

Countryside biogeography of Neotropical reptiles and amphibians

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Abstract. The future of biodiversity and ecosystem services depends largely on the capacity of human-dominated ecosystems to support them, yet this capacity remains largely unknown. Using the framework of countryside biogeography, and working in the Las Cruces system of Coto Brus, Costa Rica, we assessed reptile and amphibian assemblages within four habitats that typify much of the Neotropics: sun coffee plantations (12 sites), pasture (12 sites), remnant forest elements (12 sites), and a larger, contiguous protected forest (3 sites in one forest). Through analysis of 1678 captures of 67 species, we draw four primary conclusions. First, we found that the majority of reptile (60%) and amphibian (70%) species in this study used an array of habitat types, including coffee plantations and actively grazed pastures. Second, we found that coffee plantations and pastures hosted rich, albeit different and less dense, reptile and amphibian biodiversity relative to the 326-ha Las Cruces Forest Reserve and neighboring forest elements. Third, we found that the small ribbons of “countryside forest elements” weaving through farmland collectively increased the effective size of a 326-ha local forest reserve 16-fold for reptiles and 14-fold for amphibians within our 236-km² study area. Therefore, countryside forest elements, often too small for most remote sensing techniques to identify, are contributing ~95% of the available habitat for forest-dependent reptiles and amphibians in our largely human-dominated study region. Fourth, we found large and pond-reproducing amphibians to prefer human-made habitats, whereas small, stream-reproducing, and directly developing species are more dependent on forest elements. Our investigation demonstrates that tropical farming landscapes can support substantial reptile and amphibian biodiversity. Our approach provides a framework for estimating the conservation value of the complex working landscapes that constitute roughly half of the global land surface, and which are experiencing intensification pressure worldwide.

Key words: Anolis; anuran; community ecology; conservation biology; Costa Rica; frog; herpetology; land sharing; Las Cruces Biological Station; lizard; snake; wildlife-friendly farming.

INTRODUCTION

Of the over 7000 known vertebrate species facing extinction, nearly 40% are reptiles and amphibians (i.e., vertebrates with conservation statuses of extinct in the wild, critically endangered, endangered, or vulnerable [IUCN Global Species Programme Red List Unit 2011]). Primary threats to the global herpetofauna include habitat loss, pathogens, pollution, over-exploitation, and climate change (Gibbon et al. 2000, Stuart et al.

2004, Beebee and Griffiths 2005, Pounds et al. 2006, Whitfield et al. 2007, Sodhi et al. 2008, Warkentin et al. 2009). Considering these human impacts, it is increasingly clear that the fate of wild populations will depend in large measure on the hospitality of the 87% of the Earth’s land surface that falls outside of protected areas (Daily 2001, Coad et al. 2009, Gardner et al. 2009, Barnosky et al. 2011, Mendenhall et al. 2013a). Despite the extent of human-dominated or countryside ecosystems, their capacity to sustain wild populations of reptiles, amphibians, and other ectotherms remains poorly understood.

Countryside biogeography focuses on assessing the conservation value of human-dominated or countryside ecosystems typical of the Anthropocene in terms of their

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biodiversity, ecosystem functioning, and ecosystem services (Bignal and McCracken 1996, Daily 1997a, 2001, Crutzen and Stoermer 2000, Mendenhall et al. 2013b). The world's countryside, the increasing fraction of Earth's surfaces whose ecosystem qualities are strongly influenced by humanity, yields clues for forecasting the types of ecosystems that will exist in the future, informing decisions about what people need and want from them, and exploring the complex questions of how we decide upon and achieve our conservation goals (Daily 2001, Gardner et al. 2009, Perfecto et al. 2009). Field studies of countryside biogeography conducted within the 934-km² canton of Coto Brus in southern Costa Rica have aided in the understanding of ways to harmonize biodiversity and human activities in recent years (Gardner et al. 2009, Mendenhall 2013b). These studies have spanned an array of taxa including birds, mammals, arthropods, and plants (Ricketts et al. 2001, Hughes et al. 2002, Daily et al. 2003, Horner-Devine et al. 2003, Mayfield and Daily 2005, Brosi et al. 2007). Here we present one of the first studies on the countryside biogeography of Neotropical reptiles and amphibians.

Increasing demand for food, fuel, and fiber has changed ecosystems in ways that particularly affect the biodiversity of reptiles and amphibians (collectively, "herpetofauna"). For example, replacement of forest with agriculture typically results in simplification of vegetative structure, which has been shown to alter bird biodiversity but may have more nuanced effects on vertebrate ectotherms because of their sensitivity to associated changes in microclimate across landscapes and their relative dispersal limitations (Murcia 1995, Pringle et al. 2003, Bielby et al. 2006, Wells 2007, Hillers et al. 2008, Karp et al. 2011, 2012). Additionally, because many amphibians have a two-phase life cycle, including an aquatic larval stage, the distribution and quality of freshwater habitats in human-dominated landscapes also influences amphibian biodiversity patterns (Becker and Fonseca 2009).

Despite fundamental differences that distinguish herpetofauna from other taxa, we expected, based on taxon-indicator studies and previous findings from arthropods, birds, and nonflying mammals, that substantial reptile and amphibian biodiversity exists in human-modified habitats (Moritz et al. 2001, Ricketts et al. 2001, Daily et al. 2003, Horner-Devine et al. 2003, Mendenhall et al. 2011, 2012). We hypothesized that landscape change influences herpetofaunal biodiversity primarily at the levels of abundance and community composition, rather than species richness, and that the negative effects of forest conversion can be mitigated by conserving high numbers of relatively small remnants of minimally altered habitat on agricultural land (Mendenhall et al. 2011, 2012).

In this investigation, we characterize reptile and amphibian biodiversity across a spectrum of land use intensities including a protected forest reserve, small and

large ribbons of "forest elements" that weave through the agricultural countryside, coffee plantations, and actively grazed pastures. Moreover, we present a novel approach for identifying important habitat for tropical reptiles and amphibians by measuring tropical forest as a continuum of forest elements within taxon-specific spatial scales, rather than arbitrary categories of hospitable and inhospitable habitat types or isolated forest fragments floating in a sea, or matrix, of human-made habitats (Mendenhall 2011, Fahrig 2013). Our study has three overarching objectives: (1) to compare the species richness, abundance, and community composition of the reptiles and amphibians relative to land use and landscape context; (2) to assess the conservation value of tropical farmland for reptile and amphibian biodiversity; and (3) to identify reptile and amphibian life history traits that may confer a survival advantage in human-dominated ecosystems.

METHODS

We centered our investigation on the Las Cruces Biological Station (LCBS) and Wilson Botanical Garden located in the Coto Brus Valley in southwestern Costa Rica. The Las Cruces Forest Reserve (8°47' N, 82°57' W, 1100 m above sea level [asl]), which serves as a regional baseline of minimally altered habitat, protects ~280 ha of premontane primary and mature secondary forest (Fig. 1). The climate is characterized by a long rainy season (9–10 months) followed by a brief dry season with an average total of 3.4 m of annual rainfall (Stiles and Skutch 1989). Over 60% of the Coto Brus Valley, once forested, has been converted into cropland and pasture since the 1950s (Sansonetti 1995, Mendenhall et al. 2011).

We sampled four general habitat types at 39 locations within a 10-km radius of LCBS (Fig. 1). Elevation of sites ranged from 885 to 1410 m asl, with an average of 1120 m. The first habitat type was represented by three sites located in the primary forest of the Las Cruces Forest Reserve. Although these three sites were located within the same forest reserve and are, therefore, pseudoreplicated, no other reserves of similar size, elevation, or climate exist in the study region. We attempted to minimize any bias arising from pseudoreplication by spacing our sites 600–1300 m apart. The second and third habitat types were coffee plantations (12 sites) and actively grazed pastures (12 sites).

The fourth habitat type sampled was "countryside forest elements" embedded in agricultural land (12 sites). Countryside forest elements (CFE) included unprotected clusters of trees and various sizes and qualities of remnant native forest fragments, live fences, hedgerows, riparian strips, and the like, too small or with configurations too complex to be considered isolated forest fragments when all fine-scale forest element connections were considered (i.e., scattered trees and shrubs as small as 4 m²). The approximate size of each countryside forest element sampled for reptiles and

amphibians in this study ranged roughly from 1 to 85 ha when forest element connections of 10 m or less were used as minimum pinch points to isolate forest elements into distinct fragments. The Las Cruces Forest Reserve and its connected countryside forest elements constitute the largest in the landscape. For reference, when forest element connections of 10 m or less were used as pinch points to isolate the contiguous forest element that contained the political boundary of the Las Cruces Forest Reserve, its size was ~600 ha (Fig. 1). Each of the 12 countryside forest element sites was paired with a location in an adjacent coffee plantation or actively grazed pasture (Fig. 1.). Paired sites were an average of 150 m apart. Overall study design follows Daily et al. (2003); additional details about sites and site selection are provided by Santos-Barrera et al. (2008).

To characterize forest elements we conducted a manual classification by digitizing aerial photographs. Manual forest element classification was favored over automated approaches to facilitate accurate identification of fine-scale forest elements (i.e., scattered trees and shrubs as small as 4 m²) in a complex, agricultural system (Mendenhall et al. 2011). Orthorectified aerial photographs used in the forest element classification were from Costa Rica Airborne Research and Technology Applications (CARTA) taken in 2003 and 2005 at 2-m resolution. The forest-element map covered 23 600 ha (236 km²) and included all sampling locations. The area was delineated to encompass all study locations sampled in previous studies of this region by Stanford University's Center for Conservation Biology (e.g., Ricketts et al. 2001, Daily et al. 2003, Horner-Devine et al. 2003, Mayfield and Daily 2005, Brosi et al. 2008, Mendenhall et al. 2011, 2012). Forest elements digitized at a 2-m resolution over this extent included primary and secondary forest wherever it existed, *charral* (early secondary forest), scattered trees in coffee plantations and pastures, large shrubs, live fences, hedgerows, nonnative timber plantations, fruit tree plantations, and nonnative garden ornamentals. The final map (Fig. 1) was verified in the field from multiple vantage points, comparison with previous studies in the landscape, and comparison with 150 random samples across the landscape. Existing maps of river systems at a 5-m resolution and a digital elevation model were also used in analyses (Centro Nacional de Investigación Geo-Ambiental, Costa Rica).

From 2002 to 2004, we conducted annual surveys in both wet and dry seasons (six total surveys). Each survey used two complementary techniques: diurnal and nocturnal visual-encounter surveys (VES) (Crump and Scott 1994), and drift-fences trapping with pitfall and funnel traps (Corn 1994). VES entailed two observers walking two, 1-km transects at each site or split between paired sites over two hours; this was repeated twice during each of the six surveys, totaling 1296 observer-hours. Drift fences with pitfall and funnel traps were used at each site or split between paired sites. At each

site drift fences were arranged in two parallel lines, 50 m apart (except at paired sites). Each line contained three pitfall traps (19-L plastic buckets, 30 cm in diameter) at 10-m intervals, with two tubular funnel traps (1.5 m long, 20 cm in diameter, open at both ends) placed on opposite sides along the drift fence. Drift fences operated for 72 hours at each location during annual wet- and dry-season surveys. Total trapping effort amounted to 11 664 trap-hours (evenly distributed during day and night) with 162 pitfall and 108 funnel traps.

The original study design included 12 sites straddling countryside forest elements and adjacent coffee plantations or pastures (Fig. 1). Encounters of reptiles and amphibians from these sites were originally lumped and analyzed as a single site (see Santos-Barrera et al. 2008). At these 12 sites VES and drift fence sampling was split (i.e., half the standard sampling effort was conducted at all 12 countryside forest element sites, 6 coffee plantation sites, and 6 pasture sites). Split effort was evenly divided by conducting one VES transect and setting one drift fence with pitfall traps and funnels in each of the paired sites. After preliminary analysis it was obvious that sites straddling two habitat types had two unique reptile and amphibian biodiversity signals (Appendix A: Fig. A3). Because sampling in each habitat type was separated by a considerable distance (distance = 145 ± 22 m; mean \pm SE), all sites straddling two habitat types were considered separate in analyses. Uneven sampling effort and modeling are explained in *Statistical analyses*.

For identification, we consulted published sources on the local and regional herpetofaunas (Duellman 2001, Schlaepfer and Gavin 2001, Savage 2002, Solórzano 2004), along with the records of the Las Cruces Biodiversity Database and the University of Costa Rica herpetological collection. Species that could not be identified readily in the field were transported to the Las Cruces Biological Station laboratory for identification and then released at the point of capture the following day. Animals were not marked.

Finally, we consulted published literature (e.g., Savage 2002) to explore characteristics of reptiles and amphibians that may confer a survival advantage in human-dominated ecosystems (Mayfield and Daily 2005, Hillers et al. 2008, Suazo-Ortuño et al. 2008). These traits included snout-vent length (SVL) and general habitat stratum for reptiles. Only a few reptile traits were used because data were scant for the suite of reptile species in our study. For amphibians, traits included SVL, larval habitat (i.e., oviposition habitat), average number of offspring, general habitat stratum, and, although not a life history trait, IUCN Red List status.

Statistical analyses

We tested for effects of the four general habitat types on species richness estimates and relative abundance of each taxon using one-way ANOVAs.

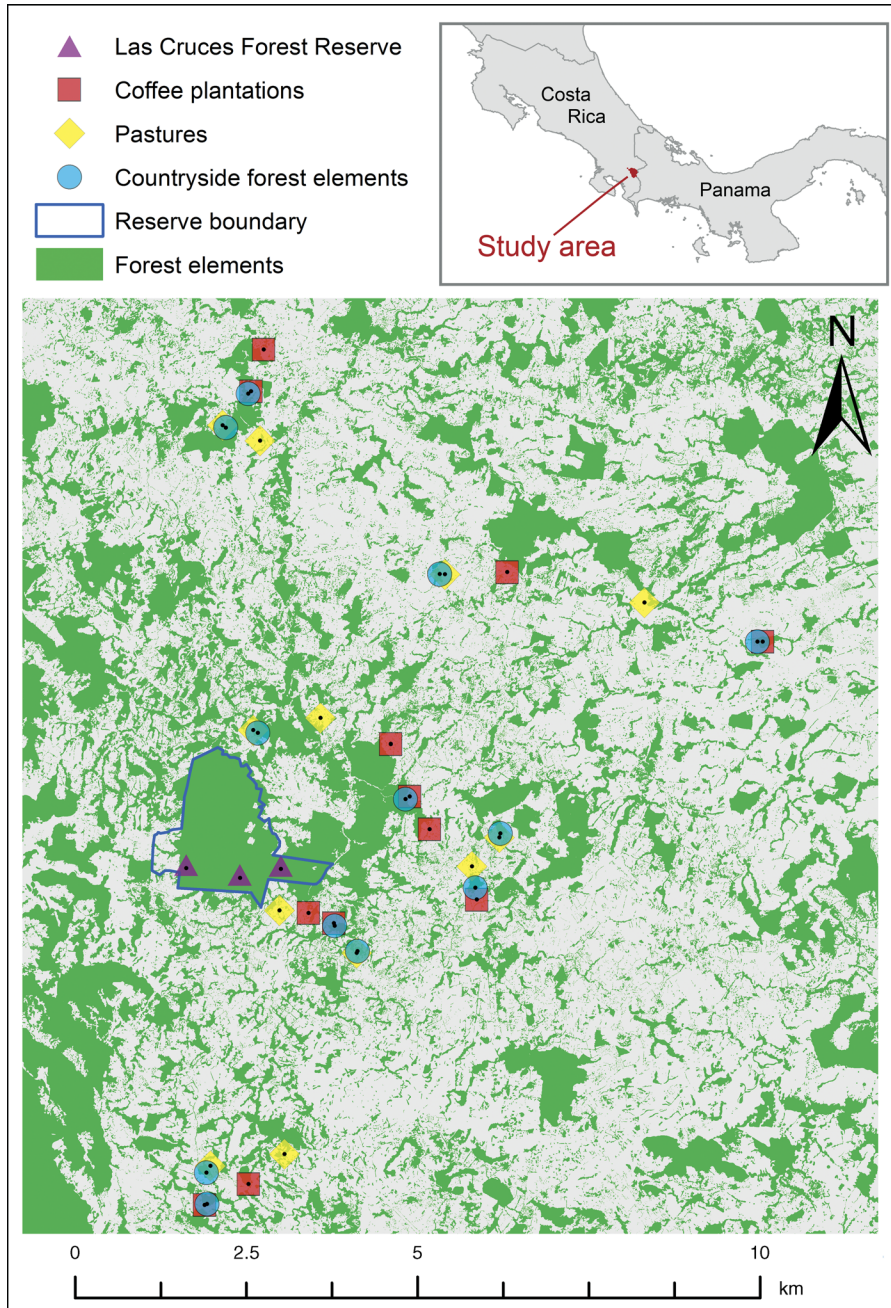


FIG. 1. Map displaying a portion of the 236-km² study area in Coto Brus, Costa Rica, containing reptile and amphibian sampling locations. Black points inside symbols show exact sampled locations. The Las Cruces Forest Reserve of the Organization for Tropical Studies Las Cruces Biological Station is the largely green area outlined in blue.

Chao species richness estimates of reptiles and amphibians were used because they perform well with low sample sizes and uneven effort (Chao 1987). Chao species richness estimates for each site were log-transformed to meet assumptions of ANOVA. Relative abundance was approximated using raw capture totals at each sampling location. Raw capture totals were doubled at the 24 paired sites with half the

sampling effort. All raw capture totals were log transformed to meet assumptions of ANOVA. Tukey honestly significant difference (HSD) post hoc tests were used for pairwise comparisons of different habitat types for species richness estimates and relative abundance. All species and morphospecies were used to calculate Chao species richness estimates and compare relative abundances.

To measure differences in reptile and amphibian abundance-based community composition, we compared Chao abundance-based similarity coefficients for each sampling location (Chao et al. 2004). We used Chao abundance-based similarity coefficients because they are resistant to biases introduced by unequal sampling (e.g., paired sites; Chao et al. 2004). All 67 species and all captures were included in community analyses, including all morphospecies. For both reptiles and amphibians, nonmetric multidimensional scaling (MDS) plots of Chao abundance-based similarity coefficients and area-proportional Euler diagrams were used to illustrate community similarity and overlap. Permutational multivariate analysis of variance (PERMANOVA) tests were used on Chao abundance-based similarity coefficients to identify reptile and amphibian abundance-based community similarities between habitat types.

To assess the conservation value of tropical farmland, we linked observed changes in reptile and amphibian biodiversity, namely with abundance-based community composition level, with the landscape context at taxon-specific spatial scales. To quantify change in reptile and amphibian biodiversity, we again used Chao abundance-based similarity coefficients to calculate the similarity of a given site on farmland to the three sampling locations in the Las Cruces Forest Reserve. The three Chao abundance-based similarity coefficients for each farmland site and the three Las Cruces Forest Reserve sites were averaged to create an abundance-based community composition, "Similarity to Las Cruces Forest Index," for each sampling location and taxon. Sites with fewer than two species observed were omitted from the index because community dissimilarity measures are based on multidimensional comparison, and sites with a single species are one-dimensional. A total of six sites were omitted for the reptile index (two countryside forest element, two coffee plantation, and two pasture sites for reptiles) and three omitted for the amphibian index (all coffee plantation sites); these sites were only removed for the Similarity to Las Cruces Forest Index and analysis. All species were used to create the Similarity to Las Cruces Forest Index. After checking for normality, the Similarity to Las Cruces Forest Index was used as a response variable with a variety of site-specific explanatory variables in a generalized linear mixed-effects modeling (GLMM) approach explained in a later paragraph.

Using results from the PERMANOVA tests, corroborated by regression tree analysis, we identified forest elements (described previously) as the major landscape features defining reptile and amphibian biodiversity measured through abundance-based community composition. To determine the taxon-specific spatial scale for which forest elements had the greatest effect on reptile and amphibian biodiversity, we measured the proportion of forest elements at multiple scales and used them to explain the Similarity to Las Cruces Forest

Index for each taxon using GLMM models. The proportion of forest elements was calculated within 32 concentric circles with radii ranging from 50 to 1000 m from the approximate middle of each sampling location (i.e., 16 circles starting at a 50-m radius and increasing by 10 m up to a radius of 200 m, and 16 circles starting at a 200-m radius and increasing by 50 m up to a radius of 1000 m).

A single spatial scale for each taxon was selected by comparing different GLMMs that used proportion of forest elements within one of 32 concentric circles as an explanatory variable (i.e., multiple, autocorrelated measures of forest element area from different concentric circles were not used in a single model). Models were compared using corrected Akaike Information Criterion (AIC_c). Site pairing as a random effect and a variety of nonlinear relationships were tested and compared using the GLMM framework (Zuur et al. 2009). The best models were selected to be used as predictive models to estimate reptile and amphibian biodiversity change within the determined taxon-specific spatial scale in areas not directly sampled over our 236-km² study area. We used the results produced by extrapolating our linear models across the habitat map to assess the conservation value of tropical farmland for reptile and amphibian biodiversity based on abundance-based community similarity.

Finally, linear regression and one-way ANOVAs were performed to identify patterns between species dependence on forest elements and selected traits. Significance levels were corrected for multiple tests using Bonferroni adjustments.

RESULTS

In total, we recorded 1678 captures of 67 species (Appendix D: Table SIMILARITY). Reptiles were represented by 692 captures of 39 species (23 snakes and 16 lizards). Amphibians were represented by 986 captures of 28 species (26 anurans, one caecilian, and one salamander). We found considerable variation in the number of captures across species, ranging from the most abundant reptile and amphibian species (the lizard *Anolis [Norops] polylepis*, 447 records; the frog *Craugastor stejnegerianus*, 415 records) to 17 singletons (13 snakes, one lizard, and three anurans). Four unique species (one lizard, one snake, and two anurans) represented by 18 individuals were not identified to species before release, but are included in all analyses as morphospecies. A list of all species recorded and their occurrence in different habitat types is provided in Appendix D. We also include a list of encounters of species found in the study area outside of our sampling and analyses (Appendix D). All identified species encountered in the study are native to Coto Brus, Costa Rica.

Chao species richness estimates were relatively high across all habitat types, including coffee plantations and actively grazed pastures. Chao species richness estimates

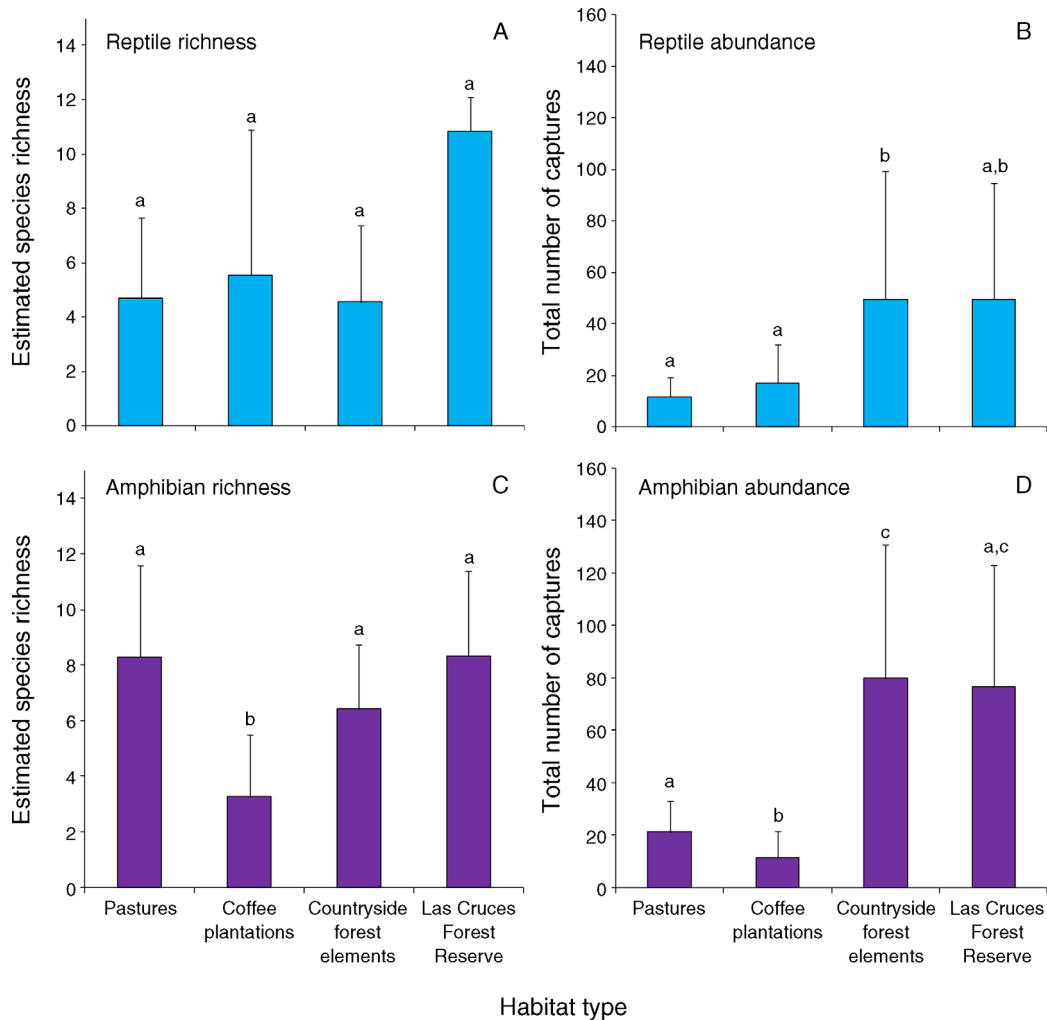


FIG. 2. Tropical farmland supports a substantial number of reptile and amphibian species, but at lower abundances than do tropical forest elements. Bar charts show the mean (\pm SD) of estimated species richness estimates (Chao 1987; see *Methods: Statistical analyses*) and raw captures for reptiles and amphibians by habitat type in Coto Brus, Costa Rica. Different lowercase letters above bars indicate significant differences between habitat types in post hoc analyses (HSD, $P < 0.05$).

did not vary significantly by habitat type for reptiles (ANOVA, $F_{3,35} = 2.391$, $P = 0.09$, Fig. 2A), but did vary for amphibians (ANOVA, $F_{3,35} = 7.95$, $P < 0.001$, Fig. 2B). Post hoc HSD analysis confirmed that coffee plantations hosted significantly fewer amphibian species than other habitat types (Fig. 2). Species richness estimates were not explained well by forest element size. Species–area relationships were weak for reptiles ($R^2 = 0.107$, $P = 0.04$, $n = 39$ and $R^2 = 0.039$, $P = 0.24$, $n = 37$ when Las Cruces Forest Reserve sites were averaged) and absent for amphibians ($R^2 = 0.015$, $P = 0.45$, $n = 39$; Appendix A: Fig. A1). Moreover, species richness estimates were not explained by distance to the Las Cruces Forest Reserve for reptiles ($R^2 = 0.005$, $P = 0.68$, $n = 39$) or for amphibians ($R^2 = 0.003$, $P = 0.95$, $n = 39$; Appendix A: Fig. A2).

The relative abundance of reptiles and amphibians was different between habitat types, but forest elements

in the countryside hosted the highest relative abundances of reptiles and amphibians. Overall abundance for both reptiles (ANOVA, $F_{3,35} = 5.17$, $P = 0.005$; Fig. 2C) and amphibians (ANOVA, $F_{3,35} = 17.54$, $P < 0.001$; Fig. 2D) varied significantly. Post hoc HSD analyses revealed that reptile and amphibian abundances in countryside forest elements were not significantly different from those in the Las Cruces Forest Reserve, but coffee plantations and pasture hosted significantly lower relative abundances of reptiles and amphibians than did countryside forest elements. Detection bias was not accounted for in comparisons of relative abundance because animals were not marked.

Among the 28 amphibian and 39 reptile species, we found two partially overlapping communities, one associated with forest and one with agriculture (Fig. 3). Of the 67 total species identified, 40% were found in both communities. Of the remaining species, 22% were

forest-element-limited (found only in forest elements including the reserve, of which five species (one frog, one lizard, and three snakes) were captured only in the Las Cruces Forest Reserve) and, perhaps more interestingly, 37% were agri-limited (found only in coffee plantations or pastures). These percentages do not include any species extirpated from the region or account for detection biases.

Community analyses revealed fundamental differences in reptile and amphibian biodiversity determined by the presence of forest elements at a sampling site. Specifically, there were differences in reptile and amphibian communities between the four general habitat types (PERMANOVA: $F_{3,34} = 3.67$, $P < 0.001$; $F_{3,34} = 2.45$, $P = 0.01$ for reptiles and amphibians, respectively). We found stronger differences when sites were lumped into two categories of forest elements (all countryside forest elements and the Las Cruces Forest Reserve) and agricultural habitat types (pasture and coffee plantations; PERMANOVA: $F_{1,36} = 6.67$, $P < 0.001$; $F_{1,36} = 5.60$, $P = 0.01$ for reptiles and amphibians, respectively). Pair-wise comparisons of the reptile biodiversity significantly favored binary categories ($t = 5.57$, $P < 0.001$) over the four general habitat types ($t = 0.90$, $P = 0.55$). For amphibians the binary categories performed slightly better ($t = 7.03$, $P < 0.001$) than the four specific habitat types ($t = 1.99$, $P = 0.015$). We found forest elements to be the major landscape variable determining observed biodiversity patterns after performing regression tree analysis to explain the Similarity to Las Cruces Forest Index using habitat type, elevation, or distance to nearest river (Appendix B: Figs. B1 and B2). Therefore, further analyses concentrated on the role of forest elements and spatial scales played in determining reptile and amphibian abundance-based community composition.

Through high-resolution classification of habitats, we found that forest elements at a fine-scale in the countryside are the most important variable shaping the reptile and amphibian biodiversity to be similar to the Las Cruces Forest Reserve. Comparisons of GLMMs revealed that the proportion of countryside forest elements within a 50-m neighborhood scale (CFE₅₀) for reptiles and an 80-m neighborhood scale (CFE₈₀) for amphibians best explained their similarity to Las Cruces Forest Reserve Indices (Appendix C: Figs. C1 and C2). Asymptotic relationships or random effects of paired site sampling did not significantly improve model fit or performance ($P > 0.05$ or $\Delta AIC_c > 4.0$). Linear models using CFE₅₀ and CFE₈₀ had the lowest AIC_c of all models compared and performed well in explaining the Similarity to Las Cruces Forest Reserve Index for reptiles ($R^2 = 0.328$, $P < 0.001$, $n = 30$, Fig. 4A; Appendix C: Table C1) and amphibians ($R^2 = 0.334$, $P < 0.001$, $n = 33$, Fig. 4C; Appendix C: Table C2), respectively. Predictive linear models using CFE₅₀ and CFE₈₀ were extrapolated to estimate the reptile and amphibian biodiversity, respectively, of the 236-km²

study area not directly sampled (i.e., to remotely predict the reptile and amphibian biodiversity).

After estimating the distribution of reptile and amphibian biodiversity in the 236-km² study area, we estimated countryside forest elements to provide the vast majority of habitat for reptiles and amphibians associated with the Las Cruces Forest Reserve. In the 236-km² (23 600 ha) study area, countryside forest elements on farms contributed 4200 ha of land predicted to support a reptile biodiversity similar to that found in the reserve (within the standard deviation of, or greater than the mean values for, the similarity to Las Cruces Forest Index for reptiles = 0.60 ± 0.04 , $n = 3$) and 3650 ha predicted to support an amphibian community with a composition similar to that in the reserve (within the standard deviation of, or greater than the mean values for, the Similarity to Las Cruces Forest Index for amphibians = 0.75 ± 0.09 , $n = 3$). Collectively, within the extent of the 236-km² study area, countryside forest elements on farmland effectively increased the size of the Las Cruces Forest Reserve an estimated 16-fold for reptiles and 14-fold for amphibians (Fig. 4B and D).

Moreover, countryside forest elements on farmland are not insular habitat patches embedded in an inhospitable matrix for most species, but rather an important habitat type among a collection that organisms use. The majority of reptile and amphibian species in this study used an array of habitats. When we graph the proportion of sampling effort-adjusted captures encountered in each of the four habitat types for the 28 species with ≥ 5 samples per species, an understanding of what constitutes a species' habitat emerges (Fig. 5). We find 7 of 12 reptile and 11 of 16 amphibian species using combinations of agriculture (pasture and/or coffee) and forest elements (countryside forest elements and/or the reserve). The remaining 39 species with < 5 samples were captured in the following breakdown across habitat types: 18 species found only in pasture and/or coffee, 12 found only in countryside forest elements and/or the reserve (5 of those 12 were found only in the reserve), and 9 found in both.

Countryside forest elements and agricultural plots also constitute habitat for species threatened by extinction in our study. The IUCN Red List statuses showed that the critically endangered red-eyed stream frog (*Duellmanohyla uranachroa*) and the vulnerable Cerro Utyum robber frog (*Craugastor podiciferus*) were exclusively recorded on private farms in this study, all but one capture in countryside forest elements (Fig. 5). Moreover, the Camron climbing salamander (*Bolitoglossa lignicolor*), which is vulnerable to extinction, was only observed in pastures and a coffee plantation. Several other species of concern not directly sampled in our study were found in the region, some using human-made habitats, including a vulnerable turtle species and three frog species listed as vulnerable, endangered, or critically endangered (Appendix D).

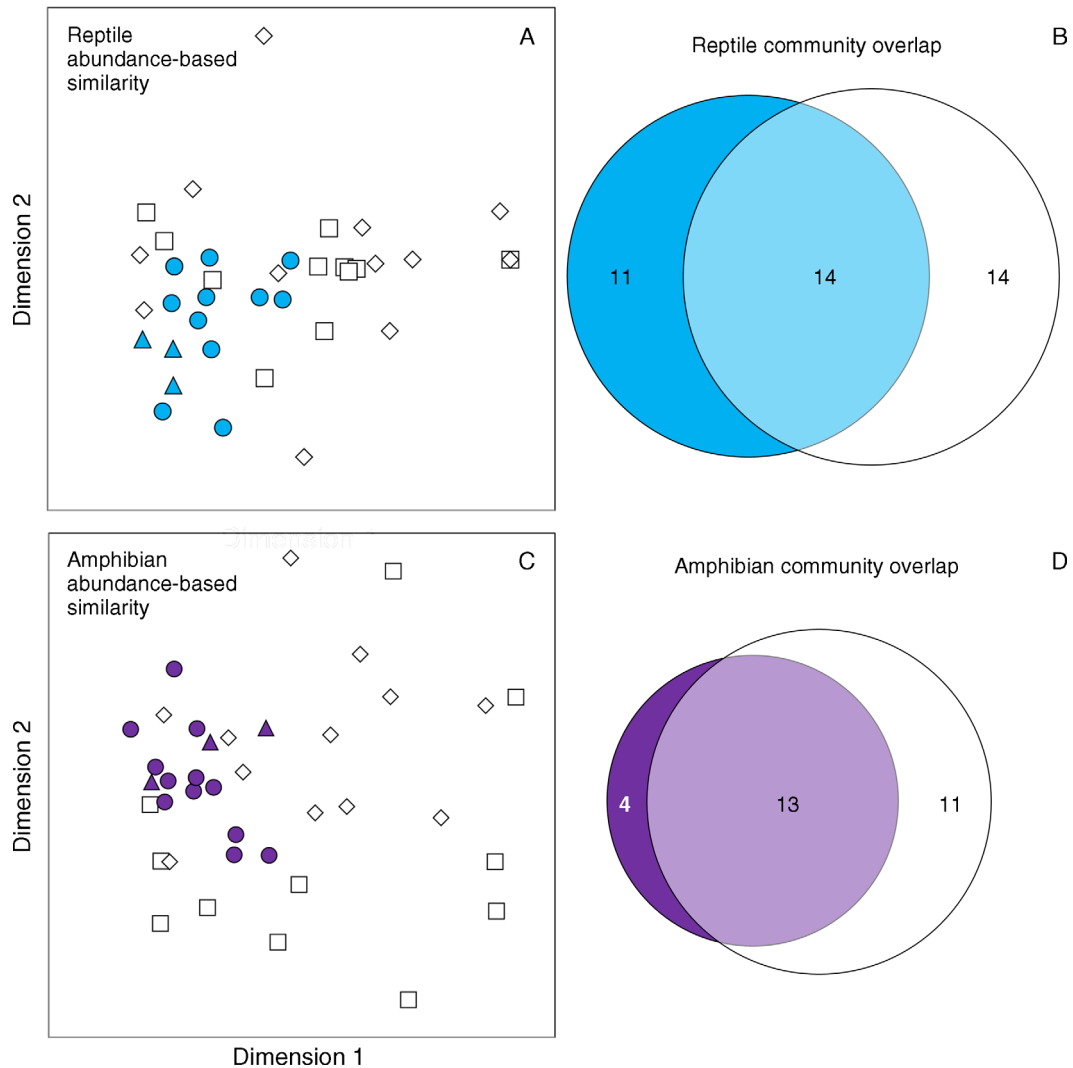


FIG. 3. Reptiles and amphibians are organized into two overlapping communities based on each species' dependence on forest elements. Similarity plots show differences and overlap between forest and agricultural biodiversity for reptiles and amphibians, using multidimensional scaling plots derived from Chao abundance-based similarity coefficients (see *Methods: Statistical analyses*). Each point summarizes abundance-based community similarity for a sampling site; closer proximity between points indicates greater similarity. Triangles represent sampling locations inside the Las Cruces Forest Reserve ($n = 3$), circles represent countryside forest elements ($n = 12$), open squares represent coffee plantations ($n = 11$), and open diamonds are actively grazed pastures ($n = 12$). Reptile biodiversity differences are summarized in plot (A) (stress = 0.24) and amphibians in plot (C) (stress = 0.23). To illustrate community overlap, two-way, area-proportional Euler diagrams are shown for (B) reptiles and (D) amphibians. Numbers in each area correspond with the total number of species encountered in each habitat type. The circle comprising the overlap and shaded areas represents the "forest community" for each taxon. The circle comprising the overlap and open areas represents the "agricultural community" for each taxon.

We found that snout–vent length (SVL) and larval habitat were correlated with the degree of anuran forest dependency. We found larger anurans are less forest affiliated ($R^2 = 0.417$, Bonferroni adjusted $P = 0.046$, $n = 15$; Fig. 6A). One-way ANOVA of larval habitat and adult forest affinity varied significantly (ANOVA $F_{2,12} = 9.501$, Bonferroni adjusted $P = 0.017$). Post hoc HSD analysis revealed that anurans whose larval stages are in moving streams, or that undergo direct development in terrestrial habitats, have higher forest element affinities

than species whose larvae develop in ponds (Fig. 6B). No relationships were found between reptile habitat affinity and reptile SVL general habitat stratum.

DISCUSSION

There is clearly no substitute for reserves that protect primary forest (Gibson et al. 2011), but our investigation demonstrates that tropical farmland can support substantial native reptile and amphibian biodiversity when countryside forest elements are considered and managed

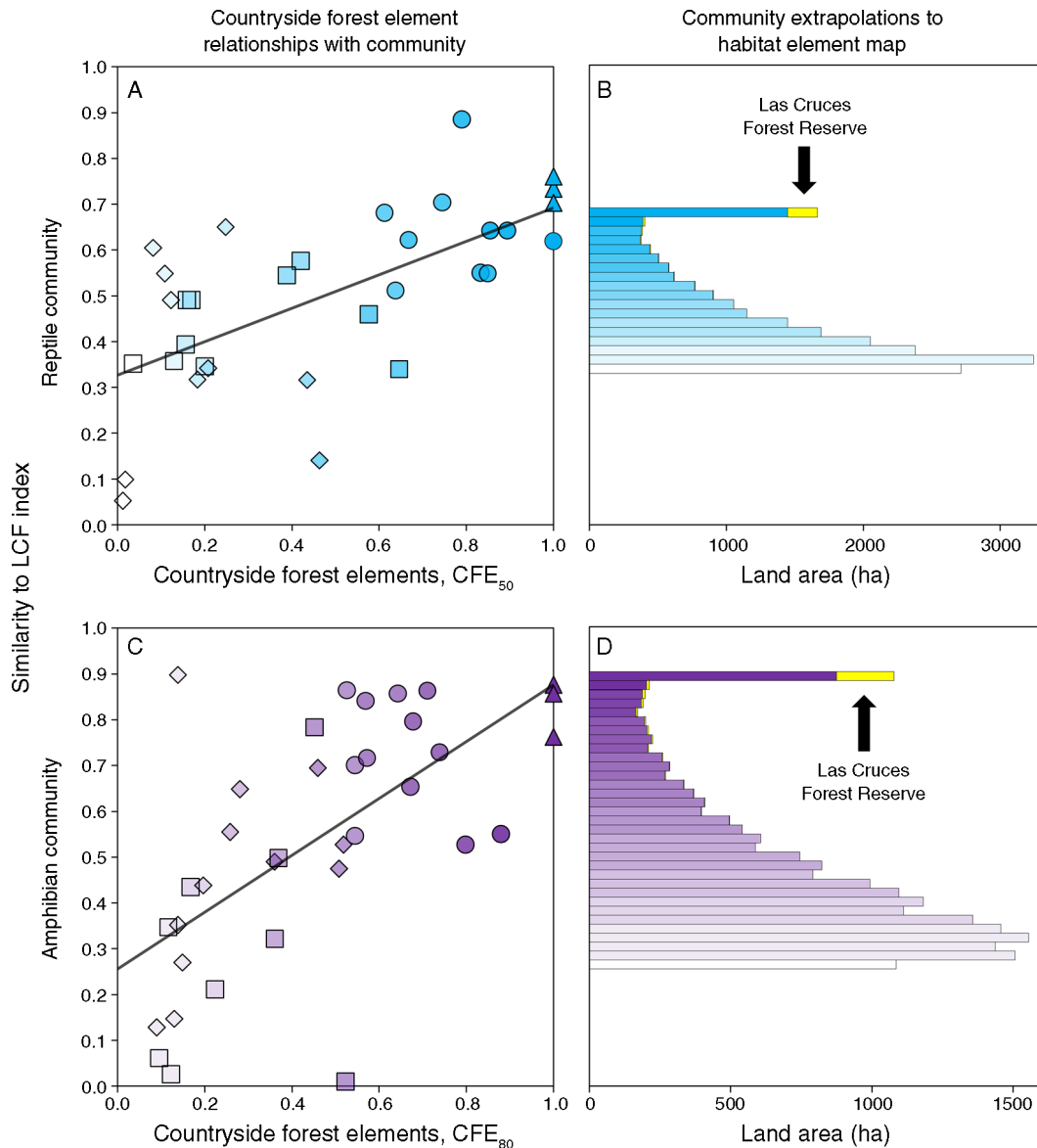


FIG. 4. Reptile and amphibian communities increasingly resembled those found in the Las Cruces Forest Reserve (LCF) as the proportion of countryside forest elements increased within the taxon-specific radii of 50 and 80 m, respectively. Plots illustrate reptile and amphibian community relationships with countryside forest elements, at these scales and extrapolations of these relationships to $\sim 236 \text{ km}^2$ of Coto Brus, Costa Rica. (A) Reptile biodiversity is more similar to the Las Cruces Forest Reserve community when the proportion of countryside forest elements within 50 m (CFE₅₀) increases ($R^2 = 0.328$, $P < 0.001$, $n = 30$). (C) Amphibian communities are most correlated with the proportion of countryside forest elements at 80 m (CFE₈₀, $R^2 = 0.394$, $P < 0.001$, $n = 33$). Darker shading of symbols and bars corresponds to an increasing proportion of countryside forest elements. Circles represent sites located in countryside forest elements, squares represent coffee plantations, and diamonds are actively grazed pastures. Panels (B) and (D) show the distribution of land and the estimated reptile and amphibian biodiversity it hosts. Yellow bars indicate land in the Las Cruces Forest Reserve. Shading of bars corresponds with the proportion of countryside forest elements.

at taxon-specific spatial scales. We find coffee plantations and actively grazed pastures to host rich, albeit different and less dense, reptile and amphibian biodiversity compared to the 326-ha Las Cruces Forest Reserve, the only regional baseline that exists in the premontane life zone where the study was conducted (Holdridge 1979). We also find that the ribbons of countryside forest elements weaving through farmland

sustain reptile and amphibian biodiversity similar to that in the Las Cruces Forest Reserve. Our findings highlight the role that countryside forest elements play in facilitating the persistence of tropical biodiversity in farmland where protected areas do not exist and may be infeasible.

Globally, reptile and amphibian responses in human-dominated ecosystems vary markedly depending on the

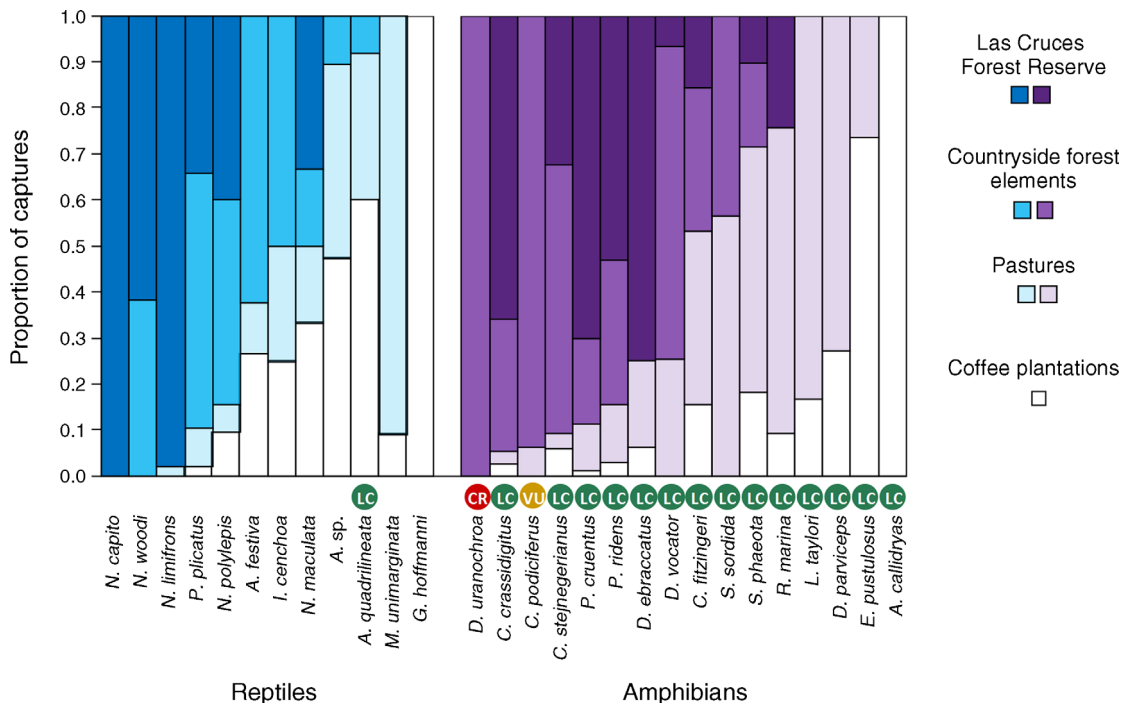


FIG. 5. Most species are not restricted to a single habitat type and use combinations of agriculture and forest elements. The bars show the proportion of individuals sampled in different habitat types in Coto Brus, Costa Rica. Proportions are adjusted for effort and are from adequately sampled reptile and amphibian species (≥ 5 captures). IUCN redlist status is indicated by the circles above each species name. Green circles represent least concern, the yellow circle is vulnerable to extinction, and the red circle represents critically endangered. Species without redlist status circles have not been evaluated by IUCN. See Appendix D for complete scientific names.

specific fauna examined, the biogeographic setting, and the degree and type of ecosystem alteration. Various studies report significant increases (Suazo-Ortuño et al. 2008), decreases (Vallan 2000, Hillers et al. 2008), and lack of changes (Urbina-Cardona et al. 2006, Dixo and Martins 2008, Luja et al. 2008) in species richness of reptiles and amphibians in human-dominated landscapes. Reptile and amphibian communities often do not react in similar ways, highlighting that life history differences among these taxa may complicate predictions of biodiversity change in response to habitat and land use change. Despite the difficulty inherent in quantifying how biodiversity responds to ecosystem change, several other countryside biogeography studies of Neotropical reptiles and amphibians corroborate our findings that substantial reptile and amphibian biodiversity exists in human-dominated landscapes, and potentially changes dramatically the way we value these habitats. For example, Urbina-Cardona et al. (2006) found similar numbers of native amphibian species across pastures, forest edges, and forest-interior sites in Veracruz, Mexico (Urbina-Cardona et al. 2006). Another study from Veracruz, conducted in a landscape where $\sim 10\%$ of the original forest cover remains, highlighted the importance of maintaining forest elements in pastures and coffee plantations to support

native, forest-dependent frogs on farmland (Pineda and Halffter 2004). Despite these findings, there remains much to be done, but the conservation value of human-made habitats is being increasingly quantified and recognized as viable habitat that can aid in the conservation of biodiversity if managed accordingly.

Our approach linking changes in reptile and amphibian biodiversity with countryside forest elements and human-made habitats, at a fine spatial scale and over an extensive area, improves understanding of the future of biodiversity in human-dominated ecosystems. This approach allows for a more holistic measure of the conservation value of land owned and managed by farmers in Coto Brus. We estimate that, collectively, countryside forest elements beyond the borders of the local reserve provide the remaining $\sim 95\%$ of habitat utilized by forest-dependent reptile and amphibian biodiversity in our study region. Countryside forest elements form a network of habitat that weaves through the landscape, and exist because it is maintained by the farmers. It remains an unanswered question as to why Costa Rican farmers maintain these networks of countryside forest elements that constitute 33% of all farmland in the study region. Moreover, these networks of countryside forest elements on farmland contribute 4200 ha and 3650 ha of habitat predicted to support

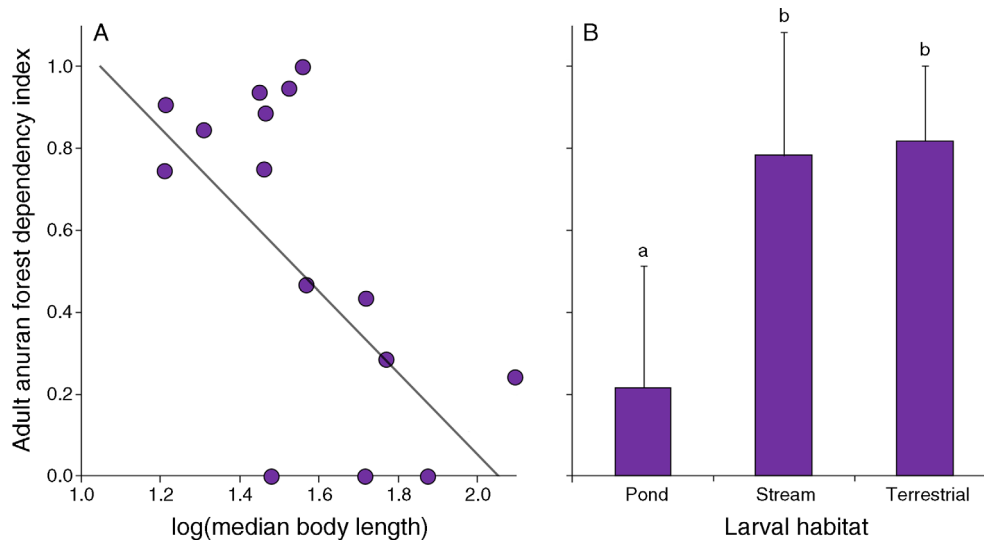


FIG. 6. Relations of (A) anuran body length (measured as snout-to-vent length, in millimeters) and (B) larval habitat to forest dependency in Coto Brus, Costa Rica. Smaller anurans are more forest dependent, while larger species are more frequent in coffee plantations and pastures. Species whose larvae depend on streams or that have terrestrial young are more dependent on forest elements, while species that require ponds often use coffee plantations and pastures. Different lowercase letters above bars indicate significant differences between larval habitat types in post hoc analyses (HSD, $P < 0.05$).

reptile and amphibian biodiversity, respectively, similar to that found inside the Las Cruces Forest Reserve, effectively boosting the total coverage of the local reserve from 0.01% of the total land area to ~15–18% within the 236 000-ha study area. This percentage of high-quality countryside forest habitat on farmland is impressive considering that only 13% of global land surface and 9.8% of the entire tropical biome are formally protected (Coad et al. 2009, Schmitt et al. 2009). Moreover, our methods of quantifying all trees on the landscape break free from simplistic and unrealistically homogenized representations of habitat configuration in “biodiversity-friendly” farming landscapes by capturing the great variety of forest element sizes and configurations that actually exist in tropical working landscapes (Mendenhall 2011, Fahrig 2013). The fine-scale forest elements we accounted for in our study are consistently unaccounted for in the remote sensing information widely available, but are now easily quantified using conservation drone technology (Koh and Wich 2012).

Similar to previous studies using arthropods, birds, and nonflying mammals, we found that countryside forest elements also increase the hospitality of pastures and coffee plantations and create a myriad of intermediate habitats for many forest-dependent species (Mendenhall 2013b). Pasture and coffee plantations with an increasing proportion of countryside forest elements within the taxon-specific radii of 50 m for reptiles and 80 m for amphibians hosted biodiversity that increasingly resembled that found in the Las Cruces Forest Reserve. We hypothesize that these radii reflect relative habitat use spatial scales and dispersal distances typical of each

taxon (Fahrig 2013). Also, the herpetofauna is not restricted to forest elements; for example, the edges between forest elements and actively farmed land create a variety of intermediate habitats that blur the boundaries of forest and nonforest (Schlaepfer and Gavin 2001, Santos-Barrera and Urbina-Cardona 2011). The extent of these intermediate habitats is considerable, and they provide an immense resource for many species, especially those using combinations of agriculture and forest.

Our results also indicate that differences in reptile and amphibian biodiversity exist between coffee plantations and pastures. Additional study is needed to examine how the type and intensity of agricultural habitats affect tropical biodiversity. For example, we observed significantly lower amphibian species richness in coffee fields, possibly an artifact of the difficulty inherent in detecting amphibians in dense coffee stands compared to open pastures. It is also possible that the typical use of chemical inputs in Coto Brus coffee plantations may have eliminated some sensitive species (Bellamy 2011). Differences in the hospitality of human-made habitats were spotlighted in a study in Mexico that found higher conservation value of coffee plantations compared to corn plantations because of the favorable microclimate conditions and the arboreal elements common in coffee, but absent in cornfields (Santos-Barrera et al. 2008).

Beyond habitat availability and connectivity, there are other important characteristics of human-dominated landscapes that may facilitate the conservation of biodiversity. In the context of amphibian biodiversity conservation, populations occurring in human-dominated landscapes may be less susceptible to pathogens,

specifically the pathogen causing the most severe amphibian declines around the globe, *Batrachochytrium dendrobatidis* (i.e., chytrid fungus) (Skerratt et al. 2007). Guilherme Becker and Zamudio (2011) discovered that “amphibians are disproportionately affected by emerging diseases in pristine environments, and that, paradoxically, disturbed habitats may act as shelters from disease” (Becker and Zamudio 2011). Human-made and modified habitat as shelter from disease coupled with our findings that substantial amphibian biodiversity exists in human-dominated landscapes increases the potential conservation value of countryside landscapes like Coto Brus, Costa Rica. Additional study is needed to examine the trade-offs and mechanism in the relationship between disturbed habitats and disease mitigation (Mendenhall et al. 2013a).

Our findings that anurans of small body size, and reproductive modes tied to flowing water or terrestrial direct development, have high forest affinities, are supported by previous studies (Hero et al. 2005, Becker et al. 2007, Suazo-Ortuño et al. 2008, Becker and Fonseca 2009, Dixo and Metzger 2010). Desiccation stress caused by higher temperatures and lower canopy cover in human-made habitats may be a strong biological filter for amphibians (Murcia 1995, Urbina-Cardona et al. 2006, Hillers et al. 2008). Larger body size serves to decrease an animal’s desiccation rate (Wells 2007). This possibly explains why we find large-bodied amphibian species occupying human-made habitats more frequently than small-bodied species. Amphibians that reproduce in still water are more closely associated with human-made habitats. Human activity tends to create breeding sites for amphibians as ranchers provide water sources for livestock, farmers irrigate crops, ditches and dirt roads facilitate and sustain large puddles, and tilapia farms build elaborate networks of ponds with seasonal use. These manmade water sources are exploited as oviposition sites by many amphibians spanning a range of forest affinities (e.g., *Dendropsophus ebraccatus*, *Smilisca phaeota*; L. O. Frishkoff, *personal observation*).

The link between modified habitats and still-water breeding amphibians is supported by a recent experiment conducted in Brazil (Silva et al. 2012) in which artificial ponds were placed at various distances from a forest edge. Ponds located at forest fragment edges or 50 m away from the edge in human-made habitats attracted the greatest number and diversity of tropical still-water breeding amphibians compared to ponds located 50 and 100 m inside forest fragments and 100 and 200 m away from the edge in human-made habitats. Our findings support these patterns, but there remains opportunity for future work to explain why still-water breeding amphibians are more species rich and more abundant at forest fragment edges or just outside forest fragments.

Terrestrial direct developers, in contrast, require humid leaf litter for their eggs to develop, which is less available in human-made habitats. Similarly, eggs of

riparian breeders, often laid on vegetation above stream courses, may be particularly vulnerable to desiccation in areas lacking sufficient tree cover. Our trait-based study on reptiles included only a few traits, limited by availability of information; further study is needed to determine if there are readily discernible reptile characteristics that confer survival advantages in human-dominated landscapes.

Extinction and changes in biogeography rank among the most potent effects that humans exert on the planet (Cardinale et al. 2012, Hooper et al. 2012). Our study provides a framework to predict changes in biogeography at fine scales, but we were not able to explore the consequences of local reptile and amphibian extirpation in our study area. We found limited data on the historical herpetofauna in the Las Cruces Forest Reserve (e.g., Scott et al. 1976), and local extinctions have not been documented. To our knowledge, no baseline records of the pre-deforestation local herpetofauna exist. One study, limited to leaf-litter herpetofauna, reported a total of 13 species, of the 67 captured and 20 observed species in our field study (Scott et al. 1976; see also Appendix D). Therefore, there is no historical baseline for our results, but the rate at which amphibian and reptile species have gone extinct in recent years suggests that local extinctions may have occurred. We hope to provide a baseline for future research with this study, and have included an incomplete list of anecdotal observations in Appendix D.

The existence of an “extinction debt” remains poorly understood for reptiles and amphibians. Extinction debts are the potential for future loss of species and populations because the remaining habitat after modification is not sufficient for long-term persistence (Tilman et al. 1994, Gagné and Fahrig 2010). Patterns of high bird biodiversity in an Indian tropical countryside, continuously cultivated for more than 2000 years, suggest that high countryside biodiversity, at least for birds, is not an artifact of extinction debt (Ranganathan et al. 2008). For mammals, however, there have been at least six recent local extinctions in our Costa Rican study area, resulting from habitat loss, dogs, pesticides, and hunting (Daily et al. 2003). Many mammal species, however, do use pastures and coffee plantations, at least partially.

Extinctions in the more distant past are even more difficult to evaluate. The Coto Brus Valley in Costa Rica has a long history of deforestation. While the current landscape was shaped primarily by deforestation starting in the 1950s (Sansonetti 1995, Mendenhall et al. 2011), sediment core analyses reveal a 3000-year history of agriculture, forest clearing, and fire in the region up to the 16th century (Clement and Horn 2001). Recent findings suggest that pre-Columbian societies throughout the Americas were not sparsely settled in wilderness, but rather were huge populations and economies that heavily influenced the lands and biodiversity around them, making some types of human-dominated ecosys-

tems and countryside biodiversity less evolutionarily novel than previously thought (Mann 2005).

From a policy perspective, our results provide a basis for estimating the conservation value of human-dominated, agricultural landscapes that constitute roughly half of the of global land surface (Ellis et al. 2010). Assessing the conservation value of the world's countryside ecosystems is critical as pressure intensifies on potentially arable lands. The projected near-doubling of food production by 2050 (Alexandratos et al. 2006), if pursued through expansion of the industrial agricultural model (Green et al. 2005, Phalan et al. 2011) may liquidate countryside forest elements and the countless wildlife populations they sustain today (Perfecto et al. 2009, Fischer et al. 2011, Mendenhall et al. 2013a), and make protected areas more insular and vulnerable, especially with projected ecosystem range shift induced by climate change (Loarie et al. 2009, Laurance et al. 2012).

Overall, our results suggest that fine-scale forest (or other native ecosystem elements), too small for conventional remote sensing techniques and therefore missed in many land classification and conservation assessments (Mendenhall et al. 2011), can make tropical farmland hospitable to a variety of reptile and amphibian species. Moreover, important ecosystem elements on farmland are likely critical to conserving biodiversity and the benefits it provides to society in the long term. For example, in the near future wildlife-friendly farmland may be essential to the survival of biodiversity within protected areas by facilitating ecosystem range shifts caused by climate change (Loarie et al. 2009), preventing reductions in genetic diversity caused by isolation (Goldberg and Waits 2010), and reestablishing subpopulations that experience local extinctions under metapopulation dynamics (Ricketts 2001, Ray et al. 2002). Conservation enhancements and appropriate incentives to conserve important ecosystem elements that make the countryside wildlife-friendly will increase the effectiveness of existing protected areas and secure ecosystem services in the long term (Daily 1997b, Kareiva et al. 2011, Mace et al. 2012).

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SUPPLEMENTAL MATERIAL

Appendix A

Additional analyses of reptile and amphibian biodiversity responses to forest area metrics, Euclidean distance to the local forest reserve, and general habitat type where sampling occurred ([Ecological Archives E095-072-A1](#)).

Appendix B

Regression tree analyses of Similarity to Las Cruces Index relationships with general habitat type, elevation, and Euclidean distance to nearest river ([Ecological Archives E095-072-A2](#)).

Appendix C

Detailed model selection and tables of regression coefficients for linear relationships between reptile and amphibian Similarity to Las Cruces Forest index and percentage of countryside forest elements at different spatial scales ([Ecological Archives E095-072-A3](#)).

Appendix D

Detailed list of reptile and amphibian captures and observations organized by general habitat type ([Ecological Archives E095-072-A4](#)).