 2018), and differences in the diel activity of species timing may influence the outcome of species interaction by decreasing resource use overlap and chances of direct confrontation (Kronfeld-Schor and Dayan 2003, Gaston 2019).

Ecological communities are often statically framed and spatially determined by subjective criteria or by habitat boundaries (Wiens 1989, Leibold et al. 2004), with spatial grain – resolution of spatial observations – ascribed to the dimensions of sampling units. In turn, the temporal appreciation of communities usually highlights the duration of studies, with resolution – determined by sampling intervals – assumed

to depict a set of interacting species with invariant activity within diel cycles (Figure 1-a). For instance, seasonal overlap of species activity influences the interaction potential of species (Carter et al. 2018) and long-term shifts in phenology are expected to alter the dynamics of species coexistence (Rudolf 2019). However, within-season species activity is largely variable and seldom constant over a diel period (McCann et al. 2017, Gaston 2019), as for distinct daily patterns of foraging time (Fraser et al. 2004, Kronfeld-Schor et al. 2013) and breeding activity (Schwartz and Bee 2013, Schalk and Saenz 2016). The circadian activity of species is determined by endogenous mechanisms adapted to optimize energetical costs, which is expressed with a plasticity of responses over varying biotic and abiotic conditions (Kronfeld-Schor and Dayan 2003, Kronfeld-Schor et al. 2013). In accordance, differences in diel activity among coexisting species (Figure 1-b) would promote distinct patterns of community composition across diel periods (Figure 1-c). If short-term variation in community composition is predictable over distinct ecological conditions, we might expect that differences in species activity may have implications for the structure of ecological communities.

Tropical anurans are an appropriate group to test for short-term community dynamics. Anuran communities are highly diverse, with most species active during the rainy season (Hödl 1977) and often restricted to habitats tightly associated to water bodies (Duellman and Trueb 1994). Pond-breeding species gather in communal egg-laying sites during reproduction and advertise calls to attract mates (Schwartz and Bee 2013). Diel activity is largely variable across species and often specific to abiotic factors (Gottsberger and Gruber 2004) but largely unexplored for entire ecological communities, especially for hyperdiverse ecosystems (Devries et al. 2008, Castro-Arellano et al. 2010, Ulloa et al. 2019). This research gap owns to the tradition of daytime research given challenging conditions to address nocturnal phenomena on the past (Gaston 2019). However, modern techniques enabling high-resolution data sampling in terrestrial systems have been improving our understanding of diverse ecological phenomena once challenged by practical issues (Rocchini et al. 2016, Gaston 2019). Amongst, automated acoustic devices enable systematic collection of environmental sounds that provide new opportunities to investigate behavioral and ecological aspects of terrestrial animals that use acoustic communication (Sugai et al. 2019a). Therefore, there is a synergistic potential in revisiting the “nocturnal problem” (Gaston 2019) with advents in acoustic monitoring.

The structure of amphibian communities is influenced by biotic and environmental factors and spatial dynamics associated with distinct spatial and temporal scales. Local and landscape environmental structures are largely responsible to define the range of suitable sites for reproduction and persistence of amphibian species (Van Buskirk 2005, Sugai et al. 2019b) while also influence dispersal dynamics into new habitats (Werner et al. 2007, Signorelli et al. 2016). However, community dynamics promoted by diel variation in species activity have been investigated to a lesser extent, particularly given constraints in investigating multiple sites concurrently. As such, the drivers of the diel variation in species composition of anurans communities are still largely unknown (Ulloa et al. 2019). Whether short-term dynamics are pervasive and predictable in communities, it might support understanding how distinct ecological processes shape natural communities.

Here, we investigate short-term dynamics of tropical anuran communities. Specifically, we address (1) whether species composition vary across hours and diel activity periods and how is it influenced by the environmental structure, and (2) whether variation in diel compositional differences is consistent communities over a gradient of environmental structure.

6.3 Methods

6.3.1 STUDY AREA AND ENVIRONMENTAL CHARACTERIZATION

We studied pond-breeding anuran communities in an area of approximately 100 km² located in the south region of the Pantanal wetlands in Brazil, Aquidauana municipality. Breeding activity takes place on the rainy season (October–April), with mean monthly temperatures and precipitation ranging from 20.1 to 33.2 °C and 96 to 231 mm (Fick and Hijmans 2017). Because most tropical anurans achieve the highest activity levels in the peak of the rainy season (Duellman and Trueb 1994), we concentrated sampling in the end of January/17 which corresponded to the month with highest precipitation levels for that season (231 mm, Fick and Hijmans 2017). Vegetation from this southernmost region is influenced by the neighboring Cerrado biome (tropical savanna), with heterogeneous vegetation types composed by grasslands, open wood savanna, and forested woodland (Evans and Costa 2013). Freshwater ponds used by anurans are embedded in such vegetation types and characterized by floating and emergent aquatic vegetation bounded by a strip of terrestrial habitat composed of grassy and herbaceous vegetation (Prado et al. 2005).

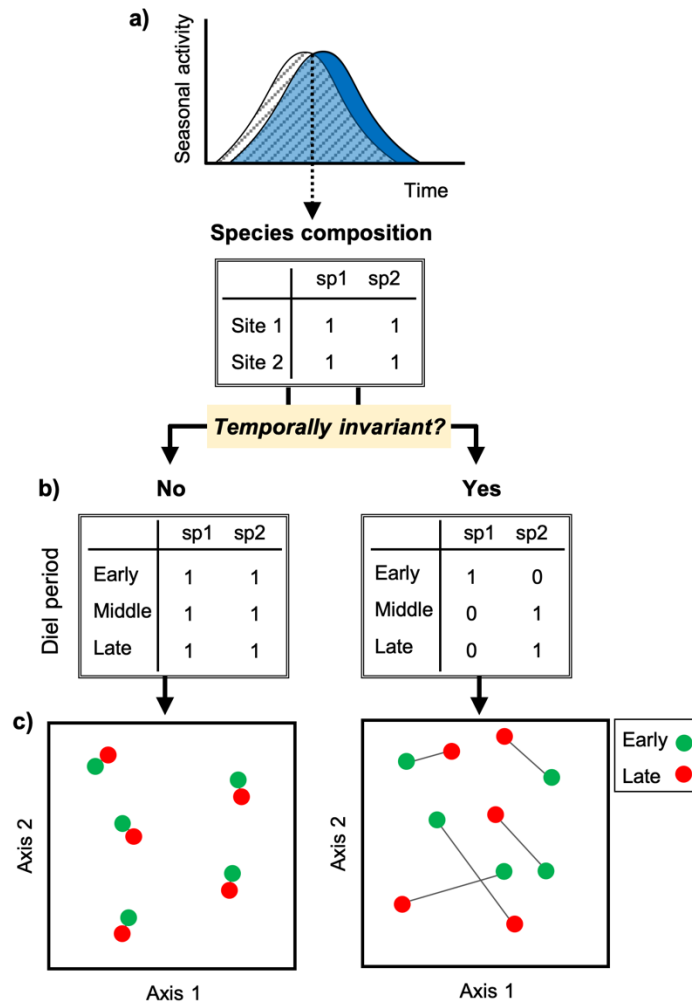


Figure 1. Diel compositional variation and potential consequences for community-wide patterns. In a given time on seasonal activity, two overlapping species sampled at a site (a) are assumed to have consistent diel activity (b-left), and the corresponding communities would show similar composition across distinct diel periods (c-left). Conversely, species can show distinct diel activity patterns (b-right), and the resulting composition of communities would vary across distinct diel periods (c-right).

The selection of sampling sites involved the use of geographic information system to i) define 500 points randomly distributed on the limits of the ponds and selected those apart at a minimum of 1km ($n = 72$), ii) calculate the Normalized Difference Vegetation Index – NDVI (Rouse et al. 1974) from RapidEye3A satellite images (5-meter pixel size, RapidEye AG 2011) within 200m-radius buffers ($125,663.6\text{m}^2$) on each point, iii) select 39 sites spanning the range of NDVI values to represent a gradient of vegetation heterogeneity, from landscapes containing dense forest to grass-dominated areas. At the monitoring sites, we sampled terrestrial and aquatic variables to characterize local habitat structures. For each of the 39 sites, we i) determined 15-meter trails for both sides of the margins of the pond, ii) at each 3-

meter intervals over the trail, we deployed a 3-meter perpendicular transect projected into the pond (aquatic habitat) and another into the terrestrial portion (terrestrial habitat), totalizing 90m² of sample area for each pond. On each terrestrial transect, we deployed a line and measured the lengths (cm) occupied by a) bare ground, b) grass > one meter, c) grass < one m, and d) shrub vegetation. Additionally, at each 1-meter interval, we determined the Leaf Area Index (LAI) as a proxy of vegetation openness, as it represents the ratio of foliage area to ground area (Bréda 2003). We measured LAI using a LAI-2200C Plant Canopy Analyzer model (LI-COR Biosciences 1992) using a 45° view cap. For the aquatic transects, we measured the lengths occupied by a) exposed aquatic surface, b) aquatic vegetation, c) grass > 20cm, d) grass < 20cm, e) shrub vegetation, and at each 1-meter interval, we measured pond depth. The measures for each variable were summed to each site, except for LAI, which were averaged. All environmental variables for aquatic, terrestrial, and landscape vegetation heterogeneity were standardized to zero mean and unit variance.

We performed a principal component analysis (PCA) on the aquatic and terrestrial habitat variables to reduce dimensionality using R package *vegan* (Oksanen et al. 2018). Aquatic habitat was represented by two axes (59%) summarizing gradients of i) typical aquatic vegetation in deep ponds to shallow ponds overflowed into the surrounding grassland due rainfall, and ii) deep ponds with free water surface to shallow ponds dominated by shrublands (Table S1, Figure 2a). Terrestrial habitat was represented by two axes recovering 68% of variation and summarizing i) grassland heterogeneity and ii) forested areas. (Table S1, Figure 2b).

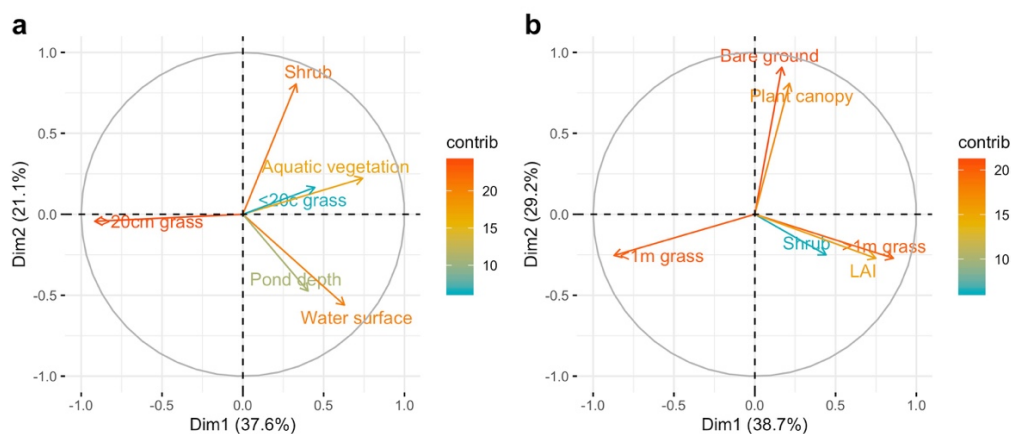


Figure 2. Loading plots showing the two principal axes from a principal component analysis on a) aquatic habitat and b) terrestrial habitat from ponds inhabited by anurans in south Pantanal, Brazil.

6.3.2 ANURAN COMMUNITIES

We conducted passive acoustic monitoring to register acoustically active anurans for 3 to 5 continuous days using 22 automated acoustic recorders that were rotated among sites during a total period of 10 days (SM4, SM3, and SM2 from Wildlife Acoustics). We deployed recorders on trees or wooden stakes up to 10 meters from the pond. Recording schedule consisted in 2 minutes of stereo recording each 20 minutes, starting one hour before sunset until one hour after sunrise (approximately from 16:30h to 07:30h, UTC -4). Recordings were performed at a 44.1 kHz sample rate with a gain of 6 dB and 12 dB on each channel. Detection and identification of anuran species were performed manually by the main author using visual inspection of spectrograms (FFT=512, Hamming window) and aural recognition with Audacity (Audacity Team 2018) and Raven 1.4 (Bioacoustics Research Program 2014). The high overlap with bird and invertebrate chorusing activity on the first and final hours of monitoring increased inaccuracy of identification and potential false negatives, so we restricted our analysis from 19:00 until 04:00 hours.

Anuran communities are usually circumscribed as the sum of all species present at one or more consecutive nights at a given site. Here, for each site, we assess the composition of signaling species within each monitored hour (all species recorded in the three samples taken at each 20 minutes), and the total sets of species registered within a day, hereafter referred as local communities. To represent nocturnal variation in species composition, we assessed the correspondence between signaling and the respective local community using the Jaccard dissimilarity coefficient, an index broadly used to represent spatial beta diversity (Jost et al. 2010). We calculated Jaccard dissimilarity values using R package *vegan* (Oksanen et al. 2018), but transformed them in similarity values ($1-d_{ij}$) to ease interpretation, and refer to them as diel similarities hereafter. Because diel similarities use local community as reference, a decrease in diel similarities indicates that signaling communities are a subset instead of a repeated set of species composing local communities. This approach i) allows us to deploy linear combinations among variables and account for non-independency among observations and ii) is more similar to a raw-data approaches and thereby, more adequate to explain variation in species composition in spite of distance-based methods (Tuomisto and Ruokolainen 2006).

6.3.3 NULL MODELS AND VARIATION ON SPECIES COMPOSITION ALONG NOCTURNAL PERIODS

We generated null models to break hourly-related structures on species composition by allowing species to be drawn from the local community registered at a given day, irrespective of hour. For each signaling community, we generated 1,000 null communities, calculated correspondence to the local community (null diel similarity) and determined the mean null diel similarity. We calculated standardized effect sizes using the difference between the mean null and the observed diel similarities from each signaling community, divided by the standard deviation of diel similarities from the respective null signaling communities. Increasing positive and negative values of standardized effect sizes of diel similarities indicate that the correspondence of signaling and local communities are higher or lower than expected without the effect of hour, respectively. We used one-sample *t* tests to determine if standardized effect sizes were different from zero (Ingram and Shurin 2009).

To test if the correspondence between signaling and local communities were different on early (19:00 to 21:00), middle (–00:00), and late (–03:00) nocturnal periods of activity, we fitted a linear mixed model using period as fixed factor, and site and monitoring day as random intercepts. We checked residuals normality and homoscedasticity on Q-Q plots and performed model inference with a likelihood-ratio test with a null model containing only random effects (Forstmeier and Schielzeth 2011). Confidence intervals for model coefficients were estimated with 1,000 bootstrap iterations using package *lme4* (Bates et al. 2015). We assessed the effect of individual predictors with iterative likelihood-ratio tests over reduced models using the function *drop1* in R package *lme4* (Bates et al. 2015).

As a visual resource to examine variation in species composition between early and late nocturnal periods, we obtained the centroid of a non-metric multidimensional scaling (nMDS) for the combination of all signaling communities on each site for early and for late periods. A low variation in species composition between early and late periods would be represented by small distances between the periods (Figure 1-c).

6.3.4 DRIVERS OF SHORT-TERM COMMUNITY COMPOSITION AND CONGRUENCE ACROSS COMMUNITIES

To determine if the environmental structure influence the degree of correspondence between signaling and local communities, we fitted three linear mixed models on diel similarity values, each with the following fixed factors: (1) local aquatic habitat, using the two first axes from a PCA representing gradients of aquatic vegetation structure, (2) local terrestrial habitat represented by the two first axes from a PCA representing gradients of terrestrial vegetation heterogeneity, and (3) landscape vegetation heterogeneity represented by mean and standard deviation of NDVI within 200-meter radius buffers. On each model, we used nocturnal period as a covariate, and site and monitoring day as random intercepts.

To address whether the variation of diel similarities is consistent across communities, we first determined the variance of diel similarities for each day. Larger variances indicate that species composition varies inconsistently across days, while lower variances indicate variation in species composition to be more consistent. We fitted three linear mixed models on the variances of diel similarities, each one using aquatic habitat, terrestrial habitat, and landscape vegetation heterogeneity variables as fixed factors, and site as random intercept. We log-transformed variance of similarities to comply with model residuals to normality and conducted the same protocol abovementioned to check residual Q-Q plots, model inference, and to estimate confidence intervals of coefficients.

Finally, we explored the influence of landscape heterogeneity and local terrestrial and aquatic habitat structures on total community similarities using of all species registered on each site over all monitored days with a distance-based redundancy analysis (Legendre and Anderson 1999). We used Jaccard dissimilarity index on the total composition of communities as a function of the mean and standard deviation of NDVI (landscape heterogeneity measures), and the selected axes from the principal component analysis on terrestrial and aquatic habitat structures. To assess the significance of constrained eigenvalues, we performed 1000 permutations computed pseudo-F statistics (Legendre and Legendre 2012). We used R package *vegan* (Oksanen et al. 2018) to perform distance-based redundancy analysis.

6.4 Results

6.4.1 COMPOSITIONAL VARIATION IN NOCTURNAL ACTIVITY

The composition of signaling communities (sets of species recorded within each monitored hour) were overall highly similar to local communities (sets of species recorded within each day; $x = .69$), ranging from .64 to .73 across hours. The highest diel similarities were associated to early hours and tended to decrease over the night (Table 1). Accordingly, when compared to null expectations of signaling communities, observed diel similarities were higher on early hours (19:00 to 21:00 h) and lower on later hours (00:00 to 03:00 h) periods (Table 1, Figure 3a).

Within early, middle, and late nocturnal periods, the correspondence of signaling and local communities tended to be lower on the middle and late periods ($\chi^2 = 66.9$, $p < 0.001$, $\beta = 0.73$, -0.04 , -0.08 , respectively, Table S2). nMDS ordinations revealed that for communities taken as the sum of species registered at each site and nocturnal period, compositional similarities showed varying degrees of similarities between early and late periods (Figure 3b), contrasting null expectations of widespread short-term compositional variation across communities.

6.4.2 ENVIRONMENTAL DRIVERS OF DIEL SIMILARITIES AND ITS VARIATION

We found that irrespective of period, diel similarities were slightly influenced by one gradient of aquatic habitat ($\chi^2 = 14.3$, $p < 0.001$, $\beta = 0.04$, $p < 0.001$), and no effect was found with environmental descriptors of landscape and terrestrial habitats (Table S2). Specifically, signaling communities from deeper ponds containing aquatic vegetation were more similar to local communities and thus, showed less compositional variation in nocturnal activity, whereas lower similarities to local communities were found for signaling communities from shallow and overflowed ponds upon grassland fields (Figure 4a).

By assessing the variance of diel similarities for each day, we found variation of similarities to be influenced by landscape heterogeneity and local terrestrial habitat structure. Specifically, lower variance, indicating higher consistency in the variation of diel similarities, was associated with ponds surrounded by less heterogeneous terrestrial habitats ($\chi^2 = 8.1$ $p = 0.018$, $\beta = 0.14$) and embedded in landscapes dominated by grassland vegetation ($\chi^2 = 6.6$ $p = 0.038$, $\beta = 0.25$; Figure 4b-c, Table S3). Conversely, we found higher variance in communities located at sites where the adjacency of

ponds was composed by heterogeneous shrub and herbaceous vegetation, and the contextual landscapes were characterized by denser woody vegetation, as woody savanna and forested areas (Figure 4b-c).

Table 1. Compositional similarities between signaling (total species per hour) and local (total species per day) anuran communities from south Pantanal wetlands. Similarities are represented by one minus Jaccard dissimilarity index (Jacc. Obs.) and summarized with a standardized effect size from communities null to hourly structures ($\bar{x}$ Jacc. stand.), which were tested for differences from zero (one sample t-test). Confidence interval correspond to 95%.

		Jacc. obs.	$\bar{x}$ Jacc. stand.	Lower CI	Upper CI	t-value	p-value
Total		0.69	0.00	-0.05	0.05	0.02	0.985
Hour	19:00	0.73	0.27	0.09	0.45	2.98	0.003
	20:00	0.73	0.38	0.21	0.55	4.31	<0.001
	21:00	0.73	0.32	0.17	0.47	4.26	<0.001
	22:00	0.71	0.15	-0.01	0.30	1.89	0.060
	23:00	0.69	0.00	-0.15	0.16	0.03	0.978
	00:00	0.67	-0.16	-0.31	-0.01	-2.15	0.033
	01:00	0.65	-0.33	-0.47	-0.18	-4.38	<0.001
	02:00	0.67	-0.21	-0.35	-0.06	-2.86	0.005
	03:00	0.64	-0.42	-0.58	-0.26	-5.11	<0.001

Distance-based redundancy analysis revealed that a fraction of variation in total species composition was explained by the environmental descriptors from local (terrestrial and aquatic habitats) and landscape contexts ($R^2 = 0.247$, adjusted $R^2 = 0.106$, $p = 0.015$). The two first axes of this constrained ordination reveal a similar direction of the effects of terrestrial and landscape variables on the variation of species composition across sites and further an effect of the structure of aquatic habitats (Figure 5).

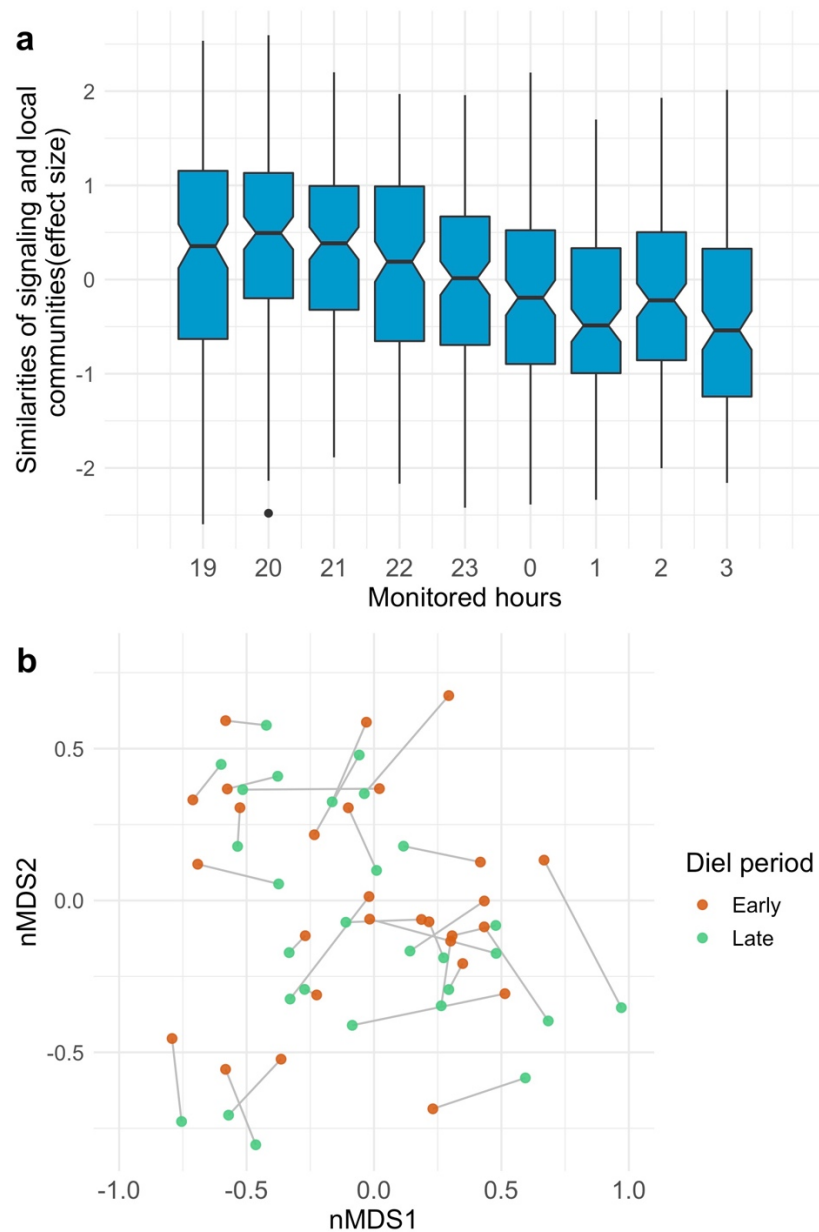


Figure 3. Short-term compositional similarities between hourly signaling and local communities of anurans from south Pantanal wetlands in Brazil. (a) Boxplots of standardized effect sizes of Jaccard similarity values from 19:00 to 03:00 h, with notches represents 95% confidence interval around the median. (b) Centroids from ordinations of non-metric multidimensional scaling (nMDS) for the combination of each community and early (red) or late (green) nocturnal periods. Closer connected dots indicate communities with similar composition between nocturnal periods.

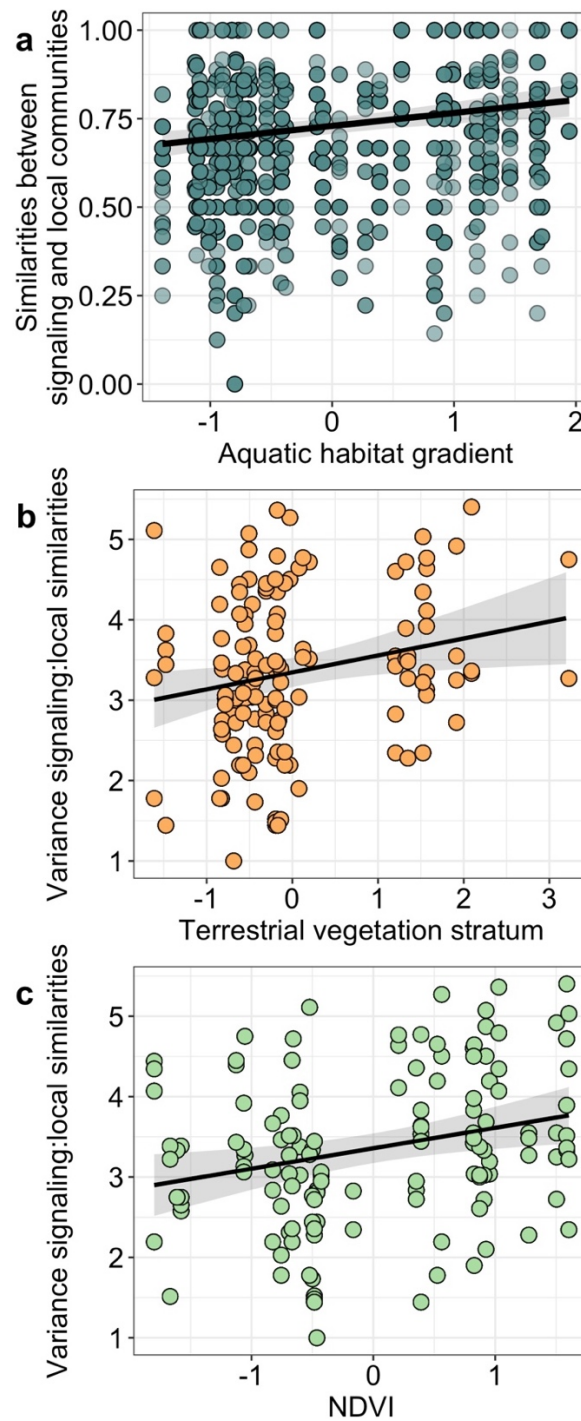


Figure 4. Relationships between short-term compositional similarities between hourly signaling and local communities of anurans and environmental variables in south Pantanal wetlands, Brazil. (a) Positive relationship between compositional differences among signaling and local anuran communities and a gradient of aquatic habitats from characteristic ponds (with aquatic vegetation) to shallow ponds overflowed to seasonal flooding grasslands (first axis of a principal component analysis – PCA). (b) Positive relationship between the variance of short-term compositional differences of local communities and a gradient of terrestrial habitat representing an increase in grassland heterogeneity and (c) an increase in canopy cover on the landscape (200 m buffer).

6.5 Discussion

Ascertaining spatial and temporal framings of communities may provide insights on how distinct ecological processes operate and shape natural communities (Soininen 2010, Van Allen et al. 2017, Viana and Chase 2019). A deeper look in the temporal grain of communities at varying scales unveiled widespread variation in species composition at distinct nocturnal periods and across anuran communities. Specifically, compositional variation of anuran communities over nocturnal periods (diel similarities) was associated with a gradient from temporary to permanent aquatic habitats. However, by addressing the variation of diel similarities over different days, we found inconsistent patterns across communities promoted by local terrestrial habitat structure and landscape heterogeneity. Our main findings indicate that anuran communities in the Pantanal wetlands might experience temporal partitioning across nocturnal periods and that environmental context have a role in modulating compositional variation of communities over a diel cycle.

A decay of short-term compositional similarities over nocturnal periods imply in a broad effect of diel timing on the calling activity of anuran communities. Such variability on calling activity patterns may reflect physiological, behavioral, and ecological mechanisms tuned to diel cycles. In anuran choruses, early arriving males are more successful in establishing spatial dominance by decreasing costs to elicit aggressive calls for territorial defense, which are also less attractive to females (Wells 2007, Wells and Schwartz 2007). A large correspondence between signaling and local communities at early nocturnal periods places early call advertising as a common strategy across species. Chorus formation can initiate with few signaling individuals that induce other males to start calling in a chain reaction among signalers (Brooke et al. 2000, Wells and Schwartz 2007, Llusia et al. 2013), which confer the benefit of optimizing calling energetic costs, minimizing predation risk, and increasing attractiveness for mates (Schwartz and Bee 2013). The subsequent decay of chorusing activity across species may reflect mechanisms determined by pacemakers from the nervous central system tuned by diel timing (Greenfield 2015) or to be the output of acoustic interactions between conspecifics and heterospecifics (Gerhardt and Huber 2002, Marshall et al. 2006). Individuals may avoid call overlap with neighbors by alternating notes at very fine temporal scales or by displaying clustered patterns of activity and silence (“unison bout singing”) that last from few seconds to several minutes (Schwartz 1991, Aihara et al. 2019). Although evidence of such behavioral

displays comes from single-species chorus formation, tropical choruses are rather composed by multiple species, and mounting evidence suggest heterospecific stimuli to elicit responses on individuals' activity patterns (Marshall et al. 2006, Phelps et al. 2006, Goodale et al. 2010, Both and Grant 2012, Gil et al. 2018). As such, interspecific inhibition of signaling can be an important phenomenon driving the temporal structuring of choruses composed by multiple species (Schwartz and Bee 2013).

Additionally, factors associated with environmental structure can influence the decay and variability of community-wide signaling activity (Wells 2007). Although fluctuations in temperature and relative humidity can also influence the levels of species calling activity on the short-term, such effects are largely variable for distinct species (Gottsberger and Gruber 2004, Schalk and Saenz 2016) that would otherwise, in the studied system, produce an unclear pattern over nocturnal periods. Alternatively, the observed relationships suggest that environmental selection and dispersal also play a role in short-term dynamics of anuran communities. Irrespective of nocturnal period, the gradient of aquatic habitats from permanent to temporal ponds had an influence on the correspondence of signaling communities to local communities. Because vegetation heterogeneity has a fundamental role in the role of environmental niche selection and dispersal dynamics in shaping the structure of communities (Cottenie 2005, Vellend 2010), we contend that such processes may might also influence community-wide diel activity patterns.

The structural complexity of breeding sites ranging from permanent to temporal ponds led to variations in the diel the correspondence between signaling and local communities. On one hand, the aquatic vegetation of breeding ponds influence species occurrence and abundance by offering distinct conditions for species to occupy sites to advertise calls and encounter mates (Wells 2007). A higher complexity on the vertical vegetation stratum of ponds decreases spatial overlap for semi-terrestrial and arboreal species, often yielding species-diverse communities (Hödl 1977, Silva et al. 2011). Conversely, overflowed ponds due accumulated precipitation create new temporary habitats that are rapidly colonized by explosive breeders (Prado et al. 2005). In such temporary aquatic habitats, amphibian communities are largely influenced by extinction-colonization dynamics at the regional and local scales, often leading to large variations in seasonal community composition (Trenham et al. 2003, Urban 2004, Richter-Boix et al. 2007, Werner et al. 2007). Such dynamics rely in the order and timing of species arrival, where early species constraint opportunities for late arrivals by depleting resources and modifying available niches for colonization

(Fukami 2015). Likely, a higher stochastic component on communities located at temporal aquatic habitats may determine an overall tendency towards lower similarities to local communities.

Although the decay of diel similarities was associated with nocturnal period and aquatic habitat, the variability of diel similarities was influenced by local terrestrial and landscape contexts. The terrestrial context of aquatic habitats influences potential colonizing species given its influence in individual movements from retreat to breeding sites and in providing refuges during breeding season interludes (Wells 2007, Becker et al. 2010, Sinsch 2014). As such, a higher local proportion of shrublands surrounding ponds promotes more opportunities for arboreal species to perch and advertise calls, while a predominance of grassland fields is more suitable for terrestrial and fossorial species (Prado et al. 2005, Valério et al. 2016). At the landscape context, forested areas provide shelters against high temperatures and low humidity levels during daylight and decrease resistance for movement among habitat patches and within the home range of species (Bowler and Benton 2005, Buskirk 2012, Silva et al. 2012). Conversely, the high solar incidence in open grassland formations is a strong constraint for the persistence and movement of species unable to cope with intense evaporative water loss (Rothermel 2004). Such limitations imposed by local and landscape terrestrial structure are associated with mechanisms of environmental selection and dispersal dynamics on the structuring of anuran communities (Trenham et al. 2003, Ernst and Rödel 2005, Keller et al. 2009, Becker et al. 2010). Thereby, environmental heterogeneity may increase the likelihood of distinct order and timing of early arrivals on different nights, which may lead to distinct outputs on diel similarities.

We argue that the variation of diel similarities on markedly distinct environments may reflect short-term spatial dynamics from distinct sets of species associated with distinct habitats. According to the distance-based constrained ordinations, it was possible to identify strong relationships among environmental structure and specific species. *Phyllomedusa azurea* and *Leptodactylus fuscus* were associated with grassland fields characterized by low-stratum and homogeneous vegetation. *P. azurea* vocalizes on the ground and over grassy vegetation and deposit eggs in leaves from vegetation above flooded fields (Rodrigues et al. 2007), and *L. fuscus* shelters in burrows on the ground and underneath grass huddles during daylight and advertise calls in open areas (Lucas et al. 2008). It is likely that homogeneous grassland fields in the Pantanal can impose constraints to the set of species able to access

aquatic habitats within these areas, and that the higher consistency in diel composition in these areas indicates that these species are persistent and recurrent across nocturnal periods. Conversely, ordinations revealed that *L. podicipinus* and *L. eleanea* were associated with forested areas, which are typical sites used for these species to advertise calls (Prado et al. 2005). *L. podicipinus* form basin-like constructions underneath forest litter to deposit eggs (Prado et al. 2002), while *L. eleanea* build underground chambers on the edge of water bodies and vocalize over forest litter (Prado et al. 2005). For anurans, environmental heterogeneity increases opportunities for species to occupy suitable sites for reproduction and foraging (Wells 2007), thus enhancing individuals' fitness with the benefit of decreased interspecific competition (e.g. spatial storage effect, Chesson 2000). Because both local and landscape heterogeneity determine the set of species capable of arriving and persisting on markedly distinct sites, we contend that the variation in nocturnal dynamics reflects spatial dynamics taking place at short timescales.

Our findings also bring up plausible effects of fine temporal resolutions on the output of species interaction potential. Such approaches have received new attention with “seasonal ecology frameworks”, which contend that changes in the timing of species activity can alter the temporal overlap of species activity, potentially affecting the strength of species interaction which may alter the structuring of communities. During reproductive seasons, increased breeding activity is followed by a rapid increase in the number of offspring (Doody et al. 2009, Buxton and Sperry 2017), and thus the presence of calling species at a given period is used to estimate species interaction potential (Carter et al. 2018). Distinct temporal offsets among competitors promotes changes in per-capita strength in competitive interactions and can lead to distinct output of species interaction (Rudolf 2019) either by enhancing stabilizing niche differences or competitive advantages among competitors (Godoy and Levine 2014). However, short-term differences in species activity can change the magnitude of competitive interactions, as for temporal segregation among signaling species (Schwartz 1987, Brumm 2006). Thus, addressing diel or short-term variation on species activity and its environmental determinants can provide new insights to estimate interaction potential among competitors.

We reinforce the importance of temporal scaling effects to inferring the role of assembly processes on ecological inference (Leibold and Chase 2017). Scaling relationships in ecological research can be described by grain (or resolution) and extent for space and duration for time (Wolkovich et al. 2014, Estes et al. 2018).

increasing the dimensions of spatial sampling units (coarser grain) increase the number of individuals and species to be registered, while environmental variables are averaged and thus coarsely represented (Wiens 1989). A mismatch between the resolution of response variable and environmental variation often leads to lower explanation of species occupancy patterns among sites (Barton et al. 2013) and thus, a weaker importance of environment in explaining community structure (Viana and Chase 2019). Therefore, spatial grain and extent determine inference of community assembly, and research in ecology should start adopting scale-integrative inference (Camargo et al. 2019). Similarly, scaling effects on community assembly can gain insights by addressing the interaction between temporal grain/duration and spatial scale. Because circadian and diel species activity is largely reliant on competitive interactions and predation pressure (Kronfeld-Schor et al. 2013), neglecting the temporal segregation of animal diel activity in communities yields a coarser representation of co-occurring species similarly to the increase of spatial grain, leading to an ecological pattern that is unrelated to the actual mechanisms driving the assembly of communities (Gaston 2019). As such, high-resolution time series provide a means to detach within and between season effects on community structure (Hatosy et al. 2013, Martin-Platero et al. 2018), which is fundamental for improving our ability to predict species responses to global changes (Dornelas et al. 2013, Wolkovich et al. 2014).

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6.8 Supplementary Material

Table S1. Principal component analysis on environmental variables from terrestrial and aquatic habitats of ponds used by anurans in south Pantanal, Brazil. For the two principal axes of each, percentage of contribution of environmental variables and correlation to the axes.

	Axis 1		Axis 2	
	Contribution to axis (%)	Correlation	Contribution to axis (%)	Correlation
<i>Terrestrial habitat</i>				
Bare soil	1.20	0.17	47.03	0.91
Grass > 1m	31.66	0.86	4.19	-0.27
Grass < 1m	32.63	-0.87	3.68	-0.25
Shrub	8.40	0.44	3.58	-0.25
Plant canopy cover	1.98	0.21	37.31	0.81
Leaf Area Index (LAI)	24.13	0.75	4.20	-0.27
<i>Aquatic habitat</i>				
Exposed water surface	17.53	0.63	24.83	-0.56
Aquatic vegetation	24.38	0.74	3.91	0.22
Grass > 20 cm	37.23	-0.92	0.15	-0.04
Grass < 20 cm	8.81	0.45	2.18	0.17
Shrub	4.82	0.33	51.18	0.81
Pond depth	7.23	0.40	17.75	-0.47

Table S2. Results of linear mixed models fitted on short-term compositional similarities between hourly signaling and local communities of anurans from south Pantanal wetlands in Brazil using i) nocturnal period of activity, and environmental variables associated to ii) aquatic and iii) terrestrial habitats, and iv) landscape vegetation heterogeneity as fixed factors.

	X ²	df	Estimate	Std. Error	Lower CI	Upper CI	t- value	p- value
<i>Nocturnal Period</i>	66.9	2						<0.001
Early (19:00 to 21:00)			0.73	0.01	0.71	0.75	60.90	
Middle (22:00 to 00:00)			-0.04	0.01	-0.06	-0.02	-4.27	
Late (01:00 to 03:00)			-0.08	0.01	-0.09	-0.06	-8.30	
<i>Aquatic habitat</i>	14.3	2						<0.001
Intercept			0.73	0.01	0.71	0.75	63.32	
PC1			0.04	0.01	0.02	0.06	3.57	<0.001
PC2			0.01	0.01	-0.01	0.03	0.93	0.35
<i>Terrestrial habitat</i>	1.45	2						0.48
Intercept			0.73	0.01	0.71	0.75	61.01	
PC1			-0.01	0.01	-0.02	0.01	-1.06	
PC2			0.01	0.01	-0.01	0.02	0.63	
<i>Landscape</i>	0.14	2						0.93
Intercept			0.73	0.01	0.71	0.75	60.9	
NDVI			0	0.01	-0.02	0.02	-0.09	
NDVI_std			0	0.01	-0.03	0.02	-0.37	

Table S3. Results of linear mixed models fitted on the variance of short-term compositional similarities between hourly signaling and local communities of anurans from south Pantanal wetlands in Brazil using i) nocturnal period of activity, and environmental variables associated to ii) aquatic and iii) terrestrial habitats, and iv) landscape vegetation heterogeneity as fixed factors.

	χ^2	df	Estimate	Std. Error	Lower CI	Upper CI	t-value	p-value
<i>Aquatic environment</i>	2.4	2						0.294
Intercept			3.36	0.1	3.16	3.56	33.86	
PC1			-0.04	0.07	-0.17	0.1	-0.57	
PC2			-0.13	0.09	-0.31	0.05	-1.49	
<i>Terrestrial environment</i>	8.1	2						0.018
Intercept			3.36	0.09	3.17	3.54	36.4	
PC1			0.14	0.06	0.02	0.26	2.37	0.022
PC2			0.13	0.07	-0.01	0.27	1.83	0.073
<i>Landscape</i>	6.6	2						0.038
Intercept			3.36	0.09	3.17	3.55	35.71	
NDVI			0.25	0.1	0.06	0.45	2.67	0.01
NDVI_std			0	0.1	-0.19	0.19	0	



7. CONCLUSÃO GERAL

A dimensão acústica está em plena reverberação na ecologia. Diversos grupos biológicos utilizam a modalidade acústica de comunicação para mediar interações sociais e competitivas, sendo os coros matinais de aves e noturnos de anuros representações particulares desse fenômeno. Dado que os sons presentes na natureza constituem uma rica fonte de informação sobre a biodiversidade, seu monitoramento amplia a capacidade de entender e acompanhar mudanças nos ecossistemas. De forma pragmática, um som pode ser associado a uma espécie e a um estado comportamental. Com isso, técnicas de monitoramento acústico que registram dados com alta frequência por longos períodos permitem quantificar os mais diferentes sons em gravações acústicas ambientais e atribuí-los a uma localidade geográfica, servindo de base para uma miríade de questões ecológicas. Assim, os dois primeiros capítulos desta tese foram revisões sobre a literatura utilizando o monitoramento acústico em ambientes terrestres, onde pudemos tanto colocar em perspectiva a trajetória de aplicações para diversas linhas investigativas em ecologia como sintetizar práticas associadas ao desenho experimental e por fim fornecer diretrizes para futuros trabalhos.

A partir da otimização da tomada de dados com gravadores autônomos, a literatura em monitoramento acústico de ambientes terrestres ascendeu notavelmente na última década. Dentre os estudos que utilizaram esta técnica, vimos a ampliação e o aprofundamento de linhas investigativas clássicas em ecologia bem como a criação de novas linhas, como a ecoacústica, que traz uma visão holística sobre paisagens sonoras. Podemos dizer que o uso do monitoramento acústico caminha para ser consolidado como um método efetivo e de ótimo custo-benefício para monitorar animais. Invariavelmente, existem desafios relacionados à otimização da análise de volumosas quantidades de dados e ao manejo destas coleções para viabilizar análises integrativas e de larga escala, cuja conciliação é atualmente fundamental para entender e mitigar a resposta da biodiversidade a mudanças de habitat e ao aquecimento global.

Por outro lado, são muitas as maneiras como os dados podem ser tomados no monitoramento acústico, sendo fundamental o planejamento do desenho amostral para assegurar uma eficiente amostragem acústica. A iniciar por garantir adequada representação espacial da área de estudo. Já em cada unidade amostral, o ideal é

averiguar a área de detecção do gravador acústico e considerar a necessidade de utilizar sub-réplicas dentro da unidade. Planejar a amostragem temporal requer lembrar que quanto mais tempo o gravador estiver ligado, maior será o consumo de energia, a quantidade de dados registrados e, conseqüentemente, menor será a autonomia. Em contrapartida, aumentar a autonomia com um menor número de programações automáticas de ligar/desligar implica em diminuir a capacidade de detecção de alguns animais. Portanto, podemos tentar destinar as gravações a períodos diários com maior probabilidade de detecção dos organismos, e ainda realizar gravações de forma cíclica com determinada frequência e tempo de gravação. Para verificar a eficiência de diferentes desenhos de amostragem temporal podemos comparar dados de gravações feitas em 24 horas com aqueles dos diferentes desenhos e estimar o quanto de informação está sendo conservada ou perdida. Por fim, de acordo com os ganhos e perdas desses diferentes desenhos podemos relacioná-los aos gastos financeiros/logísticos e tomar uma decisão bem informada. Essas diretrizes aumentam a contundência das inferências ecológicas viabilizadas por meio do monitoramento acústico. Além de que, a sistematização dos registros acústicos permite agregar múltiplos estudos e organismos, auxiliando a integração de escalas e subsidiando sínteses sobre as dinâmicas da biodiversidade no planeta.

Os capítulos seguintes foram destinados a investigar a organização de comunidades por meio de monitoramento acústico. Para tanto, realizamos uma campanha para monitorar 39 comunidades de anuros com alta precisão temporal, distribuídas ao longo de um gradiente de vegetação em uma escala de paisagem. No capítulo 3, investigamos se as comunidades possuíam características acústicas compatíveis com predições de que os sinais acústicos das espécies refletem mecanismos para diminuir a interferência frente ao barulho de fundo vindo de outras espécies ou de variáveis associadas a estrutura vegetacional. Nossos resultados, no entanto, não corroboraram essas hipóteses clássicas e apontaram para outra direção, onde as comunidades se beneficiam de informação social, vindo da vocalização das espécies. Essa é, na verdade, uma perspectiva que tem obtido crescente espaço em explicações sobre como os organismos se distribuem no espaço, a qual buscamos corroborar com nossa abordagem.

Finalmente, no capítulo 4 abordamos um aspecto que frequentemente parece passar batido: a precisão temporal das comunidades. Encontramos que, em geral, o padrão de decaimento de espécies vocalmente ativas ao longo da noite é preponderante nas comunidades estudadas. Além disso, observamos que

comunidades localizadas em habitats aquáticos temporários apresentaram menor similaridade temporal ao longo da noite do que aquelas localizadas em lagoas permanentes. Verificamos que as comunidades possuem maior consistência na variação de atividade noturna quando localizadas em áreas com vegetação terrestre localmente homogênea, dominada por gramíneas e inseridas em paisagens predominantemente abertas, enquanto as comunidades em áreas localmente mais heterogêneas em vegetação e inseridas em paisagens com maior proporção de áreas florestadas apresentam menor consistência. Deste modo, discutimos que diferenças em curto prazo no padrão de atividade de espécies podem influenciar interações competitivas no espaço por partição temporal, destacando a importância de incluir espaço e, igualmente, tempo em abordagens de ecologia de comunidades.

Finalmente, espero que as revisões aqui apresentadas sejam utilizadas como referenciais rumo a padronização e melhores práticas em monitoramento acústico. Concluo a tese com expectativas de que futuros estudos possam aproximar vertentes comportamentais e sensoriais dos organismos ao entendimento de comunidades ecológicas. Os coros animais têm-se revelado orquestrado por diversos mecanismos ecológicos e comportamentais atuando em distintas escalas que acabam influenciando a coesão de um conjunto de organismos vocalmente ativos. Por meio de novas abordagens e com o advento de novas tecnologias, podemos atualizar paradigmas sobre a estruturação das comunidades e adicionar fatores sociais e ecológicos, cuja adequada representação requer a inclusão explícita de diferentes escalas temporais e espaciais.

