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# Global Ecology and Conservation

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Original research article

## Spatial and temporal variation in population dynamics of Andean frogs: Effects of forest disturbance and evidence for declines



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### ARTICLE INFO

#### Article history:

Received 6 March 2014

Received in revised form 4 June 2014

Accepted 4 June 2014

Available online 1 July 2014

#### Keywords:

Amphibian decline

Biodiversity

Capture–mark–recapture analysis

*Pristimantis*

Neotropics

### ABSTRACT

Biodiversity loss is a global phenomenon that can result in the collapse of food webs and critical ecosystem services. Amphibian population decline over the last century is a notable case of species loss because amphibians survived the last four major extinction events in global history, their current rate of extinction is unprecedented, and their rate of extinction is greater than that for most other taxonomic groups. Despite the severity of this conservation problem and its relevance to the study of global biodiversity loss, major knowledge gaps remain for many of the most threatened species and regions in the world. Rigorous estimates of population parameters are lacking for many amphibian species in the Neotropics. The goal of our study was to determine how the demography of seven species of the genus *Pristimantis* varied over time and space in two cloud forests in the Ecuadorian Andes. We completed a long term capture–mark–recapture study to estimate abundance, survival, and population growth rates in two cloud forests in the Ecuadorian Andes; from 2002 to 2009 at Yanayacu in the Eastern Cordillera and from 2002 to 2003 at Cashca Totoras in the Western Cordillera. Our results showed seasonal and annual variation in population parameters by species and sex. *P. bicantus* experienced significant reductions in abundance over the course of our study. Abundance, apparent survival, and population growth rates were lower in disturbed than in primary or mature secondary forest. The results of our study raise concerns for the population status of understudied amphibian groups and provide insights into the population dynamics of Neotropical amphibians.

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## 1. Introduction

Amphibians survived the last four major extinction events in the history of earth (Wake and Vredenburg, 2008), yet their current extinction rates and risk for future population decline are among the highest of any taxonomic group (Stuart et al., 2004). Drivers of amphibian population declines include land use change, climate change, disease, environmental contaminants, invasive species, and exploitation for the food, pet, and medical trade (Beebee and Griffiths, 2005; Blaustein and Kiesecker, 2002). Despite the severity of the threats they face and their significance to research focused on biodiversity loss, amphibians are one of the least studied taxonomic groups (Lawler et al., 2006).

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Baseline population vital rates, including abundance, survival, and population growth rates, are critical for determining extinction risk and population trends. Mark–recapture studies are a particularly robust method for determining population vital rates because they can control for a number of variables that might influence the detection of individuals, including survival, probability of capture, population growth rate, movement of individuals, and any variables that might co-vary with these parameters. Deforestation has contributed to population declines in tropical amphibians (Brook et al., 2003; Gardner et al., 2007; Pandit et al., 2007). Yet the effect of deforestation could only be detected over a longer time frame (Todd and Rothermel, 2006). Long term monitoring is essential to accurately distinguish drivers of population dynamics, assess extinction risk (Bonebrake et al., 2010; Pechmann et al., 1991), and rigorously estimate population parameters (Funk et al., 2003).

The tropical Andes are an important focal region for studies on amphibian population dynamics because little is known about this biodiversity hotspot where high levels of diversity and endemism are at high risk of loss (Myers et al., 2000). Amphibian species in the tropics are more likely to experience threats from pathogens, climate change, and land-use change (Hof et al., 2011). High elevation, aquatic species in central and South America are generally thought to be the most susceptible to population decline (Stuart et al., 2004), but this conclusion may be biased because so little is known about the status of other amphibian groups. While there are some examples of studies that have completed robust estimates of population parameters of amphibians in the Neotropics (Ryan et al., 2008; Lampo et al., 2011; McCaffery and Lips, 2013), many amphibian population studies lack rigorous methods. An evaluation of studies published from 2006 to 2013 in South American herpetology journals showed that the majority (81%–95%) did not take into account bias related to imperfect detectability (Guimaraes et al., 2014). Mark–recapture analyses have not been used to estimate population vital rates for frogs from the genus *Pristimantis*. The absence of rigorous estimates of population parameters prevents accurate assessments of extinction risk, spatial patterns in population dynamics, and species differences for vulnerable regions and taxonomic groups.

The genus *Pristimantis* contains 462 described species (AmphibiaWeb, 2014), with more being discovered each year, making it the most speciose vertebrate genus in the world. *Pristimantis* frogs are distributed widely throughout the Neotropics from 0 to 4100 m above sea level (Carvajalino-Fernández et al., 2011). *Pristimantis* species are direct-developing (i.e. they hatch from eggs as small froglets) and are considered to have a lower population threat status and risk of population decline (Green, 2003), in part because they are not dependent on aquatic habitat for reproduction (Becker et al., 2007). There are many data deficient species in this group, but population decline or local extinction have been reported for some *Pristimantis* species in Costa Rica, Panama, Puerto Rico, Guatemala, Dominican Republic, Columbia, and Brazil (Hedges, 1993; Lips, 1999; Young et al., 2001). Reliable estimates of vital rates across more species in this genus are required to determine whether the species are persisting more successfully than other groups or if *Pristimantis* species are declining un-noticed by scientists and conservation professionals. Understanding how population parameters such as abundance, survival, and population growth vary across time, space, species, and sex is the first step in determining conservation status and trends.

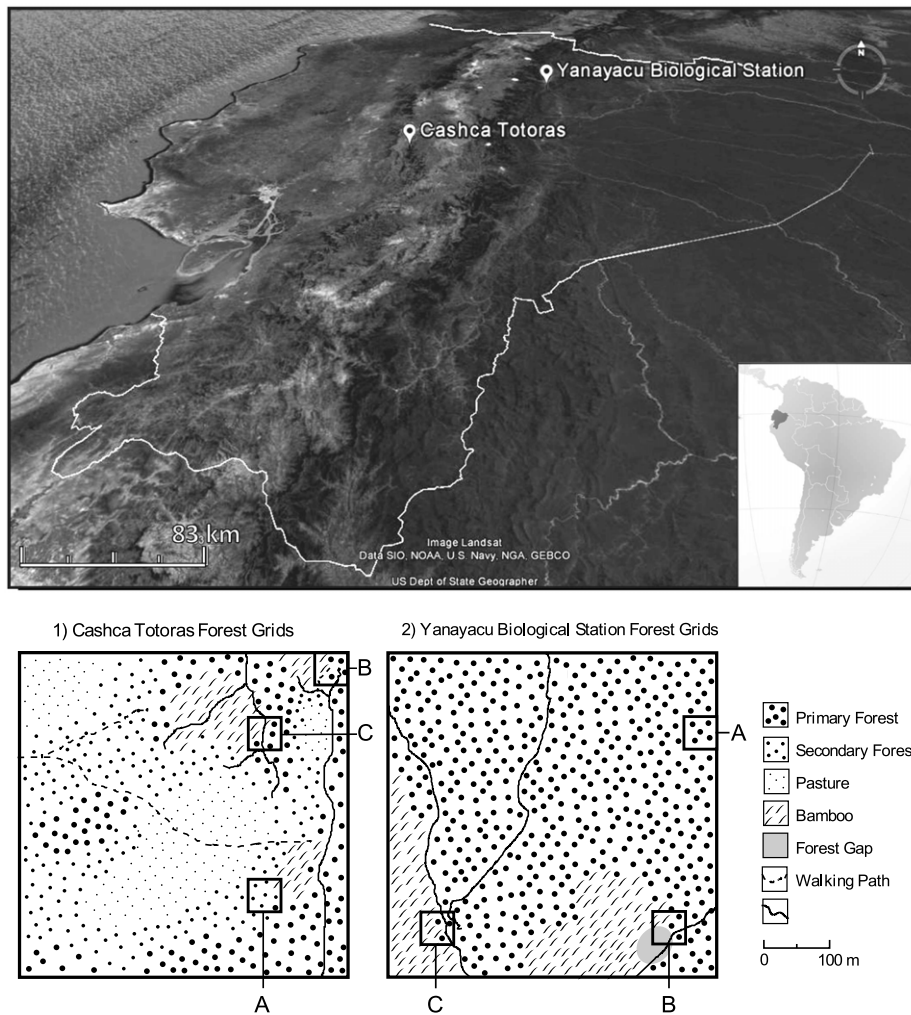
We conducted a long-term study to understand the population dynamics and demography of *Pristimantis* frogs in the Ecuadorian Andes. We collected 4 years of data, from 2002 to 2009, and used mark–recapture modeling to determine (1) whether populations of seven *Pristimantis* species are growing, stable, or in decline, and (2) whether apparent survival, population growth rates, and abundance estimates differed among forest patches and/or species. Our study attempts to fill a critical gap in amphibian decline research by testing models that evaluate the effect of local variation in habitat, seasonal and interannual variation, species, and sex on population vital rates of seven *Pristimantis* species using a long-term capture–mark–recapture analysis. The results of our study are relevant to the conservation of an understudied, diverse, and potentially at-risk taxonomic group in one of the most vulnerable regions of the world.

## 2. Materials and methods

### 2.1. Study regions

We monitored populations of *Pristimantis* species in two regions in Ecuador, Bosque Protector Cashca Totoras, Bolívar Province (1° 43' S, 78° 58' W, 3000–3200 m) and Yanayacu Biological Station, Napo Province (0° 35' S, 77° 53' W, 1900–2400 m; Fig. 1). In each region, we randomly selected three, 50 m × 50 m grids within a 500 m × 500 m area for population monitoring (Fig. 1). At Yanayacu Biological Station, we monitored all grids 11 times from May 2002 to May 2009 (May 2002, August–September 2002, April 2003, August–September 2003, December 2003, January 2007, April 2007, June–July 2007, January–February 2009, March–April 2009, and May 2009). Thus, there was a gap of approximately three years in the middle of our sampling period due to a lapse in research funds. At Bosque Protector Cashca Totoras, we monitored all grids 6 times approximately every other month from March 2002 to November 2003. We estimated population vital rates at both sites but population declines could only be detected robustly at Yanayacu, where the sampling period spanned 8 years.

The sampling sites differed in terms of habitat composition, temperature, precipitation, and timing of the wet season. Undisturbed, primary forest dominates the region at Yanayacu Biological Station and the plant community is diverse. For trees greater than 5 cm in diameter breast height, Lauraceae is the most speciose family, followed by Moraceae, Fabaceae, and Solanaceae (Valencia, 1995). The forest at Bosque Protector Cashca Totoras is more disturbed, consisting of a mixture of pasture, primary cloud forest, secondary cloud forest, and stands of evergreen bamboo (genus *Chusquea*). Yanayacu



**Fig. 1.** Location and forest composition of study regions and monitoring grids. Satellite image generated by GoogleEarth version 7.1.2.2041.

Biological Station, on average, receives about 3.0 cm more average annual precipitation and is 5 °C warmer per month than Bosque Protector Cashca Totoras, based upon weather station data within 13 km and 300 m elevation of monitoring grids (Ferdon, 1950). Yanayacu Biological Station is located on the east side of the Cordillera Oriental of the Andes mountain range in the Napo Province. On the eastern slope of the range, warm air from the Amazonian lowlands forced upward by the Andes Mountains generates precipitation. Bosque Protector Cashca Totoras is located on the west side of the Cordillera Occidental of the Andes, where Pacific Ocean currents drive rainfall patterns. Peak rainfall occurs from January–April at Bosque Protector Cashca Totoras (Ferdon, 1950) and from April–September at Yanayacu Biological Station (Greeney, 2010).

Sampling grids at each site differ in habitat composition (Fig. 1). Cashca Totoras contained the most disturbed grid. Grid A was located within secondary forest in close proximity to a cow pasture. Grids B and C at Cashca Totoras contained a mixture of primary forest and bamboo located within 50 m of a cow pasture and secondary forest. Yanayacu sampling grids were far less disturbed with all grids located within primary forest. Grid A at Yanayacu contained primary forest. Grid B contained primary forest, bamboo stands, and a forest gap caused by a wind storm. Grid C contained primary forest and a bamboo stand.

Tropical Andean localities contain high diversity and abundance of *Pristimantis* species. Yanayacu Biological Station has one of the richest known amphibian faunas of comparable altitude in the Tropical Andes containing 20 identified species of amphibians including 9 species from the genus *Pristimantis* (*P. bicantus*, *P. eriphus*, *P. inusitatus*, *P. gladiator*, *P. petersi*, *P. leucopus*, and three unidentified species of *Pristimantis* (referred to as *P. sp.1*, *P. sp.2* (aff. *eriphus*), and *P. sp.3* (*w-nigrum* complex))) (Guayasamin and Funk, 2009). Over the course of our study, we found five species from the genus *Pristimantis* at Bosque Protector Cashca Totoras (*P. phoxocephalus*, *P. w-nigrum*, *P. pyrromerus*, *P. truebae*, and *P. simonbolivari*). We focused our analyses on the seven most common species in each region, *P. bicantus*, *P. eriphus*, *P. inusitatus*, and *P. petersi* at Yanayacu Biological Station and *P. pyrromerus*, *P. truebae*, and *P. simonbolivari* at Bosque Protector Cashca Totoras.

## 2.2. Field sampling

During each primary sampling period, we sampled each monitoring grid 5–7 days in succession. Each monitoring grid was composed of 10 parallel, linear transects 50 m in length and separated by 5 m. We captured and identified all individuals encountered within 2.5 m of each transect. Therefore, our surveys covered the entire 50 m × 50 m grid area. We captured all frogs encountered and collected data on their location of capture within sampling grids, species, age class, sex, and snout-vent length. Only frogs at least 1.5 mm in length were individually marked for capture–mark–recapture analyses.

To create individually identifiable codes, we clipped a median of three toes on each individual greater than 1 cm in length. No more than two toes were clipped on each foot. While toe clipping can have biologically negative effects on study subjects, most studies examining this method have empirically determined that toe-clipping poses little risk to most herpetofauna, if implemented correctly (Perry et al., 2011). Moreover, toe-clipping can be the best method for studies on small amphibians when few marking alternatives are available, and the information gained is relevant to conservation of that species (Correa et al., 2013; Funk et al., 2005; Grafe et al., 2011; Perry et al., 2011; Swanson et al., 2013). All field workers received the same training in field protocols and field workers changed over time.

## 2.3. Capture–Mark–Recapture (CMR) analyses

To estimate the abundance, apparent survival, and population growth rate of *Pristimantis* species in monitoring grids, we used capture–mark–recapture models, a method shown to provide accurate and precise population parameter estimates for these *Pristimantis* species (Funk et al., 2003). We evaluated whether the *Pristimantis* populations were growing, stable, or in decline, and whether population vital rates differed among forest grids and/or species. To estimate apparent monthly survival, we used Cormack–Jolly–Seber models in program MARK (White and Burnham, 1999). Cormack–Jolly–Seber models use capture–recapture histories to develop maximum likelihood estimates of the probability of apparent survival ( $\phi$ ) and capture ( $p$ ). The probability of apparent survival is the likelihood both that an individual survived and that the individual did not permanently emigrate out of the monitoring area over the interval of time between sampling periods. Our models take into account unequal time periods between sampling sessions. Including the probability of capture in maximum likelihood models controls for the potential that an individual may survive yet evade capture during a sampling session.

We evaluated Cormack–Jolly–Seber models for each species and tested the degree to which monitoring grid, sex, number of toes clipped, and time (monitoring period) affected apparent monthly survival probability ( $\phi$ ) and how grid, sex, and monitoring period affected capture probabilities ( $p$ ). We controlled for the potential effect of toe-clipping on capture probabilities by including the number of toes clipped as a covariate in population models (Williams et al., 2002). We also controlled for the potential effect of differences in field workers and differences in the number of days included within primary sampling sessions by including sampling period as a covariate in our analyses. We restricted the number of predictor variables associated with each structural parameter ( $\phi$  or  $p$ ) to two because sample sizes and capture probabilities were low, and preliminary analyses indicated that more complex models could not converge. When capture probabilities were extremely low for sub-groups of a specific sex of a *Pristimantis* species within a specific grid, we eliminated those groups from the analysis (Appendix 1). We tested 29 models of apparent survival for *P. pyrrhomerus*, *P. simonbolivari*, *P. truebae*, *P. bicantus*, *P. eriphus*, and *P. petersi* and 15 models of apparent survival for *P. inusitatus*, a species for which we could not evaluate the effect of grid because capture and recapture rates were too low in two of the three monitoring grids. We included models within two QAICc values of the top model in model averaging to estimate apparent survival probabilities.

We estimated abundance ( $N$ -hat) and its associated variance for all *Pristimantis* species at each monitoring grid using Chapman's unbiased version of the Lincoln–Peterson Estimator (Seber, 1982) following Funk et al. (2003). Due to the complexity of Huggins closed capture model, small sample sizes, and relatively low recapture rates, we were unable to use Huggins closed capture model to estimate abundance. By contrast, Chapman's estimator performs well with small sample sizes (Menkens and Anderson, 1988). This method uses the number of individuals captured on each of two sessions and the number of individuals re-captured on the second session to estimate abundance. We estimated abundance for each sampling period using the Lincoln–Peterson Estimator by collapsing the five to seven days of surveys into two parts, the first three days of sampling and the last two to four days of sampling.

Using data collected from both Yanayacu Biological Station and Bosque Protector Cashca Totoras in March 2002–December 2003, we evaluated population growth rates ( $\lambda$ ) for species and monitoring grids over time. We used Pradel models that use maximum likelihood models to estimate the probability of apparent survival ( $\phi$ ), probability of capture ( $p$ ), and population growth rate ( $\lambda$ ). To control for the effect of apparent survival ( $\phi$ ) and capture probability ( $p$ ), we used the best predictor variable among species, region, grid, and time for each parameter, and then varied the predictor variables associated with population growth rate ( $\lambda$ ). We tested eight models (Appendix 3) and used model averaging of models within two QAICc values of the top model (Burnham and Anderson, 2002) to estimate population growth rates for each species and monitoring grid at Yanayacu Biological Station and Cashca Totoras.

## 3. Results

From 2002 to 2009, we marked 221 *P. pyrrhomerus* individuals, 968 *P. simonbolivari* individuals, 199 *P. truebae* individuals, 179 *P. bicantus* individuals, 316 *P. eriphus* individuals, 208 *P. petersi* individuals, and 171 *P. inusitatus* individuals. Abundance

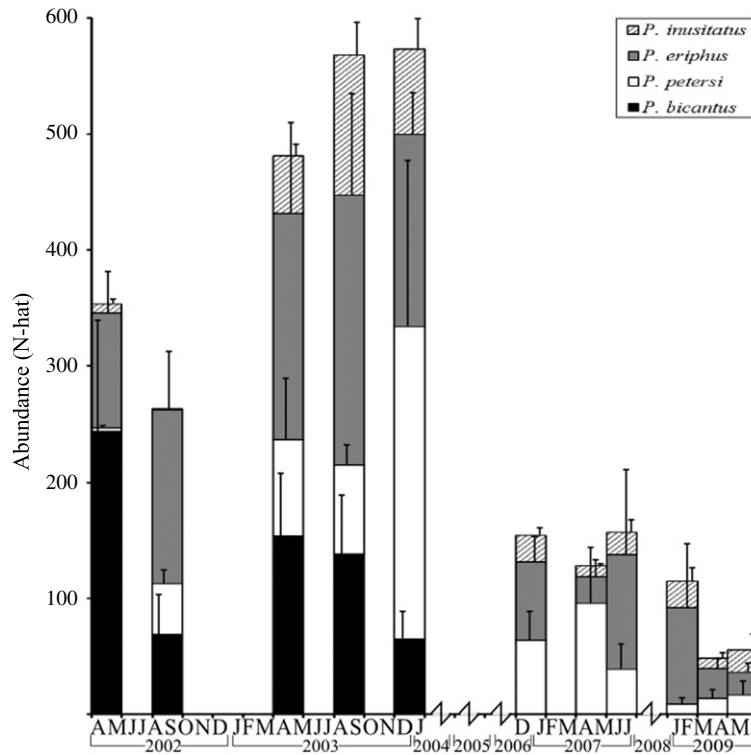


Fig. 2. Abundance estimates with standard error bars for *Pristimantis* species at Yanayacu Biological Station from 2002 to 2009.

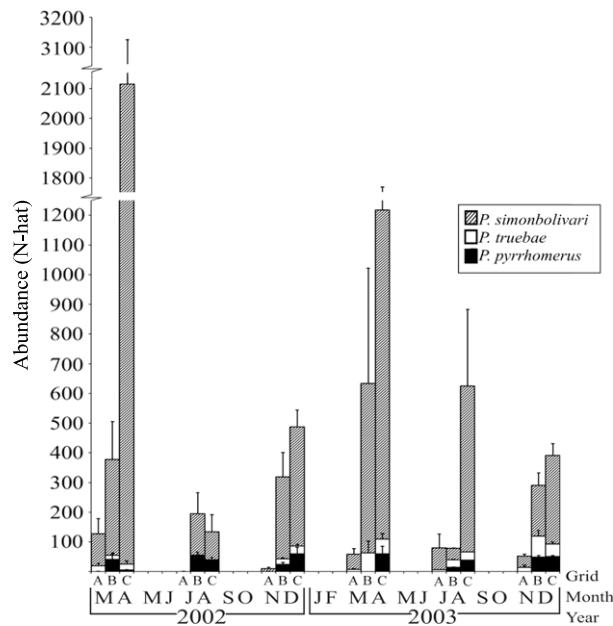


Fig. 3. Abundance estimates with standard error bars for *Pristimantis* species at Cashca Totoras from 2002 to 2003.

estimates showed that the population of one *Pristimantis* species is in decline while others display seasonal and interannual variation in abundance. Also, model results (Appendices 2, 3) and vital rate estimates (Figs. 2–5) showed that apparent survival, population growth rates, and abundance estimates differed among forest patches, species, sex, and number of toes clipped.

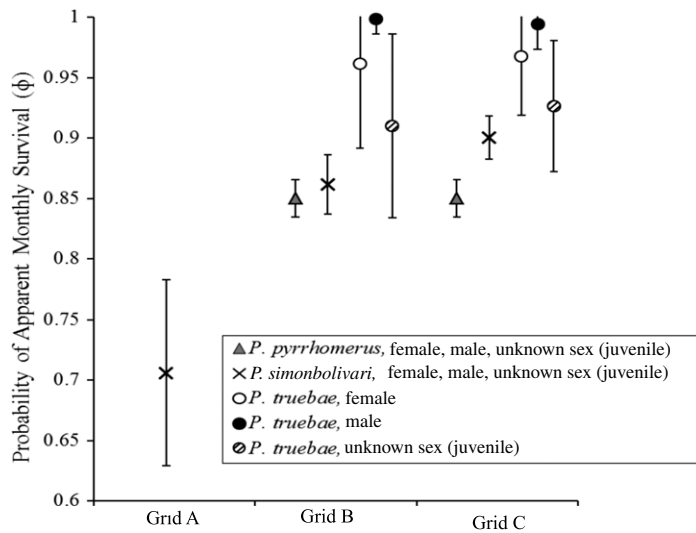


Fig. 4. Probability of apparent monthly survival among monitoring grids at Cashca Totoras by *Pristimantis* species and sex from 2002 to 2003.

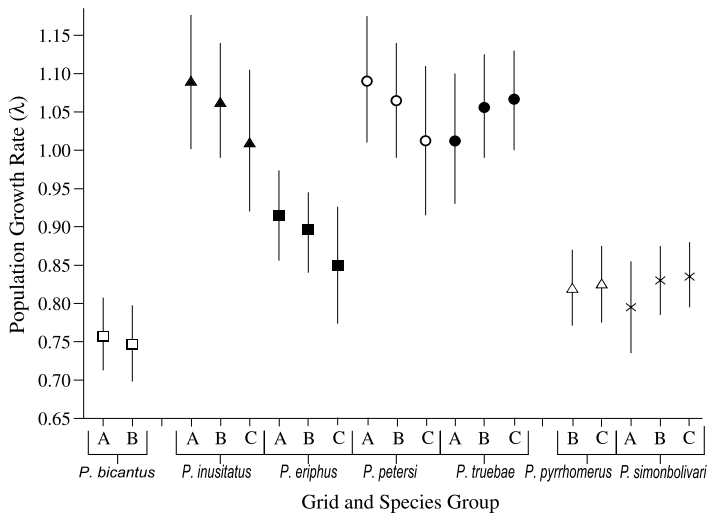


Fig. 5. Estimated population growth rate ( $\lambda$ ) for all common *Pristimantis* species found at Yanayacu Biological Station and Cashca Totoras from 2002 to 2003.

### 3.1. Temporal trends in *Pristimantis* population parameters

At Yanayacu, abundance estimates show baseline fluctuations and indicate a population decline in *P. bicantus*. Abundance estimates of *P. bicantus* at Yanayacu Biological Station indicate a potential population crash that occurred sometime between January 2004 and December 2006 (Fig. 2). All three other species at Yanayacu had lower average abundance from January 2007 to June 2009, but none of the abundance estimates for each of those species exceeded the lowest estimate those species from 2002 to 2003. Furthermore, estimates of population growth rates among species corroborate the evidence for population decline in *P. bicantus*. *P. bicantus* had among the lowest population growth rate (0.75–0.77) of any species (all other species at Cashca Totoras, 0.80–1.09) in either of the sampling sites from 2002 to 2003 (Fig. 4). Therefore, despite higher abundances of *P. bicantus* from 2002 to 2003, the population may have already been experiencing a downward trend.

At Bosque Protector Cashca Totoras, no *Pristimantis* species declined in abundance over 21 months from 2002 to 2003, but there was some evidence for seasonally driven fluctuations in abundance (Fig. 3). *P. simonbolivari* was over twice as abundant (1731–2523 individuals) during the wet season (March–April) than any of the other sampling periods (234–506 individuals) in both 2002 and 2003.

Apparent monthly survival for all species across all grids ranged from 0.22 to 0.70. For all species except *P. inusitatus*, apparent monthly survival was constant over time. Apparent monthly survival for *P. inusitatus* did not display an overarching positive or negative trend over time.

### 3.2. Variation in population parameters based on species, grid, and other covariates

There were clear differences in population parameters among species. *P. simonbolivari* had the highest estimated abundance of any species in our study. During the first sampling session, estimated abundance for *P. simonbolivari* was more than 100 times greater than either of the other two common species at Bosque Protector Cashca Totoras (Fig. 2). Species also differed from one another in their population growth rate. *P. inusitatus*, *P. petersi*, *P. truebae* had higher population growth rates (1.01–1.09) than *P. bicantus*, *P. pyrromerus*, and *P. simonbolivari* (0.75–0.84) (Fig. 4).

Local scale habitat differences also helped to explain differences in population vital rates for *Pristimantis* species. Grid A at Cashca Totoras was composed nearly entirely of secondary forest, only 4% of the grid was bamboo forest and 4% primary forest and located 25 m away from a cattle pasture. Grid B was composed of 27% bamboo and 63% primary forest and located 50 m away from the nearest cattle pasture. Finally, 50 % of grid C at Cashca Totoras was composed of bamboo forest while 50% was composed of primary forest. Grid was a predictor of apparent monthly survival in top models for *P. simonbolivari* and *P. truebae* at Cashca Totoras (Appendix 2). Grid was also an important predictor of population growth rate in top models for all species from 2002 to 2003 (Appendix 3). Abundance, apparent monthly survival, and population growth rates for each species at Cashca Totoras were significantly lower in grid A at Cashca Totoras than within any other grid at Cashca Totoras (Figs. 3–5). Average abundance of all species in grid A was 55 individuals, in grid B was 316 individuals, and grid C was 829 individuals. Apparent monthly survival in grid A (0.22–0.26) was lower than grid B (0.52–0.59) or grid C (0.66–0.70). Estimated population growth rate of *P. truebae* at grid A was 1.02 whereas at grid B, it was 1.06 and at grid C, it was 1.07. For *P. simonbolivari* estimated population growth rate in grid A was 0.80, at grid B it was 0.83, and at grid C it was 0.84.

Differences among vital rates based upon forest grids were less pronounced at Yanayacu, where forest grids were located in less degraded habitat (Fig. 4). At Yanayacu, grid A was composed entirely of primary forest. Grid B covered an area that was 40% primary forest, 35% bamboo forest, and 25% wind gap. Grid C was composed 50% of primary forest and 50% of bamboo forest.

Sex and the number of toes clipped were also linked to population vital rates in some *Pristimantis* species. Sex was an important predictor of apparent survival for *P. truebae*, *P. bicantus*, and *P. petersi* in top Cormack–Jolly–Seber models (Appendix 2). For *P. truebae*, the lowest probabilities of apparent survival occurred among juveniles that have an unknown sex (0.91), whereas the highest probabilities of apparent survival tended to occur among males (1.00) (Fig. 5). Number of toes clipped was a predictor of apparent survival for *P. truebae*, *P. bicantus*, *P. inusitatus*, and *P. petersi* in top Cormack–Jolly–Seber models (Appendix 2). Probability of apparent survival decreased if we clipped more than three toes for these species. The number of toes clipped in our study did not affect probability of apparent survival in any of the other *Pristimantis* species.

## 4. Discussion

Through rigorous estimation of population parameters, we documented the population dynamics and trends of an understudied amphibian genus in a key biodiversity hotspot. Few studies have focused on species from the genus *Pristimantis* and no studies have used capture–mark–recapture methods to estimate abundance, apparent survival, and population growth rates. Our findings fill a significant gap in the field of conservation biology and illustrate the value of focusing research efforts on understudied species and ecosystems. Species may decline to extinction before we understand their interaction with complex and dynamic ecosystems. Our results showed that a direct-developing frog species, *Pristimantis bicantus*, experienced a large reduction in population size in an Ecuadorian cloud forest from 2002 to 2009. *Pristimantis* species exhibited differences in population parameters over time and space. In our study, *P. simonbolivari* abundance varied with wet and dry seasons. In addition, the abundance, survival, and population growth rate for *P. simonbolivari*, *P. pyrromerus*, and *P. eriphus* was the lowest in grid A at Cashca Totoras, the grid with the greatest proportion of disturbed, secondary forest and closest proximity to cattle pastures. Our results provide baseline population data and suggest that the role of species traits, climate change, forest disturbance, and disease should be further explored through targeted experimental work. Anthropogenic disturbance may threaten the persistence of *Pristimantis* species.

### 4.1. Temporal trends in *pristimantis* population parameters

Constant apparent monthly survival in nearly all the species we studied may reflect the relative stability of tropical environments and a shared characteristic among Neotropical amphibians. In temperate environments, amphibians can exhibit large differences in survival and abundance among years related to extreme temperature, precipitation, and hydroperiod (Semlitsch et al., 1996; McCaffery and Maxell, 2010). By contrast, constant apparent monthly survival of Neotropical adult amphibians has been observed in *Litoria pearsoniana*, a small arboreal stream-breeding treefrog (Murray et al., 2009); *Espadarana prosoblepon*, a stream-breeding glass frog (McCaffery and Lips, 2013); and *Atelopus cruciger*, a stream-breeding harlequin toad (Lampo et al., 2011). Fluctuations in abundance over time may be caused by pulsed recruitment or differences in survival of juvenile life stages.

Our results indicate that the abundance of *Pristimantis* species fluctuates widely over time. Short-term fluctuations suggested a sensitivity to seasonal patterns of precipitation and temperature. The highest abundance of *P. simonbolivari* occurred at the end of the rainy season during the months of March and April at Bosque Protector Cashca Totoras. Larger population

sizes during the rainy season may be caused by episodic recruitment (Pechmann et al., 1991) or by higher survival when conditions are favorable. In some species, longer-term trends were evident in addition to wide, short-term fluctuations. Our results indicated a steep decline in *P. bicantus* at Yanayacu Biological Station with a population die-off occurring sometime from 2004 to 2006. This steep decline marked a decrease in abundance that was greater than seasonal and interannual fluctuations observed over previous sampling sessions during 2002–2003.

Our results contradict previously held beliefs that direct-developing species do not exhibit wide fluctuations in population size due to their independence from aquatic habitat (Green, 2003; Marsh, 2001). We used robust methods to reveal a potential die-off in one *Pristimantis* species and seasonal fluctuations associated with precipitation and temperature. Large and frequent changes in population size may make *Pristimantis* species more vulnerable to local extinction from demographic or environmental stochasticity (Doak et al., 1994; Engen and Saether, 1998). We show that the absence of aquatic larvae does not make direct developing species invulnerable to population decline.

#### 4.2. Environmental variables influencing *pristimantis* population parameters across spatial scales

Our results suggest that habitat disturbance, altering local forest patches and level of landscape fragmentation, may pose a threat to *Pristimantis* species. The grid located in secondary forest in close proximity to a cattle pasture had the lowest abundance, survival, and population growth rate at Cashca Totoras. The other two grids at that site contained primary forest, streams, and stands of bamboo and were located farther away from pasture (Fig. 1). Our results are consistent with other studies that have found that forest disturbance, canopy cover, slope, and distance to streams affect *Pristimantis* populations (Cubides and Urbina-Cardona, 2011; Marsh and Pearman, 1997; Pearman, 1997). Forest habitat type, fragmentation, and edge effects have long been recognized as key features that influence population dynamics (Fahrig, 2003; Folt and Reider, 2013; Funk and Mills, 2003; Laurance et al., 2002; Marsh and Pearman, 1997).

Ecuadorian forests suffer the highest deforestation rates in South America (Dislich et al., 2009) therefore this form of environmental disturbance may pose one of the greater threats to *Pristimantis* species. Our study suggests that forest disturbance negatively affects the abundance, apparent survival, and population growth rate of *P. pyrhomerus*, *P. simonbolivari*, and *P. truebae*. However, until more experimental work has been completed we do not know if this response characterizes all species in this genus. Although habitat fragmentation and destruction can have wide ranging effects across taxa, species respond differently to environmental disturbance (Sutton et al., 2013).

Regional differences in population parameters were difficult to assess in our study because the type of *Pristimantis* species, climate, and degree of forest disturbance and fragmentation varied between study sites. In our study, *Pristimantis* species from different cloud forests in Ecuador did not exhibit widely different patterns in apparent survival and population growth rates. However, across the range of the genus *Pristimantis*, there are wide differences in climate, disturbance, and species composition that may interact in complex ways to influence population trends in *Pristimantis* species. For example, demographic parameters including density and age structure often interact with spatial dynamics and extrinsic environmental dynamics (Marsh and Trenham, 2001; Pellet et al., 2006). One Neotropical frog *Edalorhina perezi*, selects reproductive pools across space in a manner that balances the cost of competition with con-specific tadpoles with the risk of desiccation and predation by aquatic insects (Murphy, 2003).

#### 4.3. Variation in population parameters based on species

Monthly apparent survival estimates for the *Pristimantis* species in this study fall at a lower end of the range observed in other Neotropical amphibians. Monthly Apparent Survival for *Litoria pearsoniona*, *Espadarana prosoblepon*, and *Atelopus cruciger*, three species representing a wide range of Neotropical amphibian taxa, is 0.4–0.9 (Lampo et al., 2011; McCaffery and Lips, 2013; Murray et al., 2009). Apparent monthly survival estimates for all species in all forest grids was 0.4–0.7 except for estimates for species in grid A and Cashca Totoras, where the estimate for apparent monthly survival was 0.2–0.3. Lower apparent survival relative to other species and forest patches may be due to higher rates of mortality or higher rates of movement outside of monitoring grids.

Unique species traits within the *Pristimantis* genus may explain differences in the population dynamics of individual species. *Pristimantis* species differ in body size and use of habitat. In some organisms, body mass and body temperature, through their effects on metabolic rate, can explain variation in fecundity and mortality (Savage et al., 2004). In addition, differences in population dynamics may be related to microhabitat differences in prey base, type and degree of predation pressure, and microclimate, which vary vertically across forest canopies. Syntopic *Pristimantis* species segregate vertically across the forest canopy (Blair and Doan, 2009; Guayasamin and Funk, 2009).

Differences in population parameters based on species, sex, and age were consistent with known natural history of *Pristimantis* species. Lower apparent survival among juveniles was expected because some amphibians and other r-selected species often experience high mortality rates in early life stages (Vanbuskirk and Smith, 1991). *Pristimantis* males are often territorial, vocalizing from a fixed point on top of leaves or other vegetation to attract females, which appear to move more (Lynch and Duellman, 1997). Lower apparent survival among females may be attributable to their movement outside of monitoring grids to seek suitable mates, rather than mortality. Our results showed that even for species from the same genus inhabiting cloud forests in the same region of Ecuador, levels of abundance and population dynamics might differ



widely. *Pristimantis simonbolivari* was far more abundant than any of the other species at Bosque Protector Cashca Totoras or Yanayacu Biological Station. Specialization in a narrow ecological niche and microhabitat may explain the species-specific responses across grids and monitoring regions. Forest disturbance and climate change affect components of cloud forest ecosystems in different ways. For example, we might expect that *P. bicantus*, a species found nearly exclusively at heights less than 0.5 m above the ground, would be disproportionately affected by reductions in soil moisture.

#### 4.4. Future steps

Future steps in amphibian decline research in Central and South America should strive to collect robust and long-term population data, higher resolution of data across taxonomic groups, and more accurate and widespread monitoring of climate so that it is possible to correlate climate with demography (McCaffery and Maxell, 2010). It would also help to investigate the role of disease in the population dynamics of a wider range of Neotropical amphibians. Specifically, to increase capture probabilities and survival of marked individuals, we suggest using larger monitoring grids (100 m × 100 m), and clipping no more than three toes on each frog or using, supporting findings of Swanson et al. (2013) or use photo identification methods. Our results also highlight the need to incorporate local habitat characteristics into population models and predictions. In the absence of amphibian monitoring at high temporal and spatial resolution, it is difficult to determine the relationship between climate and the population dynamics of declining amphibian species. Apparent survival, recruitment, and dispersal can be affected by climatic conditions (Allmon, 1991; Cayuela et al., 2012; Griffiths et al., 2010). Climate also influences species interactions and community dynamics that are related to population dynamics and conservation status (Taylor et al., 2013). Ecuador's temperatures have risen by 0.1 °C per decade since 1939, with the rate of warming tripling in the last 25 year (Corfield, 2008), indicating the urgency of understanding how changing climate may affect future population trends.

## 5. Conclusions

Using capture–mark–recapture techniques, we were able to document population abundance, survival, and population growth rates for four *Pristimantis* species over an eight year period and three additional *Pristimantis* species in a different region over a two year period. The results of our study highlight the value of robust population studies and show differences in abundance, apparent survival, and population growth rates that may be associated with seasonal climate and forest disturbance. We also provided evidence for a population decline in *P. bicantus*. Our results indicate a previously unknown vulnerability among Neotropical amphibians and suggest that *Pristimantis* species may be more at risk to stochastic dynamics, climate change, and habitat disturbance than previously thought. Our results additionally suggest the need for high-quality experimental work focused on how climate change, habitat destruction and fragmentation, and disease may influence understudied amphibians in one of the most at-risk regions of the world.

## Acknowledgments

This study was made possible through research funds from the Fulbright Commission, Declining Amphibian Population Task Force (DAPTF) Seed Grant, and a Conservation, Food, and Health Foundation Grant. We would also like to thank H. Greeney for providing accommodations at Yanayacu Biological Station and the Universidad de Bolivar for accommodations at Cashca Totoras Research Station. We would like to thank Dr. E. Muths, S. Amburgey, and 2 anonymous reviewers for their review of this manuscript. Research permits for this project were obtained from the Ministerio del Ambiente (029-IC-FAU-DFP) in Ecuador. This project was approved by the University of Montana Institutional Animal Care and Use Committee (ACC 034-00).

## Appendix A. Supplementary data

Supplementary material related to this article can be found online at <http://dx.doi.org/10.1016/j.gecco.2014.06.002>.

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