



Research Article

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Abstract

The extensive clearing and modification of forests by anthropogenic activities is a major driver of biodiversity loss. Declines of common species are especially concerning because of the potentially large cascading effects they might have on ecosystems. Regrowth of secondary forests may help reverse population declines by restoring habitats to similar conditions prior to land conversion but the value of these secondary forests to fauna is not well understood. We compared the abundance of a direct-developing terrestrial frog, *Craugastor stejnegerianus*, in riparian and upland habitats of pasture, secondary forest, and mature forest sites. Mean abundance per transect was lower in upland pasture compared to mature forest. Secondary forest had similar abundance to mature forest regardless of age. We show that conversion of forest habitat to pasture represents a conservation threat to this species. However, riparian buffers help mitigate the negative effect of conversion of forest to pasture, and regrowth of secondary forest is an effective management strategy for restoring the abundance of this common leaf-litter species.

Introduction

The Latin American and Caribbean (LAC) region is a key area for the preservation of biodiversity, containing approximately one-third of the world's forests, half of its tropical forests (Blackman et al. 2014) and half of the world's terrestrial species (UNEP 2010). Over the last century, LAC forests have undergone large-scale destruction by anthropogenic activities (FAO 2020), resulting in negative consequences for biodiversity (Wright and Mueller-Landau 2006) and ecosystem services (FAO 2020).

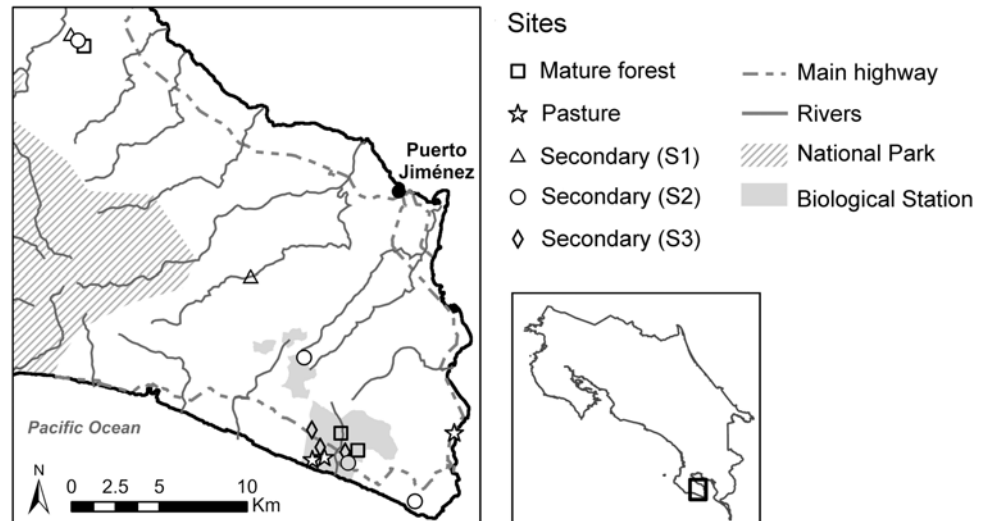
A main driver of forest loss in the LAC region is conversion of forest to pasture (Willaarts et al. 2014). Conversion of forest to pasture results in major structural and abiotic changes to the habitat. Pastures have higher temperatures (Herrera-Montes and Brokaw 2010; Nowakowski et al. 2017), more variation in temperature (Herrera-Montes and Brokaw 2010), lower leaf-litter cover (Díaz-García et al. 2017), and reduced humidity (Díaz-García et al. 2017) and soil moisture compared to forest habitats (Holl 1999). Amphibians may be particularly vulnerable to forest-to-pasture conversion because they are small-bodied, have limited vagility, and are susceptible to desiccation, which can affect dispersal and reduce survival in open-canopy habitats (Nowakowski et al. 2013; Rittenhouse et al. 2008, 2009; Rittenhouse and Semlitsch 2006).

There is mounting evidence of the negative consequences of deforestation on amphibians (Beebe and Griffiths 2005; Brook et al. 2003; Nowakowski et al. 2018; Silvano and Segalla 2005). There are key gaps in understanding and escalating concerns over declines of many common species and the resulting broad consequences these declines might have on ecosystems (Gaston 2010, 2011; Whitfield et al. 2007). However, there is also growing recognition of the potential of large-scale tropical forest restoration to mitigate some of these negative effects (Chazdon et al. 2009; Gillespie et al. 2012; Hernández-Ordóñez et al. 2015; Herrera-Montes and Brokaw 2010; Thompson et al. 2018). Some parts of the LAC region have seen shifting social, political, and economic trends in forest and conservation policy (Barbieri and Carr 2005; Grau et al. 2003; Kull et al. 2007; McDonald 2008; Southworth and Tucker 2001) that are driving reduction in forest cover loss and secondary forest gain (Aide et al. 2012; Aide and Grau 2004).

Generally, secondary forest has higher amphibian species richness and abundance than human-modified landscapes (e.g., pasture, agriculture) and lower species richness and abundance than mature forest (Thompson and Donnelly 2018). However, there is variation in species-specific response (Thompson and Donnelly 2018). Some trends in interspecific differences are thought to be attributed to particular ecological traits such as thermal tolerance, desiccation tolerance, breeding requirements, and specialised habitat associations (Ash 1997; Gardner et al. 2007; Rios-López & Aide 2007; Vallan 2002). Amphibian response to succession and land-use change can be affected by presence of specific habitat features. For example, riparian buffers can be an important management strategy to maintain amphibian abundance in logged forest (Guzy et al. 2019; Vesely and McComb 2002). Riparian habitats are common

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Figure 1. Map of study sites in the Osa Peninsula, Costa Rica in pasture (P), secondary forest < 17 years old (S1), secondary forest 17–27 years old (S2), secondary forest > 27 years old (S3), and mature forest (MF).



features in lowland rainforests and species composition and habitat structure is known to vary between riparian and non-riparian habitat (Bolt et al. 2020; Drucker et al. 2008; Sabo et al. 2005). However, past studies on forest succession and amphibians in the tropics are primarily focused only on upland habitat or do not distinguish riparian zones as a different habitat (e.g., Hernández-Ordóñez et al. 2015; Hilje and Aide 2012).

The objective of our study was to compare the abundance of a direct-developing terrestrial frog, *Craugastor stejnegerianus*, among pasture, secondary forest, and mature forest sites to determine if (1) conversion of forest habitat to pasture represents a threat to this species, and if so, (2) does regrowth of secondary forest mitigate negative effects on the abundance of *C. stejnegerianus*, and (3) does response differ by habitat type (upland, riparian). Although *C. stejnegerianus* is common throughout its range (Savage 2002), there is little available information regarding its ecology and the impacts of land management on this species (Twining and Cossel 2017).

Materials and methods

Study species

Stejneger's Robber Frog (*Craugastor stejnegerianus*) is a small, directly developing, leaf-litter frog that is distributed from northwestern Costa Rica to Panama in the western humid lowlands and premontane slopes. In Costa Rica, the distribution also extends into the western central valley and the periphery of the Atlantic lowlands in proximity to Laguna Arenal. It is considered a diurnal species (Savage 2002); however, it has also been reported to be active at night, especially on rainy nights during breeding (Gómez-Hoyos et al. 2016; Twining and Cossel 2017). *Craugastor stejnegerianus* has been observed in mature forest, secondary forest, coffee plantations, and pasture (Santos-Barrera et al. 2008; Scott 1976).

Study sites

The Osa Peninsula (southwestern Costa Rica, 8°25'29.0"N 83°21'23.7"W) is dominated by tropical lowland wet forest (Holdridge et al. 1971) and characterised by a large contiguous plot of forest (Corcovado National Park) surrounded by forest fragments of varying size and age embedded in a matrix of

agriculture and pasture land. The Osa Peninsula has two distinct seasons, dry and wet. A marked dry season occurs from January to March when monthly precipitation averages <200 mm. The wet season occurs from April to December, with a several-week period of little rainfall usually occurring in late July and /or early August (*veranillo*). Rainfall peaks in October and starts to decrease in December nearing the dry season (McDiarmid and Savage 2005).

We surveyed a chronosequence of secondary forest sites regenerating from pasture in the Osa Peninsula, Costa Rica (Figure 1). Sites consisted of replicates of each of five forest stages: pasture (P, three replicates), secondary forest < 17 years old (S1, two replicates), secondary forest 17–27 years old (S2, four replicates), secondary forest > 27 years old (S3, three replicates), and mature forest (MF, three replicates) for a total of 15 field sites all located under 300 masl. We defined mature forest as forest with a history of minimal human disturbance and containing large-diameter old trees. However, it is possible that these forests could have had some historic selective logging. We calculated forest ages and land-use history by using a combination of aerial photographs and interviews with landowners and binned forest into age groups following a previous study that focused on vegetation succession in the Sarapiquí region of Costa Rica (Letcher & Chazdon 2009). Pasture and secondary forest sites were located adjacent to or as close to mature forest as possible.

Amphibian and reptile surveys

We conducted diurnal and nocturnal visual encounter surveys along linear transects (Crump and Scott 1994). To sample across seasons, we aimed to survey each site three times annually, once during the marked dry season (January to March) and twice during the rainy season. We sampled six sites during a pilot period between September 2014 and December 2014 and all 15 sites annually between January 2015 and December 2016 for a total of six to seven sampling occasions per site. At each site, we established six randomly placed 50 x 2 m transects and sampled them repeatedly during the study; three transects were in riparian habitat and three in upland habitat. We defined upland as habitat at least 35 m from any water features and riparian transects were located along stream banks. There was one S1 secondary forest site (< 17 years old) that was too small to place six transects while maintaining at least 35 m from other transects, streams, and the

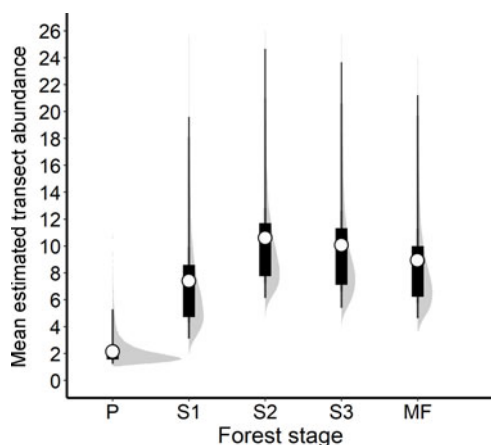


Figure 2. Mean (white circle) estimated abundance per transect for pasture (P), secondary forest < 17 years old (S1), secondary forest 17–27 years old (S2), secondary forest > 27 years old (S3), and mature forest (MF). Black bars indicate 50% credible intervals (CIs) and error lines represent 95% CIs. Grey shaded areas represent the posterior distribution density curves.

edge. Therefore, only 4 transects (two in upland and two in riparian habitat) were placed at this site. In total, we conducted 1,128 transect surveys.

N-mixture models

N-mixture models are a class of models that allow for estimation of population size from replicate count data regardless of the identity of the individual, allow for the estimation of abundance, and account for imperfect detection (Royle 2004). Additionally, effects of covariates can be incorporated into the abundance and detection model. We selected N-mixture models for analysis because we anticipated detection to be highly variable in our surveys and these models allowed us to account for predicted sources of variation (such as surveying during drastically different seasons).

The N-mixture model is composed of two model parts: 1) the abundance model that estimates the local abundance at a site i , (N_i), with mean local abundance λ , and 2) an observation model that links N_i with detection probability p , $y_{ij} \sim \text{binomial}(N_i, p_{ij})$, where y_{ij} represents counts at a site i during replicate survey j . To estimate abundance, N-mixture models use a binomial distribution to model the detection process and a separate distribution to model the dispersion of individuals among sampling units (Royle 2004; Royle & Nichols 2003). We modelled abundance using a Poisson (log link) distribution and a zero-inflated Poisson distribution. The two models had similar results and similar goodness-of-fit but the Poisson distribution had better convergence and so we report results from that model.

We estimated the effect of forest stage and habitat (upland, riparian) on abundance. We estimated survey-specific covariates time of day (TOD) and season for probability of detection. We converted categorical variable forest stage to dummy variables using mature forest as the reference group, and categorical variables TOD (nocturnal: 0, diurnal: 1), season (wet: 0, dry: 1), and habitat (upland: 0, riparian: 1). For abundance, we included the nested effect of transect in site as a random effect to account for multiple transects within sites ($\eta_{\text{site}[i]}$). For detection, we included random transect-survey effects (η_{ij}).

Detection probability was expressed with a logit-linear regression coefficient, formulated as

$$\text{logit}(p_{ij}) = \alpha_0 + \alpha_1 \text{TOD}_j + \alpha_2 \text{season}_j + \eta_{ij},$$

$$\eta_{ij} \sim \text{Normal}(0, \sigma^2)$$

where p is the detection probability at transect i during survey j , α_1 is the model coefficient for TOD, and α_2 is the model coefficient for season.

Abundance was expressed as a log-linear regression coefficient, formulated as

$$\begin{aligned} \log(\lambda_i) = & \beta_0 + \beta_1 P_i + \beta_2 S1_i + \beta_3 S2_i + \beta_4 S3_i + \beta_5 \text{Habitat}_i \\ & + \beta_6 P_i * \text{Habitat}_i + \beta_7 S1_i * \text{Habitat}_i + \beta_8 S2_i * \text{Habitat}_i \\ & + \beta_9 S3_i * \text{Habitat}_i + \eta_{\text{site}[i]}, \end{aligned}$$

$$\eta_{\text{site}[i]} \sim \text{Normal}(0, \sigma^2)$$

where λ is the abundance at transect i , β_s are the model coefficients for forest stage (P, S1, S2, and S3), habitat, and the interaction between forest stage and habitat.

We used MCMC with 180,000 iterations of three chains each. The first 90,000 were removed as burn-in and then chains were thinned by 30. A total of 9,000 samples across the three chains were used to approximate posterior summary statistics, model coefficients, and credible intervals. We evaluated convergence by visual inspection of chain mixing plots and by the Gelman and Rubin statistic, which was < 1.05 for all monitored parameters (Gelman and Rubin 1992). We evaluated goodness-of-fit through a posterior predictive check (Bayesian p-value: 0.51, c-hat: 1.00). We ran models by calling programme JAGS (Plummer 2003) from R v4.0.1 (R Core Team 2021) using package jagsUI (Kellner 2021). Data and code are available at: https://github.com/MichelleThompson86/CRASTE_SecForests.

Results

We detected *C. stejnegerianus* at every site except for one (pasture site). Raw counts of *C. stejnegerianus* per transect survey ranged from zero to 13 individuals. There were 37 observations in pasture, 49 in Stage 1 secondary forest, 211 in Stage 2 secondary forest, 152 in Stage 3 secondary forest, and 128 in mature forest for a total of 577 observations.

N-mixture models

Mean probability of detection per individual was 0.014 (95% CI 0.006–0.022). Estimated mean λ (local [transect] abundance) was 9.606 (95% CI 2.975–28.268). When upland and riparian habitats are considered together, the mean abundance per transect was 4.06 times higher in mature forest compared to pasture. (Figure 2; pasture mean estimated abundance = 2.19, 95% CI 1.22–5.28, mature forest mean estimated abundance = 8.90, 95% CI: 4.61–21.22). When compared to mature forest, estimated abundance of *C. stejnegerianus* was significantly lower in upland pasture sites (Table 1, Figure 3). We found a significant positive interaction between pasture and habitat (Table 1). Secondary forest sites had abundances similar to mature forest sites, regardless of forest stage and habitat type (Table 1, Figures 2 and 3). TOD did not have a significant effect on probability of detection (Table 1). There was a higher probability of detection in the dry season compared to the wet season (Table 1).

Table 1. Mean effects (α , β) and 95% credible intervals (CIs) for abundance (λ) and probability of detection (p). Abbreviations for forest stage: pasture (P), secondary forest < 17 years old (S1), secondary forest 17–27 years old (S2), and secondary forest > 27 years old (S3).

Parameter	Estimate	2.5%	97.5%
p			
$\alpha_{1\text{Time of day}}$	0.207	-0.152	0.585
$\alpha_{2\text{Season}}$	1.426	1.020	1.866
λ			
$\beta_{1\text{P}}$	-4.643	-7.482	-2.515
$\beta_{1\text{S1}}$	-0.486	-1.811	0.768
$\beta_{1\text{S2}}$	0.354	-1.428	0.607
$\beta_{1\text{S3}}$	0.184	-0.943	1.789
$\beta_{1\text{Habitat}}$	0.060	-0.606	0.735
$\beta_{1\text{P}^*\text{Habitat}}$	3.699	1.687	6.451
$\beta_{1\text{S1}^*\text{Habitat}}$	-0.395	-0.793	1.575
$\beta_{1\text{S2}^*\text{Habitat}}$	0.795	-0.034	1.632
$\beta_{1\text{S3}^*\text{Habitat}}$	-0.249	-1.134	0.617

Bold values indicate a significant effect (95% CI that does not include zero).

Discussion

Our findings show that small populations of *C. stejnegerianus* can persist in pastures but that pasture is no substitute for forest. Mean abundance per transect was lower in upland pasture compared to mature forest. However, riparian buffers partially mitigate the negative effect of conversion to pasture and regrowth of secondary forest on pasture habitats restores abundances similar to those in mature forest.

Our results are consistent with other research that, in general, craugastorid frogs are sensitive to habitat change. For example, a review on the effects of land-use conversion on amphibians estimated a 9.3-fold decrease in abundance of craugastorid frogs as a result of habitat alteration (Nowakowski et al. 2018) and Ficetola et al. (2008) found lower density of calling males of *C. fitzingeri* in pasture compared to secondary and primary forest. Leaf litter provides a refuge for many direct-developing frogs for all or most of their life stages (Ryan et al. 2015; Scott 1976). Leaf-litter dwelling frogs with direct development of eggs, such as *C. stejnegerianus*, require humid conditions for development, and terrestrial-developing species are often small-bodied with high surface-to-volume ratios and low heat tolerances (Nowakowski et al. 2017; Scheffers et al. 2013), which can result in vulnerability to desiccation and thermal stress in open-canopy habitats such as pasture (Duarte et al. 2012; Hoffman et al. 2021; Tracy et al. 2010).

We found a higher probability of detection in the dry season compared to the wet season. This result was opposite of our prediction. We provide two hypotheses for this outcome. First, it was often raining during many of the surveys during the wet season and this can make it hard to see, potentially affecting detection. Second, leaf-dropping events in tropical forests are generally higher in the dry season than in the wet season resulting in high leaf-litter depths in the late dry or early very wet season (Frankie et al. 1974; Levings & Windsor 1984). Leaf-litter dynamics are known to affect herpetofauna densities (Folt 2017; Guyer 1988; Whitfield et al. 2014). Changes in density can be a result of bottom-up effects of increased arthropod food resources with increasing

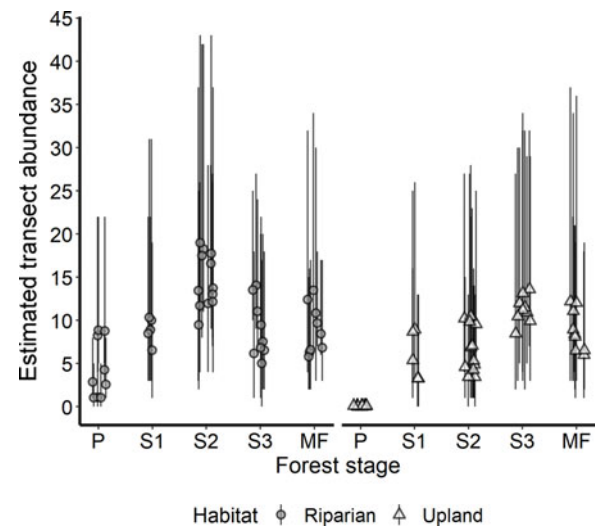


Figure 3. Estimated abundance (λ) for each riparian (circle) and upland (triangle) transect in pasture (P), secondary forest < 17 years old (S1), secondary forest 17–27 years old (S2), secondary forest > 27 years old (S3), and mature forest (MF). Error bars represent 95% confidence intervals.

litter depth (Folt 2017; Guyer 1988; Levings & Windsor 1984; Lieberman & Dock 1982; Toft 1980) or top-down effects of predator dynamics (Folt 2017). Furthermore, Ryan et al. (2015) reported a decrease in leaf-litter amphibians, including *C. stejnegerianus*, during a high rainfall, La Niña event. We did not test for differences in abundance between seasons but it is possible an increase in frog density and/or activity in the high levels of leaf litter during the dry season affected the probability of detection.

Declines in common, non-threatened species have received less conservation attention than threatened and rare species (Redford et al. 2013). Declines in common species are particularly alarming because proportionally small declines can result in the loss of a large number of individuals, faunal biomass, interactions, and ecosystem services, and declines in common species can often signal declines in the overall abundance of assemblages (Gaston 2010; Gaston & Fuller 2008). Terrestrial leaf-litter amphibians play important roles in ecosystems such as nutrient cycling and energy flow of forest ecosystems because they can be present at high densities and they are efficient at converting invertebrate biomass into usable energy (Beard et al. 2002, 2003; Best & Welsh 2014; Davic & Welsh 2004). *Craugastor stejnegerianus* is a common species throughout its range (San Vito: Ryan et al. 2015; Santos-Barrera et al. 2008; Scott 1976; Golfito: Barquero 2003; Dehling 2005; San Ramón: Acosta-Chavez et al. 2019; Rincon: Ryan et al. 2015; Scott 1976) and can be present at extremely high densities. For example, Scott (1976) estimated a density of 4,586/ha at Las Cruces Biological Station and 431/ha at Rincón de Osa, Costa Rica. Our transect study design did not result in density estimates but the model allowed us to estimate a total abundance of 160.254 (95% CI 83–282) in our mature forest transect sampling area, and 39.374 (95% CI 22–95) in our pasture transect sampling area, which we interpret as our transects crossing the home range or habitat use of this quantity of individuals in the mature forest and pasture transects sampled (a total of 18 transects measuring 50 × 2 m in each habitat type). The estimate of individual probability of detection was low, which can lead to unreliable estimates of abundance (Royle 2004). Therefore, abundance estimates should

be interpreted with caution. While not directly comparable, considering the estimates of 431–4,586/ha by Scott (1976), our abundance estimates seem plausible. Therefore, conversion of forest to pasture and resulting reduction in abundance of this species likely has significant negative consequences for ecosystem function.

Even if low abundances of *C. stejnegerianus* are present in pasture habitats, these small populations are likely to be at heightened risk of stochastic local extinction (Lande 1993; Wissel et al. 1994) and may rely on nearby source forest habitat to persist. Restoration of forests in human-modified habitats is an effective management strategy for conserving this leaf-litter species. The estimated time to recovery is short. Secondary forests less than 17 years of age already had comparable abundances to mature forests. This time to faunal recovery aligns with the timeline of canopy physical structure (Clark et al. 2021) and above-ground biomass (Letcher & Chazdon 2009) during lowland tropical forest regeneration. However, our secondary forest and pasture sites were located close to mature forest remnants, embedded in a landscape that still has considerable forest cover. Therefore, our results showing a rapid increase in the abundance of *C. stejnegerianus* during secondary forest succession likely represents a best-case scenario.

Some of our pasture riparian sites were buffered by sparse, scattered trees and others were closer to meeting regulations for riparian forest buffers under Costa Rican law (at least 15 m width). The positive effect for the interaction term between pasture and habitat indicates the size of the negative effect of pasture on abundance is mediated by habitat type. The negative effect pasture has on abundance is partially offset by the presence of riparian habitat. Therefore, our results support the strategy of maintaining remnant natural vegetation, such as remnant trees or riparian buffers, for persistence of amphibian populations in modified landscapes, and this is reinforced by the results of other studies (e.g., herpetofauna: Robinson et al. 2013; fish: Lorion & Kennedy 2009; birds: Mitchell et al. 2018; Thompson et al. 2022). These results highlight the importance of policy such as Costa Rica Forestry Law (no. 7575), which describes restrictions for clearing trees in riparian zones. However, current regulations and enforcement of the protection of riparian buffers in modified landscapes without also protecting surrounding mature forests may not sufficiently protect the habitat that is crucial to amphibian species.

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Competing interests. The authors declare none.

Ethical statement. The authors assert that all procedures contributing to this work comply with applicable national and institutional ethical guidelines on the care and use of laboratory or otherwise regulated animals.

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