Biol Invasions (2021) 23:373–378
https://doi.org/10.1007/s10530-020-02385-4

INVASION NOTE

The enemy within: consequences of the invasive bullfrog on native anuran populations

Stephanie da Silva Silveira · Murilo Guimarães

Received: 18 October 2019 / Accepted: 8 October 2020 / Published online: 23 October 2020

Abstract The bullfrog, *Lithobates catesbeianus*, is one of the most important invasive anurans, affecting especially native anurans due to their similar habits. Here we used a hierarchical co-occurrence model fit in a Bayesian framework to investigate the effects of the bullfrog on two native frog species from southern Brazil, 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 activity and microhabitat use 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.

Graphic abstract

The bullfrog, *Lithobates catesbeianus*.
Photograph by Natália Dallagnol Vargas

Keywords Exotic frog · Co-occurrence · Niche theory · Habitat use · *Lithobates catesbeianus*

Introduction

According to niche theory, species with similar functional traits are more likely to co-occur, while coexistence may promote competition and species exclusion (Leibold et al. 2009). The introduction of a non-indigenous competitor is especially critical,

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Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10530-020-02385-4) contains supplementary material, which is available to authorized users.

S. S. Silveira · M. Guimarães (✉)
Programa de Pós-Graduação em Biologia Animal, Departamento de Zoologia, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil
e-mail: mu.guima@gmail.com

because native species share no evolutionary history with invasive species and thus, may be unable to cope with new competitors (Kats and Ferrer 2003). Such interaction can result in several temporary or permanent effects for resident species (Simberloff et al. 2013), including shifts in activity and behavior, and thus, influencing habitat use patterns over time (Mayer et al. 2015).

The bullfrog, *Lithobates catesbeianus*, is one of the best-known invasive amphibian species worldwide and it has been related to population losses mainly due to competition and predation (Blaustein and Kiesecker 2002). Currently, biological invasions are among the main causes of worldwide amphibian declines (Kats and Ferrer 2003) and the invasive amphibians represent a real threat to native amphibians, given their niche similarities. Understanding the response of native populations to an invasive species can be critical to understand the invasion process, to predict future outcomes and to develop better management strategies. Here we test the hypothesis that the presence of the bullfrog induces population disruption in native species. We predict that native species will show opposite activity and habitat use patterns, or at least that such spatiotemporal relationships will be weakened, when the bullfrog is present at a site.

Materials and methods

We performed our study in southern Brazil (Online Resource 1), where there are invasive populations of bullfrog (Both et al. 2011). The study area lies in a transitional zone between seasonal forests, grasslands and coastal dune forests. We sampled 58 ponds (hereafter 'sites'), mostly inside private land. Sites varied in size, between 0.0045 km^2 and 7.85 km^2 with the surrounding landscapes including a variety of anthropogenic modifications such as livestock grazing, roads and urban settlement. We selected adults of two common native frog species that share life-history traits with the bullfrog, including activity patterns and microhabitat use, the lesser swimming frog, *Pseudis minuta* (Pseudidae), and the criolla frog, *Leptodactylus latrans* (Leptodactylidae) (Langone 1994; Zank et al. 2008). All three species co-occur in the study area (Online Resource 2).

We surveyed sites during the breeding season (austral spring and summer), from October 2017 to March 2018, which we assumed closure according to the assumption of occupancy modeling. Two to four trained observers sampled sites using the independent observer method (Borchers et al. 1998), where observers performed sampling with no communication with each other. Thus, observers represented single independent visits at a site and sampling occasion. Given that not all sites were surveyed in all months, we had a total of two to six visits on each site along the breeding season. We recorded the presence of the three species using 10-min auditory search plus 10-min visual search per site, always after sunset, between 7 pm and 1 am. Along with the species detection/non-detection data, we recorded nocturnal activity (the time when sampling occurred, recorded as minutes after midnight, 'time'), activity along the breeding season (date of sampling according to the Julian calendar, 'date') and water temperature ('twater'). These temporal covariates were used to understand species ´activity patterns by including them in the detection probability parameter, which is related to physical activity (Strebel et al. 2014). We collected information on pond area ('area') and proportion of macrophyte vegetation cover ('veg') to estimate the effects of microhabitat use. These spatial covariates were included in the estimation of occupancy probability. For the analysis, the numerical covariates were centered and scaled to have zero mean and one standard deviation. All covariates were included as logit-scale parameters in linear models.

We fitted the Waddle et al. (2010) co-occurrence occupancy model that considers one species as dominant (here, the bullfrog) and the other as subordinate (the native species), as a prey-predator approach. Occupancy and detection of the subordinate is modeled conditional on the presence or absence of the dominant (Waddle et al. 2010). The model distinguishes the ecological process, which means the presence or absence of a species, the occupancy probability (ψ), from the observation process, which describes measurement error in the presence/absence of a species at a site, the detection probability (p) (Kéry and Royle 2016).

We addressed potential issues of pseudoreplication within localities (see Online Resource 1) by including a random normal variable *eps* with zero mean and variance *thau.alpha* (Online Resource 3). 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 spatial structure of sites nested within the four localities. We conducted the analysis in software JAGS (Plummer 2003) run through R (R Core Team 2019), via the jagsUI package (Kellner 2014). We used a Bayesian mode of inference with MCMC techniques and vague priors for all parameters (Kéry and Royle 2016) (details in Online Resource 3). 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 species in the presence and absence of the invader. We used the 95% credible intervals (CRI) for all posterior distributions to measure uncertainty in parameter estimates.

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%; Online Resource 4). Most detections of the lesser swimming frog came from auditory cues, while the criolla frog was mostly found visually. Point estimates of detection and occupancy probabilities of both native species were similar both in the presence and in absence of the bullfrog with superimposed credible intervals (Online Resource 5).

Activity of the lesser swimming frog was 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. 1, Online Resource 6). However, there was no effect when the bullfrog was onsite ($\alpha_{date.pm.with}$ = − 3.89, CRI − 12.61 to 4.402; Fig. 1). 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. 1, Online Resource 6), 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. 1, Online Resource 6). 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 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. 1). Water temperature was not related to activity of the native species (Fig. 1, Online Resource 6).

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. 2) and vegetation cover ($\beta_{veg.pm.without}$ = 9.03, CRI 1.54 to 27.49, Fig. 2, Online Resource 6). However, both effects were unimportant 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. 2, Online Resource 6). Neither pond size nor vegetation cover influenced occupancy probability of the criolla frog, either in the presence or absence of bullfrog (Fig. 2, Online Resource 6).

Discussion

In our study, the bullfrog presence did not change the proportion of ponds occupied by the two native species. On the other hand, the abundance of the lesser swimming frog was nine to ten times lower in sites invaded by the bullfrog in Uruguay, about 350 km from our sampling area (Gobel et al. 2019). Thus, native population stability and persistence should be assessed using multiple approaches to detect variations on individuals, populations and the relationship with habitat. Although we found the pairs invasive-native species in a relatively small number of sites and detection probability was sometimes low, potentially affecting the precision of our estimates (see simulation scenarios in Waddle et al. 2010), the presence of the bullfrog may have disrupted the relationship between native species, activity and microhabitat use in most cases.

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, later on the night. The criolla frog showed no 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). Bullfrog calls are louder, long-lasting and cover a

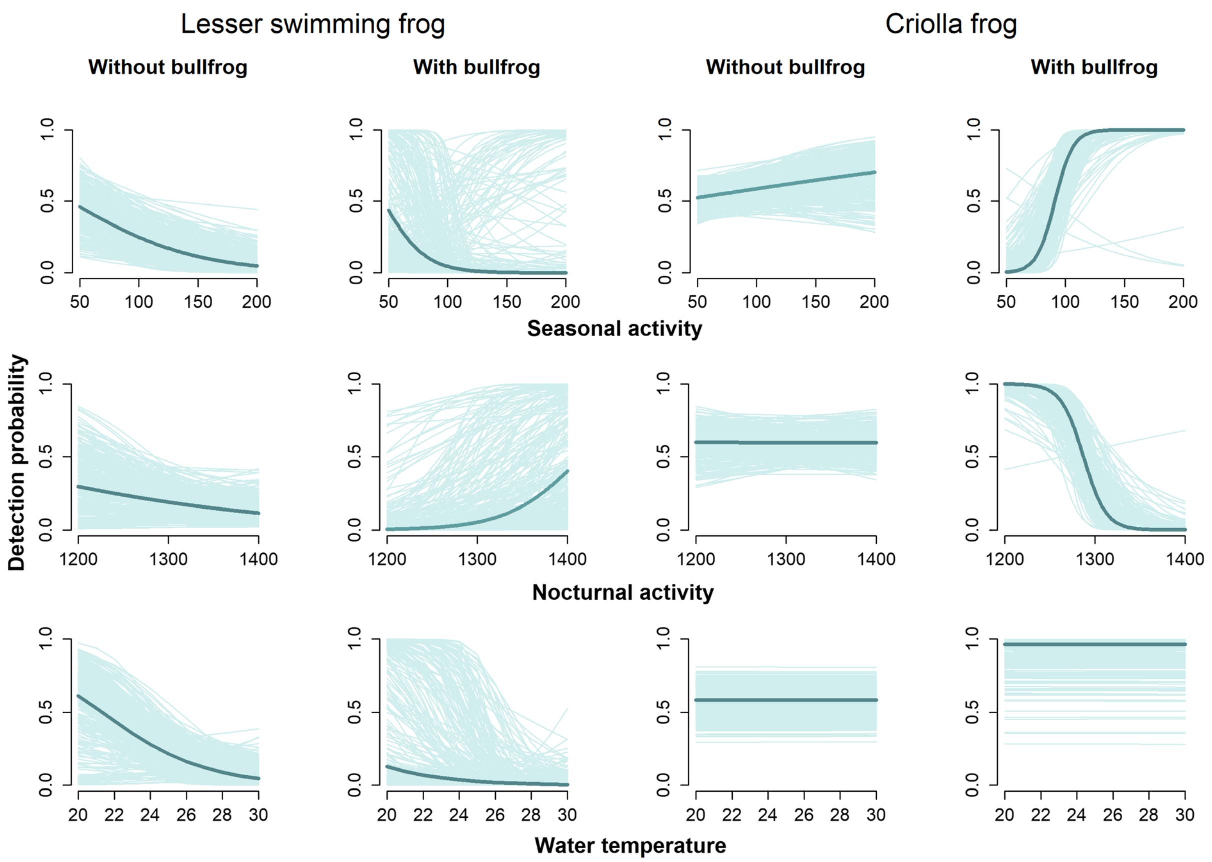

Fig. 1 Relationship between detection probability and seasonal activity (Julian day), nocturnal activity (minutes after midnight) and water temperature (degrees Celsius) for the lesser swimming frog and the criolla frog in the presence and in the absence of the invasive bullfrog. Dark blue lines show the posterior means and light blue lines show estimation uncertainty, based on 300 random posterior distributions sampled

broad frequency spectrum than native species, masking the acoustic signal or changing calling activity of native anurans (e.g. Zank et al. 2008; Both and Grant 2012). Additionally, bullfrog calls can also hinder the ability of observers to detect calling anurans in the ponds. Our results support previous information from the literature, showing that invasive amphibians, such as the bullfrog (Kiesecker and Blaustein 1997) and the cane toad, *Rhinella marina* (Greenlees et al. 2007), as well as other alien species induce changes in behavioral activity of native amphibians (Nunes et al. 2019).

The presence of the bullfrog in our study broke the strong and positive relationship between the lesser swimming frog, the amount of pond vegetation cover and pond size. Invasive species may force native species to low-quality areas, such as observed in Hawaiian coral reefs (Schumacher and Parrish 2005). These behavioral responses observed in native populations may lead to changes in species' habitat use patterns (e.g. Hoare et al. 2007, Mayer et al. 2015). 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. Unlike the lesser swimming frog, none of the spatial covariates influenced habitat use of the criolla frog neither in presence nor in the absence of the bullfrog. We suspect that, at least three life history characteristics may explain this finding. First, the criolla frog presents a lack of specificity to habitat types, and diet. Second, while adult lesser swimming frogs attain around 25% of bullfrog adult body size, adult criolla frogs are about 65%, which may reduce agonistic interactions. Third, the criolla frog seems to share less habitat preferences with the bullfrog than the lesser swimming frog. Native species sharing more similar functional traits

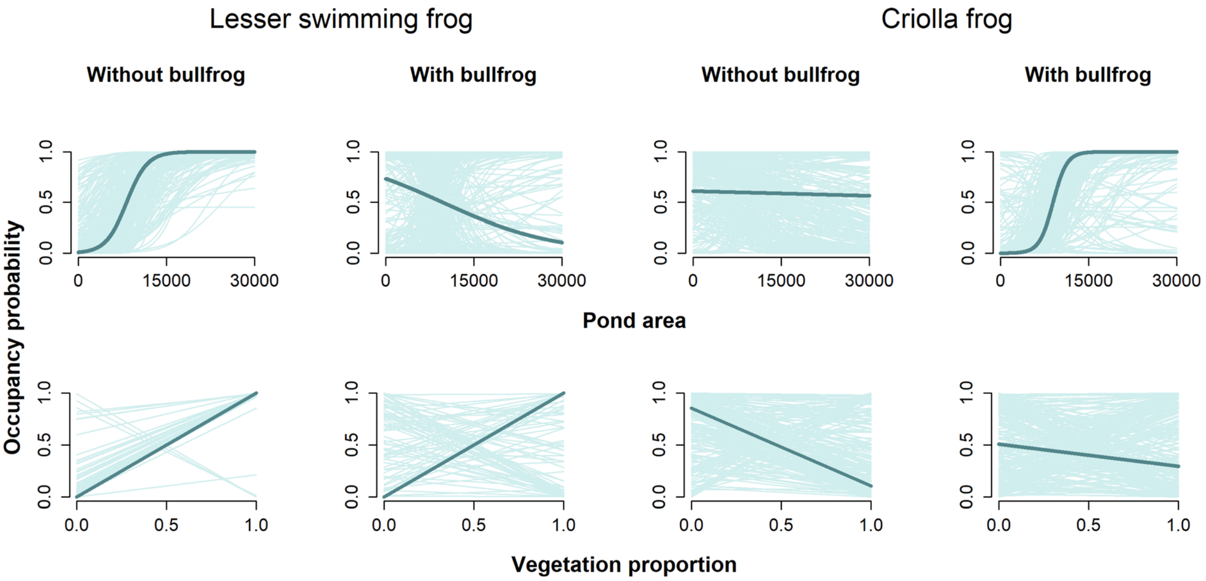

Fig. 2 Relationship between occupancy probability and pond area (square meters) and vegetation proportion (% cover) for the lesser swimming frog and the criolla frog in the presence and in the absence of the invasive bullfrog. Dark blue lines show the posterior means and light blue lines show estimation uncertainty, based on 300 random posterior distributions sampled

with invaders are the main species expected to suffer the consequences of such interactions (Sebastián et al. 2015).

The disruptions observed here in activity and microhabitat use for the native species suggests spatio-temporal disturbances potentially induced by the bullfrog. The persistence of a species 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.

Acknowledgements We thank Larissa Bailey, Marc Kéry, John Measey, Camila Both, Caroline Zank, Maria João Pereira and three anonymous reviewers for their comments and Victoria Graves for the English review. We are grateful to our field crew for helping in data collection, and to the landowners that kindly allowed us access to their land. We also thank PPGBAN, Laura Verrastro and Fundação de Apoio da Universidade Federal do Rio Grande do Sul for financial support. SS and MG were both supported by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) with a master and a postdoc (PNPD) scholarship, respectively. This study was conducted during a time of great political and economic difficulty in Brazil. Beyond their substantial cuts to research budgets, we also feel great dissatisfaction with the manner in which the Brazilian government has been attacking environmental agencies, researchers and universities. It is unacceptable to politicize rather than prioritize scientific investigation.

Authors 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.

References

Blaustein AR, Kiesecker JM (2002) Complexity in conservation: lessons from the global decline of amphibian populations. Ecol Lett 5:597–608. https://doi.org/10.1046/j.1461-0248.2002.00352.x

Borchers D, Zucchini W, Fewster R (1998) Mark-recapture models for line transect surveys. Biometrics 54:1207–1220

Both C, Grant T (2012) Biological invasions and the acoustic niche: the effect of bullfrog calls on the acoustic signals of white-banded tree frogs. Biol Lett 8:714–716. https://doi.org/10.1098/rsbl.2012.0412

Both C, Lingnau R, dos Santos-Jr AP et al (2011) Widespread Occurrence of the American Bullfrog, *Lithobates catesbeianus* (Shaw, 1802) (Anura: Ranidae), in Brazil. South Am J Herpetol 6:127–134. https://doi.org/10.2994/057.006.0203

Brooks SP, Gelman A (1998) General methods for monitoring convergence of iterative simulations. J Comput Graph Stat 7:434–455. https://doi.org/10.1080/10618600.1998.10474787

Gobel N, Laufer G, Cortizas S (2019) Changes in aquatic communities recently invaded by a top predator: evidence of American bullfrogs in Aceguá, Uruguay. Aquat Sci 81:1–11. https://doi.org/10.1007/s00027-018-0604-1

Greenlees MJ, Brown GP, Webb JK et al (2007) Do invasive cane toads (*Chaunus marinus*) compete with Australian frogs (*Cyclorana australis*)? Austral Ecol 32:900–907. https://doi.org/10.1111/j.1442-9993.2007.01778.x

Hoare JM, Pledger S, Nelson NJ, Daugherty CH (2007) Avoiding aliens: behavioural plasticity in habitat use enables large, nocturnal geckos to survive Pacific rat invasions. Biol Conserv 6:510–519. https://doi.org/10.1016/j.biocon.2006.12.022

Kats LB, Ferrer RP (2003) Alien predators and amphibian declines: review of two decades of science and the transition to conservation. Divers Distrib 9:99–110. https://doi.org/10.1046/j.1472-4642.2003.00013.x

Kellner K (2014) jagsUI: Run JAGS (specifically, libjags) from R: an alternative user interface for rjags. R package version 1.1

Kéry M, Royle J (2016) Applied hierarchical modeling in ecology: analysis of distribution, abundance and species richness using R and BUGS. Academic Press, San Diego

Kiesecker JM, Blaustein AR (1997) Population differences in responses of red-legged frogs (*Rana aurora*) to introduced bullfrogs. Ecology 78:1752–1760

Langone JA (1994) Ranas y sapos del Uruguay (Reconocimientos y aspectos biológicos). Mus Damaso Antonio Larrañaga, Ser Divulg 5:1–123

Leibold MA, Mcpeek MA, Mcpeek A (2009) Coexistence of the niche and neutral perspectives in community. Ecol Soc Am Stable 87:1399–1410

Mayer M, Brown GP, Zimmermann B et al (2015) Habitat use of the introduced cane toad (*Rhinella marina*) and native frog species in tropical Australia. J Trop Ecol 31:531–540. https://doi.org/10.1017/S0266467415000474

Nunes AL, Fill JM, Davies SJ et al (2019) A global meta-analysis of the ecological impacts of alien species on native amphibians. Proc R Soc B Biol Sci 286:20182528. https://doi.org/10.1098/rspb.2018.2528

Plummer M (2003) JAGS: a program for analysis of bayesian graphical models using Gibbs sampling. In: Hornik K, Leisch F, Zeileis A (eds) Proceedings of the 3rd international workshop on distributed statistical computing. https://www.r-project.org/conferences/DSC-2003/

R Core Team (2019) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org

Schumacher BD, Parrish JD (2005) Spatial relationships between an introduced snapper and native goatfishes on Hawaiian reefs. Biol Invasions 7:925–933. https://doi.org/10.1007/s10530-004-2983-6

Sebastián OS, Navarro J, Llorente GA, Richter-boix Á (2015) Trophic strategies of a non-native and a native amphibian species in shared ponds. PLoS ONE 10:e0130549

Simberloff D, Martin JL, Genovesi P et al (2013) Impacts of biological invasions: what's what and the way forward. Trends Ecol Evol 28:58–66. https://doi.org/10.1016/j.tree.2012.07.013

Strebel N, Kéry M, Schaub M, Schmid H (2014) Studying phenology by flexible modelling of seasonal detectability peaks. Methods Ecol Evol 5:483–490. https://doi.org/10.1111/2041-210X.12175

Waddle JH, Dorazio RM, Walls SC et al (2010) A new parameterization for estimating co-occurrence of interacting species. Ecol Appl 20:1467–1475. https://doi.org/10.1890/09-0850.1

Zank C, Di-Bernardo M, Lingnau R et al (2008) Calling activity and agonistic behavior of Pseudis minuta Günther, 1858 (Anura, Hylidae, Hylinae) in the Reserva Biológica do Lami, Porto Alegre, Brazil. South Am J Herpetol 3:51–57. https://doi.org/10.2994/1808-9798(2008)3%5b51:caaabo%5d2.0.co;2