# Lowland extirpation of anuran populations on a tropical mountain

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**Background.** Climate change and infectious diseases, threaten animal and plant species even in natural and protected areas. To cope with these changes, species may acclimate, adapt, move or decline. Here, we test for shifts in anuran distributions in the Luquillo Mountains (LM), a tropical montane forest in Puerto Rico by contrasting occurrence probabilities from historical (1931-1989) and current data (2015/2016). **Methods.** Historical data were gathered through the Global Biodiversity Information Facility (GBIF) and published literature and the current data were collected using acoustic recorders along three elevational transects. **Results.** In the recordings, we detected the 12 native frog species known to occur in LM. Over a span of ~25 years, two species have become extinct and four species suffered extirpation in lowland areas. As a consequence, low elevation areas in the LM (< 300 m) have lost at least six anuran species. **Discussion.** We hypothesize that these extirpations are due to the effects of climate change and infectious diseases, which are restricting many species to higher elevations and a much smaller area. Three lines of evidence support our hypothesis: 1) LM is a protected reserve without any obvious land use change in the past 80 years. 2) An increase in temperature and the frequency of dry periods coincided with amphibian declines. And 3) *Batrachochytrium dendrobatidis* was found in the preserved skins of frog specimens coinciding with the beginning of anuran declines in LM. Our study confirms the general impressions of amphibian population extirpations at low elevations, and corroborates the level of threat by IUCN

1 **Lowland extirpation of anuran populations on a tropical mountain.**

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41   **Abstract**

42

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44   natural and protected areas.  To cope with these changes, species may acclimate, adapt, move or
45   decline.  Here, we test for shifts in anuran distributions in the Luquillo Mountains (LM), a
46   tropical montane forest in Puerto Rico by contrasting occurrence probabilities from historical
47   (1931-1989) and current data (2015/2016).
48   **Methods.** Historical data were gathered through the Global Biodiversity Information Facility
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52   span of ~25 years, two species have become extinct and four species suffered extirpation in
53   lowland areas.  As a consequence, low elevation areas in the LM (< 300 m) have lost at least six
54   anuran species.
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56   infectious diseases, which are restricting many species to higher elevations and a much smaller
57   area.  Three lines of evidence support our hypothesis: 1) LM is a protected reserve without any
58   obvious land use change in the past 80 years. 2) An increase in temperature and the frequency of
59   dry periods coincided with amphibian declines. And 3) *Batrachochytrium dendrobatidis*
60   was found in the preserved skins of frog specimens coinciding with the beginning of anuran
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64   **Keywords:** acoustic monitoring, ARBIMON, occupancy, elevation, climate change, infectious
65   disease

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87 **Introduction**
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89       The 21$^{th}$ century marks an era in which biodiversity is threatened at the global scale.
90 Although habitat loss and degradation due to human activities are the main threats to animal and
91 plant species around the world (WWF 2016), populations of many species are declining even in
92 natural and protected areas (Hedges 1993; Stuart *et al.* 2004; Lips *et al.* 2005; Skerratt *et al.*
93 2007; Collins, Crump & Lovejoy III 2009). To explain these declines in undisturbed habitats,
94 scientists have focused on the widespread effects of climate change and infectious diseases.
95 Climate change is linked to local extinctions and has altered species distributions and abundance,
96 causing an overall shift toward higher latitudes and altitudes (Parmesan 2006; Seimon *et al.*
97 2007; Raxworthy *et al.* 2008; Lenoir *et al.* 2008; Chen *et al.* 2011; Ficetola & Maiorano 2016).
98 Infectious diseases, such as chytrisiomycosis, have also caused local extinctions and population
99 declines around the world, especially in cool moist enviroments charcteristic of many upland
100 tropical areas (Whitfield, Lips & Donnelly 2016) altering the spatial distribution of many species
101 (Pounds *et al.* 2006; Di Rosa *et al.* 2007; Kiesecker & Skelly 2011; Lips 2016).
102       Although an increasing number of studies have documented changes in species
103 distributions in tropical regions (Pounds, Fogden & Campbell 1999; Raxworthy *et al.* 2008;
104 Chen *et al.* 2011; Feeley *et al.* 2011; Forero-Medina *et al.* 2011; Harris *et al.* 2012), the majority
105 of information on range shifts comes from temperate regions, (Lenoir & Svenning 2014),
106 resulting in large uncertainties in predicting the responses of tropical species to different global
107 changes scnearios (Feeley & Silman 2011). Nevertheless, a recent study has shown that
108 hundreds of species have already suffered local extinction in the tropics (Wiens 2016). In
109 addition, tropical montane areas are among the most threatened ecosystems due to global
110 warming (Still, Foster & Schneider 1999; Williams, Jackson & Kutzbach 2007) and the flora and
111 fauna in these areas are expected to suffer the greatest proportion of extinctions due to climate
112 change (Sekercioglu *et al.* 2008). From a conservation perspective, this is particular troublesome
113 given that tropical montane areas harbor a large portion of the world biodiversity and have high
114 levels of endemism (Gradstein, Homeier & Gansert 2008).
115       Here we address the question: Have there been elevational shifts in anuran distributions
116 within the largest protected area in Puerto Rico? To answer this question, we compared the
117 historical and current elevational distributions of 12 species within the Luquillo Mountains.
118 Specifically, we quantified species occurrence along an elevation gradient (~ 0 – 1,050 m) and
119 tested for shifts in anuran distributions by comparing occupancy probabilities between historical
120 (1931-1989) and current data (2015-2016). Our study provides a quantitative description of
121 elevational shifts in anuran species in a tropical mountain, and a quantitative baseline for future
122 studies of these species.
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127 **Materials & Methods**

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129      *Study site*

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131      The study was conducted in the Luquillo Mountains (LM) in north-eastern Puerto Rico
132 (Fig. 1). The majority of LM is protected by the El Yunque National Forest (EYNF), also known
133 as the Luquillo Experimental Forest, which is the largest protected area (115 km$^2$) of primary
134 forest in Puerto Rico (Lugo 1994). The LM spans an elevational range from 100 to 1074 m and
135 its highest peak is only 8 km from the ocean, creating a steep elevation gradient. This protected
136 site is ideal for testing for elevational shifts for three reasons: 1) There have been no direct
137 effects of land use change during the last 80 years in the LM; 2) The LM comprises three main
138 peaks (Pico del Este – 1051 m, Pico del Yunque -1050 m, Pico del Toro – 1074 m) allowing the
139 establishment of several elevational gradients; and 3) There has been extensive research
140 documenting abiotic and biotic changes along the elevational gradient. For instance, the LM
141 elevational gradient has a positive relationship with rainfall, runoff, humidity, cloud cover and
142 wind velocity (Briscoe 1966; García-Martinó *et al.*, 1996; Weaver & Gould 2013) and a negative
143 relationship with temperature, forest growth, and canopy height (Weaver & Murphy 1990;
144 Weaver 2000; Wang *et al.* 2003; Weaver & Gould 2013). Temperature declines with elevation
145 from ~ 26.5°C in the lowlands to ~ 20°C at the mountain top (Waide *et al.* 2013). Annual
146 rainfall ranges from 2450 mm yr–1at lower elevations to over 4000 mm yr–1at higher elevations
147 (Waide et al. 2013). In addition, the distribution of plants and animals are also affected by this
148 elevation gradient (Gould, Gonzalez & Rivera 2006; González *et al.* 2007; Gould *et al.* 2008;
149 Willig *et al.* 2011; Brokaw *et al.* 2012; Weaver & Gould 2013; Campos-Cerqueira & Aide
150 2016).

151      *Species*

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153      The anuran community in the LM includes 13 native species of tree frogs commonly
154 referred to "coquis" (*Eleutherodactylus spp*.) and one native frog species from the
155 *Leptodactylidae* family. The coquis are terrestrial-breeding, direct-development species, and
156 calling and reproductive activity occurs year-round (Stewart & Pough 1983; Woolbright 1985;
157 Stewart 1995; Joglar 1998). All coqui species are very vocal throughout the night and most
158 species have a peak of vocal activity around 20:00 (Villanueva-Rivera 2014). *Eleutherodactylus*
159 *coqui* is one the most studied species in Puerto Rico. Both males and females are strongly
160 territorial, and they rarely move more than five meters from their retreat sites (Woolbright 1985;
161 Woolbright 1996; Joglar 1998). Ten of the 13 species tree frogs are endemics to Puerto Rico and
162 eight are listed in the IUCN Red List (Table 1).

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166    *Historical data*

167        The historical data was acquired through the compilation of all available information
168    about the species distributions in published and open sources (Table S1, Table S2, TableS3).
169    While some data sets provided quantitative information about the presence of the species
170    associated with a specific georeferenced location (e.g. GBIF 2016, Joglar 1998; Drewry & Rand
171    1983), others data sets (e.g. Schwartz & Henderson 1991; Rivero 1998) provided qualitative
172    information about species distribution range that was used to support the quantitative data.  The
173    information about species distribution from the historical data sets were acquired using different
174    sampling methods, from opportunistic observations to mark-recapture and acoustic monitoring.
175    Rather than being a drawback, the use of these complementary methods may increase species
176    detactability.  As far as we know, our compilation is the most comprehensible collection of
177    historical data on anuran distributions (i.e. occurrence) in the Luquillo Mountains in Puerto Rico.

178        For a record to be included in our quantitative historical data set, it had to fulfill three
179    criteria: 1) the record had to include a georeferenced locality or a specific geographical
180    description that enabled us to georeference the locality; 2) the record had to be within the LM
181    area; and 3) the record had to be before 1990.  We used records before 1990 because this date
182    coincides with the decline of many populations of coqui species in the LM (Burrowes, Joglar &
183    Green 2004), and in addition we created a gap of ~25 years between the historical and current
184    data sets.  All geographical coordinates from the GBIF data set were checked and corrected
185    (Table S2).
186
187    *Current data*
188
189        We collected acoustic data from 67 sites in the LM along three elevational transects (84 –
190    1049 m) between March and May of 2015 and again in April and May of 2016.  The elevational
191    transects took advantage of roads and trails, but all audio recorders were placed more than 200 m
192    from any road.  Each elevational transects started in the lowlands and reached one of the three
193    main mountain peaks of the Luquillo mountains (East Peak, Toro Peak, El Yunque Peak).  Along
194    each elevational transect, two audio recorders, separated at least by 200 m, were deployed at
195    ~100-m elevational intervals.  Audio recorders collected data at each site for approximately one
196    week and were then moved to another elevation transect.  Both male and female
197    *Eleutherodactylus* species are territorial species, and *E. coqui* does not move more than five
198    meters from their retreat sites (Stewart & Pough 1983; Woolbright 1985; Gonser & Woolbright
199    1995).  Calls of all the anuran species from our study site were brodcasted at different distances
200    from the audio recorder, and we estimated the detection range to be ~50 m.  Therefore, a site is
201    defined as a three-dimensional hemisphere with a radius of approximately 50 m around the
202    recorder.  Given that the recorders were separated by >200 m we assumed that they were
203    independent samples.  All recordings were analyzed, permanently stored, and available in the

204    Automated Remote Biodiversity Monitoring Network (ARBIMON) (arbimon.sieve-
205    analytics.com/project/elevation/dashboard).
206          Audio recorders (LG smartphone enclosed in a waterproof case with an external
207    connector linked to a Monoprice microphone) running the ARBIMON Touch application
208    (https://play.google.com/store) were used to collect the audio recordings.  Audio recorders were
209    placed on trees at the height of 1.5 m and programmed to record 1 minute of audio every 10 min
210    for a total of 144 – 1-minute recordings per day.  We manually inspected all recordings from
211    18:00 to 5:00 (65,187 1-minute recordings ) and marked the presence and absence of each focal
212    species for each day.
213
214    ***Analysis***
215    ***Historical distributions - GLM models***
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217          Within the LM, anurans were historically reported from 51 sites, ranging from 39 to 1045
218    m.  The compilation of all historical data provided valuable information about the presence of
219    species, but no data about species absences.  Since our goal was to predict species occurrence
220    from the historical data and because predictive methods such as generalized linear models
221    (GLM) require absence data, we generated pseudo-absence data by assigning an absence where
222    there were no reports for species from a site.  This procedure allowed us to fit GLM models,
223    which is recommended when absence data are not available (Chefaoui & Lobo 2008).  In this
224    way, all species with a collection record from a site were listed as present, and all other species
225    were listed as absent.  This approach provides greater model performance than using randomly
226    sampled pseudo-absence (Lütolf, Kienast & Guisan 2006).  We used this dataset to fit
227    generalized linear models (GLM) using a logistic function in R.  Although we are aware that the
228    estimation of occurrence probability using logistic regression may be unrealistic (Ward *et al.*
229    2009; Royle *et al.* 2012) and may underestimate occupancy probability (Kéry, Gardner &
230    Monnerat 2010; Lahoz-Monfort, Guillera-Arroita & Wintle 2014), the use of more appropriate
231    analysis (e.g. Maxlike – Royle *et al.* 2012) were precluded for two reasons: 1) overall sparse data
232    due to a small data set, and 2) lack of repeated visits to the same locality.  Nevertheless, our
233    historical quantitative data matches with the available qualitative information about species
234    distribution (Schwartz & Henderson 1991; Rivero 1998), and it provides the best summary of the
235    past distributions of these species.
236          Because we were interested in testing for elevational shifts, we included information
237    about elevation as a standardized continous covariate represented by a linear (*elevation*) and a
238    quadratic (*elevation+elevation$^2$*) function.  In addition, we included a null model with only the
239    intercept (Null model) in a total of three model parametrizations for each species, simply
240    depicted as:
241

242   *(1) Occupancy ~ Null*
243   *(2) Occupancy ~ Elevation*
244   *(3) Occupancy ~ Elevation + Elevation²*

245

246   We used the glmulti package (Calcagno & de Mazancourt 2010) of R software for model
247   selection based on the lowest AIC value.  We compared models using AIC, and we estimated
248   occupancy profiles by model-averaging all models with ΔAIC < 2.0

249

250   **Current distributions - Occupancy models**

251

252   We used a detection/non-detection matrix summarized by day from the acoustic monitoring
253   data set to fit single-species single-season occupancy models using the package Unmarked in R
254   (Fiske & Chandler 2011).  Because we have a relatively small number of anuran species in LM
255   and because all the focal species were detected several times we chose to use single-species
256   models.  We also assume that the population was close between the two years to reduce model
257   complexity and because change in occupied sites between years were very small for all species
258   (average of 2.45 sites, SD = 2.42).  We did not include *E. coqui* in occupancy analyses because
259   the first species was present in all sampling sites.
260   The occupancy state of each sampling site was estimated taking into account imperfect
261   detection, following the standard maximum likelihood hierarchical approach introduced by
262   (Mackenzie *et al.* 2002).  Our models contain a sampling level describing the probability of
263   detection conditioned on occupancy ($p$), and an underlying biological level describing the
264   probability ($\psi$) that a site is occupied.  Both $p$ and $\psi$ were allowed to vary according to elevation.
265   To estimate elevational profiles of occupancy ($\psi$) for each species we constructed a set of
266   competing hypothesis of how occupancy and detection changed over *elevation* (Kéry, Gardner &
267   Monnerat 2010).  *Elevation* is a standardized continuous covariate represented by a linear
268   (*elevation*) and a quadratic (*elevation + elevation²*) function.  In addition, we included a null
269   model with only the intercept. resulting in a total of nine models per species (Table S4).  An
270   example of the most parametrized occupancy model can be described as:

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272   Biological level - Occupancy ($\psi$)
273   logit ($\Psi$)= $\beta_0$+ $\beta_1$elevation+ $\beta_2$elevation²

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275   Sampling level - Detectability ($p$)
276   logit ($p$)= $\beta_4$+ $\beta_5$elevation+$\beta_6$elevation²

277

278   We compared models using AIC, and we estimated occupancy profiles across the range
279   of elevations sampled by model-averaging all models with ΔAIC < 2.0.  All models were fitted
280   using the package Unmarked in R (Fiske & Chandler 2011).  To compare changes in species
281   distributions between historical and current data we conservatively estimated the species

282  distribution range by selecting sites with probability of occupancy equal or higher than 0.1.  By
283  using this conservative approach to determine species range limits we excluded sites with low
284  likelihood to be occupied by the species.  Only range shifts greater than 100 meters were
285  considered significant.
286
287  **Results**
288
289  ***Naïve occupancy data***
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291        A total of 51 unique sampling localities were extracted from our historical compilation in
292  the LM over a period of 58 years (1931 to 1989).  The most widespread species was *E. coqui* (n
293  = 27 sites) and *E. portoricensis* (n = 25 sites), while *E. hedrick* (n = 4 sites), *E. unicolor* (n = 3
294  sites) and *E. cochranae* (n = 3 sites) were relatively rare (Fig. 2).  The total numbers of species
295  detected varied across the sites with a maximum of eleven species detected at one low elevation
296  site (371 m).
297        In contrast, 67 sampling localities were surveyed in 2015 and 2016 and the 12 native frog
298  species known to currently occur in the LM were detected.  These species included:
299  *Lepidodactylus abilabris, E. antillensis, E. cochranae, E. brittoni, E. coqui, E. wightmanae, E.*
300  *hedricki, E. unicolor, E. gryllus, E. locustus, E. richmondi,* and *E. portoricensis.*  We did not
301  detect two species *(E. eneidae* and *E. karlschmidti)* that are considered extinct (Burrowes et al.,
302  2004).  The most widespread species was *E. coqui*, detected in all sampling sites (n = 67), and
303  the least common species were *E. locustus* and *E. richmondi* (n = 4).  The total numbers of
304  species detected varied across the sites with a maximum of seven species detected at one high
305  elevation site (800 m).  The naïve occupancy data suggests that six species (*E. portoricensis, E.*
306  *gryllus, E. locustus, E. richmondi, E. eneidae, E. karlschmidti*) no longer occur below 500 meters
307  (Fig. 2).
308
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310  ***Occupancy modelling***
311
312        Elevation plays an important role in amphibian distribution because models with the
313  covariate *Elevation* performed better (ΔAIC < 2) than the null model for the majority of species
314  in the historical data set ( n=11/14) as well in current data ( n=9/11) (Table 1). Overall, the
315  occurrence probability increases with the increase of elevation in four species (*E. portoricensis,*
316  *E. gryllus, E. unicolor,* and *E. locustus*), while there was a negative relationship between
317  occurrence and elevation in four species (*E. brittoni, L. albilabris, E. antillensis,* and *E.*
318  *cochranae*) (Table 1, Fig. 3).  The occurrence probabilities of *E. richmondi* and *E. hedricki*
319  assume a bell-shape distribution with higher occupancy probabilities at intermediary elevation.
320  The historical occurrence distribution of *E. wightmanae* indicates a higher occupancy probability

321   at intermediate elevations, while the current occurrence distribution shows a slight increase of
322   occurrence with elevation.
323      The main difference between the past and present distributions of the species can be
324   described by two features: 1) the level of the occupancy probabilities and 2) changes in the
325   distributional range.  There was a decrease in the level of occupancy probabilities in five species
326   (*E. richmondi, E. wightmanae*, *E. locustus, E. antillensis,* and *E. cochranae*), while there was an
327   increase in the levels of occupancy probability for six species (*E. portoricensis, E. gryllus, E.*
328   *unicolor, E. hedricki, E. brittoni,* and *L. albilabris*) (Fig 3).  Four species showed a significant
329   range contraction (>100m) for the lower end of the elevational distributions (Fig. 4): *E.*
330   *portoricensis* (207 to 508 m), *E. gryllus* (39 to 654 m), *E. locustus* (191 to 333 m), *E. richmondi*
331   (39 to 654 m). There was also signficant range contraction for the upper end of the elevational
332   distribution of two species: *E. richmondi* (1045 to 800 m) and *E. antillensis* ( 618 to 216 m).  In
333   addition, we detected a range expansion at the low end of the elevational distribution in *E.*
334   *unicolor* (908 to 523 m) and a range expansion on the upper end of *E. hedricki* (649 to 1020 m).
335      Overall, detection probabilities were high for all species (0.40 > p < 1.00) indicating that
336   our acoustic survey provides a robust methodology for detecting anuran species.  Moreover, the
337   high detection probabilities estimated provide robust evidence for the lowland extirpation of
338   some species.
339
340   **Discussion**
341
342      In this study, we present quantitative evidence of changes in the distributions of anuran
343   species along an elevational gradient in a protected tropical mountain.  Over a span of ~25 years,
344   two species became extinct and four species suffered extirpation in lowland areas.  As a
345   consequence, low elevation areas in the LM (< 300 m) have lost at least six anuran species.  This
346   pattern of local extinction in low elevation sites has been observed for many other species around
347   the world, and climate change is thought to be the major culprit (Wiens 2016).  Furthermore, the
348   impacts of global warming are expected to have extensive negative impacts on species richness
349   in lowland tropical areas (Colwell *et al.* 2008).  One possible explanation for population
350   extirpation at the lower end of species distributions is that species may be exceeding their
351   maximum thermal tolerance (Deutsch *et al.* 2008) due to warming temperatures.  Moreover, the
352   loss of species in tropical lowlands is especially troublesome given that there are rarely species
353   from hotter areas to colonize the lowlands (Colwell *et al.* 2008).
354      Although our results indicate changes in the elevational distributions of some species, there
355   were two limitations with the historical data: 1) lack of information on non-detection and 2)
356   absences of replicate visits in a short time frame.  Consequently, our historical data set may have
357   false absences, biasing our comparisons.  In addition, we were not able to estimate detection
358   probabilities, which can lead to bias and an underestimation of occupancy probabilities (Kéry,
359   Gardner & Monnerat 2010).  Misidentification error and taxonomic changes could also be a
360   relevant source of bias.  Moreover, all historical data inherently suffer from geographical

361   imprecision and survey-specific characteristics such as effort, different methodologies, and
362   variability in observer skills (Tingley & Beissinger 2009).  Despite these intrinsical limitations,
363   our historical quantitative data set reflects the available qualitative description of species
364   distribution range, and it offers our best knowledge about the historical distribution of the
365   species.
366       Although these limitations limits inferences on colonization, we can provide inferences for
367   local extinction (Tingley and Beissinger 2009).  For instance, there are many records, including
368   museum specimens, indicating that *E. gryllus* historically occurred in lower elevation sites (e.g.
369   300 m) and now it can only be found above 600 m.  Any bias and underestimation of occurrence
370   probabilities would be more likely to affect our comparisons when the occurrence probabilities
371   from the historical data sets are lower than the current occurrence probabilities.  Therefore, the
372   historical biases in the data results in conservative estimates of range contractions.
373       The observed pattern of species extirpation at low elevations areas is supported by long-term
374   monitoring projects centered around the El Verde Field Station (350 - 450 m) (Stewart 1995)
375   (Woolbright 1997).  The El Verde Field Station is the most studied site in LM and there is strong
376   evidence that of the seven species that were relatively common before 1990, only *E. coqui and*
377   *E. hedricki* are still common, while  *E. gryllus*, *E. portoricensis*, *E. richmondi*, *E. eneidae*, and *E.*
378   *wightmanae*  are now locally extinct (Drewry & Rand 1983; Woolbright 1997; Stewart 1995)
379   (GBIF, 2016).  Woolbright (1997) extended his study beyond the El Verde Field Station and
380   noted an overall pattern of local extinctions at lower elevation sites within the Tabonuco forest.
381   Furthermore, *E. richmondi*, *E. wightmanae*, and *E. locustus* were also described to have become
382   locally extinct at middle (661 m) and high elevation sites (850 m) in EYNF around 1990 (Joglar
383   & Burrowes 1996).  Our study confirms the results of these two long-term studies given that *E.*
384   *locustus*, *E. richmondi*, *E. gryllus*, *E. portoricensis* and *E. wightmanae* are now relatively rare in
385   the LM and, with the exception of *E. wightmanae,* these species no longer occur in low
386   elevations (< 500 m).  Anecdotal descriptions of elevational shifts indicate an upward shift for *E.*
387   *gryllus, E. portoricensis,* and *E. richmondi* and a downward shift for *E. hedricki* (Joglar 1998).
388   Our results also agree with a general upward shift for *E. gryllus, E. portoricensis,* and *E.*
389   *richmondi*, but there is no evidence for a downward shift for *E. hedricki.*
390       The declines and extirpations of the anurans populations in Puerto Rico between 1970 and
391   1990 (Moreno 1991; Stewart 1995; Woolbright, 1996; Burrowes, Joglar & Green 2004), has
392   intrigued the scientific community since many of these declines have happened in protected
393   areas.  We hypothesized that the distributions shifts documented in this study are the
394   consequence of climate change and chytrid fungus, as previously proposed by other researchers
395   (Joglar & Burrowes 1996; Burrowes, Joglar & Green 2004; Lips *et al.* 2005).  Evidences for this
396   hypothesis can be summarized as follow: First, there has been no obvious direct anthropogenic
397   impact in the LM during the period of decline, and the LM remains one of the best-preserved
398   forests in Puerto Rico.  Second, studies have shown a significant increase in annual mean
399   temperature ($0.007^{o}C$ $yr^{-1}$) over 62 years (1932-1994) in the lowlands (100-450m) of LM
400   (Greenland & Kittel 2002), and a significant increase in the mean minimum temperature and a

401  decrease in mean precipitation from 1970 to 2000 in the East Peak (1051 m) (Lasso & Ackerman
402  2003). In addition, analyses of climate data from local weather stations showed an increase in
403  the frequency of dry periods and prolonged dry seasons between 1970 and 1990, coincident with
404  amphibian declines (Stewart 1995; Burrowes, Joglar & Green 2004). Models also suggest that
405  warming temperatures will continue with drier wet seasons, and drier dry seasons in the LM and
406  the Caribbean (Scatena 1998; Campbell *et al.* 2011). Although *Eleutherodactylus* frogs do not
407  depend on water bodies for reproduction, these species need cool temperatures and humid sites
408  to prevent dehydration and desiccation of eggs, and prolonged periods of drought significantly
409  decreased *E. coqui* population densities in the EYNF (Stewart 1995). Prolonged drought can
410  also reduce foraging success of coquis (Woolbright & Stewart 1987). In addition, there is a
411  negative impact of drought on the behavior and activity patterns of *E. coqui* (Pough *et al.* 1983;
412  Stewart 1995), as well as on the infection levels of the pathogenic chytrid fungus (Longo,
413  Burrowes & Joglar 2010).
414      The *Batrachochytrium dendrobatidis* fungus (Bd) is another potential cause of widespread
415  amphibian decline. Bd has been identified in more than 700 species of amphibians, and it has
416  been associated with species extinctions, mass mortality events, and population declines (Stuart
417  *et al.* 2004; Lips *et al.* 2005; Lips *et al.* 2006; Skerratt *et al.* 2007; Lips 2016). Although no die-
418  offs have been observed in Puerto Rico, there is evidence linking Bd and amphibian declines
419  (Burrowes, Joglar & Green 2004; Longo *et al.* 2013). Bd was found in the preserved skins of *E.*
420  *coqui* collected in 1978, and *E. karlschmidti* collected in 1976, coinciding with the beginning of
421  declines of these species in the LM (Burrowes, Joglar & Green 2004), and it has been detected in
422  nine *Eleutherodactylus* species as well as in *Leptodactylus albilabris* (Burrowes, Longo & Joglar
423  2008). While Bd may pose a serious threat to frogs in EYNF, studies are needed to assess its
424  impact on species distributions along the entire elevational gradient.
425      There is also evidence supporting the interacting effects of climate change and Bd as main
426  cause of amphibian declines (Pounds et al. 2006; Grant *et al.* 2016). In Puerto Rico, the
427  synergetic effect of climate change and disease have been proposed to explain local declines
428  (Burrowes, Joglar & Green 2004). Climate change may act directly on the pathogen by trigging
429  outbreaks, and in the host, it may change behavior, phenology, and physiology (Burrowes 2009),
430  and consequently increase its susceptibility to the pathogen. For instance, coquis stressed by
431  dehydration aggregate in humid refuges during dry periods, which likely increases the
432  probability of disease transmission (Longo, Burrowes & Joglar 2006)
433      Although climate change and infectious diseases are the main culprit for the anuran declines
434  in Puerto Rico (Joglar & Burrowes 1996; Burrowes, Joglar & Green 2004; Lips *et al.* 2005),
435  hurricanes could also contribute to species declines in EYNF (Woolbright, 1991; Woolbright,
436  1997). For instance, two coquis species (*E. portoricensis* and *E. unicolor*) may have been
437  extirpated from El Verde area (350 m) by Hurricane Hugo in 1989 (Woolbright 1997).
438  Nevertheless, some coqui species were apparently not affected by this hurricane, and the density
439  of *E. coqui* rapidly recovery to pre-hurricane levels. The same pattern of increase in abundance
440  of *E. coqui* was observed after the Hurricane Georges (1998) in Maricao, Puerto Rico, while the

441 abundance of two other species declined (*E. richmondi* and *E. brittoni*) (Vilella & Fogarty 2005).
442 Long-term monitoring of all amphibian species is needed to understand the impact of hurricanes
443 on their populations and distributions given that the frequency of hurricanes is expected to
444 increase as global warming increses (O'Brien *et al*. 1992).
445    Our study provides a quantitative description of elevational shifts in anuran species in a
446 tropical mountain, and a quantitative baseline for future studies of these species.  From a
447 conservation perspective, we identified species that may be more vulnerable to extinction due to
448 range contractions and because these species are being pushed to higher elevations where there is
449 much less land area.  For example, our acoustic data showed that four species no longer occur
450 below 500 m (*E. locustus, E. richimondi, E. portoricensis. E. gryllus*).  Furthermore, *E.*
451 *richimondi* was only found in a narrow elevational range (<350 m), and both *E. richimondi* and
452 *E. locustus* are now relatively rare.  Possibly, the most vulnerable species is *E. gryllus* that reach
453 its highest occupancy probabilities above 900 m, only 174 m from the top of the mountain.  The
454 extremely narrow elevational ranges exhibited by these species are especially worrisome because
455 there are only limited connections to other high elevation forest sites in Puerto Rico, and this
456 would require extensive movement through lowland forests, agricultural lands, and urban areas.
457    These shifts in distribution along the elevation gradient are creating new ecological
458 communities, which could impact ecosystem function given that anurans are the largest
459 component of nocturnal biomass of all vertebrates in Puerto Rico (Stewart 1995) and are
460 fundamental components of the food web (Beard *et al.* 2003; Whiles *et al.* 2006). While
461 historically the distributions of 11 coqui species overlapped in the lowlands (371 m), today the
462 elevation with the greatest richness (seven species) occurs at 800 m.  Of greatest concern, is the
463 loss of six coqui species below 500 m.  This biotic attrition in the lowlands is likely to change
464 interspecific interactions affecting the function of these biological communities (Colwell *et al*.
465 2008).
466
467    **Conclusions**
468
469    In this study, we have shown how acoustic surveys can be used to monitor species, provide
470 data to confirm general impressions of amphibian population extirpations at certain
471 sites/elevations, and corroborate the level of threat of species as considered by IUCN.  Two
472 critically endangered species (*E. eneidae* and *E. karlschmidti*) have not been detected since 1974
473 and 1990, despite our efforts and those of previous researchers.  Two species considered
474 critically endangered (*E. locutus* and *E. richmondi*) and two endangered species (*E. portoricensis*
475 and *E. gryllus*) suffered range contractions > 100 m caused by extirpation in the lowlands.  Here,
476 we provide recommendations to improve the conservation of these threatened species: 1) The
477 establishment of a long-term monitoring project to monitor species distributions.  Widespread,
478 frequent, and long-term monitoring is necessary to understand the causes and consequences of
479 amphibian decline, and to focus conservation and management activities (Lips *et al.* 2005); 2)
480 captive breeding of the four species that suffered lowland extirpation.  Captive breeding is often

481  the easiest and most cost-effective method to manipulate and conserve the population of many
482  species (Brooks, Wright & Sheil 2009; Zippel *et al.* 2011).

483

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485

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487

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492  **References**

493

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718  **Figures and tables**

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721  Figure 1.  Map of the Luquillo Mountains and their location in NE Puerto Rico.  The black
722  circles represent sites sampled in 2015/2016 and circles with a dot represent sites with historical
723  data.  Different colors represent differences in elevation (m).

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726  Table 1. Comparison of elevation distribution of 14 frog species in the Luquillo Mountains,
727  Puerto Rico.  Given are IUCN status (EN = endangered; CR = Critically endangered; VU =
728  Vulnerable; LC = Low concern, † =Extinct, * = Endemic), the best supported occupancy model
729  (Elev = elevation; NA = not analyzed) and the cumulative Akaike's Information Criterion weight
730  for all models with those terms (Weight).

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733  Figure 2. Comparison of raw data on species presence along the elevation gradient for 14 frog
734  species in the Luquillo Mountains, Puerto Rico.  Open circles represent positive detections from
735  historical data and black circles represent positive detections from current data.

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737  Figure 3: Historical (black line) and current (blue line) estimated elevation distributions of 11
738  frog species in Puerto Rico. The observed data are show in open circles (historical) and blue
739  circles (current).  The historical and current elevation profiles were estimated by model-
740  averaging all models with ΔAIC < 2.0.  The grey and blue shaded area represent the 95%
741  confidence intervals. Data for the two extinct species (*E. eneidae* and *E. karlschmidti*) and *E.*
742  *coqui*, which occur at all elevations in the historical and current data are not included.

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745  Figure 4. Summary of elevational range changes for 14 species. Significant shifts (>100 m) are
746  in red for extirpations and green for colonization, while no-significant shifts are in grey.

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Comparison of elevation distribution of 14 frog species in the Luquillo Mountains, Puerto Rico.

Table 1. Comparison of elevation distribution of 14 frog species in the Luquillo Mountains, Puerto Rico. Given are IUCN status (EN = endangered; CR = Critically endangered; VU = Vulnerable; LC = Low concern, † =Extinct, * = Endemic), the best supported occupancy model (Elev = elevation; NA = not analyzed) and the cumulative Akaike's Information Criterion weight for all models with those terms (Weight).

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5  for all models with those terms (Weight).

| Species | IUCN status | Distributions (m) | | | | Occupancy modeling | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Historic | Current | Shift Lower range | Shift Upper range | Best model (H) | Best model (C) | Weight (H) | Weight (C) |
| E. portoricensis* | EN | 207-1045 | 508-1049 | **-301** | +4 | Elev$^2$ | Elev$^2$ | 0.70 | 0.50 |
| E. gryllus* | EN | 39-1045 | 654-1049 | **-615** | +4 | Null | Elev | 0.38 | 0.65 |
| E. locustus* | CR | 191-1045 | 333-1049 | **-142** | +4 | Elev | Null | 0.67 | 0.55 |
| E. richmondi* | CR | 39-1045 | 654-800 | **-615** | **-245** | Elve$^2$ | Elev$^2$ | 0.54 | 0.84 |
| E. wightmanae* | EN | 39-1015 | 84-1049 | +45 | +34 | Elev$^2$ | Null | 0.93 | 0.60 |
| E. hedricki* | EN | 329-649 | 362-1020 | +33 | **+371** | Elev$^2$ | Elev$^2$ | 0.59 | 1.00 |
| E. unicolor* | VU | 908-1045 | 523-1049 | **385** | +4 | Elev | Elev | 0.71 | 0.54 |
| E. brittoni* | LC | 39-740 | 84-800 | +45 | +60 | Elev | Elev$^2$ | 0.52 | 0.87 |
| L. albilabris | LC | 39-1045 | 84-1049 | +45 | +4 | Null | Elev | 0.64 | 0.59 |
| E. coqui | LC | 39-1045 | 84-1049 | +45 | +4 | Null | NA | 0.64 | NA |
| E. antillensis | LC | 39-618 | 84-216 | +45 | **-402** | Elev | Elev | 0.70 | 0.70 |
| E. cochranae | LC | 39-222 | 84-245 | +45 | +23 | Elev | Elev | 0.48 | 0.55 |
| E. eneidae* | CR† | 268-1045 | NA | NA | NA | Elev$^2$ | NA | 0.52 | NA |
| E. karlschmidti* | CR† | 130-786 | NA | NA | NA | Elev$^2$ | NA | 0.50 | NA |

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Map of the Luquillo Mountains and their location in NE Puerto Rico.

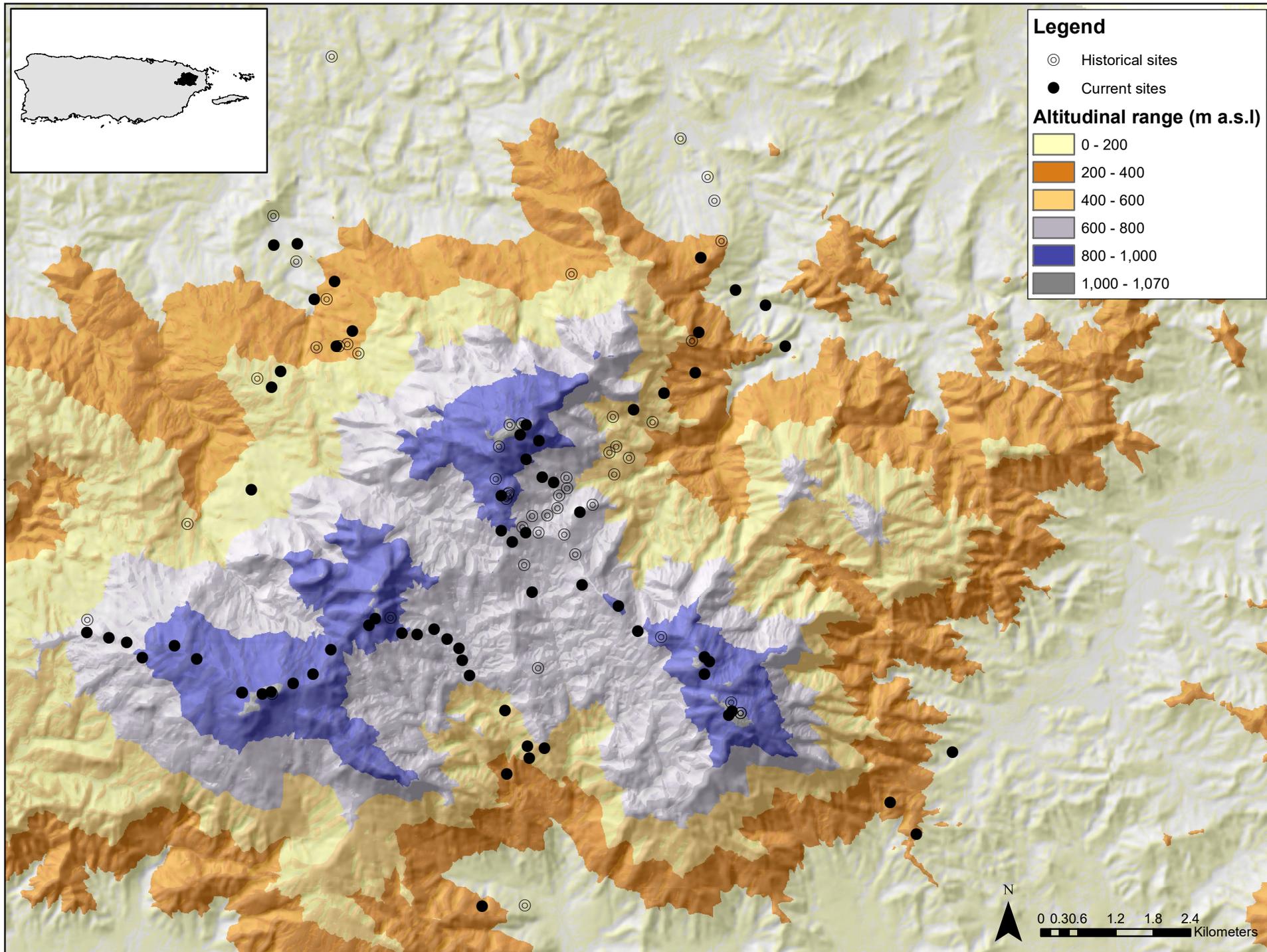
Figure 1. Map of the Luquillo Mountains and their location in NE Puerto Rico. The black circles represent sites sampled in 2015/2016 and circles with a dot represent sites with historical data. Different colors represent differences in elevation (m).

Comparison of raw data on species presence along the elevation gradient for 14 frog species in the Luquillo Mountains, Puerto Rico.

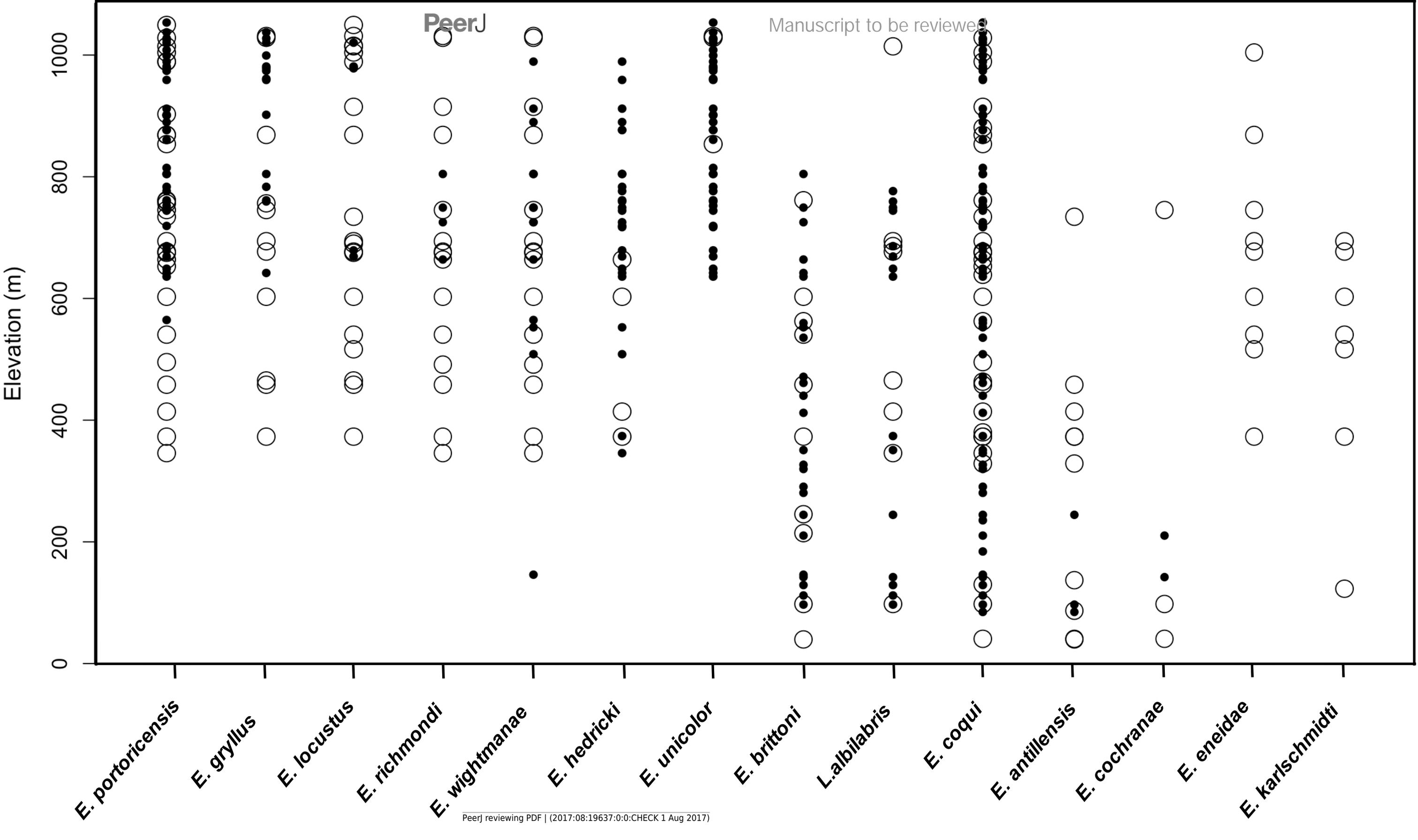
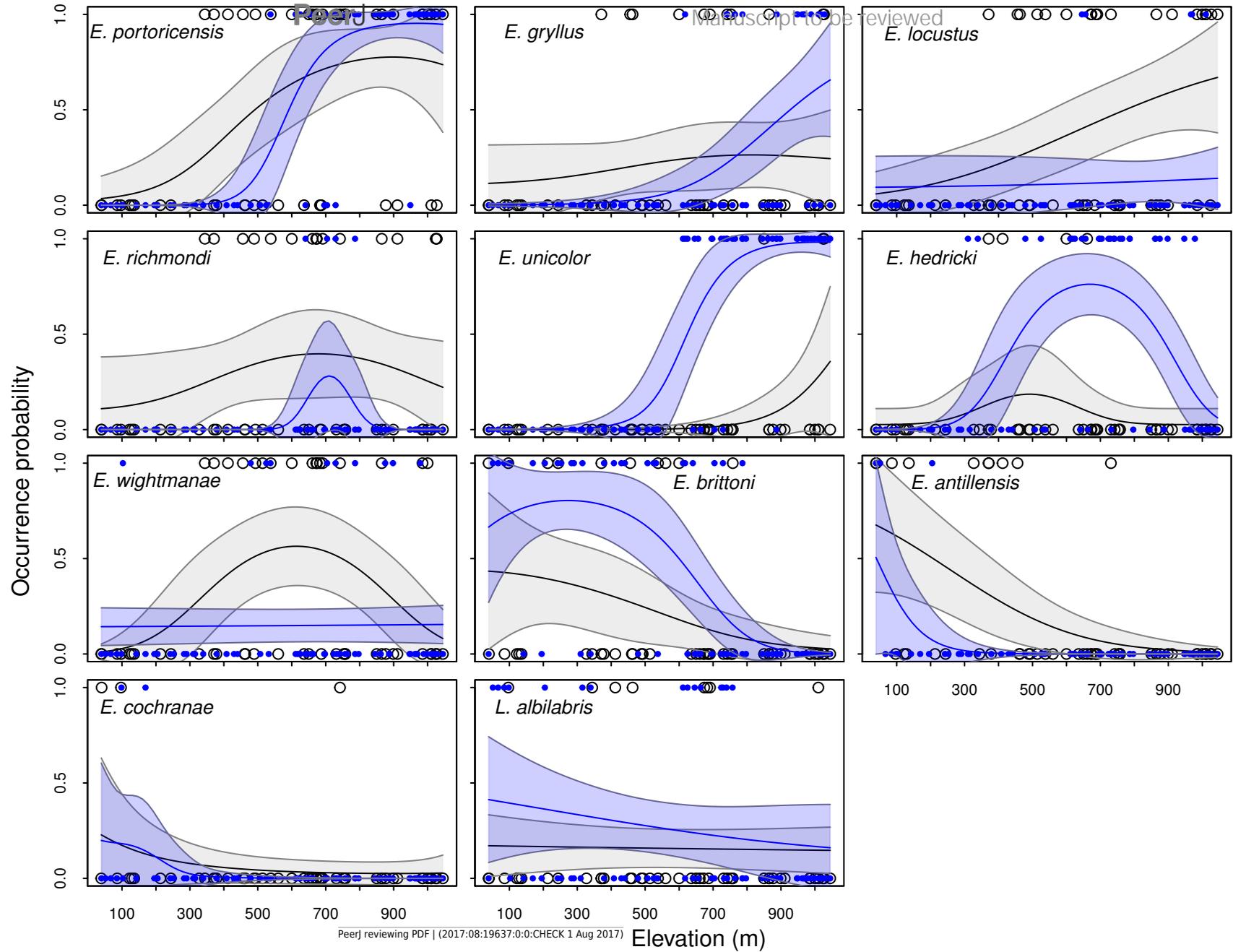
Figure 2. Comparison of raw data on species presence along the elevation gradient for 14 frog species in the Luquillo Mountains, Puerto Rico. Open circles represent positive detections from historical data and black circles represent positive detections from current data.

Historical (black line) and current (blue line) estimated elevation distributions of 11 frog species in Puerto Rico.

Figure 3: Historical (black line) and current (blue line) estimated elevation distributions of 11 frog species in Puerto Rico. The observed data are show in open circles (historical) and blue circles (current). The historical and current elevation profiles were estimated by model-averaging all models with ΔAIC < 2.0. The grey and blue shaded area represent the 95% confidence intervals. Data for the two extinct species (*E. eneidae* and *E. karlschmidti*) and *E. coqui*, which occur at all elevations in the historical and current data, are not included.

Occurrence probability

Elevation (m)

Summary of elevational range changes for 14 species.

Figure 4. Summary of elevational range changes for 14 species. Significant shifts (>100 m) are in red for extirpations and green for colonization, while no-significant shifts are in grey.