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## HABITAT ALTERATION AFFECTS AMPHIBIAN ASSEMBLAGES IN RAJAH SIKATUNA PROTECTED LANDSCAPE OF BOHOL, PHILIPPINES

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**Abstract.**—Anthropogenic habitat alteration is one of the major drivers of biodiversity loss worldwide. Here, we present the results of an investigation into the responses of amphibian assemblages to a gradient of habitat alteration in Rajah Sikatuna Protected Landscape (RSPL) of Bohol, Philippines. We compared the abundance, species richness, diversity, and composition of amphibians among different habitat types (lower montane forests, dipterocarp forests, riparian areas, grassland, and agricultural areas), and we also examined their relationships with environmental and habitat characteristics. We recorded 318 individuals from 18 amphibian species, belonging to seven families. We found that amphibian abundance, species richness, and diversity differed significantly between habitat types with less disturbed habitats (i.e., forests and riparian areas) generally greater than highly altered habitats (i.e., grassland through agricultural areas). The amphibian fauna of forests and riparian areas were primarily composed of rainforest- and stream-dependent species while highly altered habitats (grassland and agricultural areas) were associated with open-habitat specialists and disturbance-tolerant species. The most important environmental variables influencing patterns of amphibian diversity in the area included grass cover, litter depth, ground relative humidity, and temperature. In summary, the assemblages of amphibians in the RSPL, Bohol, were affected by habitat alteration, highlighting the importance of the sustained protection efforts of the landscape.

**Key Words.**—Central Visayas; dipterocarp forests; disturbance-tolerant; diversity; tropical rainforest

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### INTRODUCTION

Biodiversity typically declines as a result of anthropogenic habitat alteration such as conversion, fragmentation, and deforestation (Riemann et al. 2017). For amphibians, a lack of suitable habitat, especially for arboreal species, is associated with a reduction in species richness (Peltzer et al. 2006). Previous research has investigated some of the consequences of disturbance on amphibian communities. For example, Cruz-Elizalde et al. (2016) and Decena et al. (2020) reported that disturbed areas had fewer species than protected or undisturbed environments. Furthermore, generalist species typically predominated in disturbed habitats whereas species of conservation concern were more prevalent in undisturbed environments. In areas where Tropical Rainforests are continuing to deteriorate and shrink in size, habitat modification has had significant effects on amphibian species that depend on forest ecosystems (Alcala et al. 2004). Some species of amphibians, however, may be able to withstand some habitat alteration as long as a significant portion of forest cover is retained (Herrmann et al. 2005).

Habitat alteration often changes specific environmental characteristics such as canopy cover, leaf litter cover, understory density, temperature, humidity, elevational gradient, and forest patch size and shape, which have been shown to affect amphibian diversity and occurrence (Urbina-Cardona et al. 2006; Laurencio and Fitzgerald 2010; Russildi et al. 2016; Decena et al. 2020). The loss or reduction in canopy cover can substantially result in the decline of species, especially rainforest-specialist amphibians because canopy cover provides necessary habitat conditions (Cortés-Gómez et al. 2013). More importantly, microclimatic conditions (e.g., temperature and humidity) are determinants of amphibian diversity because these mainly affect physiological and reproductive activities, and subsequently the survival of species (Vallan 2002).

The Philippine archipelago is recognized as one of the most important centers of herpetofaunal diversity in Southeast Asia (Diesmos et al. 2002), wherein amphibians are represented by 112 species, at least 80% of which are endemic (Diesmos et al. 2015). The country has high amphibian diversity and endemism, yet faces threats from habitat alteration and degradation,

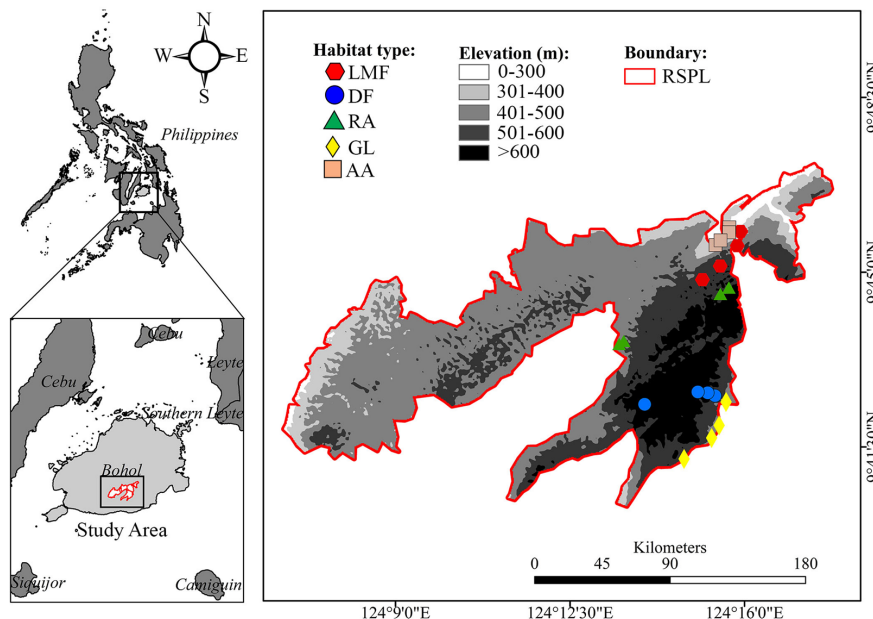
as well as from natural catastrophes (e.g., typhoons), agricultural expansion and urbanization, invasive species, and hunting for food (Liu et al. 1993; Sodhi et al. 2004; Lasco et al. 2013; Diesmos et al. 2015). Although the knowledge of amphibians in the Philippines has increased dramatically in the last few decades (Baron et al. 2021), the majority of investigations during this time have centered primarily on species discovery and taxonomy, including studies by Siler et al. (2011), Brown et al. (2013), Sanguila et al. (2016), Binaday et al. (2017), and Baron et al. (2021). Quantitative studies exploring the effects of habitat alteration and fragmentation on amphibian communities in the country are limited (see Diesmos 2008 and Decena et al. 2020). Therefore, we conducted the current study to explore the response of amphibian assemblages across a gradient of habitat alteration in the Rajah Sikatuna Protected Landscape (RSPL), Bohol, Philippines. The specific objectives of the study were twofold: to quantify any differences in abundance, species richness, and diversity of amphibians among habitat types representing a gradient of habitat alteration; and to examine how environmental and habitat variables influence the amphibian occurrence and diversity patterns.

**MATERIALS AND METHODS**

**Study area.**—The RSPL is a protected and Key Biodiversity Area (KBA; Fig. 1) characterized mainly by forested limestone hills, grasslands, and natural

springs in the island province of Bohol in Central Visayas, Philippines (Aureo et al. 2020; <https://www.keybiodiversityareas.org/site/factsheet/9780>). It is the largest remaining tract of natural forest in Bohol, with an average elevation of 400 m. The area is composed of 88% limestone forest, 10% agricultural areas, and 2% grassland with a total area of 10,452.60 ha (<https://ppdo.bohol.gov.ph/maps/municipal-maps/3rd-district/guindulman/thematic-maps/network-of-protected-areas-for-agriculture-and-agro-industrial-development-npaad/>; <http://datazone.birdlife.org/site/factsheet/rajah-sikatuna-protected-landscape-iba-philippines>). The climate of the study area is characterized as equatorial rainforest-fully humid (Kottek et al. 2006), having a more-or-less evenly distributed rainfall throughout the year with no dry season (Lantican 2001). The area has an average annual rainfall of 1,360.2 mm and temperature of 27.7° C (Japan International Cooperation Agency 2012).

**Habitat types.**—The habitat types that we sampled were lower montane forests, dipterocarp forests, riparian areas, grassland, and agricultural areas. Lower montane forests were a less-disturbed habitat characterized by the presence of the tree species White Lauan (*Shorea contorta*), Philippine Mahogany (*Shorea squamata*), and Manggachapui (*Hopea acuminata*) from the family Dipterocarpaceae with some mixed tree species and are usually located at an elevation of 600 m. We defined dipterocarp forests as habitat that was dominated by



**FIGURE 1.** Location of the Rajah Sikatuna Protected Landscape (RSPL) of Bohol Island, Philippines. The right panel indicates the boundary of the study area (RSPL), and the study transects for each habitat type. (Map was generated using ArcMap 10.3; Esri, Redlands, California, USA). Habitat types are lower montane forests (LMF), dipterocarp forests (DF), riparian areas (RA), grassland (GL), and agricultural areas (AA).

dipterocarp trees. Dipterocarp forests are characterized by a closed canopy, less understory vegetation, and thicker leaf litter in comparison to montane forests. This habitat was also considered less altered as we observed minimal anthropogenic disturbances. Meanwhile, we defined riparian areas as habitats with trees and shrubs located adjacent to waterways such as streams or rivers. The riparian areas we considered in the study were those with permanent streams or with flowing water during the sampling period. All the riparian areas sampled were located within forest areas, and thus, these had minimal disturbance as with the abovementioned forest types. Grassland areas were disturbed habitats characterized by vegetation dominated by grasses and were usually located along forest edges. Grassland habitats were generally abandoned slash-and-burn cultivation areas. The agricultural areas were represented by cultivations for semi-annual crop production and were considered highly altered. In addition, agricultural areas together with grasslands were both originally less disturbed habitats, particularly dipterocarp or montane forests before disturbance and conversion.

**Amphibian sampling.**—We randomly established twenty  $20 \times 100$  m strip transects across the five habitat types with the distance between adjacent transects ranging from 0.1 to 70 km. Within a transect, three persons surveyed amphibians in the morning at 0600–1000 and in the evening at 1900–2300. We employed visual encounter and acoustic methods to exhaustively search for anurans in all available microhabitats such as on the ground, under rocks and logs, in leaves and leaf litter, on vegetation and trees, and in water. We returned all displaced objects to their original position to avoid further disturbance during searching. We limited our searches to approximately 1 h per transect to avoid pseudo-replication, with four transects being sampled per day/night (Supsup et al. 2020). We sampled each transect 22 times at the habitat types and spent 1,320 h (22 sampling sessions per transect  $\times$  20 transects  $\times$  1 h  $\times$  three people) or 440 h/person for the entire duration of the sampling. We started our surveys 22 July 2019 and ended 7 October 2019. We spent the first 11 d, 22 July to 1 August, in the lower montane forests, 5–15 August in grasslands, 19–29 August in the dipterocarp forests, 9–19 September in riparian areas, and 27 September to 7 October in agricultural areas. Generally, we sampled transects in a specific habitat type in clustered dates as we could not sample combinations of transects from different habitats primarily due to logistical constraints. Though there could be the effect of the seasons on the pattern of the diversity/assemblage of amphibians, this might be minimal as the climate of the study area is characterized by the absence of dry season, rather than by more or less evenly distributed rainfall throughout the year.

**Species collection and identification.**—For each species collected, we photographed and measured standard morphometric measurements, adapted from the Guidelines for Amphibians and Reptiles Survey of the Haribon Foundation (Haribon Foundation 2001), to support species identification. We made the preliminary identifications using AmphibiaWeb (<https://amphibiaweb.org/>) and the criteria of the International Union for Conservation of Nature (IUCN) Red List (IUCN 2018). We sent photographic vouchers and morphometric measurements to the Philippine National Museum for confirmation and verification. We collected specimens of species that were difficult to identify and preserved them following the standard preservation techniques by Heyer et al. (1994). The collected specimens were temporarily located at Bohol Island State University, Bohol.

**Measurement of environmental variables.**—We measured 10 environmental variables: (1) canopy cover (%); (2) grass cover (%); (3) fern cover (%); (4) elevation (m); (5) litter depth (cm); (6) air temperature ( $^{\circ}$ C); (7) air relative humidity (%); (8) ground relative humidity (%); (9) soil pH; and (10) soil temperature ( $^{\circ}$ C). We estimated canopy cover using a convex spherical densiometer and we used the quadrat-grid method ( $1 \times 1$  m) to estimate fern and grass cover at every 20 m interval along the transect (Barker 2001). We measured the litter depth by inserting a graduated ruler through the litter until reaching the soil. For measuring the relative humidity and temperature, we used a digital thermohygrometer. Finally, we measured soil pH using a portable pH meter. We measured all environmental variables in each transect during amphibian sampling.

**Data analysis.**—We calculated the abundance, species richness, and diversity (Shannon-Wiener) of amphibians for each strip transect across the different habitat types (lower montane forests, dipterocarp forests, riparian areas, grassland, and agricultural areas) using the PAST 3.22 (Hammer et al. 2001). To illustrate the adequacy of our sampling effort for amphibians, we generated a species accumulation curve for each of the habitat types sampled using the function `specaccum` in the `vegan` package of R (Gotelli and Colwell 2001).

We determined the descriptive statistics (mean  $\pm$  standard error) for each environmental variable across the different habitat types (Appendix). We carried out Pearson's Product Moment Correlation to test multicollinearity between environmental variables, and we excluded the variables with high multicollinearity for performing the last statistical analysis (Generalized Additive Model [GAM]). We tested data on amphibian abundance, species richness, and diversity for normality using the Kolmogorov-Smirnov test. We tested for equal variances using Levene's test. For data that were

normally distributed and homoscedastic, we performed One-way Analysis of Variance (ANOVA) to test for differences in amphibian abundance, species richness, and diversity between habitat types (lower montane forests, dipterocarp forests, riparian areas, grassland, and agricultural areas) representing a gradient of disturbance. Afterward, we performed Tukey’s post-hoc test whenever there were significant differences at  $\alpha = 0.05$ . Also, we used a Welch ANOVA test when the variable being tested was heteroscedastic. We performed the Games-Howell post-hoc test when differences were significant at  $\alpha = 0.05$ . We carried out all the above-mentioned analyses in SPSS version 20.0 for Windows (IBM Corporation; Armonk, New York, USA).

We used Non-metric Multidimensional Scaling (NMDS) ordination to explore similarities in amphibian assemblages among habitat types. We performed NMDS ordination from the Bray dissimilarity matrix of pairwise dissimilarities between strip transects based on the abundance data. We performed the NMDS using the function metaMDS in the R package vegan (Oksanen 2019). In constructing the ordination diagram, we used 20 random starting configurations, with the final configuration that minimized the stress of the ordination configuration retained for plotting. For this analysis, we considered only those species with an abundance of at least three individuals. Furthermore, to support the results of the NMDS, we performed an Analysis of Similarities (ANOSIM) permutation test in the vegan package of R (Oksanen 2019) with 5,000 random permutations of the dissimilarity matrix to test for differences in species assemblages among habitat types.

To examine the occurrence of amphibian species in relation to environmental variables across a gradient of habitat alteration, we fitted linear vectors into the NMDS ordination using the function envfit in the vegan

package of R (Oksanen 2019). We performed the analysis using the same species abundance data and the environmental variables. We evaluated the significance of the environmental variables using a permutation test with 1,000 random permutations.

Finally, we explored the relationships between amphibian abundance, species richness, and diversity with environmental variables using the GAM in the R package mgcv (<https://cran.irsna.fr/web/packages/mgcv/mgcv.pdf>). We performed GAM using a Poisson error structure and logarithmic link functions for count data (abundance and species richness) while we used a Gaussian error structure and identity link function for continuous data (diversity). We retained only the environmental variables with correlations ( $r$ ) < 0.65 for analysis, which included grass cover, elevation, litter depth, air temperature, air relative humidity, and ground relative humidity (Table 1).

We initially performed the GAM analysis with a full model fitted with smooth-terms for all the selected environmental variables. In the initial fitting, some of the environmental variables appeared to be best fitted by smooth-terms with effective degrees of freedom (edf) equal to one, indicating simple linear relationships. Thus, in the following fitting, we expressed these terms as linear terms. We obtained the final model by dropping the least significant environmental variables one at a time and selected the one with the lowest Akaike’s Information Criterion (AIC). We illustrated the shape of the response curves associated with each term by plotting the partial effects. Moreover, we also checked the residual plot for each of the models. We performed the species accumulation curve, NMDS, ANOSIM, fitting of linear vectors, and GAM analyses using R version 4.1.0 (R Development Core Team 2021).

**TABLE 1.** Correlation matrix of 10 environmental variables measured in strip transects in Rajah Sikatuna Protected Landscape (RSPL) of Bohol Island, Philippines. Variables are canopy cover (CC), grass cover (GC), fern cover (FC), elevation (E), litter depth (LD), air temperature (AT), air relative humidity (ARH), ground relative humidity (GRH), soil pH (SpH), and soil temperature (ST). Significant correlations are denoted by one asterisk (\*:  $P < 0.05$ ) or two asterisks (\*\*:  $P < 0.01$ ).

	CC	GC	FC	E	LD	AT	ARH	GRH	SpH	ST
CC	1									
GC	-0.62**	1								
FC	0.37	-0.27	1							
E	0.73**	-0.34	0.47*	1						
LD	0.82**	-0.51*	0.33	0.63**	1					
AT	-0.39	-0.24	0.01	-0.35	-0.41	1				
ARH	0.61**	-0.27	0.20	0.49*	0.54*	-0.31	1			
GRH	0.68**	-0.48*	0.67**	0.55*	0.57**	0.05	0.45	1		
SpH	0.81**	-0.75**	0.23	0.61**	0.82**	-0.20	0.27	0.53*	1	
ST	-0.76**	0.73**	-0.52*	-0.53*	-0.56*	-0.16	-0.59**	-0.89**	-0.60**	1

## RESULTS

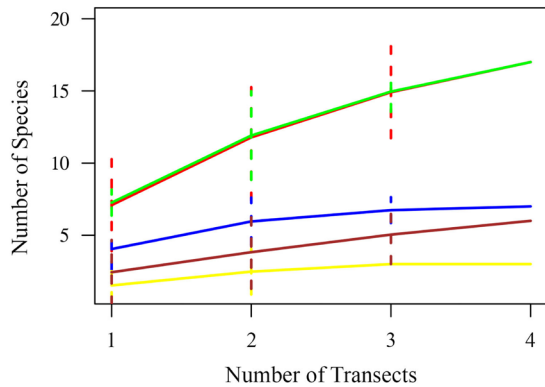
**Species richness and diversity.**—We recorded 318 individuals from 18 amphibian species, belonging to seven families in RSPL, Bohol (Table 2). The most abundant species was Guenther’s Forest Frog (*Platymantis guentheri*), which accounted for 15% of the total number of amphibians captured. The species accumulation curves for amphibians in the habitat types dipterocarp forests, agricultural areas, and grassland are close to the asymptote (Fig. 2), indicating that our

surveys detected most species likely to occur in these habitat types. On the other hand, species accumulation curves for lower montane forests and riparian areas showed a lack of asymptote, suggesting incomplete sampling efforts (Fig. 2).

Amphibian abundance differed significantly among habitat types ( $F_{4,15} = 4.62$ ,  $P = 0.012$ ; Fig. 3); it was higher in riparian areas compared to the highly altered habitats, i.e., grassland and agricultural areas (Tukey’s HSD,  $P < 0.05$ ). Amphibian abundance in altered habitats, however, did not differ significantly with

TABLE 2. Occurrence and abundance of amphibian species in the different habitat types in Rajah Sikatuna Protected Landscape (RSPL) of Bohol Island, Philippines. Species code is for reference in Figure 4. Red List refers to International Union for Conservation of Nature (IUCN) Red List status (IUCN 2022): data deficient (DD), least concern (LC), near threatened (NT), and vulnerable (VU).

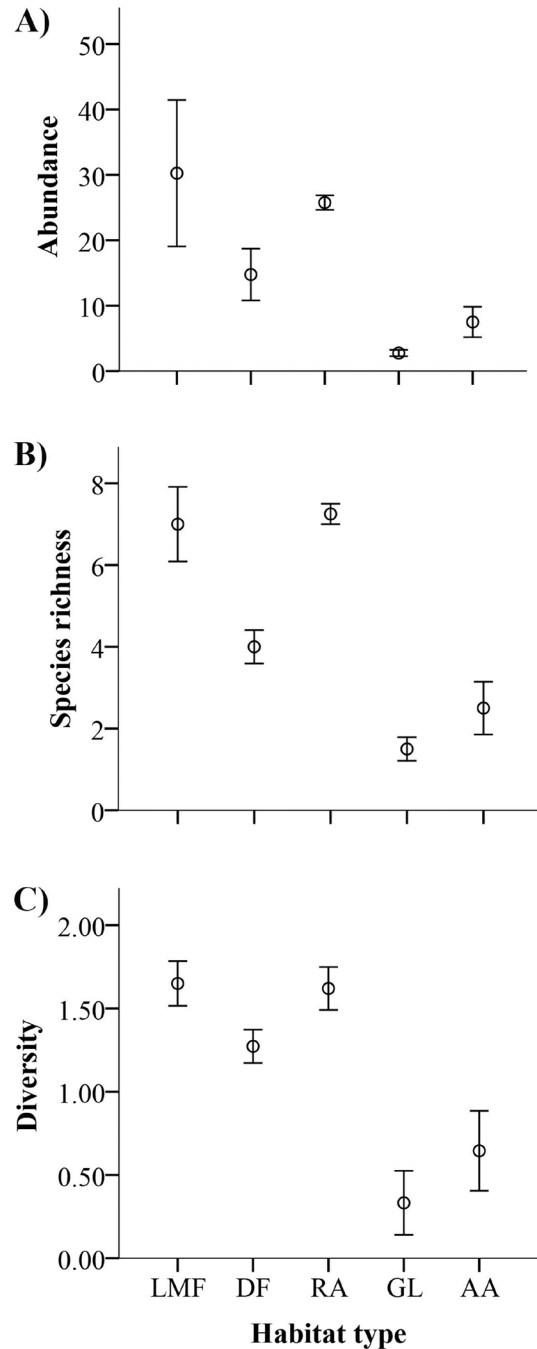
Family/Species	Species Code	Habitat type					Red List
		Lower mon-tane forests	Dipterocarp forests	Riparian areas	Grassland	Agricultural areas	
<b>Bufonidae</b>							
Cane Toad ( <i>Rhinella marina</i> )	Rm			3	6	17	LC
<b>Ceratobatrachidae</b>							
Philippine Wrinkled Ground Frog ( <i>Platymantis corrugatus</i> )	Pc	4	15	21			LC
Guenther’s Forest Frog ( <i>Platymantis guentheri</i> )	Pg	12	16	21			VU
Dumeril’s Wrinkled Ground Frog ( <i>Platymantis dorsalis</i> )	Pd	4		1			LC
<b>Dicroglossidae</b>							
Brackish Frog ( <i>Fejervarya moodiei</i> )	Fm	21	7	3		2	DD
Small Disked Frog ( <i>Limnonectes leytensis</i> )	Ll	4		5			LC
Giant Visayan Frog ( <i>Limnonectes visayanus</i> )	Lv	3		3		4	NT
Common Puddle Frog ( <i>Occidozyga laevis</i> )	Ol	2		8	2	4	LC
<b>Megophryidae</b>							
Mindanao Horned Frog ( <i>Megophrys stejnegeri</i> )	Ms	8		5			LC
<b>Microhylidae</b>							
Black-spotted Sticky Frog ( <i>Kalophrynus pleurostigma</i> )	Kp	9	10	2			LC
<b>Ranidae</b>							
Big-eyed Frog ( <i>Pulchrana grandocula</i> )	Pug	17		3			LC
Zamboanga Frog ( <i>Saguirana everetti</i> )	Se	12		2			NT
Black-spotted Rock Frog ( <i>Stauroids natator</i> )	Sn	7		2			LC
<b>Rhacophoridae</b>							
Frilled Tree Frog ( <i>Kurixalus appendiculatus</i> )	Ka	1		11			LC
<i>Philautus</i> sp.	Psp	1	3				DD
Common Tree Frog ( <i>Polypedates leucomystax</i> )	Pl	2	4	6	3		LC
Harlequin Tree Frog ( <i>Rhacophorus pardalis</i> )	Rp	5	4	5		2	LC
Mindanao Flying Frog ( <i>Rhacophorus bimaculatus</i> )	Rb	4		2			LC



**FIGURE 2.** The species accumulation curves display the species richness with the number of transects sampled among the five habitat types in Rajah Sikatuna Protected Landscape (RSPL) of Bohol Island, Philippines. Vertical dashed lines are confidence intervals. Habitat types are lower montane forests (red), dipterocarp forests (blue), riparian areas (green), grassland (yellow), and agricultural areas (brown).

lower montane forests and dipterocarp forests (Tukey’s HSD,  $P < 0.05$ ). Amphibian species richness differed significantly among habitats ( $F_{4,15} = 21.64$ ,  $P < 0.001$ ) and was significantly higher in lower montane forests and riparian areas than in grassland and agricultural areas (Tukey’s HSD,  $P < 0.05$ ; Fig. 3). Furthermore, species richness in dipterocarp forests did not differ significantly with agricultural areas (Tukey’s HSD,  $P > 0.05$ ) but was significantly higher than grassland (Tukey’s HSD,  $P < 0.05$ ). Lastly, amphibian diversity differed significantly among habitats ( $F_{4,15} = 12.56$ ,  $P < 0.001$ ) with montane forests, dipterocarp forests, and riparian areas having significantly higher diversity than the altered habitats, grassland, and agricultural areas (Tukey’s HSD, all  $P$ s  $< 0.05$ ; Fig. 3).

**Species composition.**—There was a clear differentiation in amphibian assemblages among habitat types as indicated by the absence of overlapping habitat polygons between less disturbed habitats (forests and riparian areas) and highly altered habitats (grassland and agricultural areas; Fig. 4). Amphibian species composition differed significantly among habitat types (ANOSIM  $R = 0.354$ ,  $P = 0.004$ ). Based on the NMDS ordination space, certain amphibian species were associated with specific habitat types (Fig. 4). For example, Black-spotted Sticky Frog (*Kalophrynus pleurostigma*), Philippine Wrinkled Ground Frog (*Platymantis corrugatus*), *Philautus* sp., and *P. guentheri* were associated with dipterocarp forests, whereas Harlequin Tree Frog (*Rhacophorus pardalis*), Mindanao Flying Frog (*Rhacophorus bimaculatus*), Brackish Frog (*Fejervarya moodiei*), Small Disked Frog (*Limnonectes leytenis*), Frilled Tree Frog (*Kurixalus appendiculatus*), Big-eyed Frog (*Pulchrana grandocula*), Mindanao



**FIGURE 3.** The (A) abundance (number of individuals recorded), (B) species richness, and (C) diversity (Shannon-Wiener) of amphibians among the different habitat types in Rajah Sikatuna Protected Landscape (RSPL) of Bohol Island, Philippines. Habitat types are lower montane forests (LMF), dipterocarp forests (DF), riparian areas (RA), grassland (GL), and agricultural areas (AA). Symbols represent the mean with standard error.

Horned Frog (*Megophrys stejneri*), Zamboanga Frog (*Saguirana everetti*), Black-spotted Rock Frog (*Staurois natator*), and Dumeril’s Wrinkled Ground



**TABLE 4.** Summary statistics for GAM analyses for abundance, species richness, and diversity relationships with selected environmental variables for amphibians in Rajah Sikatuna Protected Landscape (RSPL) of Bohol Island, Philippines. Abbreviations are standard error (SE), effective degrees of freedom (edf), and Chi-square (Chi sq).

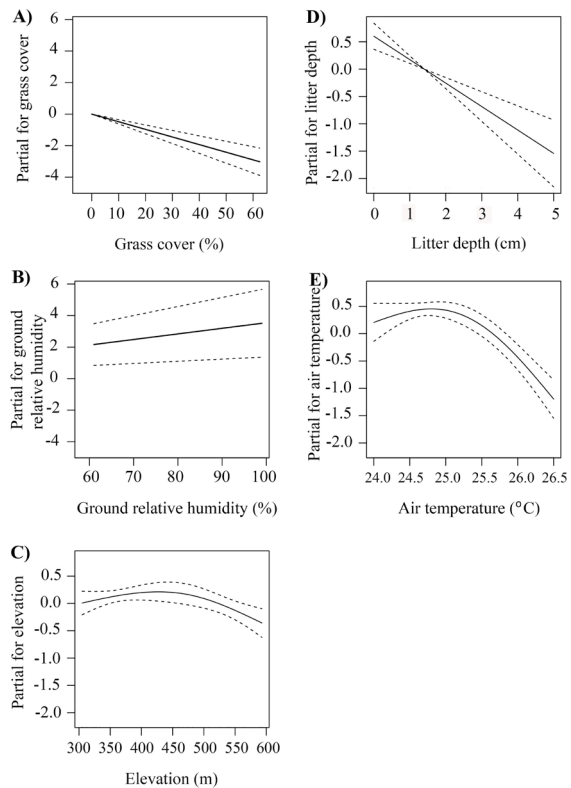
	Estimate	SE	Z	P-value
<b>Abundance</b>				
Parametric coefficients				
Intercept	0.110	0.889	0.124	0.901
Grass cover	-0.048	0.007	-6.974	< 0.001
Ground relative humidity	0.035	0.011	3.268	0.001
Smooth terms				
s(Elevation)	edf	df	Chi sq	P-value
s(Litter depth)	1.856	1.979	8.422	0.0115
s(Air temperature)	1.000	1.000	25.472	< 0.001
Adjusted R <sup>2</sup>	1.960	1.998	55.974	< 0.001
	0.632			
<b>Species richness</b>				
Parametric coefficients				
Intercept	-0.322	1.287	-0.250	0.803
Grass cover	-0.016	0.008	-1.952	0.051
Ground relative humidity	0.023	0.015	1.504	0.133
Smooth terms				
s(Air temperature)	edf	df	Chi sq	P-value
Adjusted R <sup>2</sup>	1.737	1.931	3.452	0.194
	0.678			
<b>Diversity</b>				
Parametric coefficients				
Intercept	Estimate	SE	t	P-value
Elevation	1.736	0.478	3.633	0.002
	-0.001	0.001	-1.343	0.198
Smooth terms				
s(Litter depth)	edf	df	F	P-value
Adjusted R <sup>2</sup>	1.946	1.997	13.66	< 0.001
	0.648			

**DISCUSSION**

Our study suggests that less disturbed habitats, particularly lower montane forests, and riparian areas, support species-rich and diverse amphibian assemblages. Such habitats harbor most of the forest or stream-dependent amphibian species documented in this study, mainly dominated by the vulnerable (VU) *P. guentheri*, and other least concern (LC) or data deficient (DD) species such as *P. corrugatus*, *F. moodiei*, and *P. grandocula* (IUCN 2022). These results can be explained by the presence of a variety of microhabitats and suitable environmental conditions, characterized by the presence of shade, microclimatic amelioration, higher moisture level, and organic matter, which are all essential to many amphibians (Bury and Corn 1991;

Naughton et al. 2000). In addition, less disturbed and structurally complex habitats support amphibian communities with a greater diversity of reproductive modes. For example, lotic and lentic bodies of water are used by amphibian species that lay eggs in water and have free-living aquatic larvae (Vallan 2002). Likewise, interior forest habitats are crucial to amphibians that breed by direct development (Delima et al. 2007). We commonly encountered the direct-developing *P. guentheri* and *P. corrugatus* in forest habitats in our study area. Conversely, altered habitats of grassland and agricultural areas had the lowest amphibian species richness and diversity. Anthropogenic habitat disturbances in the form of slash-and-burn, logging activities, and crop cultivation are detrimental, especially for sensitive amphibian species (Decena

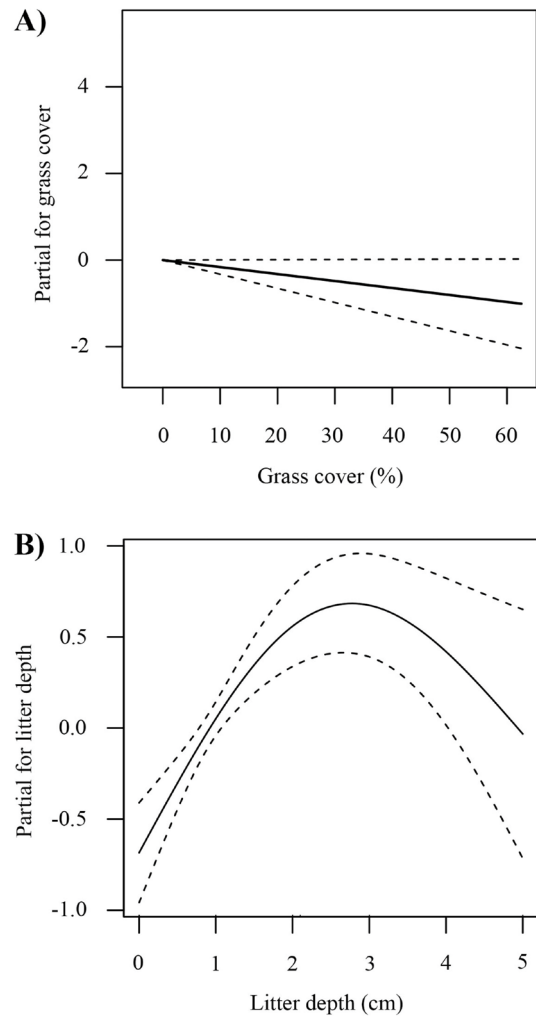




**FIGURE 5.** Partial effects of (A) grass cover, (B) ground relative humidity, (C) elevation, (D) litter depth, and (E) air temperature in GAM model for amphibian abundance in Rajah Sikatuna Protected Landscape (RSPL) of Bohol Island, Philippines. Dashed lines indicate the standard errors for each model term.

et al. 2020). According to Gonzalez and Dans (1997) and Mallari et al. (2013), the diversity of amphibians is inversely correlated with the degree of disturbance and human encroachment on the ecosystem.

Amphibian species composition differed markedly among habitat types. In general, less altered habitats (i.e., forests and riparian areas) were composed of stream-dependent species, whereas highly altered habitats (i.e., grassland and agricultural areas) were composed of open-habitat and disturbance-tolerant species. The clustering among the species on the NMDS axes could reflect variation in structural and habitat quality, for example, less disturbed habitats (forests and riparian areas) are characterized by a higher canopy cover, fern cover, litter depth, relative humidity, and soil pH, whereas altered habitats (grassland and agricultural areas) are characterized by higher grass cover, air temperature, and soil temperature. This observed pattern of species composition is consistent with the findings in some previous studies on tropical amphibians (Gillespie et al. 2012; Cruz-Elizalde et al. 2016; Decena et al. 2020, 2023). In our study area, the most notable and abundant amphibians in forests or riparian areas



**FIGURE 6.** Partial effects of (A) grass cover and (B) litter depth in GAM model for amphibian species richness and diversity, respectively, in Rajah Sikatuna Protected Landscape (RSPL) of Bohol Island, Philippines. Dashed lines indicate the standard errors for the model term.

were *P. corrugatus*, *P. guentheri*, and *P. grandocula*. These species are known to deposit their eggs or breed in microhabitats such as leaf litter or leaves and running water (IUCN 2022), which are typical characteristics of less disturbed habitats. In contrast, the dominant species in the grassland and agricultural areas was *R. marina*, a disturbance-tolerant and alien-invasive species (Diesmos et al. 2006). Similarly, Decena et al. (2020) observed *R. marina* thriving in highly disturbed habitats (pasture areas), though they have also documented the Common Green Frog (*Hylarana erythraea*), another abundant non-native species in the lowlands of Babatngon Range in Leyte Island. The presence of these amphibian species in highly transformed environments suggests a high tolerance to habitat alteration (Cruz-Elizalde et al. 2016).

Our study demonstrated that species composition is significantly influenced by variations in environmental variables, particularly habitat structure and microclimatic conditions. Most amphibian species documented in our study area were associated with more structurally complex habitats (i.e., forests and riparian areas), which is indicative of greater habitat quality. For example, a thick leaf-litter cover provides sufficient moisture levels and food resources for amphibians for foraging, courtship, and egg-laying (Welsh and Droege 2001). High canopy cover and density of woody plants provide an important habitat condition for rainforest-specialist amphibian species (Cortés-Gómez et al. 2013). Habitats with higher atmospheric humidity are home to amphibian species that spawn eggs outside of water bodies such as in leaves, litter, and on rock surfaces, as this prevents the desiccation of egg masses (Vallan 2002). In our study area, some of the amphibians that exhibit such reproductive modes include *L. leytensis*, *R. bimaculatus*, *R. pardalis*, and *P. corrugatus* (Brown et al. 2013; IUCN 2022). Moreover, our study shows that lower soil acidity is associated with the occurrence of amphibians, particularly ground-dwelling species (e.g., *P. corrugatus*, *K. pleurostigma*). In contrast, highly altered habitats (grassland and pasture) were characterized by higher soil temperature and grass cover, which can be directly associated with the loss of structural complexity (e.g., trees and canopy cover; Vallan 2002). These habitat conditions favored the dominance of disturbance-tolerant species including *R. marina* as well as *O. laevis* and *L. visayanus* (Sanguila et al. 2016; IUCN 2022).

Changes in ground habitat structure (e.g., grass cover and litter depth) influence the abundance and diversity of amphibians (Urbina-Cardona et al. 2006; Hillers et al. 2008; Suazo-Ortuño et al. 2008). In our study, increasing grass cover was associated with lower amphibian abundance and species richness, indicating that habitat alteration characterized by the establishment of grasses is unable to support a diverse amphibian community. This trend was likewise observed in the study of Urbina-Cardona et al. (2006) wherein amphibian species richness, particularly of forest species, was negatively correlated with grass cover. As expected, most amphibians sampled in our study area were forest or stream-dependent species, and grass-dominated habitats were associated primarily with *R. marina*, which is a disturbance-tolerant and invasive alien species (Diesmos et al. 2006; Cortés-Gómez et al. 2013; Sanguila et al. 2016). Moreover, although amphibian abundance declined with increasing litter depth, diversity peaked with intermediate or thicker litter depth. Previous investigations have shown the relative importance of litter to the maintenance of tropical amphibian diversity as it provides suitable habitat conditions for many

species (Urbina-Cardona et al. 2006; Cortés-Gómez et al. 2013). Specifically, litter can function as a buffer that stabilizes microhabitat conditions (Hillers et al. 2008) by substantially contributing to a higher humidity (Urbina-Cardona et al. 2006).

The loss in habitat structural complexity of an ecosystem through habitat degradation results in an undesirable change in microclimatic conditions (Vallan 2002). We showed that amphibian abundance declines with increasing temperature, while it increased with increasing ground relative humidity. In general, habitat alteration in our study area was characterized by increased temperature and decreased relative humidity, which negatively affected amphibian communities, in line with the results of previous studies (Vallan 2002; Urbina-Cardona et al. 2006; Decena et al. 2020). In particular, open and degraded habitats with higher temperatures are typically inhospitable to amphibians (Cruz-Elizalde et al. 2016) mainly because of the high risk of dehydration (Rothermel and Semlitsch 2002). In addition, higher temperatures and increased evaporation enhanced by the loss in canopy cover may reduce pond persistence (Hillers et al. 2008), eventually affecting the reproduction of pond-breeding populations of amphibians. Likewise, decreasing relative humidity adversely affects amphibian communities, especially those that do not spawn in running waters or ponds (Donnelly and Crump 1998). Eggs deposited on litter, leaves, and rocks would be more likely to dry out if atmospheric humidity decreases (Vallan 2002). Therefore, there is a need to protect the remaining primary habitats and restore degraded ones to enhance microclimatic conditions that would favor the maintenance of diverse amphibian communities in the study area.

Lastly, elevation appeared to be a determinant of amphibian abundance, which decreased at higher elevations, a similar pattern that was also observed by Carvalho-Rocha et al. (2021) for other tropical amphibians. Lower amphibian abundance in higher elevations is likely due to increasing environmental constraints (Körner 2007), and especially a reduction of microhabitat diversity (Khatiwada et al. 2019). The absence of permanent aquatic microhabitats (e.g., lentic and lotic water bodies) at higher elevations limits the reproduction of many amphibian species (Nuñez et al. 2010).

The results of our study showed that amphibian assemblages in RSPL, Bohol, differ across habitats representing a gradient of habitat alteration. The less disturbed habitats, i.e., montane forests and riparian areas, generally had greater amphibian abundance, species richness, and diversity in comparison to the highly disturbed habitats, i.e., grassland and agriculture. Therefore, the occurrence and diversity of amphibians

in those less disturbed habitats can be the basis for monitoring and prioritizing protection. Furthermore, our results indicate that good habitat quality is mainly characterized by lower temperatures, higher relative humidity, and less grass cover. Management and restoration actions should aim to improve these environmental characteristics to promote the persistence and diversity of amphibian communities in RSPL.

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## Herpetological Conservation and Biology

**APPENDIX.** Environmental variables measured along the 100-m long  $\times$  20-m wide strip transects in Rajah Sikatuna Protected Landscape (RSPL) of Bohol Island, Philippines, in five habitat types. Variables are canopy cover (CC), grass cover (GC), fern cover (FC), elevation (E), litter depth (LD), air temperature (AT), air relative humidity (ARH), ground relative humidity (GRH), soil pH (SpH), and soil temperature (ST). Values are mean  $\pm$  standard error, and n = 20.

Habitat Type	Environmental Variable									
	CC (%)	GC (%)	FC (%)	E (m)	LD (cm)	AT ( $^{\circ}$ C)	ARH (%)	GRH (%)	SpH	ST ( $^{\circ}$ C)
Lower Montane Forest	94.00 $\pm$ 2.04	0.00 $\pm$ 0.00	0.58 $\pm$ 0.23	424.00 $\pm$ 57.87	1.75 $\pm$ 0.48	25.00 $\pm$ 0.00	79.50 $\pm$ 1.50	84.00 $\pm$ 0.00	6.30 $\pm$ 0.00	24.00 $\pm$ 0.00
Dipterocarp Forest	94.75 $\pm$ 1.25	0.00 $\pm$ 0.00	1.05 $\pm$ 0.42	528.50 $\pm$ 7.82	3.25 $\pm$ 0.63	24.25 $\pm$ 0.14	80.00 $\pm$ 0.00	83.00 $\pm$ 2.00	6.75 $\pm$ 0.03	25.00 $\pm$ 0.00
Riparian Areas	87.00 $\pm$ 3.76	0.00 $\pm$ 0.00	5.08 $\pm$ 2.08	532.50 $\pm$ 33.94	2.03 $\pm$ 0.03	25.25 $\pm$ 0.25	85.25 $\pm$ 3.90	91.25 $\pm$ 4.19	6.10 $\pm$ 0.07	22.75 $\pm$ 0.25
Grassland	0.00 $\pm$ 0.00	51.25 $\pm$ 7.40	0.00 $\pm$ 0.00	351.25 $\pm$ 36.32	0.00 $\pm$ 0.00	24.50 $\pm$ 0.35	76.00 $\pm$ 1.35	69.75 $\pm$ 6.13	5.40 $\pm$ 0.04	28.75 $\pm$ 0.95
Agricultural Areas	0.00 $\pm$ 0.00	2.50 $\pm$ 2.50	0.00 $\pm$ 0.00	312.25 $\pm$ 5.36	0.00 $\pm$ 0.00	26.50 $\pm$ 0.00	74.00 $\pm$ 0.00	74.50 $\pm$ 0.29	5.90 $\pm$ 0.00	26.00 $\pm$ 0.00