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**INSTITUTO DE BIOCÊNCIAS  
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**INIMIGO ENTRE NÓS: AS CONSEQUÊNCIAS DA INTERAÇÃO ENTRE  
ANFÍBIOS NATIVOS E INVASORES**

**PORTO ALEGRE  
2019**

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Dissertação apresentada ao Programa de Pós-Graduação em Biologia Animal, Instituto de Biociências da Universidade Federal do Rio Grande do Sul, como requisito parcial à obtenção do título de Mestre em Biologia Animal.

Área de concentração: Biologia e Comportamento Animal

Orientador: Prof. Dr. Murilo Guimarães

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Aprovada em \_\_\_\_\_ de \_\_\_\_\_ de \_\_\_\_\_.

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*"O resto é mar, e tudo que eu não sei contar  
São coisas lindas que eu tenho pra te dar  
Vem de mansinho a brisa e me diz  
É impossível ser feliz sozinho"*

*Tom Jobim*

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## RESUMO

Invasões biológicas podem causar uma série de efeitos negativos em populações nativas e são principalmente preocupantes quando lidamos com grupos em declínio mundial, como anfíbios. A rã-touro, *Lithobates catesbeianus*, é um anfíbio anuro com alto potencial invasor, sendo considerada uma das 100 piores espécies invasoras do mundo pela IUCN. Aqui, nós avaliamos os efeitos da rã-touro em populações de anuros nativos, usando um modelo hierárquico de co-ocorrência com abordagem bayesiana. Não encontramos diferenças nas probabilidades de detecção e ocorrência das espécies nativas quando na presença e ausência da rã-touro. Porém, o uso do habitat e atividade das espécies nativas se mostrou diferente nos dois cenários. A presença da rã-touro causa um distúrbio em populações nativas, que pode alterar o comportamento e uso de habitat em resposta à essa invasão. Ao longo do tempo, essas mudanças podem gerar consequências mais graves, como deslocamento de espécies nativas para áreas menos favoráveis e até mesmo declínios populacionais. Este trabalho fornece informações pertinentes a respeito dos efeitos sutis de espécies invasoras e como eles podem ser avaliados em populações nativas.

**Palavras-chave:** invasão biológica, modelagem de co-ocorrência, atividade, uso de habitat, rã-touro

## ABSTRACT

Biological invasions can cause several negative effects in populations and are specially concerning when we deal with groups in decline, such as amphibians. The bullfrog, *Lithobates catesbeianus*, is an amphibian anuran with a high invasive potential, being considered one of the 100 world's worst invasive alien species, by IUCN. Here, we evaluate the effects of the bullfrog in native anuran populations, using a hierarchical co-occurrence model with bayesian approach. Also, we evaluate what is the main focus of publications on the effect of alien anurans. We found little differences in the detection and occurrence probabilities of the native species when in the presence and absence of the bullfrog. However, activity and habitat use of the native species was different in both scenarios. The presence of the bullfrog cause a disturbance in native populations that may alter behaviour and habitat use in response to this invasion. Over time, these changes can result in serious consequences such as displacement of native species to sites less favourable and even population declines. Our work provides relevant information about the subtle effects of invasive species and how they can be evaluated in native populations.

**Keywords:** bioinvasion, co-occurrence modelling, activity, habitat use, bullfrog



## INTRODUÇÃO GERAL

Invasões biológicas são consideradas uma das maiores causas de perda de biodiversidade e modificação de ecossistemas no mundo (Simberloff *et al.* 2013). Desde o início da revolução industrial, com o aumento do comércio e transporte internacional, a introdução de espécies exóticas vem crescendo mundialmente. Este problema é agravado por perturbações antrópicas, que incluem mudanças no clima global e ciclos biogeoquímicos, tornando os ecossistemas mais frágeis e suscetíveis ao estabelecimento de espécies invasoras (van Wilgen *et al.* 2014; Medeiros 2015).

Por definição, espécie exótica é aquela introduzida pelo homem fora de sua área de distribuição atual ou passada, de forma intencional ou acidental. A espécie exótica se torna invasora quando sua introdução ameaça a biodiversidade nativa. Apesar de menos de 20% de todas as espécies exóticas se tornarem invasoras (IUCN 2017), os efeitos ecológicos e socioeconômicos negativos que estas causam são incalculáveis (van Wilgen *et al.* 2008; MacIsaac *et al.* 2011).

Existem diversos fatores ligados ao sucesso de uma espécie invasora, tais como hábitos alimentares generalistas, ausência de predadores e parasitas nativos, grande plasticidade ecológica, altas taxas de reprodução e variabilidade genética (Ehrlich 1989). Espécies invasoras competem por recursos com espécies nativas, introduzem patologias, induzem mudanças em comportamentos e nichos ecológicos e reduzem a variabilidade genética, podendo levar a declínios e extinções populacionais (Mooney & Cleland 2001; Vilà *et al.* 2010). As invasões, além de causarem impactos negativos em populações, afetam comunidades e ecossistemas, e podem alterar o ciclo de nutrientes, teias alimentares, modificar a hidrologia de bacias hidrográficas, reduzir a complexidade de habitats e riqueza de espécies (Simberloff *et al.* 2013).

O reconhecimento dos problemas causados por invasões propiciou o crescimento de uma área de estudo chamada de Ciência da Invasão ou *Invasion Science* (MacIsaac *et al.* 2011). Ainda que subestimado, acredita-se que aproximadamente oito novos primeiros registros de espécies invasoras são registrados por ano no mundo, e para maioria dos táxons esse número mostra sinais de aumento ao longo tempo (Seebens *et al.* 2017). Atualmente, de acordo com a Global Invasive Species Database, 175 espécies invasoras estão presentes no Brasil. Somente na zona

costeira brasileira foram registradas 58 espécies exóticas, sendo nove (16%) delas consideradas invasoras (Lopes et al. 2009).

Apesar do crescente aumento na taxa de invasões, os efeitos das espécies invasoras ainda estão pouco descritos (Crossland et al. 2008). Neste contexto, uma preocupação importante é avaliar a resposta de grupos biológicos sensíveis, como os anfíbios, que desempenham papel diferenciado nos ecossistemas importando e exportando energia entre o ambiente aquático e o terrestre. O declínio mundial de anfíbios é hoje amplamente reconhecido e tem levantado questões importantes acerca de suas possíveis causas, além de motivar interesse por ações de conservação (Blaustein & Kiesecker 2002; Beebe & Griffiths 2005). Dentre as principais ameaças estão a perda e degradação de habitats e a radiação ultravioleta (Kiesecker et al. 2001). Recentemente, os efeitos da introdução de espécies exóticas vêm ganhando mais atenção (Bellard et al. 2016; McCallen et al. 2019).

No Brasil se conhecem seis espécies de anfíbios com populações invasoras confirmadas (Forti et al. 2017). Considerando as similaridades de comportamento e uso de hábitat, interações negativas entre anfíbios nativos e exóticos já são descritas em diversos sistemas. Anfíbios invasores contribuem para o declínio de populações de anfíbios nativos (Kats & Ferrer 2003), e a ausência de história evolutiva compartilhada pode explicar este padrão (Gillespie 2001). Assim, pode-se esperar variados tipos de respostas de curto, médio e longo prazo por parte das espécies nativas, que não apresentam estratégias de defesa contra a ameaça recente.

Mesmo com a crescente preocupação com a bioinvasão e a sua relação com o declínio populacional de anfíbios, ainda há uma ampla lacuna de conhecimento a ser preenchida. Invasão biológica é um tópico que começou a receber mais atenção em estudos ecológicos somente a partir dos anos 1990 em diante, quando houve um aumento significativo no número de artigos sobre o tema (McCallen et al. 2019). Na América do Sul, por exemplo, estudos com espécies exóticas são escassos e acabam por subestimar o número de invasores e seus potenciais efeitos (Speziale et al. 2012). Ainda que exista o reconhecimento do problema e a necessidade de manejo de invasores, a ameaça de novas introduções ultrapassa a quantidade de medidas mitigadoras propostas (Early et al. 2016).

Uma das espécies de anfíbios anuros invasoras mais conhecidas é a rã-touro *Lithobates catesbeianus* (Shaw, 1802), nativa da porção leste da América do Norte.

Esta espécie possui um alto potencial invasor e atualmente é encontrada em quase 40 países de todo o mundo (Lever 2003; Kraus 2009). No Brasil, os primeiros exemplares foram introduzidos por volta de 1930, quando foi criado o primeiro ranário do país, no Rio de Janeiro. Ao longo da década seguinte, houve um crescimento da prática devido a programas governamentais de incentivo e fomento. Contudo, neste período não havia qualquer tipo de avaliação técnica para a criação de rãs-touro, ou estudos biológicos e ecológicos afim de controlar a prática e evitar a fuga dos animais para ambientes naturais. O abandono de inúmeros ranários no país, na década de 1990, devido ao fracasso da prática, resultou na fuga de indivíduos da espécie que se estabeleceram em ecossistemas naturais e persistem até hoje (Cunha & Delariva 2009).

A revisão mais recente da ocorrência de *Lithobates castesbeianus* no Brasil indica que a espécie está presente em 130 municípios, sendo que a maioria dos novos registros de ocorrência foram computados no sul e sudeste do país (Both *et al.* 2011). Essas regiões são consideradas especialmente sensíveis à invasão da rã-touro por abrigar o bioma Mata Atlântica, que apresenta condições climáticas favoráveis ao estabelecimento da espécie (Ficetola *et al.* 2007; Giovanelli *et al.* 2008).

Quando adulta, a rã-touro apresenta hábito alimentar generalista e consome uma grande variedade de presas, incluindo indivíduos da própria espécie e outros anfíbios anuros (Bury & Whelan 1984; Blaustein & Kiesecker 2002; Silva *et al.* 2009,2011). A espécie é também conhecida por registros ocasionais de predação de grandes animais como morcegos, serpentes, aves e ratos (referências em Bury & Whelan 1984; Kaefer *et al.* 2007). Girinos se alimentam preferencialmente de plantas aquáticas, mas também de pequenos invertebrados (Altig *et al.* 2007; Ruibal & Laufer 2012).

A presença de espécies invasoras pode causar uma série de implicações negativas às populações naturais. Os efeitos mais imediatos e diretos, decorrentes de predação ou competição, são normalmente os mais estudados (Kiesecker & Blaustein 1998, Silva *et al.* 2009, 2011). Por outro lado, efeitos menos evidentes são também importantes para o entendimento do processo de invasão. Mudanças de comportamento de espécies nativas podem resultar da simples presença de um invasor causando, por exemplo, o deslocamento da espécie para microhabitats menos favoráveis (Hoare *et al.* 2007). Esses efeitos podem levar um longo período para serem notados e podem ser a causa subjacente de efeitos mais críticos, como declínios

populacionais (Kiesecker *et al.* 2001, Mooney & Cleland 2001). Alterações comportamentais e de uso de habitat resultantes da interação com rã-touro já são observadas nas populações de *Rana aurora* do estado do Oregon, USA há um longo período (Kiesecker & Blaustein 1997,1998; Blaustein and Kiesecker, 2002). Acredita-se que o declínio de populações desta espécie possa estar ligado a estas interações. No Brasil, estudos indicam que a vocalização da rã-touro altera o comportamento de canto de espécies nativas e pode mascará-los no ambiente (Both & Grant 2012; Medeiros *et al.* 2017).

Considerando a crescente ameaça que invasões biológicas representam para populações nativas e a lacuna de conhecimento, este trabalho se concentra no grupos dos anfíbios e tem como objetivo geral avaliar os efeitos de espécies invasoras sobre populações nativas. Para isto, utilizamos duas espécies nativas como modelos biológicos, a rã-boiadora (*Pseudis minuta*) e a rã-manteiga (*Leptodactylus latrans*) (Fig. 1). A proposta conta com um estudo de campo envolvendo populações invasoras de rã-touro e das espécies nativas citadas. Nosso objetivo geral é avaliar o efeito da rã-touro sobre o uso de habitat e atividade das espécies nativas. Nós esperamos identificar mudanças nestes parâmetros quando compararmos populações nativas invadidas e não-invadidas pela rã-touro.



**Figura 1** Espécies alvo do trabalho. A: rã-touro (*Lithobates catesbeianus*), espécie invasora, B: rã-manteiga (*Leptodactylus latrans*) e C: rã-boiadora (*Pseudis minuta*), ambas espécies nativas do Brasil.

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# CAPÍTULO 1

THE ENEMY WITHIN: CONSEQUENCES OF THE INVASIVE BULLFROG ON NATIVE ANURAN POPULATIONS

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## **Author contributions**

Stephanie da Silva Silveira and Murilo Guimarães conceived the ideas and designed the experiment, Stephanie da Silva Silveira collected the data, Stephanie da Silva Silveira and Murilo Guimarães analyzed the data and contributed critically to the drafts and gave final approval for publication.

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## Abstract

Niche theory predicts that species with similar functional traits are more likely to co-occur, but competition may arise and species tend to differentiate along the space and time dimensions. The introduction of a novel non-indigenous competitor is especially critical, because native species share no evolutionary history with the invader and the interaction between invasive and native species may result in several detrimental effects for resident populations. The bullfrog, *Lithobates catesbeianus*, is one of the most important invasive anurans, affecting native faunas, especially anurans, due to similar traits common to all amphibians. Here we assessed the impacts of the invasive bullfrog on two native frog species from southern Brazil. We used a hierarchical co-occurrence model fit in a Bayesian framework to investigate the effects of the bullfrog on native species, testing the hypothesis that bullfrog presence changes the activity of native species and their relationship with habitat. We found that both occupancy and detection probabilities of native species were similar with bullfrog presence or absence at a site. However, we observed changes in microhabitat use and activity preferences of both native species when the bullfrog was present, suggesting that the presence of the invasive species altered the behavior of the native species. Changes induced by invasive species can result in severe long-term consequences for native species since niche differentiation may not mediate the ability of species to persist together indefinitely.

**Key-words:** bioinvasion, co-occurrence, activity, habitat use, *Lithobates catesbeianus*

## Introduction

According to niche theory, species with similar functional traits are more likely to co-occur, as they are more adapted to the same environmental conditions (Chesson 2000). At the same time, coexistence may promote competition, leading species to exclusion (Chesson 2000; Leibold et al. 2009). From the perspective of invasion ecology, the introduction of a novel non-indigenous competitor is especially critical, because native species share no evolutionary history with invaders and thus, have no defense mechanism to cope with the new competitors (Kats and Ferrer 2003; Cook and Jennings 2007). Nevertheless, the coexistence of native and invasive species may be possible if they exploit resources at different spatial or temporal scales.

The interaction between invasive and native species can result in several detrimental effects for resident populations over time and space (Mooney and Cleland 2001; Simberloff et al. 2013; Blackburn et al. 2014), leading to temporary or permanent changes in population structure and survival. Shifts in native species' activity and behavior may be triggered by an invader, influencing habitat use patterns over time (Mayer et al. 2015). Severe effects, such as mortality through predation, competition or poisoning, reduce survival and may lead populations to decline or even to become extinct (Greenlees et al. 2010; Richter-Boix et al. 2013).

The bullfrog, *Lithobates catesbeianus*, is one of the best-known invasive amphibian species, featuring on the "100 world's worst invasive alien species" list, assessed by the IUCN. It is originally from eastern North America, but currently can be found in nearly 40 countries and four continents (Lever 2003; Kraus 2009), mostly due to intentional introductions for farming (Ficetola et al. 2007; Giovanelli et al. 2008). Because of its generalist habits and large size, the bullfrog preys on a variety of animals, including native anurans of invaded areas (Blaustein and Kiesecker 2002; Silva et al. 2009, 2011). In the United States, bullfrog has been related to population losses of pacific treefrogs, foothill yellow-legged frogs and red-legged frogs, mainly due to competition and predation (Blaustein and Kiesecker 2002). In Brazil, the bullfrog was introduced in the 1930's and so far, no record of population decline or extinction for any other species exists, although impacts on anuran species and communities have been reported (Silva et al. 2011; Both and Grant 2012; Medeiros et al. 2017).

Native amphibians may be the group most affected by the bullfrog, since they are potential competitors, given the similarity of their niche. Currently, one third of amphibians are at risk of extinction, and bio-invasion is among the main causes of worldwide population declines in the group (Knapp and Matthews 2000; Kats and Ferrer 2003). Understanding the response of native populations to a novel non-indigenous species can be critical to understand the invasion process, to predict future outcomes and to develop better management strategies (Zarnetske et al. 2013; Gallien and Caboni 2017).

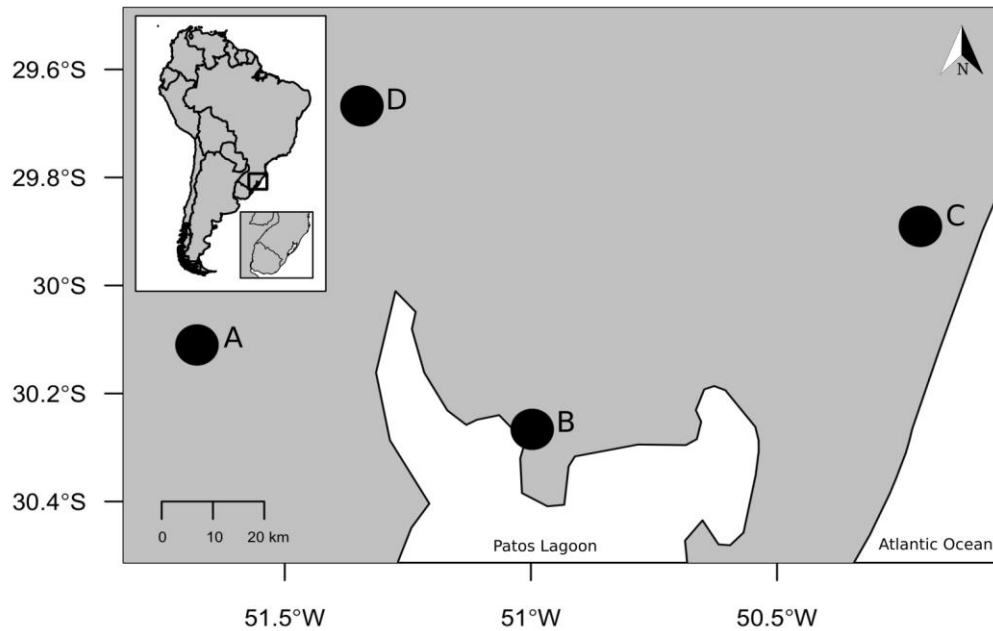
Here we investigate potential changes induced by the bullfrog on native frog species by testing the hypothesis that the presence of the bullfrog induces native species' population disruption. We predict that native species will show differences in habitat use and activity when the bullfrog is present at a site. To test these ideas, we use a co-occurrence occupancy model that corrects the inferences about presence and absence of these species for imperfect detection and allows detection error of native species to differ according to bullfrog presence or absence.

## **Material and methods**

### **Study area and species**

We performed our study in southern Brazil, state of Rio Grande do Sul (Fig. 1). The study area lies in a transitional zone between seasonal forests, grasslands and coastal dune forests (Hasenack et al. 2017). The climate in the region is subtropical, with rainfall distributed throughout the year and mean annual temperatures between 18°C and 22°C (Moreno 1961; Maluf 2000). The bullfrog is currently distributed mainly in the eastern portion of Brazil (Giovanelli et al. 2008; Both et al. 2011), and is considered invasive throughout all the study area.

For our study, we searched for permanent ponds in private lands and protected areas in the eastern part of the state, assessed according to permission, costs and logistics. We were able to select 58 ponds in four different localities spanning a region of 6,600 km<sup>2</sup> (Fig. 1). Ponds (hereafter 'sites') varied in size, between 0.0045km<sup>2</sup> and 7.85km<sup>2</sup>, and were mostly inside private land, where the surrounding landscapes included a variety of anthropogenic modification such as livestock grazing, roads and urban settlement. The number of sites in each locality varied from six to 23 (Fig. 1).



**Fig. 1** Study area showing the four surveyed localities in the state of Rio Grande do Sul, southern Brazil: Eldorado do Sul (A - 15 sites), Porto Alegre (B - 24 sites), Osório (C - 6 sites) and Capela de Santana (D - 13 sites)

To test our hypothesis we selected adults of two common native frog species that overlap with the bullfrog in microhabitat use and activity patterns. The lesser swimming frog, *Pseudis minuta* (Pseudidae), is an aquatic frog that is found inside ponds, floating on the water surface and is associated with available aquatic vegetation (Zank et al. 2008). The presence of bullfrog is also associated with sites with more emergent vegetation, as it provides more suitable places for oviposition (Li et al. 2011; Liu et al. 2016; Medeiros et al. 2017). Both lesser swimming frog and bullfrog also overlap in breeding period in southern Brazil, with a prolonged reproductive season, peaking in the hottest months of the year (Melchior et al. 2004; Kaefer et al. 2007). The second native species is the criolla frog, *Leptodactylus latrans* (Leptodactylidae). Differently from the lesser swimming frog and the bullfrog, the criolla frog is mainly found around or close to the edge of ponds, where they also lay their eggs, or even far from ponds, between vegetation, when not breeding (Langone 1994; Bertoluci 1998; Hartmann et al. 2010). All three species co-occur in the study area, not always together.

## **Sampling design**

The 58 sites were surveyed monthly during the breeding season (austral spring and summer), from October 2017 to March 2018. On each sampling occasion and site, we randomly selected an initial sampling point around the pond's edge. Then, two to four observers stood 30 meters apart from each other on the pond's edge, starting from the initial point. We adopted the independent observer method, where each trained observer sampled the pond with no communication with each other, representing multiple independent visits during the same sampling occasion (Borchers et al. 1998; Mackenzie et al. 2018). Sites were surveyed from two to six times, and the presence of the three species was recorded using 10-min auditory and visual cues, always after sunset, between 7 pm and 1 am, when species were active. Species were identified based on their distinct calls or visually and captured by hand only when essential for identification.

## **Microhabitat use and activity covariates**

Along with the species detection/non-detection data, we collected information on covariates that likely influence the occurrence of species. To estimate the effects of microhabitat use, we included pond area ('area') and proportion of macrophyte vegetation cover ('veg') because they are important predictors of frog habitat use, as mentioned above. Both covariates did not vary significantly during the period of the study, so we used mean values for each site. These spatial covariates were included in the estimation of occupancy probability.

We included nocturnal activity recording the time species were active at nights ('time', recorded as minutes after midnight), activity along the breeding season recording the date of sampling according to the Julian calendar ('date') and water temperature ('twater') because they are generally good predictors of frog activity (Oseen and Wassersug 2002; Zank et al. 2008). We measured water temperature with a digital skewer thermometer in the surface of the water, close to the pond edge where the surveys were conducted. These temporal covariates were used to understand species' activity patterns by including them in the detection probability parameter, which is related to physical activity, producing a strong signal in the detection probability (Strebel et al. 2014; Sutherland et al. 2016). All numerical covariates were scaled to have zero mean and one standard deviation.

## Statistical analysis

We fitted the Waddle et al. (2010) co-occurrence occupancy model to investigate statistical interactions between the species while considering the effects of covariates. In this model one species is considered as dominant (here, the invader) and the other as subordinate (the natives), as a prey-predator approach, where occurrence and detection of the subordinate is modelled conditional on the presence or absence of the dominant (Waddle et al. 2010).

The model distinguishes the ecological process from the observation process, where the latter describes measurements error in the presence/absence of a species at a site. The ecological process describes the presence or absence of a species and is governed by the occupancy probability ( $\psi$ ), the probability a species occupies a site. The observation process represents the detection probability ( $p$ ), the probability a species is detected given species' presence (Kéry & Royle 2016).

Occupancy is described as a Bernoulli random variable ( $z$ , equation 1). Waddle et al.'s (2010) model adopts three parameters to model the joint distribution of the occupancy state of the species:  $\psi^B$  (occupancy probability of dominant species),  $\psi^{A|B}$  (occupancy probability of subordinate species, given dominant is present) and  $\psi^{A|\bar{B}}$  (occupancy probability of subordinate, given dominant is absent, equation 2). Here, note an if-else statement in the parentheses of the Bernoulli.

$$(1) \quad z^B | \psi^B \sim \text{Bernoulli}(\psi^B)$$

$$(2) \quad z^A | z^B, \psi^{A|B}, \psi^{A|\bar{B}} \sim \text{Bernoulli}(z^B \psi^{A|B} + (1 - z^B) \psi^{A|\bar{B}})$$

The second submodel is represented by another Bernoulli random variable ( $y$ ). Because our ability to detect a species at a site depends on whether the species is present at that specific site, the encounter history ( $y$ ) is conditional on the binary occurrence state of the species ( $z$ , equation 3). In addition, the detection of the subordinate species is conditional on the true occurrence state of the dominant species (equation 4).

$$(3) \quad y^B | z^B, p^B \sim \text{Bernoulli}(z^B p^B)$$

$$(4) \quad y^A | z^A, z^B, p^{A|B}, p^{A|\bar{B}} \sim \text{Bernoulli}(z^A \{z^B p^{A|B} + (1 - z^B) p^{A|\bar{B}}\})$$

All microhabitat use and activity covariates were included as logit-scale parameters in a linear model (MacKenzie et al. 2002). We fitted two models, one for the pair bullfrog-lesser swimming frog and another for the pair bullfrog-criolla frog.

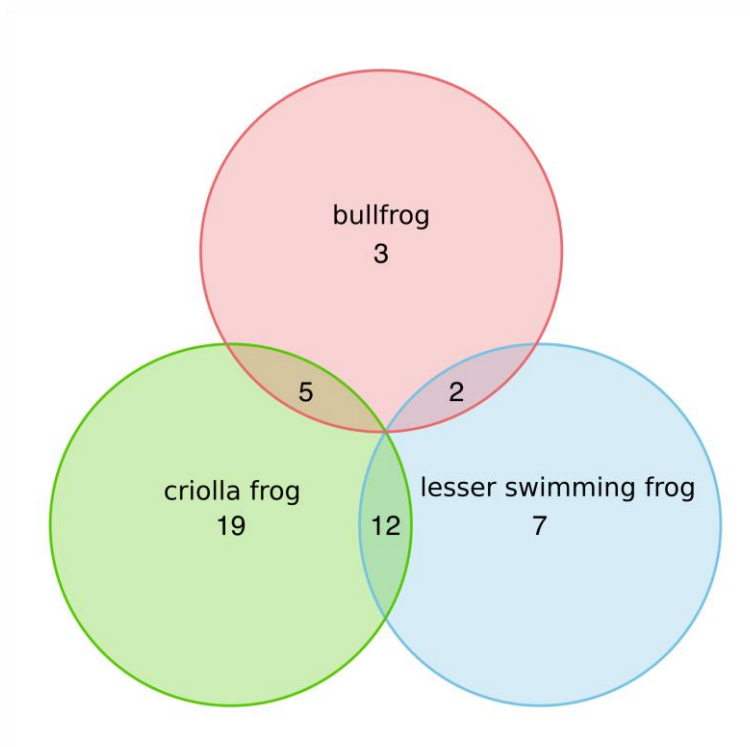
We addressed potential issues of pseudoreplication (Hurlbert 1984) to control for potential dependency among sampling units (Lazic 2010) within localities (A, B, C, D, see Fig. 1) by including a random normal variable *eps* for each model with zero mean and variance *thau.alpha* (see JAGS code in Online Resource 1), i.e., we treated *eps* as a type of block effect. With our model structure we were able to account for detection errors, to incorporate predictors of species occupancy and detection, and to account for the blocking structure represented by the sites (ponds) that were nested within the four regions.

The analysis was conducted in software JAGS (Plummer 2003) run through R (R Core Team 2019), via the jagsUI package (Kellner 2014). We employed a Bayesian approach with Markov Chain Monte Carlo, using vague priors for all parameters (Kéry and Royle 2016) (Online Resource 1). We ran 3 chains of 650,000 iterations each, with a burn-in period of 475,000 iterations, adaptation phase of 30,000 and thinning by a rate of 100, resulting in 5,250 samples for the posterior distribution for each parameter estimated (Online Resource 1). We checked chain convergence by visual inspection of trace plots and by the Brooks-Gelman-Rubin statistic (Brooks and Gelman 1998), which were always below 1.1. We present mean estimates of occupancy and detection, as well as predictor effects for the native (subordinate) species in the presence and absence of the invader (dominant). We also report the 95% credible intervals (CRI) for all posterior distributions. We assumed statistical “significance” when the 95% CRI’s for a parameter did not overlap zero.

## **Results**

We detected the bullfrog in 10 out of the 58 sites surveyed (17%), whereas the lesser swimming frog was found in 19 sites (33%) and the criolla frog in 31 sites (53%; Fig. 2). Species were found alone or in pairs within sites, but never the three at the same site. Most detections of the lesser swimming frog came from auditory cues, while the criolla frog was mostly found visually. Below we first present the estimates of detection and occupancy probabilities, and then the effects of activity and

microhabitat predictors on native species in the presence and in the absence of the invasive bullfrog.



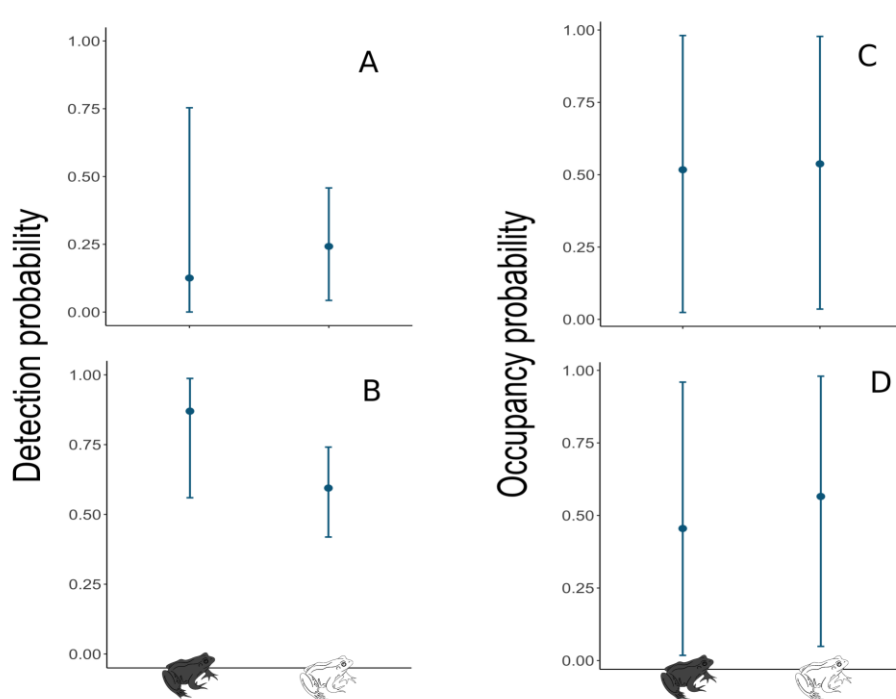
**Fig. 2** Number of co-occurring sites among species

### **Detection and occupancy patterns**

Detection probability of the lesser swimming frog was higher when the bullfrog was absent (0.24, CRI 0.04 to 0.46; Fig. 3a) than when it was present (0.12, CRI 0.00 to 0.75; Fig. 3a). Occupancy of the lesser swimming frog was similar both in the absence (0.54, CRI 0.02 to 0.98; Fig. 3c) and in the presence of the bullfrog (0.52, CRI 0.02 to 0.98; Fig. 3c).

In the bullfrog's absence, detection probability of the criolla frog was lower (0.59, CRI 0.42 to 0.74, Fig. 3b) than when the bullfrog was onsite (0.86, CRI 0.05 to 0.45, Fig. 3b). Occupancy probability of the criolla frog was slightly higher (0.56, CRI 0.05 to 0.99, Fig. 3d) when the bullfrog was absent than when it was present (0.45, CRI 0.02 to 0.96, Fig. 3d).



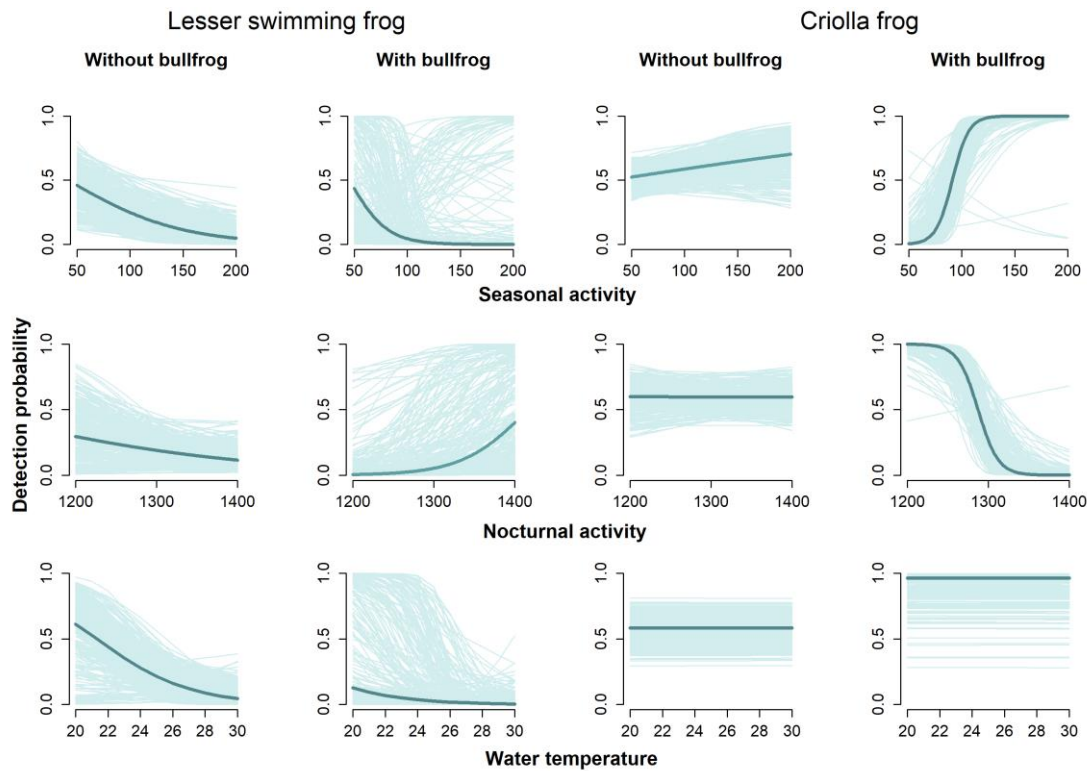


**Fig. 3** Mean detection and occupancy probabilities and the 95% credible intervals of the lesser swimming frog (A and C) and the criolla frog (B and D) in the presence (shaded frog) and absence (light frog) of the bullfrog

### Activity of native species

Activity of the lesser swimming frog was significantly higher in the beginning of the breeding season in sites the bullfrog was absent ( $\alpha_{date.pm.without} = -1.31$ , CRI -3.18 to -0.48, Fig. 4, Online Resource 2). However, such effect became non-significant when the bullfrog was onsite ( $\alpha_{date.pm.with} = -3.89$ , CRI -12.61 to 4.402; Fig. 4). Activity of the lesser swimming frog along the night did not vary when the bullfrog was absent ( $\alpha_{time.pm.without} = -0.99$ , CRI -3.31 to 1.09, Fig. 4, Online Resource 2), but with bullfrog presence, the lesser swimming frog was active later on the night ( $\alpha_{time.pm.with} = 4.52$ , CRI 0.731 to 10.47, Fig. 4, Online Resource 2). The water temperature did not influence the activity of the lesser swimming frog, regardless of the absence or presence of the bullfrog (Online Resource 2).

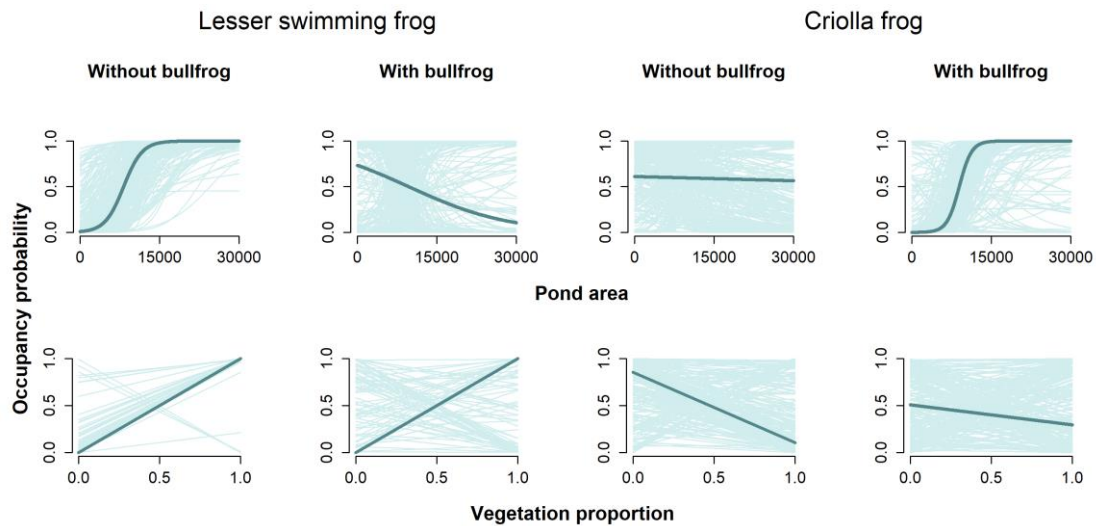
The criolla frog was equally active during the breeding season and along the nights when the bullfrog was absent. However, in the presence of the bullfrog, the criolla frog was significantly more active later in the breeding season ( $\alpha_{ll.date.with} = 9.05$ , CRI 2.59 to 15.62) and earlier at nights ( $\alpha_{ll.time.with} = -16.56$ , CRI -28.67 to -4.54; Fig. 4). Water temperature was not related to activity of the criolla frog when the bullfrog was absent or present (Fig. 4, Online Resource 2).



**Fig. 4** Relationship between detection probability and activity predictors for the lesser swimming frog and the criolla frog in the presence and in the absence of the invasive bullfrog. Dark blue lines show the posterior means and light blue lines show estimation uncertainty, based on 300 random posterior distributions sampled.

### Microhabitat use of native species

In sites with no bullfrog, occupancy probability of the lesser swimming frog was positively related to pond size ( $\beta_{pondarea.pm.without} = 8.21$ , CRI 1.42 to 25.78, Fig. 5) and vegetation cover ( $\beta_{veg.pm.without} = 9.03$ , CRI 1.54 to 27.49, Fig. 5, Online Resource 2). However, both effects were non-significant in sites including the bullfrog ( $\beta_{pondarea.pm.with} = -1.51$ , CRI -28.66 to 27.64;  $\beta_{veg.pm.with} = 7.38$  CRI -22.95 to 25.78, Fig. 5, Online Resource 2). Neither pond size nor vegetation cover influenced occupancy probability of the criolla frog, either in the presence or absence of bullfrog (Fig. 5, Online Resource 2).



**Fig. 5** Relationship between occupancy probability and microhabitat predictors for the lesser swimming frog and the criolla frog in the presence and in the absence of the invasive bullfrog. Dark blue lines show the posterior means and light blue lines show estimation uncertainty, based on 300 random posterior distributions sampled.

## Discussion

We assessed the effects of the presence of the invasive bullfrog on microhabitat use and activity of native frog species from southern Brazil. With our results, we highlight two important points. First, occupancy and detection probability estimates were relatively similar, especially considering the superimposed intervals, for both native frogs when the bullfrog was either present or absent. Second, in most cases the presence of the bullfrog disrupted the relationship between native species, microhabitat use and activity. We found the pairs invasive-native species in a relatively small number of sites, which may reflect the wide credible intervals estimated.

## Detection and occupancy patterns

In general, the results for detection probability were similar to occupancy, where estimates for native species in the presence and absence of the bullfrog were superimposed. Detection probability is always dependent on detection methods and here we combined visual and auditory cues to find species. Most detections of the lesser swimming frog came from auditory search, because the species is mostly found in the center of ponds, sometimes in relatively deep water, which difficult its visualization in large ponds. We detected the criolla frog mostly visually, since the

species is common along pond edges. Despite the different methods to find the species, both species are active in the wet season, where breeding activity is intense.

Both native lesser swimming frog and criolla frog are common species in our study area and widely distributed in southern South America (Frost 2019). The invasion of the bullfrog did not seem to change the proportion of ponds occupied by these two native species, but we suggest caution on this conclusion. The lesser swimming frog co-occurs with the bullfrog in sites about 350 km from our sampling area, in Uruguay. There, the abundance of this native frog was nine to ten times lower in sites invaded by the bullfrog, when compared to non-invaded sites (Gobel et al. 2019). In this way, native population stability and species persistence may be measured using multiple approaches to detect variations on individuals, populations and the relationship with the habitat.

### **Enemy within, part I: the bullfrog induces activity differences**

The bullfrog changed the activity pattern along the night and the breeding season for both the lesser swimming frog and criolla frog. In sites with no bullfrog, the lesser swimming frog was more active earlier in the breeding season but showed no preference along the nocturnal activity. In the presence of the bullfrog, the pattern reversed, with the lesser swimming frog showing no activity preference along the breeding season, but preference in nocturnal activity. The lesser swimming frog presents extended breeding and vocal activity, with preference for the hottest months of spring and summer (Zank et al. 2008, 2010; Huckembeck et al. 2012). Additionally, its nocturnal activity is also extended (Zank et al. 2008). Even considering the extended activity of the species, our findings show that the bullfrog presence is able to change the pattern. Similarly, the criolla frog did not present activity preferences when the bullfrog was absent. However, we observed higher activity levels later in the breeding season and earlier nocturnal activity when the bullfrog was present. Changes in activity patterns may result from behavioral responses, as a way to avoid the invader (Mayer et al. 2015). Our results support previous information from the literature, showing that invasive amphibians, such as the bullfrog (Kiesecker and Blaustein 1997) and the cane toad (Greenlees et al. 2007), as well as other alien species induce changes in behavioral activity of native amphibians (Nunes et al. 2019).

Calling activity of the bullfrog in southern Brazil and Uruguay is extended,

with individuals calling throughout the day and night (Medeiros et al. 2016; Laufer et al. 2017). Because bullfrog calls are louder, long-lasting and cover a broad frequency spectrum than native species, they can mask the acoustic signal or even change calling activity of native anurans (Capranica 1966; Nunes and Juncá 2006; Zank et al. 2008; Both and Grant 2012; Bleach et al. 2015). These features of the bullfrog calls can also hinder the ability of observers to detect other calling anurans in the ponds. Studies in Australia have shown that invasive cane toads, which also present loud calls, influence calling behavior of native species. The high competitive abilities of the bullfrog in all life stages compared to native species (Kupferberg 1997; Boelter and Cechin 2012), its predatory habits (Bury and Whelan 1984), the potential to breed nearly year-round in south Brazil (Kaefer et al. 2007) and its extended vocal activity represents a continuous latent threat in invaded sites, influencing activity and displacing native species (Kiesecker and Blaustein 1997).

Although water temperature plays a major role on anuran development and growth (Wheeler et al. 2014) we did not find any influence of this covariate on habitat use of both the lesser frog and the criolla frog either in the presence or absence of the bullfrog. However, it is paramount to consider that biotic factors may mediate the competitive interactions between invasive and native species, being crucial on the invasive success of alien species (Alcaraz et al. 2008). The abundance of the bullfrog seems to be related to photoperiod and air temperature in southern Brazil (Medeiros et al. 2016), both variables that influence water temperature. Thus, suboptimal abiotic conditions may decrease abundance of this invasive species, reducing competition pressure.

### **Enemy within, part II: the bullfrog induces microhabitat use differences**

The presence of the bullfrog broke the strong and positive relationship between the lesser swimming frog and the amount of pond vegetation cover and pond size. Species exploiting the same resources are susceptible to competitive exclusion (Weiher and Keddy 1999; Chesson 2000) and many examples of native species' declines are documented after invasion (Kats and Ferrer 2003). Invasive species may force native species to low-quality areas, such as observed for the yellowtail goatfish from Hawaii, which moved to areas farther away from the reef due to introduction of the blue-line snapper (Schumacher and Parrish 2005). As a consequence, these behavioral responses observed in native populations may lead to changes in species'

habitat use patterns (Mayer et al. 2015), which occurred with the Duvaucel's gecko from New Zealand after the introduction of Pacific rats (Hoare et al. 2007). The exclusion of invasive species may allow native species to return to their natural habitats, but given eradication is rarely feasible, native populations usually co-occur with invaders for such long periods of time that changes they induce in population structure can lead to permanent shifts (Carroll and Dingle 1996).

Unlike the lesser swimming frog, none of the spatial covariates influenced habitat use of the criolla frog neither in presence or absence of the bullfrog. Three life history characteristics may explain this finding. First, leptodactilids are widely distributed in South America (Maneyro et al. 2004; Frost 2019), especially the criolla frog, which presents a specialist-generalist diet composed mainly of terrestrial items (Teixeira and Vrcibradic 2003; Maneyro et al. 2004; Sanabria et al. 2005; Pazinato et al. 2011). In the study area, this species is fairly common, being found in most of the ponds surveyed. The lack of specificity to habitat types displayed by this frog may reflect its opportunistic behavior and wide distribution. Second, while adult lesser swimming frogs attain around 25% of bullfrog adult body size, adult criolla frogs are about 65%, which may help reduce agonistic interactions (Bury and Whelan 1984; Langone 1994). Third, the criolla frog seems to share less habitat preference characteristics with the bullfrog than the lesser swimming frog. Native species sharing more similar functional traits with invaders are the main species expected to suffer the consequences of such interactions (Roy et al. 2012; Sebastián et al. 2015).

Despite our results, even species that diverge in habitat preferences with invaders may be affected. Australian native frogs showing different habitat use preferences from the invasive cane toad were around 15% more abundant in areas where the invader was temporarily removed (Mayer et al. 2015).

### **Concluding remarks**

We assessed local co-occurrence patterns and observed changes in microhabitat use and activity for both native species. Our results suggest spatio-temporal disturbances potentially induced by the bullfrog. Such disturbances may sound subtle, given that similar occupancy and detection trends were observed for both native species in the presence and in the absence of the invader. However, the disruptions observed in microhabitat use and activity of the native species are important, and long-term effects may evolve from subtle changes of species

interaction.

After the introduction of the bullfrog in Brazil, almost 85 years ago, we still lack information on native species' responses upon its invasion. Assessing the magnitude of the effects of bioinvasion constitutes an important way to understand and predict long-term consequences, and species' persistence will be determined by a complex variety of processes across different spatial and temporal scales. Yet, niche differentiation may not mediate the ability of species to persist together indefinitely (Chesson 2000, Siepielski & McPeck 2010, Gravel et al. 2011) and we may be testifying a slow but gradual change in native species' life history caused by invaders.

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## **CONSIDERAÇÕES FINAIS**

Nós encontramos diferenças no uso de habitat e atividade das espécies nativas quando na presença e ausência da rã-touro. Nosso estudo traz à tona a preocupação com efeitos sutis e menos evidentes de invasões, mas que são de extrema importância para a persistência de populações nativas. Também, evidenciamos a necessidade de estudos de campo incorporarem erros de detecção em suas análises, como forma de diminuir potenciais incertezas e erros de estimativa. Acreditamos que este trabalho não só levanta questões importantes sobre bioinvasão, mas também serve como base para outros estudos futuros que busquem entender os efeitos sutis de invasões à nível populacional.

## Online Resource

**Online Resource 1** JAGS model and R code for the two species co-occurrence model, following Waddle et al. 2010 model

### BIOLOGICAL INVASIONS

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```
{[SEP]}# ----- Model for dominant species (L. catesbeianus 'lc') ----- # Priors[SEP]psi.lc ~  
dunif(0,1)[SEP]beta0.lc <- log(psi.lc) - log(1-psi.lc)[SEP]beta1.lc ~ dunif(-30,30) # slope on  
pond area (area)[SEP]beta2.lc ~ dunif(-30,30) # slope on pond vegetation (veg) beta3.lc ~  
dunif(-30,30) #slope for group element
```

```
p.lc ~ dunif(0,1) #detection[SEP]alpha0.lc <- log(p.lc) - log(1-p.lc)[SEP]alpha1.lc ~ dunif(-  
30,30) #slope on season activity (Date) alpha2.lc ~ dunif(-30,30) #slope on nocturnal  
activity (Time) alpha3.lc ~ dunif(-30,30) #slope on water temperature (Twater)
```

```
tau.alpha.lc <- 1 / (sd.alpha.lc * sd.alpha.lc) # sd hyperparam sd.alpha.lc ~ dunif(0,10)
```

```
# Likelihood[SEP]for (i in 1:R) { #loop over sites[SEP]z.lc[i] ~  
dbern(psiMean.lc[i])[SEP]logit(psiMean.lc[i]) <- beta0.lc + beta1.lc*area[i] +  
beta2.lc*veg[i] + beta3.lc * group[i] +
```

```
eps.lc[group[i]]
```

```
for (j in 1:T) { #loop over visits
```

```
y.lc[i,j] ~ dbern(z.lc[i] * pMean.lc[i,j])[SEP]logit(pMean.lc[i,j]) <- alpha0.lc +  
alpha1.lc*Date[i,j] + alpha2.lc*Time[i,j] + alpha3.lc*Twater[i,j]
```

```
} }
```

```
for(g in 1:4){[SEP]eps.lc[g] ~ dnorm(0,tau.alpha.lc) }
```

```
# -----Model for subordinate species (L. latrans 'll')----- [SEP]
```

```
# Priors[SEP]psi.ll.with.lc ~ dunif(0,1)[SEP]psi.ll.without.lc ~
```

```

dunif(0,1)[SEP]beta0.ll.with.lc <- log(psi.ll.with.lc) - log(1-psi.ll.with.lc)
beta0.ll.without.lc <- log(psi.ll.without.lc) - log(1-psi.ll.without.lc)
beta1.ll.with.lc ~ dunif(-30,30) # slope on pond area (area) beta1.ll.without.lc
~ dunif(-30,30) [SEP]
beta2.ll.with.lc ~ dunif(-30,30) # slope on pond vegetation (veg) beta2.ll.without.lc ~
dunif(-30,30) [SEP]beta4.ll.with.lc ~ dunif(-30,30) #group[SEP]beta4.ll.without.lc ~ dunif(-
30,30)

tau.alpha.ll <- 1 / (sd.alpha.ll * sd.alpha.ll) # sd hyperparam sd.alpha.ll ~ dunif(0,10)

p.ll.with.lc ~ dunif(0,1) [SEP]p.ll.without.lc ~ dunif(0,1) [SEP]alpha0.ll.with.lc <-
log(p.ll.with.lc) - log(1-p.ll.with.lc) alpha0.ll.without.lc <- log(p.ll.without.lc) - log(1-
p.ll.without.lc) alpha1.ll.with.lc ~ dunif(-30,30) # slope on season activity (Date)
alpha1.ll.without.lc ~ dunif(-30,30) [SEP]alpha2.ll.with.lc ~ dunif(-30,30) # slope on
nocturnal activity (Time) alpha2.ll.without.lc ~ dunif(-30,30) [SEP]alpha3.ll.with.lc ~
dunif(-30,30) # slope on water temperature (Twater) alpha3.ll.without.lc ~ dunif(-
30,30)

# Likelihood[SEP]for (i in 1:R) {[SEP]z.ll[i] ~ dbern(psi.ll[i])[SEP]logit(psi.ll[i]) <-
beta0.ll.with.lc*z.lc[i] + beta0.ll.without.lc*(1-z.lc[i]) +

beta1.ll.with.lc*z.lc[i]*area[i] + beta1.ll.without.lc*(1-z.lc[i])*area[i] +
beta2.ll.with.lc*z.lc[i]*veg[i] + beta2.ll.without.lc*(1-z.lc[i])*veg[i] +

beta3.ll.with.lc*z.lc[i]*group[i] + beta3.ll.without.lc*(1-z.lc[i]) * group[i] +
eps.ll[group[i]]

for (j in 1:T) {[SEP]y.ll[i,j] ~ dbern(p.ll[i,j])[SEP]p.ll[i,j] <- z.ll[i] *
pMean.ll[i,j][SEP]logit(pMean.ll[i,j]) <- alpha0.ll.with.lc*z.lc[i] +
alpha0.ll.without.lc*(1-z.lc[i]) +

alpha1.ll.with.lc*z.lc[i]*Date[i,j] + alpha1.ll.without.lc*(1-z.lc[i])*Date[i,j] +
alpha2.ll.with.lc*z.lc[i]*Time[i,j] + alpha2.ll.without.lc*(1-z.lc[i])*Time[i,j] +

alpha3.ll.with.lc*z.lc[i]*Twater[i,j] + alpha3.ll.without.lc*(1-z.lc[i])*Twater[i,j]

} }

for(k in 1:4) {[SEP]eps.ll[k] ~ dnorm(0,tau.alpha.ll) }

# ----- Derived quantities (both) ----- for (i in 1:R) {[SEP]tmp11[i] <-
z.lc[i]*z.ll[i][SEP]tmp01[i] <- equals(z.lc[i],0) * equals(z.ll[i], 1)

tmp10[i] <- equals(z.lc[i],1) * equals(z.ll[i], 0) tmp00[i] <- equals(z.lc[i],0) *
equals(z.ll[i], 0) }[SEP]lc.l <- sum(z.lc[i])

```

```
ll.1 <- sum(z.ll[]) lc.1.ll.1 <- sum(tmp11[]) lc.0.ll.1 <- sum(tmp01[]) lc.1.ll.0 <-
sum(tmp10[]) lc.0.ll.0 <- sum(tmp00[]) }[1][SEP][2],fill = TRUE)
```

```
sink() # End of model
```

**Online Resource 2** Posterior distributions of mean, standard deviation and 95% credible intervals of occupancy and detection predictors of the lesser swimming frog (*Pseudis minuta*) and criolla frog (*Leptodactylus latrans*) when in the presence (with) or absence (without) of the invasive bullfrog, *Lithobates catesbeianus*

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Parameter	mean	sd	2.5%	97.5%
<i>Pseudis minuta</i> (lesser swimming frog)				
psi.with	0.517	0.292	0.024	0.981
psi.without	0.537	0.286	0.036	0.978
p.with	0.126	0.206	0.000	0.754
p.without	0.242	0.116	0.043	0.458
area.with	-1.512	16.322	-28.657	27.686
area.without	8.209	6.023	1.419	25.782
veg.with	7.381	13.441	-22.950	28.717
veg.without	9.027	7.046	1.542	27.493
group.with	2.648	12.343	-13.796	28.350
group.without	2.870	7.135	-4.004	24.375
date.with	-3.893	4.045	-12.609	4.402
date.without	-1.311	0.670	-3.185	-0.480
time.with	4.252	2.542	0.731	10.467

time.without	-0.998	1.125	-3.310	1.099
twater.with	-0.914	1.872	-5.256	1.906
twater.without	-0.946	0.595	-2.149	0.333
<i>Leptodactylus latrans</i> (criolla frog)				
psi.with	0.455	0.287	0.018	0.960
psi.without	0.565	0.275	0.049	0.980
p.with	0.870	0.114	0.560	0.987
p.without	0.594	0.089	0.419	0.741
area.with	12.341	8.498	-4.172	28.028
area.without	-0.092	7.706	-12.229	23.599
veg.with	-0.284	2.574	-4.685	3.459
veg.without	-1.218	6.335	-15.232	15.790
group.with	4.077	2.645	-0.206	10.165
group.without	7.249	9.734	-1.130	29.025
date.with	9.050	3.560	2.589	15.623
date.without	0.354	0.346	-0.341	1.027
time.with	-16.560	6.658	-28.672	-4.540
time.without	-0.010	0.597	-1.187	1.123
twater.with	-3.354	1.861	-6.887	0.025
twater.without	0.165	0.319	-0.457	0.796