

RUNNING HEAD: ANOLIS LIZARDS AS BIOCONTROL AGENTS

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RUNNING HEAD: ANOLIS LIZARDS AS BIOCONTROL AGENTS

TITLE

**ANOLIS LIZARDS AS BIOCONTROL AGENTS IN MAINLAND AND ISLAND  
AGROECOSYSTEMS**

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38 **Summary**

39

- 40 1. Our knowledge of ecological interactions that bolster ecosystem function and  
41 productivity has broad applications to the management of agricultural systems. Studies  
42 suggest that the presence of generalist predators in agricultural landscapes leads to a  
43 decrease in the abundance of herbivorous pests, but our understanding of how these  
44 interactions vary across taxa and along gradients of management intensity and eco-  
45 geographic space remains incomplete.
- 46 2. In this study, we assessed the functional response and biocontrol potential of a highly  
47 ubiquitous insectivore (lizards in the genus *Anolis*) on the world's most important coffee  
48 pest, the coffee berry borer (*Hypothenemus hampei*). We conducted field surveys and  
49 laboratory experiments to examine the impact of land-use intensification on species  
50 richness and abundance of anoles and the capacity of anoles to reduce berry borer  
51 infestations in mainland and island coffee systems.
- 52 3. Our results show that anoles significantly reduce coffee infestation rates in laboratory  
53 settings (Mexico,  $P=0.03$ ,  $F=5.13$   $df=1, 35$ ; Puerto Rico,  $P=0.014$ ,  $F=8.82$ ,  $df=1, 10$ ) and  
54 are capable of consuming coffee berry borers in high abundance. Additionally,  
55 diversified agroecosystems bolster anole abundance, while high intensity practices,  
56 including the reduction of vegetation complexity and the application of agrochemicals  
57 were associated with reduced anole abundance.
- 58 4. *Synthesis and applications.* The results of this study provide supporting evidence of the  
59 positive impact of generalist predators on the control of crop pests in agricultural

60 landscapes, and the role of diversified agroecosystems in sustaining both functionally  
61 diverse communities and crop production in tropical agroecosystems.

62

63 **Keywords:** agriculture, *Anolis*, biodiversity, ecosystem services, coffee berry borer

64

## 65 **INTRODUCTION**

66 The relationship between biodiversity and ecosystem function has received much  
67 attention due to growing concerns around the negative impacts of intensified land use. Empirical  
68 and theoretical studies suggest that biodiversity stabilizes ecosystem function, as referenced in  
69 the “insurance hypothesis,” whereby functional diversity acts as a buffer for ecosystem processes  
70 amidst environmental disturbance (Ives *et al.* 2000; Yachi & Loreau 1999). These principles  
71 have been applied broadly to the management of agricultural landscapes, which vary in both  
72 structural diversity and external inputs (Altieri 1999; Perfecto *et al.* 2005). Diversified  
73 agroecosystems that model native landscapes have been shown to function as reservoirs for local  
74 biodiversity (Fahrig *et al.* 2011; Tschardt *et al.* 2005) and suitable outlets for species dispersal  
75 among metapopulation communities (Vandermeer & Perfecto 2007). Furthermore, increasing  
76 diversity can support ecosystem services that increase crop yield, such as the biological control  
77 of crop pests by natural enemies (Vandermeer *et al.* 2010, Kremen & Miles 2012). Our  
78 understanding of how trophic interactions bolster ecosystem services such as biocontrol, and the  
79 response of relevant species to habitat modification may inform both socio-economic and  
80 ecological goals of food security and biodiversity conservation.

81 The sustainable management of crop pests is an issue of increasing importance among  
82 farmers worldwide. In approximately 80 countries throughout the tropics (nearly 40% of all  
83 sovereign nations), coffee production is a leading agricultural commodity and the primary means  
84 of subsistence for nearly 20 million coffee-growing households (Perez *et al.* 2015). The coffee  
85 berry borer (CBB), *Hypothenemus hampei*, is one of the most important and devastating coffee  
86 pests, inducing 60-90% reductions in coffee yields throughout many countries including, but not  
87 limited to, Mexico, Jamaica, Malaysia, and Tanzania (Benavides & Vega 2005). The destruction  
88 of the coffee berry occurs during the life cycle of *H. hampei*; wherein reproduction occurs within  
89 the fruit, the coffee seed is consumed by the brood (during stages of development), and adults  
90 emerge to disperse for oviposition in unoccupied berries (Brun *et al.* 1995, Perez *et al.* 2015).

91 Several strategies have emerged to eliminate the berry borer, including agricultural  
92 intensification (Perfecto *et al.* 1996, Soto-Pinto 2002) and the application of insecticides (Brun *et*  
93 *al.* 1995). Insecticide application, however, has proven in many cases to be ineffective. Since the  
94 bulk of the organism's life-cycle occurs within the fruit, topical pesticides are often ineffective  
95 (Damon 2000), and in cases where it is affected CBB can quickly develop resistance to these  
96 chemicals (Vega 2015).

97 Several mechanisms have been cited as promoting the top-down control of herbivorous  
98 prey in ecological systems, with habitat complexity and predator diversity as highly relevant,  
99 especially to managed systems (Philpott *et al.* 2012, Iverson *et al.* 2014). A variety of naturally  
100 occurring biocontrol agents against the coffee berry borer have been documented, including ants  
101 (Perfecto & Vandermeer 2006, Larsen & Philpott 2010, Gonthier *et al.* 2013, Morris *et al.* 2015)  
102 and birds (Johnson & Kellermann 2010, Karp *et al.* 2013). In an experiment conducted by  
103 Johnson and Kellerman (2010), coffee plants excluded from foraging birds and bats had  
104 substantially higher coffee berry borer infestations. Furthermore, bird and bat densities were  
105 greatest in more structurally diverse farms.

106 Arboreal lizards in the genus *Anolis* (Iguanidae) are highly ubiquitous insectivores  
107 throughout the New World tropics and reach the highest population densities of any lizard in the  
108 world (Schoener and Schoener 1980, Vitt *et al.* 2003). Anoles drive the top-down regulation of  
109 arthropod communities due to their dominant presence, especially in island ecosystems (Spiller  
110 and Schoener 1990). Despite the high abundance and distribution of anoles, very few studies  
111 have addressed their functional role as predators in agroecosystems (Borkhataria *et al.* 2006,  
112 2012). An exclusion experiment in Puerto Rican shade-coffee found a negative impact of anoles  
113 on select herbivorous pests (Borkhataria 2006), while studies of anoles in natural systems  
114 indicate diets dominated by arthropods including ants (Vitt *et al.* 2003, Huang *et al.* 2008),  
115 spiders (Pacala & Roughgarden 1984, Hodge *et al.* 1999, Vitt *et al.* 2003) and beetles (Wolcott  
116 1923, Simmonds 1958). Simmonds (1958) provides evidence that anoles function as biological  
117 control against scale insects in Bermuda, while also consuming a variety of small insect prey  
118 (*e.g.*, ants) in large quantities. Whether or not anoles are important predators of the coffee berry  
119 borer, however, remains unknown.

120 *Anolis* lizards have been used broadly as a model group for the study of trait  
121 diversification and biotic interactions along environmental gradients (Losos 2009). Their

122 application to biocontrol appears most relevant due to an opportunistic feeding strategy, allowing  
123 individuals to monopolize on aggregates of prey (e.g. colonies of ants and termites) (Barbor  
124 1930; Rand *et al.* 1975; personal observation). Comparative studies on the effects of anole  
125 presence and absence in island ecosystems show a negative correlation between the presence of  
126 anoles and plant damage via the reduction of herbivorous insect pests (Pacala and Roughgarden  
127 1984). Additionally, the ability of anoles to exploit vertical niche space, including coffee bushes  
128 (Figure 1), may bolster their capacity to serve as a front line of defense against most insect pests,  
129 particularly during outbreaks.

130 Differences in the evolutionary history and complexity of mainland and island lizard  
131 assemblages have led to novel ecological differences among mainland and island *Anolis*  
132 populations (Andrews 1979). The adaptive radiation of Caribbean anoles into distinct ecomorphs  
133 that partition vertical and thermal niche space (Langerhans *et al.* 2006) is a feature that may have  
134 profound impacts on pest provisioning services along complementary gradients of  
135 intensification. Our knowledge of how critical abiotic features such as temperature (Huey 1982,  
136 Hertz 1992) and light (Leal and Fleishman 2002) generally influence species presence along  
137 gradients of land-use remains elusive. Mainland studies of anoles in agroecosystems show both  
138 an increase (Mexico; Urbina-Cardona *et al.* 2006) and decrease (Mexico; Suazo-Ortuno *et al.*  
139 2008) in richness and abundance with agricultural intensification, while studies in island systems  
140 also show a negative response to increasing disturbance (Dominican Republic; Glor *et al.* 2000)  
141 and a positive response of abundance in shifts from shade to open sun habitats (Puerto Rico;  
142 Borkhataria *et al.* 2012). The lack of comparable land-use types and intensity metrics has made  
143 inferring underlying mechanisms that drive these differences difficult.

144 The coffee agroforestry systems of Latin America have been used broadly as a model for  
145 understanding the effects of land-use intensification on biodiversity (Perfecto *et al.* 2014). Coffee  
146 is generally grown along a gradient of vegetation complexity and land-use intensity, including  
147 reduced canopy cover, reduced vegetative diversity and chemical inputs (Moguel and Toledo  
148 1999). This important feature of coffee production, in addition to the well-known ecological and  
149 biogeographic dynamics of anoles, make them a model system and taxon for studying the role of  
150 diversity and ecological complexity in biological control.

151 In this study, we conducted an experimental and field based assessment of the potential  
152 for *Anolis* lizards to reduce coffee berry borer (CBB) infestations in regions of naturally high

153 anole abundance (the Caribbean) and low anole abundance (Mainland Mexico). We investigated  
154 patterns of anole abundance and richness along a comparable gradient of agricultural  
155 intensification in the mainland and Caribbean coffee growing regions of Mexico and Puerto Rico  
156 to test the hypotheses that 1) anoles, as opportunistic and generalist predators, function to reduce  
157 CBB infestations in both mainland and Caribbean agroecosystems, and 2) differences in  
158 mainland and island community structure will result in a non-uniform response in anole richness  
159 and abundance to complementary forms of agricultural intensification, due to the stabilizing  
160 force of greater functional diversity in island ecosystems.

161 This study of generalist insectivores that exist in agricultural landscapes and are highly  
162 abundant across eco-geographic space may help to identify land-use practices that impact the  
163 ecosystem service of biocontrol. Furthermore, this approach has broad implications for  
164 understanding how phenomena such as adaptive radiation among potentially relevant species  
165 may provide ecological and evolutionary insights on the role of pre-adapted functional traits that  
166 shape community resilience to human-modified environments.

167

## 168 **2. METHODS**

### 169 **2.1 Study Sites**

170 Field surveys were conducted in the Soconusco region of Chiapas, Mexico and the Puerto  
171 Rican municipalities of Orocovis and Adjuntas during the months of June and July 2015,  
172 respectively. The coffee growing landscape in Mexico is characterized by large farms (~300  
173 hectares) with remnant patches of tropical evergreen forests making up approximately 6% of the  
174 52 km<sup>2</sup> area covered. A total of twenty-three 50 x 25 m sampling sites were surveyed along a  
175 gradient of shaded canopy cover and intensity (Fig. 1A, 1C), within an altitudinal range of ~1100  
176 to 1200 m above sea level. In Puerto Rico, coffee farms were more distinctly divided into shaded  
177 and unshaded management regimes and notably smaller in size (~ 1 – 6 ha per farm; Fig. 1B,  
178 1D). Survey sites were selected in a similar landscape of high altitude (550 m to 730 m asl)  
179 farms within a matrix of tropical forest. A total of six 50 x 25 m plots were sampled along a  
180 gradient of canopy cover and intensity analogous to that of Mexico.

### 181 **2.2 Field Survey Methods**

182 Visual encounter survey methods were used to survey for all lizards in each 1250 m<sup>2</sup> plot.  
183 Each plot was surveyed by walking each row of coffee and carefully inspecting each bush and

184 surrounding vegetation up to three vertical meters for the presence or absence of anoles. Surveys  
185 took place between 10:00 to 15:00 hours because anoles were most active during this time  
186 (personal observation). Survey time for each plot was measured as the total time required for a  
187 single person survey effort per row divided by the total number of persons involved. In each plot,  
188 the total number of individuals encountered were recorded and each individual was identified to  
189 species.

190 Following lizard surveys, we took four vertical digital canopy cover photos (DCP;  
191 adapted from Chianucci *et al.* 2014) along a grid of sixteen localities per 32 m<sup>2</sup> within the 1250  
192 m<sup>2</sup> plot area. Digital cover photography is a robust and time effective alternative to handheld  
193 densiometers, which is another common method of characterizing canopies (Chianucci *et al.*  
194 2014). All photos were taken using a point-and-shoot digital camera (Olympus Stylus Tough  
195 TG-4) using the following settings: photo lens was set to F2, aperture priority, ISO 100,  
196 automatic focus and exposure. In the field, photos were taken at a height of approximately 1.5  
197 meters. Images were collected between the hours of 10am and 3pm. All photographs for each  
198 point along the survey grid were analyzed and averaged into a single value for each plot.

### 199 2. 3 Site Classification

200 Each survey plot was scored according to five major qualitative characteristics associated  
201 with both agricultural intensification and lizard abundance common to both Mexico and Puerto  
202 Rico (Figure 2). Characteristics analyzed included road-induced edge effects (R), the application  
203 of pesticides (P), average coffee height (above or below 1.5 meters) (S), and percent canopy  
204 cover (C). An agricultural intensity index (AII) was generated using the following equation:

$$205 \quad AII=(R+P +S)-C$$

206 R (roadside), P (agrochemicals) and S (height) are binary variables given a value of 1 for  
207 presence and 0 for absence. Plots that were present approximately one meter from a vehicle path  
208 or road were assigned a value of 1, whereas interior plots were assigned a zero value.

209 Agrochemical application was determined via land owner inquiry regarding the history and  
210 current use of agrochemicals. The existent use of agrochemicals was assigned an intensity value  
211 of 1. The agrochemical varieties and brands used were not recorded. Reduced coffee height  
212 (<1.5M) was quantified as more intense and received a value of 1, while larger coffee (>1.5M)  
213 received a zero value. Percent canopy cover (C) was included as a raw cover value in decimal

214 form. Index values for each region range between -1 and 2, with a value of 2 corresponding to  
215 greatest intensity (Perfecto *et al.* 2005).

## 216 **2.4 Laboratory Experiments**

### 217 **2.4.1 Field Collection and Husbandry**

218 For laboratory experiments in both Mexico and Puerto Rico, lizards were collected by  
219 noose or butterfly net from a single coffee farm in each region that was characterized by dense  
220 canopy cover and absence of pesticide application. Individuals were collected after completing  
221 field surveys and on plots with an AII score ranging from 0-0.5. These site characteristics were  
222 chosen in order to reduce the potential for gross fitness differences among individuals. Upon  
223 collection, each individual lizard was assigned a number and GPS coordinate at the site of  
224 capture. A series of morphological measurements were collected, including snout-vent length  
225 and sex. Lizards were sexed using non-invasive transillumination technique described by Davis  
226 and Leavitt (2007), whereby a small LED light was positioned at the tail-base (contralateral to  
227 the cloaca) to illuminate the presence or absence of male hemipenes. Individuals were also  
228 inspected for the presence or absence of a dewlap, which can also indicate sex in adults. Anoles  
229 of 38 - 45 mm snout-vent length were used for each laboratory experiments because they were  
230 the most frequently encountered size class for both Mexico and Puerto Rico.

### 231 **2.4.2 Infestation Reduction Experiment**

232 The infestation reduction potential of anoles was assessed by housing an individual anole  
233 in a 60 x 60 x 60 cm BugDorm© experimental mesh tent containing a single coffee branch (Fig.  
234 3A). Experiments were conducted in a semi-outdoor laboratory with a single mesh-screen wall  
235 that provided a natural photoperiod and ambient temperatures sufficient for natural feeding  
236 activities for the lizards. Branches with bored fruits were selected from the field to ensure that  
237 the berries were ripe enough for infestation by the berry borer. All bored berries and insects were  
238 removed from each selected branch before the start of the experiment, with twenty fruits and  
239 multiple leaves left remaining on each branch. Individual branches were positioned vertically in  
240 35mm plastic canisters filled with water (Fig. 3B). The top of each canister and branch based  
241 was wrapped in Parafilm© plastic to prevent CBB mortality. Each branch was then placed in the  
242 center of an inverted plastic bowl for vertical orientation and covered by a strip of bark. Bark  
243 was used to increase basking area and allow the anole to move freely from the coffee branch to  
244 the base of the enclosure.



245 Prior to each trial, a solitary lizard was housed in each BugDorm for a minimum of 24  
246 hours to allow them to acclimate (Sanger *et al.* 2008). Berry borers were collected from infested  
247 fruits and removed carefully by splitting the fruit body and separating individual beetles from the  
248 plant material. At the start of each trial, twenty adult female berry borers were placed near the  
249 center of each branch using a coffee leaf as a platform. The platform was kept stable until all  
250 CBB had dispersed onto the branch. Following the 24-hour trial window, each coffee branch was  
251 removed and the total number of infected berries per branch (number of berries with at least one  
252 CBB hole) were recorded (Fig. 3C). Each lizard was returned to the original location of capture  
253 after the experiment was completed.

### 254 **2.4.3 Functional Response**

255 To assess the consumption potential of anoles, individuals were housed in 9.1 kilogram  
256 aerated plastic terrariums with coffee leaves as substrate for 24 hours prior to the start of each  
257 trial. Terrariums were coated with fluon (Insect-a-Slip, BioQuip, CA) at the top to prevent CBB  
258 from escaping. Cardboard barriers were placed in between terraria to prevent visibility among  
259 individuals. Terrarium holes were created using a small 16 gauge pin-needle to ensure airflow,  
260 but to prevent the beetles from escaping.

261 Adult female berry borers were obtained from infested berries collected in the field and  
262 placed into separate glass vials hours prior to the start of each experiment. CBB were housed for  
263 no longer than 24 hours to ensure borer efficacy. Berry borers were placed in the terrariums  
264 between the hours of 9-10 am and remained unaffected for 24 hours. Each trial lasted for twelve  
265 hours, after which lizards were removed from each container and all unconsumed beetles were  
266 recorded. All remaining beetles were euthanized following each experiment. Morphometric  
267 measurements taken for each individual lizard included: snout-vent length, head width, head  
268 length, tail length, front and hind limb length, in addition to sex, gravidity and species.

## 269 **2.5 Data analysis**

### 270 **2.5.1 Field Surveys**

271 Canopy cover images were analyzed using a dot grid approach to estimate canopy cover  
272 for each sample location. Interpretation of digital cover photographs using a transparent dot-grid  
273 overlay is a standard technique well suited for estimating canopy cover (Nowak *et al.* 1996).

274 An analysis of variance (ANOVA) test was used to find statistical significance between  
275 total abundance and region. Linear regressions were used to examine the effect of canopy cover

276 on total lizard abundance per region. We used generalized linear mixed models (GLMM) to  
277 examine the relative importance habitat variables on abundance.

## 278 **2.5.2 Laboratory Experiments**

279 Generalized linear models (GLM) were used to account for covariates in differences  
280 between consumption patterns (functional response) and berry borer infestation rates between  
281 treatments with and without anoles. Differences in coffee borer infestation rates were analyzed  
282 with an ANOVA.

283 Linear and non-linear models were used to fit the CBB consumption data for Mexico,  
284 Puerto Rico and the combined dataset to the following functional response models as outlined by  
285 Holling (1959 & 1965):

$$286 \text{ Type I: } P = aN$$

$$287 \text{ Type II: } P = \frac{aN}{1+hN}$$

$$288 \text{ Type III: } P = \frac{aN^2}{1+hN^2}$$

289 where  $P$  is the total number of coffee berry borers consumed,  $N$  is prey density (total number of  
290 CBB offered),  $a$  is attack rate, and  $h$  is handling time. Attack rate and handling time were not  
291 measured directly in this study and were included as constants in the model. The AIC value of  
292 each model was used to assess performance, with the lowest value indicating the best fit to the  
293 data. All statistical tests were performed in R v3.2.3 and significance was assessed at a  $P$  value  $\leq$   
294 0.05.

295

## 296 **3 RESULTS**

### 297 **3.1 Infestation reduction potential and functional response**

298 In laboratory settings, individual anoles reduced coffee berry borer infestations by an  
299 average of 49% in Mexico ( $P=0.03$ ,  $F=5.13$ ,  $df=1$ , 35) and 83% in Puerto Rico ( $P = 0.019$ ,  
300  $F=8.82$ ,  $df=1$ , 10; Figure 4). The effects of sex and gravidity on reduction potential were non-  
301 significant ( $P > 0.05$ ).

302 Manipulations of prey density reveal a Type III functional response by anoles for  
303 combined data from Mexico and Puerto Rico (Fig. 5). The combined data, however, reveals  
304 indistinguishable differences between the Type 1 and Type II AIC values (Table 1). Results

305 from a generalized linear model suggest that gravity, snout-vent length, species, and region are  
306 non-significant effects on consumption potential ( $P > 0.05$ ).

### 307 **3.2 Environmental predictors of abundance and species presence**

308 The average abundance of anoles on all coffee plots containing at least one individual  
309 was approximately twelve times greater in Puerto Rico than in Mexico (Fig. 6). Anoles were the  
310 only lizard genus found on farms in Puerto Rico (five species total), while the two species of  
311 anole known on farms in Mexico were present along with a single species of *Amiava* and an  
312 unidentified species in the genus *Mabuya* (Table 3). In Mexico, a single species of anole was  
313 dominant throughout the study area (*A. dollfusianus*), while the less dominant species were  
314 present only in plots with reduced shade cover ranging from 50-75% cover (Table 3). Both  
315 species in Mexico also favored plots with coffee plants that were on average greater than 1.5  
316 meters in height.

317 Coffee plantations in Puerto Rico were generally dominated by a single species in plots  
318 with high shade (*A. gundlachi*) and plots with low shade (*A. cristatellus*; Table 3). The less  
319 dominant species, *A. evermanni* and *A. stratulus*, also occurred more frequently in shade or sun  
320 plots, respectively. All four species generally occurred together when plots were positioned  
321 along a road or habitat edge.

322 Along a gradient of increasing agricultural intensity, both Mexican and Puerto Rican  
323 anole abundance decreased significantly (Mexico:  $R^2 = 0.278$ ,  $F = 9.48$ ,  $df = 1, 21$ ,  $P = 0.006$ ;  
324 Puerto Rico:  $R^2 = 0.539$ ,  $F = 6.85$ ,  $df = 1, 4$ ,  $P = 0.059$ ; Figure 7). In Mexico, only 11 out of 23  
325 surveyed plots contained anoles, while six of the eleven were present at the lowest index values  
326 ranging from -1.0 to 0.5. In Puerto Rico, the greatest abundance of anoles was not present at the  
327 lowest intensity value, but did show a linear decrease with increasing intensity. This trend  
328 appears to be driven by a single plot with zero anoles. The generalized linear mixed model  
329 testing the effects of canopy cover, agrochemicals, edge effects, and coffee height on anole  
330 abundance in plots in Mexico and Puerto Rico revealed significant effects of coffee height  
331 (positive) ( $P = 0.015$ ,  $Z = -2.43$ ; Table 1) and agrochemical application (negative) ( $P < 0.05$ ,  $Z = -$   
332  $3.42$ ; Table 1) on abundance in Mexico and significant effects of canopy cover (positive) ( $P =$   
333  $0.005$ ,  $Z = 2.77$ ; Table 1) on abundance in Puerto Rico. In both regions, the application of  
334 pesticides had a deleterious effect on anole abundance (Table 1), but lack of necessary

335 replication of pesticide plots in Puerto Rico ( $N = 1$ ) prevented this parameter from being used in  
336 the model.

## 337 **4 DISCUSSION**

### 338 **4.1 The biocontrol potential of *Anolis* lizards on CBB**

339 The results of this study are the first to provide evidence that anoles are capable of both  
340 consuming the coffee berry borer in high numbers (Fig. 5) and significantly reducing CBB  
341 infestations in the laboratory settings (Fig. 4). These results, combined with our field survey data  
342 showing that anole abundance is bolstered by reduced agricultural intensification (Fig. 7),  
343 suggest that anoles may be important biocontrol agents in diversified coffee landscapes,  
344 particularly in regions such as Puerto Rico where they are naturally more abundant. Furthermore,  
345 these results support several theoretical and field based studies suggesting that pest control  
346 services decline significantly when generalist predators are removed from coffee agricultural  
347 landscapes (Perfecto *et al.* 2004, Faria *et al.* 2008, Karp *et al.* 2013).

348 Predation rates by lizards are generally determined by many other factors, including prey  
349 diversity, predator size, and environmental conditions such as habitat diversity and seasonality  
350 (*e.g.*, Angilletta 2001; Pitt & Ritchie 2002). This study was conducted during the egg laying  
351 season for Mexican anoles and during the period of low berry borer abundance for both regions  
352 (Sponagel 1994), so the functional response of anoles to coffee berry borer abundances may be  
353 different in field settings at other times of the year. Realistic estimates of reduction potential  
354 would be most robust for experiments conducted in natural conditions, with natural variation in  
355 ecological factors like structural complexity and prey diversity.

356 Results from the functional response experiment imply that more data are necessary to  
357 infer a functional response curve for the combined data set or that the data better fit an  
358 alternative model (Table 1). AIC values for Puerto Rico show negligible differences between  
359 each functional response type, suggesting that more data are needed to infer a satiation point.  
360 This result also suggests that the combined data set significance may have been driven primarily  
361 by the Mexico data. Overall, however, the high consumption results from this study are  
362 concordant with several studies showing that anoles consume large numbers of insects that may  
363 have been otherwise assumed too small relative to lizard body size to reflect an important diet  
364 component (Simmonds 1958). Ultimately, the behavior of the coffee berry borer in field settings,

365 with added variables like habitat variability and co-consumption of alternative prey, may provide  
366 more realistic estimates of functional response for this genus.

#### 367 **4.2 Adaptive radiation as a predictor of disturbance tolerance**

368 Previous studies documenting the effects of agricultural intensification corroborate the  
369 results of this study that shifts from diverse ecosystems to intensified agricultural landscapes  
370 have negative effects on the functional characteristics of anole communities such as abundance,  
371 diversity, and use of vertical plant space (Glor *et al.* 2000, Borkhataria *et al.* 2012). This study  
372 additionally illustrates the deleterious effects of pesticide use in Mexico and Puerto Rico, and the  
373 significant role of dissimilar habitat variables on abundance in each region (coffee height in  
374 Mexico, canopy cover in Puerto Rico). For plots that included agrochemical applications, lizards  
375 of both regions were virtually eliminated, potentially because of reduced prey abundance, or  
376 perhaps through direct bioaccumulation of toxic substances (Mann *et al.* 2007).

377 The sympatric occurrence of distinct ecomorphs in the Puerto Rican coffee farms is  
378 posited here as the underlying mechanism leading to higher abundances at intermediate levels of  
379 intensity among island anoles (Fig. 7). Although lizards are generally assumed to favor basking  
380 sites and open habitats for thermoregulation, several mechanisms may account for a dissimilar  
381 response between island and mainland taxa. Anoles have been shown to be either  
382 thermoregulators, species that actively select favorable microhabitats, or thermoconformers,  
383 species that adopt ambient temperatures (Losos 2009). Comparative studies of the Puerto Rican  
384 anoles *A. gundlachi* and *A. cristatellus* reveal that *A. gundlachi* functions as a thermoconformer  
385 adapted to cooler environments, and *A. cristatellus* as a thermoregulator tolerant of warmer  
386 conditions (Hertz 1992, Rogowitz 1996). Our results corroborate this finding by showing  
387 increased *A. gundlachi* abundance in interior plots with high shade (Table 3), whereas *A.*  
388 *cristatellus* was most abundant in plots with the least amount of shade and along forest edges  
389 with reduced cover (Table 3). *Anolis stratulus* was also shown to share trends similar to that of  
390 *A. cristatellus*, supporting findings by Borkhataria *et al.* (2012), who showed congruent  
391 relationships to sun and shade dominance among *A. gundlachi* and *A. cristatellus*. Mainland  
392 anole species have been reported to avoid the costs of thermoregulation by selecting for  
393 environments that are relatively warmer (Vitt *et al.* 2001). The results of this study, however,  
394 suggest that mainland anoles respond more to shifts in structural diversity than to reduced cover  
395 or habitat edges.

396 A number of additional mechanisms may influence the reduction of anole diversity in sun  
397 and pesticide plots between the two regions. As discussed previously, the life history  
398 characteristics of Caribbean island and mainland anoles are understood to be fundamentally  
399 different. Anole communities within the Caribbean are limited by food resources due to high  
400 interspecific competition, whereas mainland anoles are generally limited by relatively greater  
401 levels of predation (Andrews 1979). Andrews (1979) additionally references mainland anoles as  
402 having lower survivorship and lower food intake (via less time foraging). Although mainland  
403 anoles with low abundances are not predicted to have as great of an ecosystem impact on the  
404 insect community as island anoles, they are likely more vulnerable to changes in prey  
405 availability, structural diversity, and chemical inputs.

#### 406 **4.3 Implications for management and conservation**

407 The results of this study imply that the geographic location and local environmental  
408 settings where human-disturbance takes place are both important factors that must be considered  
409 when managing at-risk species. This research suggests that the structural diversification of coffee  
410 farms functions as a benefit both to farmers, by providing the insurance of predatory diversity  
411 against pest outbreaks, and to biodiversity, by providing a hospitable landscape for persistence  
412 and dispersal.

413 In the island agroecosystems of Puerto Rico, the loss of anole biocontrol services is  
414 buffered by greater functional diversity and overall abundance, relative to Mexico, implying that  
415 islands of the greater Antilles are more equipped to respond to disturbance at the genus level.  
416 Shade adapted ectotherms such as *Anolis gundlachi* in Puerto Rico, however, will likely be  
417 isolated in forested habitat islands as the result of an increasing move toward sun coffee and  
418 deforestation, and they may be at greater extinction risk relative to species that are more tolerant  
419 to the higher temperatures experienced in more intensely managed farms (Frishkoff 2015). A  
420 study of mainland anoles by Pounds *et al.* (1999) suggested that mainland anole abundance  
421 decreases linearly in response to increasing environmental temperatures. Such declines are  
422 predicted to be further exacerbated amidst intensified agricultural landscapes and increasing  
423 global temperatures (Deutsch *et al.* 2008).

424 In conclusion, the evidence presented in this study showing that anoles reduce pest  
425 infestation potential and are adversely effected by land-use intensification has important  
426 implications for the management of agricultural landscapes to maintain ecosystem services such

427 as biological control. This understanding adds to a growing body of evidence suggesting that  
428 win-win solutions are possible in agriculture, helping both to conserve biodiversity and to  
429 promote the sustainable production of food to meet society's needs.

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618 **Figure 1.** Photograph of an adult Mexican anole, *Anolis sericeus*, perching in a coffee shrub.

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620 **Figure 2.** Representative photos of diversified shade coffee in Mexico (A), diversified shade  
621 coffee in Puerto Rico (B), intensive sun coffee in Mexico (C), intensive sun coffee in Puerto  
622 Rico (D).

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624 **Figure 3.** Laboratory setup for the experimental assessment of CBB infestation reduction. Each  
625 individual anole was paired with a single coffee branch per enclosure tent (A) and all enclosure  
626 tents were housed in a semi-outdoor laboratory with natural sunlight and ambient conditions (B).  
627 (C) is a representative photo of CBB entry holes used to assess coffee berry infestation.

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629 **Figure 4.** Mean number of coffee berries infested by the coffee berry borer ( $\pm$  1SE) in the  
629 presence and absence of *Anolis* lizards in laboratory settings.

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631 **Figure 5.** Functional response of anole predation on variations in coffee berry borer abundance  
631 in laboratory settings.

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633 **Figure 6.** Average abundance of anoles per hectare in Mexico ( $n=42.9 \pm 12.56$ ) and Puerto Rico  
633 ( $n=609.6 \pm 57.26$ ) from plots where anoles were present.

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635 **Figure 7.** (A) Variation in anole abundance along a gradient of intensity in Mexico ( $R^2 = 0.278$ ,  
636  $P = 0.006$ ) and (B) Puerto Rico ( $R^2 = 0.539$ ,  $P = 0.059$ ).

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640 **Table 1. AIC values for type I, II, and III functional response model fit to the given data for**  
 641 **Mexico, Puerto Rico and combined.**

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Functional Resp.	AIC Values		
	Mexico	Puerto Rico	Combined
Type I	293.54	167.79	475.38
Type II	290.19	167.17	475.35
Type III	288.76	166.72	479.53

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665 **Table 2. Results of a generalized linear mixed model testing the effects of canopy cover,**  
 666 **agrochemicals, edge effects and coffee height on anole abundance in plots in Mexico and**  
 667 **Puerto Rico. Asterisks denote degree of significance.**

<b>Region:</b>		Mexico						
Variable	Fixed Effects	Estimate	Std. Error	Z	Pr(> z )	Random effects	Variance	Std. Dev.
Abundance	Intercept	2.644	1.666	1.587	0.113	Plot	0.351	0.592
	Cover	-1.289	2.324	-0.555	0.579			
	Agrochem	-3.671	1.072	-3.424	0.006***			
	Road	0.2655	0.4727	0.562	0.574			
	Height	-1.706	0.703	-2.427	0.015*			
<b>Region:</b>		Puerto Rico						
Variable	Fixed Effects	Estimate	Std. Error	Z	Pr(> z )	Random effects	Variance	Std. Dev.
Abundance	Intercept	2.104	0.894	2.353	0.0186*	Plot	0.656	0.81
	Cover	3.183	1.149	2.769	0.005**			

Road -0.951 0.737 -1.289 0.197

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**Table 3. Average species abundance per characteristic of habitat intensity in Mexico and Puerto Rico.**

% Canopy Cover		Agrochemical Use		Roadside Plot		Coffee Height	
50-75%	75-100%	Yes	No	Yes	No	<1.5 M	>1.5 M



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**Mexico**

<i>Anolis dollfusianus</i>	6.8	8	0.08	5.18	7.3	6.7	1.4	8.3
<i>Anolis sericeus</i>	1.6	0	0.08	0.09	1	1.7	0	1
<i>Amiava amieva</i>	0.8	0	0.25	0.27	0.7	1	0.2	0.66
<i>Scincidae spp.</i>	3.6	0	0.17	2	3.3	2.7	0.8	2.66
<b>TOTAL:</b>	<b>12.8</b>	<b>8</b>	<b>0.58</b>	<b>7.54</b>	<b>12.3</b>	<b>12.1</b>	<b>2.4</b>	<b>12.62</b>

	% Canopy Cover		Agrochemical Use		Roadside Plot		Coffee Height	
	0 - 25%	75-100%	Yes	No	Yes	No	<1.5 M	>1.5 M
<b>Puerto Rico</b>								
<u>Trunk-Ground</u>								
<i>Anolis gundlachi</i>	1	43.5	0	46.4	7	68	N/A	46.4
<i>Anolis cristatellus</i>	30	7	0	12.4	26.5	0	N/A	12.4
<u>Trunk-Crown</u>								
<i>Anolis stratulus</i>	18	1.5	0	4.8	1.5	0	N/A	4.8
<i>Anolis evermanni</i>	1	2.5	0	5.8	2.25	9	N/A	5.8
<u>Grass-Bush</u>								
<i>Anolis krugi</i>	2	1	0	1.4	0.75	0	N/A	N/A
<b>TOTAL:</b>	<b>52</b>	<b>55.5</b>	<b>0</b>	<b>70.8</b>	<b>38</b>	<b>77</b>	<b>N/A</b>	<b>69.4</b>

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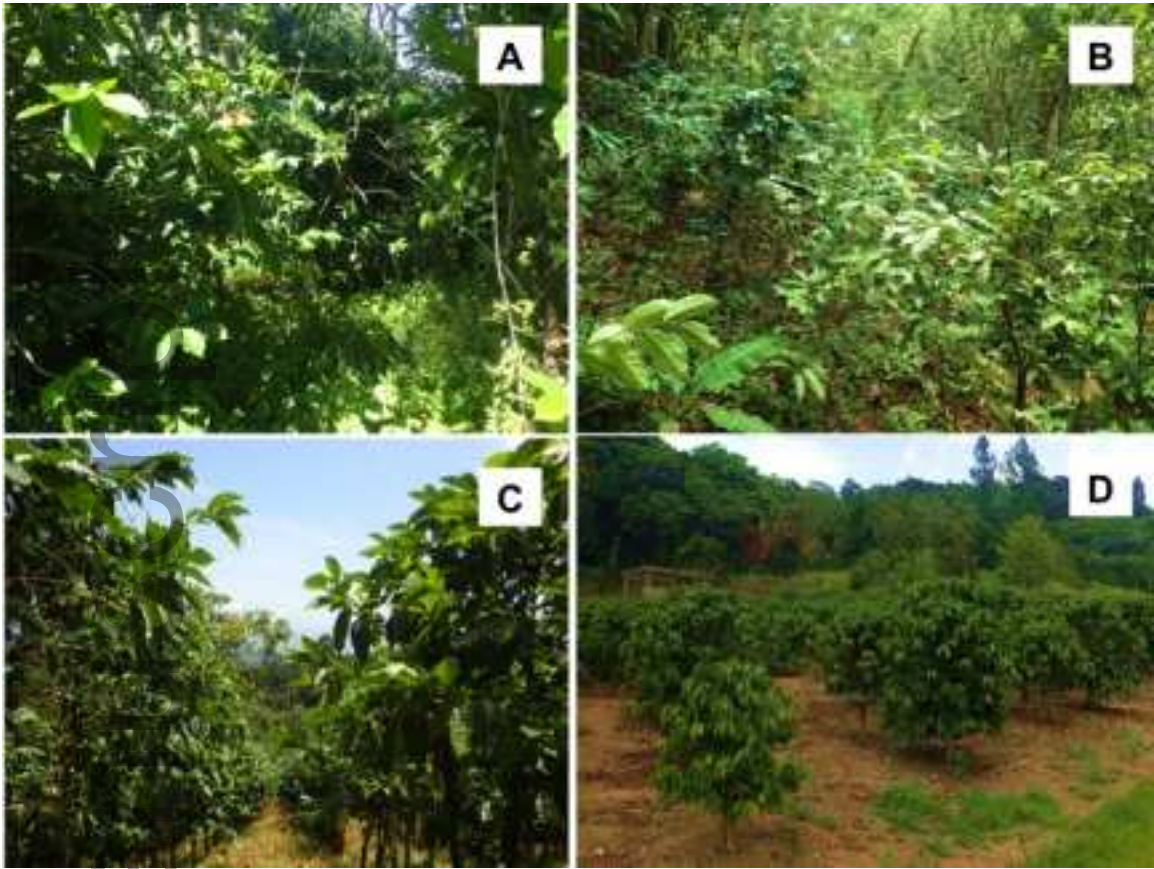
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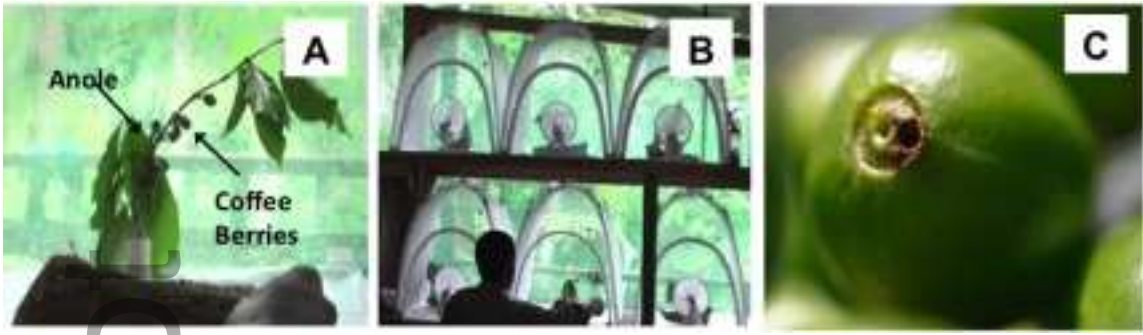


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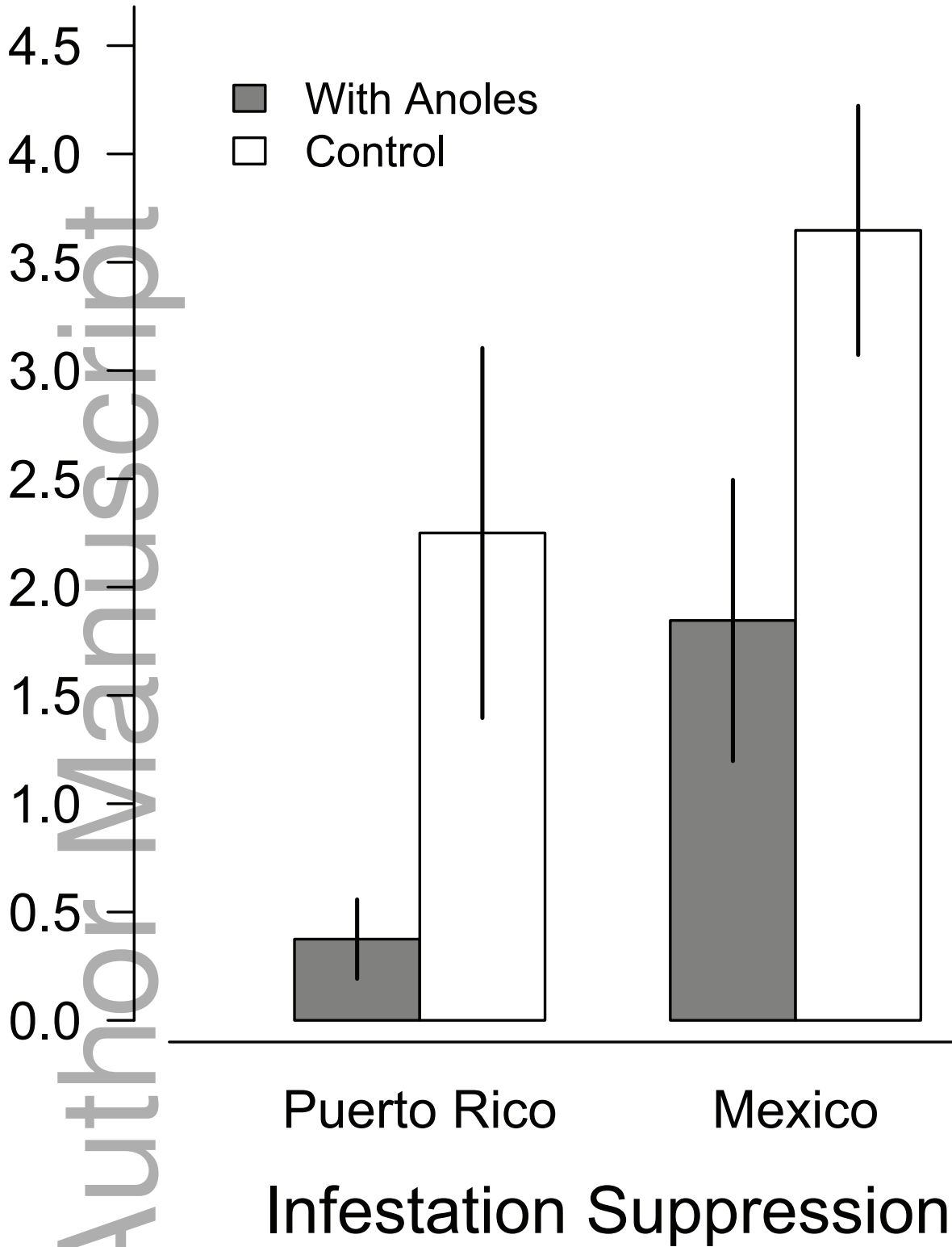


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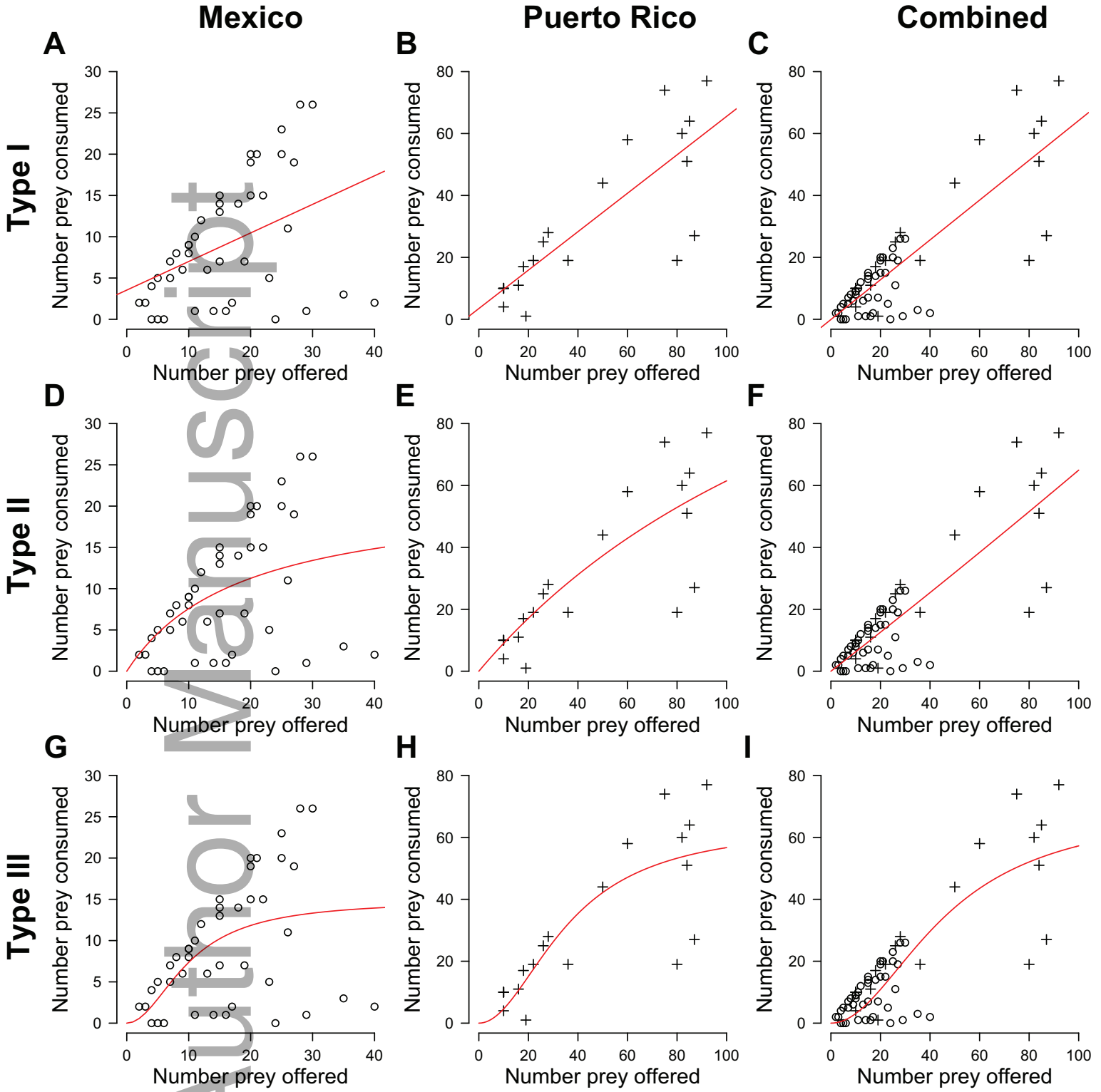
Number of Infested Berries

Per Branch



Infestation Suppression

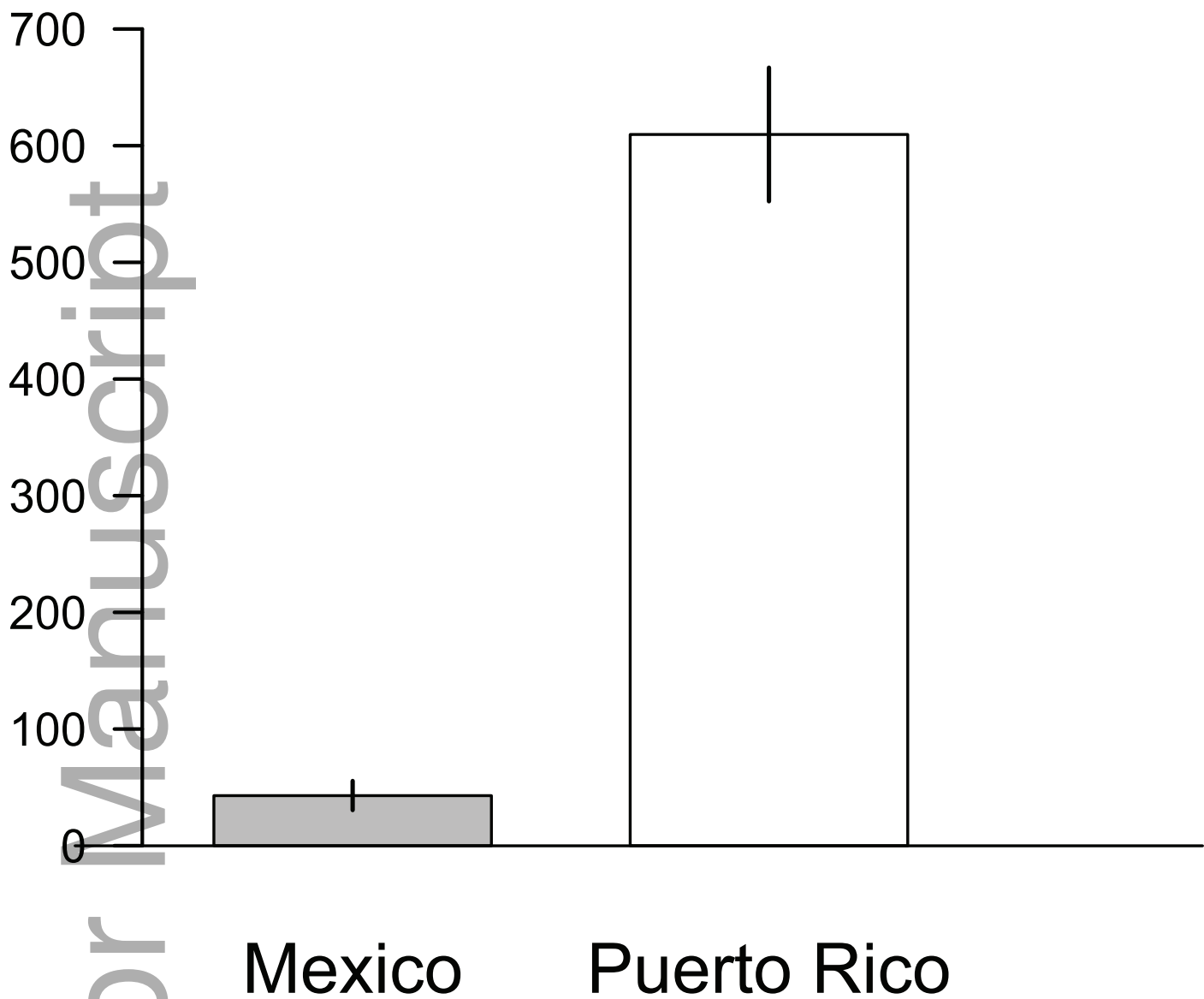
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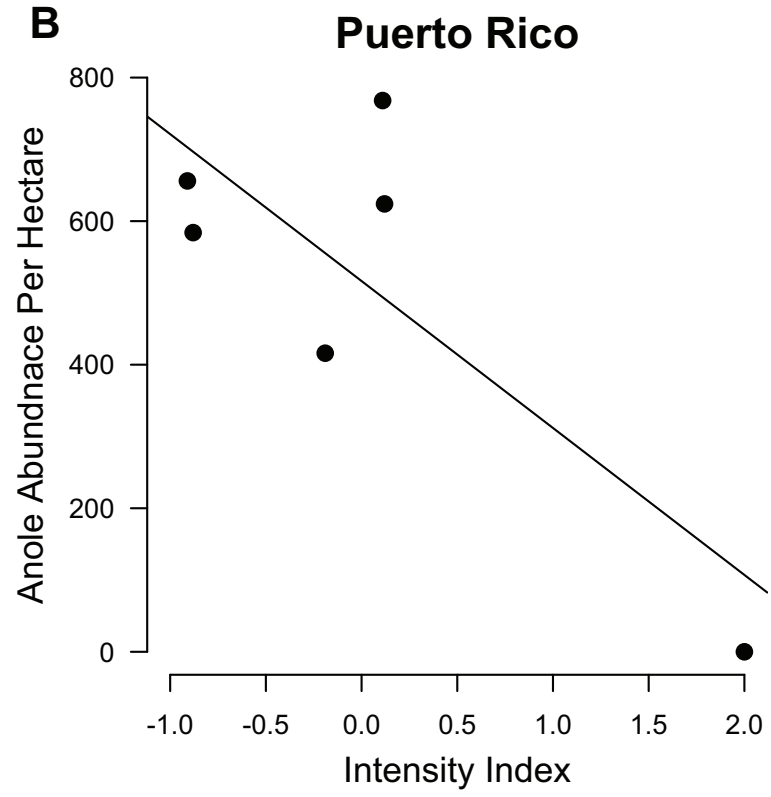
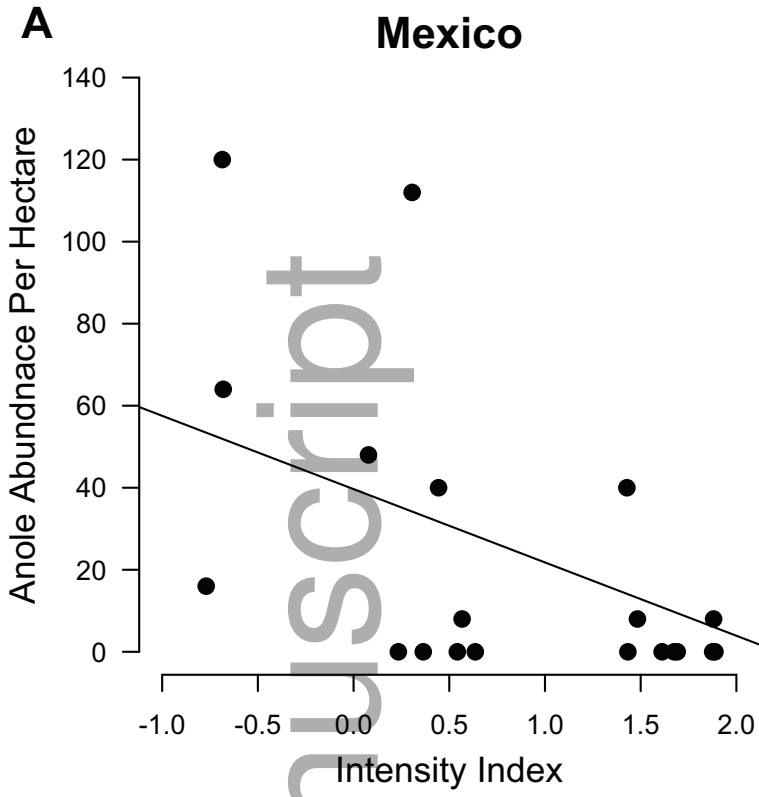


Anole Abundance Per Hectare



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