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Source: *Herpetologica*, 70(1):34-46. 2014.

Published By: The Herpetologists' League

DOI: <http://dx.doi.org/10.1655/HERPETOLOGICA-D-12-00068>

URL: <http://www.bioone.org/doi/full/10.1655/HERPETOLOGICA-D-12-00068>

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AMPHIBIAN DIVERSITY AND SPECIES COMPOSITION IN RELATION TO HABITAT TYPE AND ALTERATION IN THE MACHE–CHINDUL RESERVE, NORTHWEST ECUADOR

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ABSTRACT: Amphibians are facing extinctions worldwide as a result of numerous factors. Habitat alteration has long been implicated in the loss of biodiversity; however, we still do not know how different animal assemblages respond to habitat alteration. To investigate the impacts of anthropogenic habitat alteration on diversity, we studied amphibian assemblages across different habitats in the Chocó rainforest of northwest Ecuador. Amphibian diversity was estimated using intensive surveys along transects in primary and altered (historically logged) forest and riparian habitats, as well as along roads with varying levels of ongoing human activity. Our results suggest an interaction between habitat type and alteration on the diversity and composition of amphibian assemblages. Amphibian assemblages along rivers were the richest as well as the least impacted by habitat alteration. In addition, riparian zones harbored amphibian assemblages distinct from other habitat types, including rare and endangered species. Diversity and species richness were lower in secondary than in primary forest, suggesting that amphibian assemblages in interior forest habitat may be more vulnerable to alterations caused by logging. These findings suggest that amphibian assemblages in different habitat types (i.e., riparian vs. interior forest) may vary in vulnerability to habitat alteration. We discuss these findings in relation to land management plans that promote amphibian diversity in northwest Ecuador and recognize a good potential indicator species, *Oophaga sylvatica*, for identifying pristine habitat.

Key words: Active search; Amphibians; Disturbance; Indicator species; Logging; Primary forest; Secondary forest

OF THE 7000 known species of amphibians, approximately one-third are listed as threatened and at least 43% are in decline (Gascon et al., 2007). Along with the adverse effects of invasive species (Dukes and Mooney, 2004), disease (Cheng et al., 2011), and climate change (Beebee, 1995), habitat alteration has been proposed as an important factor in these declines (Stuart et al., 2004; Wake and Vredenburg, 2008). In the tropics, where amphibian diversity reaches its highest levels, empirical studies have reported mixed results concerning the impact of habitat alteration on amphibian species. A number of studies have demonstrated that habitat alteration causes a decrease in amphibian diversity in tropical forests (Pearman, 1997; Steininger et al., 2001; Krishnamurthy, 2003; Hamer and McDonnell, 2008). For example, Krishnamurthy (2003) reported that more than 50% of the amphibian species encountered during his

study in the Western Ghats, India, were found exclusively in primary forests. Pearman (1997), investigating habitat disturbance in Amazonian Ecuador, found less striking results but still demonstrated that amphibian richness increased with distance from altered habitat such as pasture.

Conversely, other studies have found that habitat alteration may sometimes promote amphibian diversity (Toral et al., 2002; Urbina-Cardona et al., 2006), usually along forest edges. Urbina-Cardona et al. (2006) found amphibian species richness to be highest at the forest–pasture edge habitat, which may be explained by the intermediate-disturbance hypothesis (Connell, 1978). Toral et al. (2002) found that species composition of amphibian assemblages changed markedly at the pasture–forest edge but that richness was comparable in pasture and forest. A similar pattern has been described in the Atlantic forest of Brazil, where species historically restricted to savannah habitats have been able to colonize deforested areas (Haddad and

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Prado, 2005; Vasconcelos et al., 2010); although the overall effect may be an increase in species associated with habitat alteration, the invading species are often generalist species that replace species with highly specialized life histories and more restricted ranges (Haddad and Prado, 2005). It appears that the effects of habitat alteration on amphibians depend on the nature of the disturbance, the microhabitats that are disturbed, and the metric used to assess changes in amphibian communities (e.g., richness vs. species composition). As such, a more refined understanding of the relationship between anthropogenic habitat alteration and amphibian diversity based on more case studies would be useful for management and conservation of this group.

In addition to anthropogenic alteration, naturally occurring habitat features are also likely to influence amphibian diversity. For example, riparian habitat and interior forest habitat are both crucial for amphibian species at different stages in their life cycle (Olson et al., 2007). Species differ in the extent to which they utilize riparian and terrestrial habitats (Semlitsch and Bodie, 2003; Olson et al., 2007). For example, although frogs of the genus *Pristimantis* lay their eggs in terrestrial habitats (Hedges et al., 2008), all centrolenid frogs (Savage, 2002) and many hylid frogs require streams for reproduction (Cogger and Zweifel, 1998), and most species are dependent on aquatic environments for at least part of their life cycle (Zimmermann and Simberloff, 1996; Hofer et al., 2000). As a result, amphibian diversity and abundance is often highest in riparian areas; various studies have found overall amphibian species richness to be negatively correlated with distance from streams (Dickman, 1987; Perkins and Hunter, 2006; Urbina-Cardona et al., 2006). However, the relative impact of habitat type (e.g., riparian, interior forest, or road edge) and habitat alteration (e.g., primary vs. secondary habitat) and any interactions between these factors on amphibian diversity remains poorly understood.

South America's Chocó biogeographic zone is a biodiversity hotspot consisting of humid rainforest that combines exceptionally high levels of diversity, endemism, and threats for

many taxa, including amphibians (Dinerstein et al., 1995). Chocó habitat, which extends north from northwest Ecuador along the Pacific coast of Colombia and into southwest Panamá, has experienced significant anthropogenic alteration in recent decades, mainly via forest clearing for agriculture (Dodson and Gentry, 1991; Sierra, 1996; Sierra et al., 2002). Despite the global importance of the Chocó for amphibian conservation, information on the effects of habitat alteration on amphibian diversity is lacking for the region. For example, at the Bilsa Biological Station in northwestern Ecuador, one of the last large remnants of premontane forest in the Ecuadorian Chocó and the site of a recent inventory reporting 37 amphibian species (Ortega-Andrade et al., 2010), the distribution of species in relation to habitat type and/or the effect of habitat alteration on species richness and composition has not been examined.

Our goals in the current study were as follows: (1) to assess how amphibian richness, diversity, and species composition vary across three habitat types: interior forest, riparian zones, and road edge; (2) to determine how amphibians respond to habitat alteration (e.g., primary vs. secondary forest types) in these different habitat types; and (3) to identify indicator species for each of the three habitat types. In doing so, we build upon earlier inventory work by Ortega-Andrade et al. (2010) to characterize the habitat associations of amphibian species in Bilsa Biological Station and the Ecuadorian Chocó. Our a priori hypotheses, based upon findings of similar studies in other areas, were that riparian habitats would have higher richness and diversity than terrestrial habitats, and that alteration would be associated with reduced richness and diversity in all habitat types.

MATERIALS AND METHODS

Fieldwork was conducted in Bilsa Biological Station (hereafter BBS; 0°22'N, 79°45'W; datum = WGS84) a 3500-ha private reserve operated by Fundación Jatun Sacha and located within the 70,000-ha Mache-Chindul Ecological Reserve in Esmeraldas Province, Ecuador (Fig. 1). BBS receives on average 2000–3000 mm of rain per year and average monthly temperatures range from 21 to 24°C

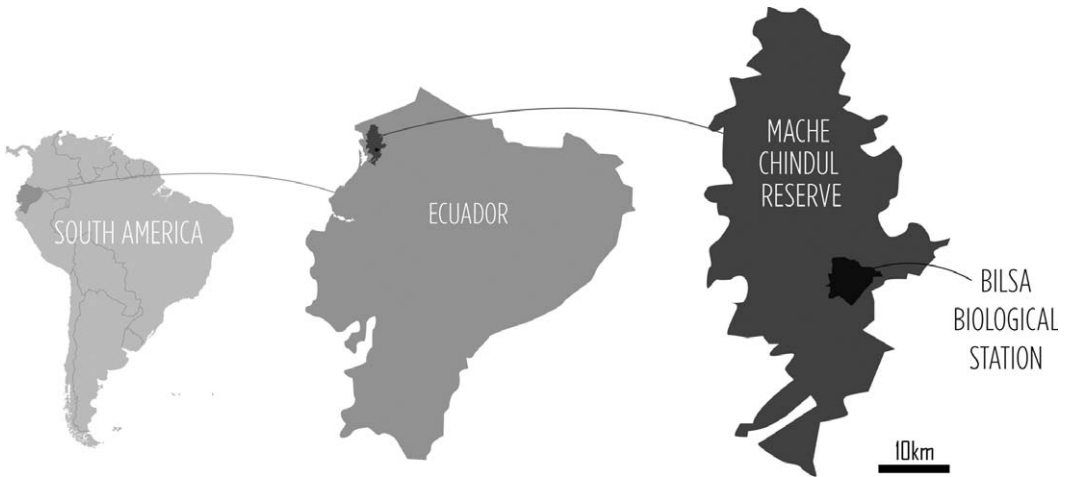


FIG. 1.—Location of Bilsa Biological Station within Mache–Chindul Reserve in Esmeraldas Province, northwest Ecuador.

(Charlat et al., 2000). The dry season begins in July and ends in December, and the wet season extends from January to June (Ortega-Andrade et al., 2010). Elevations range from 300 to 730 m above sea level, including both Humid Premontane and Humid Tropical forest life zones (Holdridge, 1967). BBS is approximately two-thirds primary forest (never logged) and one-third secondary forest that was cleared 20–30 yr ago and has been regenerating since then. Pristine forest is characterized by flora in the families Rubiaceae, Myristicaceae, Lauraceae, and Araceae; secondary forest is characterized by Melastomataceae, Rubiaceae, and Cecropiaceae (Karubian and Carrasco, 2008; JK, personal observation). All forest types included in this study are contiguous. The surrounding area contains patches of primary, selectively logged, and secondary forests interspersed among areas used for cacao cultivation, grazing livestock, and other agricultural purposes.

Sampling occurred from March to November 2007, corresponding to the last 4 mo of the rainy season and a transitional period that marks the onset of the dry season. We sampled three habitat types (riparian, interior forest, and road edge) with two or three levels of habitat alteration per habitat type (see below), for a total of seven categories of habitat sampled (Table 1). Sampling of each

habitat category was evenly distributed across each month of the study period. Riparian transect sites were established in both primary and secondary forests along the banks of streams with year-round water flow. Pairs of interior forest transects in both primary and secondary forests ran perpendicular and parallel to walking trails at randomly selected points along these trails; perpendicular transects began 5 m into the forest from the trail and the parallel transects began 5 m past the end of the perpendicular one, forming an L-shape. Habitat alteration in interior forest or forest adjacent to rivers (riparian habitat) was scored as primary and secondary based on known land use history of the site. Road-edge habitat consisted of a grassy margin approximately 2 m wide running parallel to a dirt road. The margin was maintained by cutting grass and shrubs with a machete annually; the dirt road was inaccessible by vehicles ~10 mo/yr due to muddy conditions (there was no vehicular traffic during our study), and received on average 15 humans and 10 mules walking by per day and almost no foot traffic by night (JK, personal observation). We recognized three categories of habitat alteration in road-edge habitats: (1) dirt road bordered by secondary forest on both sides, the least altered; (2) dirt road with secondary forest on one side and pasture land on the other, being intermediately altered; and (3)

TABLE 1.—Number of individual amphibians recorded in seven habitat categories in Bilsa Biological Station, northwest Ecuador; 1° = primary habitat; 2° = secondary habitat; for road-edge habitats, pasture = edge formed by road bordered by pasture on both sides, 2° = road bordered by secondary forest on both sides, mix = road bordered by pasture on one side and secondary forest on the other side (with sampling conducted on the forest side). The last two columns highlight species significantly associated with a type of habitat (forest, river, or road edge) according to an indicator species analysis. Observed indicator values (IV, in %) indicate the strength of association with that habitat, with significance levels. Conservation status categories: EN = Endangered, V = Vulnerable, NT = Near-threatened, according to International Union for the Conservation of Nature (IUCN, 2011).

Family	Species	Total	Forest		River		Road Edge			Indicator Species	
			1°	2°	1°	2°	Pasture	2°	Mix	Habitat	IV
Bufonidae	<i>Rhaebo haematiticus</i>	31	0	0	19	12	0	0	0	River	11.4°
	<i>Rhinella margaritifera</i>	37	0	0	9	28	0	0	0	River	11.4°
	<i>Rhinella marina</i>	1	0	0	0	0	0	1	0		
Caeciliidae	<i>Caecilia leucocephala</i>	1	0	0	1	0	0	0	0		
	<i>Caecilia nigricans</i>	1	0	0	0	0	1	0	0		
Centrolenidae	<i>Centrolene prosoblepon</i>	37	0	0	23	14	0	0	0	River	30.0°°
	<i>Cochranella mache</i> (EN)	2	0	0	2	0	0	0	0		
	<i>Sachatamia cf. albomaculata</i>	4	0	0	2	2	0	0	0		
	<i>Teratohyla spinosa</i>	1	0	0	1	0	0	0	0		
Craugastoridae	<i>Craugastor longirostris</i>	8	1	2	2	2	1	0	0		
Dentrobatidae	<i>Colostethus</i> sp. nov.	45	3	0	21	21	0	0	0	River	22.5°°
	<i>Epipedobates boulengeri</i>	27	1	0	16	10	0	0	0	River	24.7°°
	<i>Hyloxalus awa</i> (V)	114	0	0	79	35	0	0	0	River	72.9°°
	<i>Oophaga sylvatica</i> (NT)	20	18	0	1	1	0	0	0	Forest	12.8°°
Hylidae	<i>Hypsiboas pellucens</i>	1	0	0	0	0	1	0	0		
	<i>Hypsiboas picturatus</i>	48	0	0	18	30	0	0	0	River	27.1°°
	<i>Smilisca phaeota</i>	7	0	0	0	0	1	3	3	Road	10.6°
Leptodactylidae	<i>Leptodactylus labrosus</i>	1	1	0	0	0	0	0	0		
	<i>Leptodactylus rhodomerus</i>	2	0	0	0	0	1	1	0		
Plethodonidae	<i>Bolitoglossa</i> spp.	1	0	0	0	1	0	0	0		
Strabomantidae	<i>Pristimantis achatinus</i>	535	50	97	45	39	91	114	99	Road	52.5°°
	<i>Pristimantis parvillus</i>	3	1	2	0	0	0	0	0		
	<i>Pristimantis subsigillatus</i>	2	0	0	0	0	1	0	1		
	<i>Pristimantis walkeri</i>	4	0	3	0	0	0	0	1		
	Total	933	75	104	239	195	97	119	104		

° $P \leq 0.05$.
 °° $P \leq 0.01$.

dirt road with pasture on both sides, the most altered of the road-edge categories.

In total, we established 67 unique transects: 23 in riparian habitat, 28 in interior forest habitat, and 16 in road-edge habitat. Of the riparian transects, 12 were located in primary habitat and 11 in secondary habitat. The interior forest transects consisted of 14 transects in primary and 14 in secondary forests. The road transects consisted of five transects surrounded by pasture on both sides, five with secondary forest on one side and pasture on the other, and six with secondary forest on both sides. We sampled each of these 67 transects with one round of morning and evening sampling sessions, and 23 of these transects received a second round of morning and evening sampling sessions 2 to 3

mo apart from one another. In total, 180 sampling events along transects took place.

Sampling was conducted by GJ and RH using the active search method along transects (Heyer et al., 1994), which involved walking slowly along transects while intensively searching for amphibians on all available substrates <3.5 m in height. The 3.5 m cut-off represents a restriction in the surveyors' ability to detect individuals and not a true cut-off for amphibian presence. We can expect more individuals and quite possibly canopy specialists persisted above 3.5 m and recognize that they will have gone undetected during this study. Transect dimensions were 2 × 50 m (width × length; width sometimes varied for brief portions of riparian and road-edge transects but averaged 2 m). Transects were established and marked with flagging

tape at least 2 wk prior to sampling to avoid any effects of disturbance. Each transect was sampled twice on the same day: first in the morning from 0900 to 1100 h and then again at night from 2100 to 2300 h. All amphibians encountered during morning sampling sessions were captured and temporarily held until after the night sampling session was complete to avoid resampling the same individual twice on the same day. Species and substrate were recorded for each individual sampled. Sampled individuals were measured and photographed for subsequent identification with the assistance of experts of the local herpetofauna, before being released unharmed at the point of capture. Collecting specimens is not permitted at BBS.

To determine whether habitat structure may correlate with observed patterns of amphibian richness and diversity, we measured understory density (USD) in riparian and interior forest types. We estimated USD every 10 m along the 50-m transects, for a total of six measurements per transect. At each 10-m increment on forest transects, we placed a straight 2-m-long pole vertically in the center of the transect, and counted the number of leaves touching the pole. We did the same along riparian transects, but we placed the pole at the edge of the river and on the edge of the bank where the forest vegetation began. We averaged values for the six measurements per transect, giving an index of USD for a given transect. We obtained one value for each forest transect and two different values for riparian transects—USD at the water's edge, and USD at the bank edge.

Expected species accumulation curves (e.g., sample-based rarefaction curves), which allow for comparison of richness levels while controlling for different sample sizes, were computed independently for each habitat type using the analytical formulas of Colwell et al. (2004). As an estimation of the total number of species present in each habitat type (i.e., estimated richness), we report mean and range of four commonly employed abundance-based real richness estimators (Abundance-based Coverage Estimator, Chao1, Jack1, and Bootstrap), based on 1000 randomizations of samples without replacement.

Two diversity indices were calculated: Shannon–Wiener's and Simpson's indices (Krebs, 1999). Both of these indices treat diversity as a function of both species richness and evenness, with the Shannon–Wiener index placing more weight on rare species and Simpson's index placing less weight on rare species. Analyses described above were conducted using EstimateS v.8 (Colwell, 2006).

To assess the relative importance of habitat type (forest or riparian) vs. habitat alteration (primary or secondary), as well as their interaction on amphibian communities, we employed a general linear mixed model using residual maximum likelihood (Patterson and Thompson, 1971) in JMP v.9 (SAS Institute, 1989–2007) to test for effects on number of species observed. Road edge was not included in this analysis because the habitat alteration classification for road edge followed a different scheme than for forest and riparian habitats (i.e., three categories instead of two). Transect identification number was included as a random effect in this model to account for the fact that each transect was sampled twice (i.e., morning and evening), and in some cases more often (e.g., sampling a subset of the same transects twice, as described above).

We evaluated similarity in amphibian species composition among habitats with a detrended correspondence analysis (DCA; Hill and Gauch, 1980), in which habitat categories were ordinated according to the relative frequency of each species; down-weighting the importance of rare species did not affect qualitative results. We conducted an indicator species analysis (Dufrêne and Legendre, 1997; McCune and Mefford, 1999), in which information on both the presence and abundance of species were combined to identify species especially associated with riparian, interior forest, or road-edge habitats. The analysis produces indicator values that range from 0 (no indication) to 100 (perfect indication). Perfect indication means that presence of a species points to a particular habitat without error, based on available data. Significance of these associations was established using a Monte Carlo technique, with 1000 randomizations. DCA and indicator species analyses were conducted

in PC-Ord Version 4.41 (McCune and Meford, 1999).

RESULTS

We recorded 933 individuals representing 24 species, 17 genera, and 9 families (Table 1) during our sampling work at BBS. *Pristimantis achatinus* was by far the most abundant species, comprising more than half of the total of the individual encounters. In contrast, over half the species ($n = 13$) were represented by less than five individuals, and seven species were represented by a single individual (Table 1). The single encounter of *Teratohyla spinosa* represents a new record for the BBS.

We found no difference in USD between primary and secondary riparian habitats ($t_{68} = 0.032$, $P = 0.98$). In contrast, in interior forest habitats USD was significantly lower in primary forest than in secondary forest ($t_{52} = 5.37$, $P < 0.0001$).

Both rarefied and estimated richness values indicate that pristine and secondary river habitats, primary forest, and road edges formed by roads flanked by pasture present more species than secondary forest, roads flanked by secondary forest, or a mixture of secondary forest and pasture (Fig. 2A; Table 2A). Primary and secondary riparian habitat presented the highest values of species diversity, followed by primary forest, whereas secondary forest and road-edge habitats were the least diverse (Table 2A).

Similar results were obtained when the seven habitat categories were collapsed into three (riparian, forest, and road edge). Sample-based rarefaction indicated that riparian habitat had higher richness than interior forests and road-edge habitats at comparable sample sizes (Fig. 2B). Riparian habitat also had the highest estimated richness values, but road edges had higher values than did interior forest habitats (Table 2B). Diversity indices were highest for riparian habitat, followed by forests and then road edge.

The mixed model assessing relative importance of habitat type (in this case, river vs. forest) and habitat alteration (primary vs. secondary habitat) on observed number of species indicates that rivers had higher numbers of species, regardless of whether they occurred in primary or secondary habitat.

Habitat alteration or the interaction between habitat alteration and habitat type did not affect observed richness (Table 3).

A DCA shows that amphibian communities on rivers segregate from those in all other habitat types along a first axis explaining 79% of the variance in community composition (Fig. 3). A second axis, explaining an additional 4% of the variance, separates primary river communities from those in other habitats.

The uniqueness of river communities was also reflected by the fact that river habitats presented the highest number of indicator species ($n = 7$; Table 1). In contrast, forests had only one indicator species and road edge had two, including *P. achatinus*, which was present in all three habitat types but was especially common in road-edge habitat (Table 1). Four species were encountered only at pristine sites (i.e., primary rivers or forests: *Cochranella mache*, *T. spinosa*, *Caecilia leucocephala*, and *Leptodactylus labrosus*) whereas six species (*Smilisca phaeota*, *Pristimantis subsigillatus*, *L. rhodomerus*, *Caecilia nigricans*, *Hypsiboas pellucens*, *Rhinella marina*) were found only along road edges, but only *S. phaeota* was common enough to be considered an indicator species of road-edge habitats. We sampled three species of conservation concern: *Cochranella mache* (Endangered) was restricted to primary river habitat, *Hyloxalus awa* (Vulnerable) was restricted to river habitats, and *Oophaga sylvatica* (Near-threatened) was restricted to primary forest and river habitats.

DISCUSSION

Amphibian assemblages in BBS exhibited complex patterns in response to habitat disturbances depending on the habitat type (forest, riparian, road edge) under consideration. Assemblages in river habitats were more resilient to habitat alteration than were interior forest assemblages. The high diversity found along rivers and the vulnerability of interior forests suggests that riparian zones and primary forests in the Mache-Chindul Mountains should be made a priority for amphibian conservation.

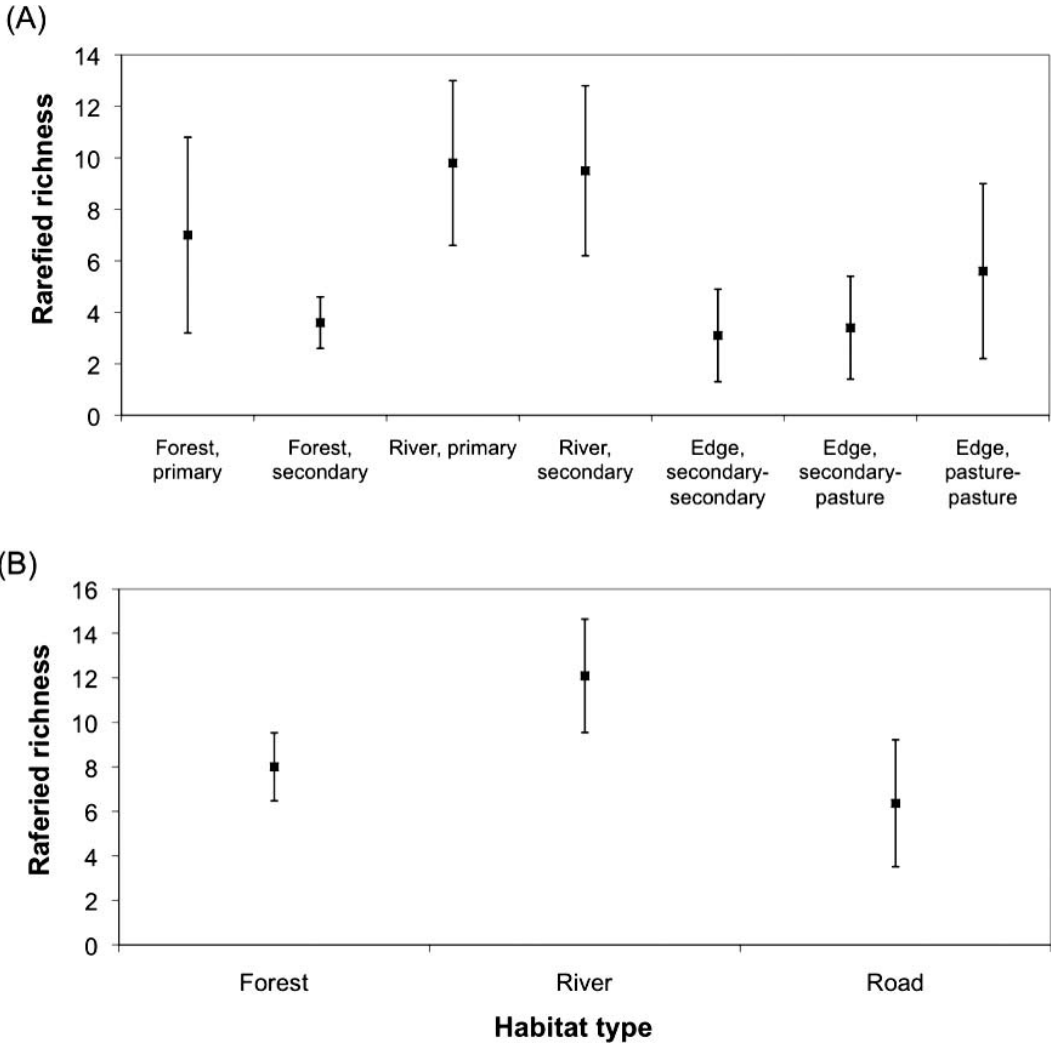


FIG. 2.—Rarefied richness (mean and 95% confidence interval) for amphibians captured in different habitat categories in Bilsa Biological Station, northwest Ecuador. Richness was compared across habitat types assuming the minimum sample of (A) 75 individuals, with seven habitat categories, or (B) 179 individuals, with habitat types combined into three categories.

Amphibian Assemblages in Forests and Along Rivers

Amphibian richness and diversity (as measured by the Shannon–Wiener and Simpson indices) were more dependent on habitat type (riparian vs. interior forest) than on habitat alteration (primary vs. secondary), with rivers presenting higher richness and diversity than interior forest. Both diversity and richness were similar between primary and secondary river sites; however, primary interior forest

was more species-rich and diverse than secondary interior forest. Rivers house higher species diversity and abundance than other habitat types, likely because they provide breeding habitat in an area that otherwise contains little standing water. Indeed, six of seven of the species identified as indicators of river habitat utilize streams for at least part of their life cycle (Savage, 2002; IUCN, 2011); the remaining species, *Colostethus* sp. nov. likely does the same, but no information has

TABLE 2.—Observed and estimated species richness (average and range of ACE, Chao1, Jack1, and Bootstrap indices), Shannon–Wiener and Simpson’s diversity indices, and total of individuals recorded for (A) each of the seven habitat categories and (B) for habitat types combined into three broad categories of amphibians in Bilsa Biological Station, northwest Ecuador.

	Richness		Diversity		Total individuals	Sampling sessions
	Observed	Estimated	Shannon–Wiener	Simpson		
(A)						
Forest						
Primary	7	13.1 (8.6–19.9)	0.9	2.0	75	16
Secondary	4	4.4 (4.0–5.0)	0.3	1.2	104	16
River						
Primary	14	17.2 (15.5–19.5)	2.0	5.7	239	18
Secondary	12	14.2 (13.0–15.5)	2.1	7.4	195	17
Road edge						
Pasture	7	16.4 (9.1–22.0)	0.3	1.1	97	8
Secondary	4	5.8 (4.8–7.7)	0.2	1.1	119	8
Mix	4	5.8 (4.8–7.7)	0.2	1.1	104	7
(B)						
Forest	8	9.3 (9.0–10.0)	0.79	1.46	179	32
River	15	17.3 (16.5–18.0)	2.09	6.69	434	35
Road edge	9	15.5 (11.1–21.6)	0.29	1.11	320	23

been published on its reproductive biology. *Rhaebo haematiticus*, *Rhinella margaritifera*, *Hypsiboas picturatus*, *Hyloxalus awa*, and *Centrolene prosoblepon* were found exclusively in river habitats, where their tadpoles develop; their distribution within BBS appears highly constrained by their reproductive requirements. Of the other two river indicators—*Epipedobates boulengeri* and *Colostethus* sp. nov.—the former is known to lay its eggs in leaf litter before transporting the tadpoles to streams to complete their development (IUCN, 2011). Our observations of the latter species suggest a similar life history. The two species were located only one and three times, respectively, away from river habitats, so although they may utilize terrestrial habitats for part of their breeding cycle, they still appear to be restricted in their distribution as a result of their reproductive ecology. The reproductive requirements of these seven indicator species account for the elevated richness and unique species composition found in river habitats.

The similar amphibian diversity and richness along primary and secondary river habitats may potentially be explained by regular disturbances along river banks caused by rising water levels during the wet season. This natural disturbance may result in a similar habitat structure along rivers in both primary and secondary forest, as represented

in the similar understory vegetation density in both habitat qualities. Real et al. (1993) explained the high amphibian diversity associated with flooded rivers on the basis of the intermediate disturbance hypothesis, which predicts that diversity will peak at intermediate levels. Diversity is predicted to be lower with no disturbance or very high disturbance due to competitive exclusion and local extinction respectively (Connell, 1978). However, in BBS the mountainous terrain and near absence of other water sources needed for reproduction is also likely to contribute to the high abundance and diversity of amphibians along rivers. Large pools of still water such as ponds, lakes, and terminal basins are absent from BBS; mountain streams with intermittent small pools provide the only suitable breeding habitat for a number of amphibian species. Puddles forming on the

TABLE 3.—Effect tests from a general linear mixed model with habitat type (river or forest), habitat disturbance (primary or secondary), and an interaction term as predictor variables, number of observed species as the response variable, and transect identity as a random effect.

	F (df)	P value
Habitat type	5.50 (1, 8.99)	<0.0001
Habitat disturbance	1.35 (1, 29.6)	0.187
Interaction	–0.18 (1, 29.6)	0.857

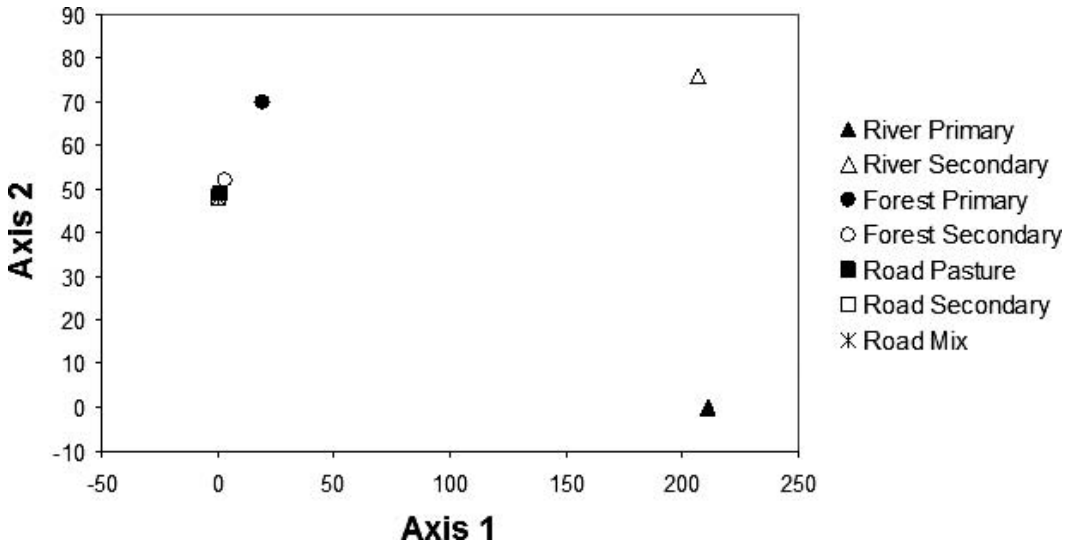


FIG. 3.—Detrended correspondence analysis ordination of seven habitat categories in Bilsa Biological Station, Ecuador, based on number of individual amphibians detected per species. The first two axes explained 83% of the variance in community composition.

road during the wet season may provide ephemeral breeding habitat for some species, but these pools exist as a result of human disturbance, and are not found in forested habitats.

Another important consideration related to the findings of this study is that in BBS areas of secondary forest are contiguous and often in close proximity to primary habitat, which may serve as a source of colonizers for secondary habitat. We would predict that more isolated secondary forests (i.e., in forest fragments) would show considerable declines in richness and shifts in species composition, as has been demonstrated for understory birds in the Mache–Chindul Reserve (RD, personal observation) and for amphibians in Bolivia and Brazil (Tocher et al., 1997; Becker et al., 2007; Watling and Donnelly, 2008).

Primary and secondary interior forest exhibited a significant difference in estimated richness levels. Like river habitats, secondary interior forests we sampled were bordered by primary forest, which may serve as a source for colonizers; however, unlike river habitats, interior forests lack the regular natural disturbances that rivers experienced with fluctuating water levels. It appears that amphibian communities in interior forests

may be more sensitive than riparian amphibian communities to dramatic disturbance events, such as logging, with effects evident as long as three decades after the event. A number of studies have demonstrated that logging and slash-and-burn agriculture impoverish amphibian diversity and richness (Pearman, 1997; Krishnamurthy, 2003; Gardner et al., 2007; Hamer and McDonnell, 2008). Changes in amphibian richness and diversity have been attributed to structural habitat alteration caused by human activity, such as changes in leaf litter cover, canopy cover, and tree size (Hillers et al., 2008) and by absence of refuge structures such as bromeliads (Galindo-Leal et al., 2003). Bromeliads are slow-growing plants that are usually absent from secondary forests (Benzing, 1980). The lack of bromeliads in both secondary forest and road-edge habitats likely explains the absence of *O. sylvatica*—whose tadpoles carry out their development in bromeliads—from these habitats. *Oophaga sylvatica* was identified as an indicator of forest habitat, with 90% of encounters of this species occurring in primary forest habitat, and none in secondary forest; like the river indicators discussed above, its distribution within BBS reflects its reproductive biology.

Additional environmental variables collected in primary and secondary forests at BBS may provide a clearer understanding of the influence of habitat structure on the patterns of amphibian diversity in BBS and species composition in the region. Similarly, a more thorough survey of amphibian communities may uncover additional species and further elucidate true levels and patterns of diversity in the BBS. Our sampling effort took place over 9 mo; a year-round sampling effort may yield more species, particularly those with specialized seasonal breeding requirements.

Amphibian Assemblages Along Road Edges

Road edges supported surprisingly high levels of amphibian richness, particularly through pasture habitat. This may be explained by the existence of temporary breeding pools that are rare in other less disturbed habitats in the reserve. Four of the six species that were found exclusively in road-edge habitats (*H. pellucens*, *S. phaeota*, *L. rhodomerus*, and *Rhinella marina*) are known to breed in still bodies of water (Savage, 2002; IUCN, 2011). Previous studies have identified structural similarities between savannah habitats and deforested areas as a major factor permitting the expansion of species into disturbed areas (Haddad and Prado, 2005). In our study, we favor the idea that access to reproductive resources has played a more important role; no natural habitats in our study area resemble road edge or pasture, so species colonizing these habitats are unlikely to be capitalizing on familiar habitat structure. Rather, the four species mentioned above more likely colonized from nearby lowlands, their range expansion facilitated by the presence of still water along the road during the wet season.

Of the species found exclusively along roads, only *S. phaeota* was found on enough occasions to be identified as an indicator species for this habitat. Like the indicator species for forests and rivers, its abundance along road habitats is likely a result of its preference for temporary pools for reproduction (IUCN, 2011). The only other indicator species for road-edge habitats was *P. achatinus*. This species was the most common species encountered during this study in all

habitats, but was particularly abundant along road edges and in secondary interior forest. Unlike the previously mentioned indicator species, the conspicuous abundance of *P. achatinus* in road-edge habitats cannot be explained by its requirements for reproduction. *Pristimantis achatinus* has direct development, with egg clutches being laid in moist terrestrial environments (Hedges et al., 2008); further analysis of environmental variables such as humidity and leaf litter depth could provide insight into the patterns of abundance for this species.

Amphibians as Indicators of Habitat Alteration

Amphibians are considered generally good indicator species due to their sensitivity to habitat alteration (Welsh and Ollivier, 1998; Pollet and Bendell-Young, 2000). Nonetheless, not all species are equally useful for this purpose. BBS has similar amphibian species richness to Jatun Sacha Reserve in Amazonian Ecuador (Pearman, 1997); however, some taxa in BBS demonstrate markedly different patterns in response to habitat alteration. At the Amazonian Jatun Sacha Station, Pearman (1997) found that species richness of the genus *Pristimantis* declined with proximity to pasture, suggesting that *Pristimantis* may be a useful indicator assemblage for assessing the disturbance in tropical wet forest. *Pristimantis* species at BBS, however, exhibited the greatest richness in secondary interior forest and in road habitats and all but one (*P. achatinus*) were very rare. These findings suggest that *Pristimantis* has little value as an indicator assemblage for assessing the disturbance in premontane or humid tropical forest in the Mache–Chindul. Desiccation is a real threat for most amphibians and the higher humidity levels at premontane sites likely allow more species to flourish in pasture and edge settings than at lowland rainforest sites (Toral et al., 2002).

Four species (*Cochranella mache*, *T. spinosa*, *Caecilia leucocephala*, and *L. labrosus*) encountered during this study were found exclusively in pristine interior forest or river habitats. All of these species were only encountered once or twice over the course of 9 mo, thus making them poor indicator

species. *Oophaga sylvatica*, however, is a good candidate as an indicator species for pristine forest habitat since it: (1) was the second most abundant amphibian found along pristine interior forest transects during this study and was only observed once in secondary habitat; (2) is easily identifiable; (3) is vocal during the day; and (4) is widespread in the region. All of these traits make its detection easy and feasible. Surveys for the presence of *O. sylvatica* in other pristine (or disturbed) forest habitat across its range are needed, however, before adopting this species as a suitable indicator of quality pristine forest habitat.

Conservation and Management Implications

Although the DCA revealed similarities in amphibian communities in interior forest and along roads, much of the result reflects more the pattern of abundance of *P. achatinus* than an overall similarity between the amphibian communities of the two habitats. Each of these habitat categories was strongly dominated by *P. achatinus*, whereas other species were found in relatively low abundance. DCA showed that river habitats, on the other hand, hosted a unique and much more even amphibian community structure with no single species dominating the habitat, as demonstrated by the high values of Shannon–Wiener or Simpson’s diversity compared to other habitats. In general, the species that were indicative or exclusively found in road habitats tended to be widespread and all were listed as being of Least Concern by the International Union for Conservation of Nature (IUCN, 2011). These results are congruent with those of Ficetola and De Bernardi (2004), which suggested that habitat disturbance results in impoverished amphibian compositions made up of common and robust species. Rivers supported an endemic undescribed species (*Colostethus* sp. nov.; G. Vigle, personal observation), and one Endangered (*Cochranella mache*) and one Vulnerable (*Hyloxalus awa*) species. This highlights the importance of considering species composition and the conservation status of individual amphibian species, and not defining conservation priorities solely on the basis of species richness levels (Pearman, 1997).

The high diversity, presence of rare or endangered species, and apparent resilience of riparian amphibian assemblages to habitat alteration in the form of logging has implications for the conservation and restoration of amphibian diversity in western Ecuador. For riparian areas, protecting existing forest and promoting new forest growth along rivers should be made a priority for amphibian conservation in this part of the world. Interior forest amphibian assemblages in BBS demonstrated lower diversity but more vulnerability to habitat alteration than amphibian assemblages along rivers, suggesting that pristine, unlogged interior forests should also receive conservation attention over altered interior forests. Given the mosaic structure of the disturbed and pristine habitats in BBS, more research focused on amphibian responses to habitat fragmentation is required to create land-management plans that will sustain amphibians in the Chocó rainforest well into the future.

Acknowledgments.—We are grateful for the assistance provided by staff of the Jatun Sacha Foundation and Bilsa Biological Station, and to the local residents in our study area for conserving their forests and making this work possible. Thanks to D. Cabrera, L. Carrasco, F. Castillo, P. Mena, and J. Olivo for assistance in the field and to M. Yanes-Muñoz and M. Ortega-Andrade at the Museo Ecuatoriano de Ciencias Naturales for help with identifications of photographs of specimens. Thanks to S. Bondrup-Nielsen, T. Herman, S. Mockford, and D. Stewart at Acadia University for early edits on this manuscript. Thanks to D. Blackburn, M. Chatfield and D. McAlpine for thoughtful comments about the manuscript before submission. Research was supported by the Conservation, Food and Health Foundation; Disney Worldwide Conservation Fund; National Geographic Society; and National Science Foundation (OISE-0402137). All research was conducted with approval of the Ecuadorian Ministry of the Environment (Permit 009-CI-FAU-DRE-MA).

LITERATURE CITED

- Becker, C.G., C.R. Fonseca, C.F.B. Haddad, R.F. Batista, and P.I. Prado. 2007. Habitat split and the global decline of amphibians. *Science* 318:1775–1777.
- Beebee, T.J.C. 1995. Amphibian breeding and climate change. *Nature* 374:219–220.
- Benzing, D.H. 1980. *The Biology of the Bromeliads*. Mad River Press, USA.
- Charlat, S., O.R. Thatcher, N. Hartman, M. Saillan, and E. Vooren. 2000. Survey of *Alouatta palliata* at the Bilsa Biological Reserve, north-west Ecuador. *Neotropical Primates* 8:40–44.

- Cheng, T.L., S.M. Rovito, D.B. Wake, and V.T. Vredenburg. 2011. Coincident mass extirpation of neotropical amphibians with the emergence of the infection fungal pathogen *Batrachochytrium dendrobatidis*. *Proceedings of the National Academy of Sciences of the United States of America* 108:9502–9507.
- Cogger, H., and R. Zweifel. 1998. *Encyclopedia of Amphibians and Reptiles: A Comprehensive Illustrated Guide by International Experts*. Academic Press, USA.
- Colwell, R.K. 2006. EstimateS: Statistical estimation of species richness and shared species from samples, Version 8. Available at <http://purl.oclc.org/estimates>. Archived by WebCite at <http://www.webcitation.org/6AJOsKPPc> on 30 August 2012.
- Colwell, R.K., C.X. Mao, and J. Chang. 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology* 85:2717–2727.
- Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302–1310.
- Dickman, C.R. 1987. Habitat fragmentation and vertebrate species richness in an urban environment. *Journal of Applied Ecology* 24:373–381.
- Dinerstein, E., D.M. Olson, D.J. Graham, A.L. Webster, S.A. Primm, M.P. Bookbinder, and G. Ledec. 1995. *A Conservation Assessment of the Terrestrial Ecoregions of Latin America and the Caribbean*. The World Bank, USA.
- Dodson, C.H., and A.H. Gentry. 1991. Biological extinction in western Ecuador. *Annals of the Missouri Botanical Garden* 78:273–295.
- Dufrêne, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67:345–366.
- Dukes, J.S., and H.A. Mooney. 2004. Disruption of ecosystem processes in western North America by invasive species. *Revista Chilena de Historia Natural* 77:411–437.
- Ficetola, G.F., and F. De Bernardi. 2004. Amphibians in a human-dominated landscape: the community structure is related to habitat features and isolation. *Biological Conservation* 119: 219–230.
- Galindo-Leal, C., J.R. Cedeño-Vázquez, R. Calderón and J. Augustine. 2003. Arboreal frogs, tank bromeliads and disturbed seasonal tropical forest. *Contemporary Herpetology* 2003: N1. Available at <http://www.cnah.org/ch/ch/2003/1/index.htm>. Archived by WebCite at <http://www.webcitation.org/6L77VEI9V> on 13 November 2013.
- Gardner, T.A., E.B. Fitzherbert, R.C. Drewes, K.M. Howell, and T. Caro. 2007. Spatial and temporal patterns of abundance and diversity of an East African leaf litter amphibian fauna. *Biotropica* 39:105–113.
- Gascon, C., J.P. Collins, R.D. Moore, D.R. Church, J.E. McKay, and J.R. Mendelson, III (Eds). 2007. *Amphibian Conservation Action Plan*. IUCN/SSC Amphibian Specialist Group, Switzerland and UK.
- Haddad, C.F.B., and C.P.A. Prado. 2005. Reproductive modes and their unexpected diversity in the Atlantic forest of Brazil. *Bioscience* 55:207–217.
- Hamer, A.J., and M.J. McDonnell. 2008. Amphibian ecology and conservation in the urbanising world: a review. *Biological Conservation* 141:2432–2449.
- Hedges, S.B., W.E. Duellman, and M.P. Heinicke. 2008. *New World direct-developing frogs (Anura: Terrarana): molecular phylogeny, classification, biogeography, and conservation*. *Zootaxa* 1737:1–182.
- Heyer, W.R., M.A. Donnelly, R.W. McDiarmid, L.C. Hayek, and M.S. Foster (Eds). 1994. *Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians*, 1st Ed. Smithsonian Books, USA.
- Hill, M.O., and H.G. Gauch. 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetatio* 42:47–58.
- Hillers, A., M. Veith, and M.O. Rodel. 2008. Effects of forest fragmentation and habitat degradation on West African leaf-litter frogs. *Conservation Biology* 22:762–772.
- Hofer, U., L.-F. Bersier, and D. Borcard. 2000. Ecotones and gradient as determinants of herpetofaunal community structure in the primary forest of Mount Kupe, Cameroon. *Journal of Tropical Ecology* 16:517–533.
- Holdridge, L.R. 1967. *Life Zone Ecology*. Tropical Science Center, San Jose, Costa Rica.
- [IUCN] International Union for Conservation of Nature. 2011. *The IUCN Red List of Threatened Species*. Version 2011.2. Available at www.iucnredlist.org. Archived by WebCite at <http://www.webcitation.org/6AJQwcNMg> on 30 August 2012.
- Karubian, J., and L. Carrasco. 2008. Home range and habitat preferences of the Banded Ground-cuckoo (*Neomorphus radiolosus*). *Wilson Journal of Ornithology* 120:205–209.
- Krebs, C.J. 1999. *Ecological Methodology*, 2nd Ed. Benjamin Cummings, USA.
- Krishnamurthy, S.V. 2003. Amphibian assemblages in undisturbed and disturbed areas of Kudremukh National Park, central Western Ghats, India. *Environmental Conservation* 30:274–282.
- McCune, B., and M.J. Mefford. 1999. *PC-ORD: Multivariate Analysis of Ecological Data*, Version 4.41. MjM Software, USA.
- Olson, D.H., P.D. Anderson, C.A. Frissell, H.H. Welsh, and D.F. Bradford. 2007. Biodiversity management approaches for stream-riparian areas: perspectives for Pacific Northwest headwater forests, microclimates, and amphibians. *Forest Ecology and Management* 246:81–107.
- Ortega-Andrade, H.M., J. Bermingham, C. Aulestia, and C. Paucar. 2010. Herpetofauna of the Bilsa Biological Station, province of Esmeraldas, Ecuador. *Check List* 6:119–154.
- Patterson, H.D., and R. Thompson. 1971. Recovery of inter-block information when block sizes are unequal. *Biometrika* 58:545–554.
- Pearman, P.B. 1997. Correlates of amphibian diversity in an altered landscape of Amazonian Ecuador. *Conservation Biology* 11:1211–1225.
- Perkins, D.W., and M.L. Hunter. 2006. Effects of riparian timber management on amphibians in Maine. *Journal of Wildlife Management* 70:657–670.
- Pollet, I., and L. Bendell-Young. 2000. Amphibians as indicators of wetlands formed from oil sand effluent. *Environmental Toxicology and Chemistry* 19:2589–2597.
- Real, R., J.M. Vargas, and A. Antúnez. 1993. Environmental influences on local amphibian diversity: the role of floods on river basins. *Biodiversity and Conservation* 2:376–399.

- SAS Institute. 1989–2007. JMP[®], Version 9. SAS Institute, USA.
- Savage, M.J. 2002. The Amphibians and Reptiles of Costa Rica: A Herpetofauna Between Two Continents, Between Two Seas. University of Chicago Press, USA.
- Semlitsch, R.D., and J.R. Bodie. 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. *Conservation Biology* 17:1219–1228.
- Sierra, R. 1996. La deforestación en el noroccidente del Ecuador, 1983–1993. *EcoCiencia*, Ecuador.
- Sierra, R., F. Campos, and J. Chamberlin. 2002. Assessing biodiversity conservation priorities: ecosystem risk and representativeness in continental Ecuador. *Landscape and Urban Planning* 59:95–110.
- Steininger, M.K., C.J. Tucker, J.R.G. Townshend, T.J. Killeen, A. Desch, V. Bell, and P. Ersts. 2001. Tropical deforestation in the Bolivian Amazon. *Environmental Conservation* 28:127–134.
- Stuart, S.N., J.S. Chanson, N.A. Cox, B.E. Young, A.S.L. Rodrigues, D.L. Fischman, and R.W. Waller. 2004. Status and trends of amphibian declines and extinctions worldwide. *Science* 306:1783–1786.
- Tocher, M.D., C. Gascon, and B.L. Zimmermann. 1997. Fragmentation Effects on a Central Amazonian Frog Community: A Ten Year Study. University of Chicago Press, USA.
- Toral, C.E., P. Feinsinger, and M.L. Crump. 2002. Frogs and a cloud-forest edge in Ecuador. *Conservation Biology* 16:735–744.
- Urbina-Cardona, J.N., M. Olivares-Pérez, and V.H. Reynoso. 2006. Herpetofauna diversity and environment correlates across a pasture-edge-interior ecotone in tropical rainforest fragments in the Los Tuxtlas Biosphere Reserve of Veracruz, Mexico. *Biological Conservation* 132:61–75.
- Vasconcelos, T.S., T.G. Santos, D.C. Rossa-Feres, and C.F.B. Haddad. 2010. Similarity of ground-dwelling anuran (Amphibia) composition among different vegetation physiognomies in a mesophytic semideciduous forest from southeastern Brazil. *North-Western Journal of Zoology* 6:275–285.
- Wake, D.B., and V.T. Vredenburg. 2008. Are we in the midst of the sixth mass extinction? A view from the world of amphibians. *Proceedings of the National Academy of Sciences of the United States of America* 105:11466–11473.
- Watling, J.L., and M.A. Donnelly. 2008. Species richness and composition of amphibians and reptiles in a fragmented forest landscape in northeastern Bolivia. *Basic and Applied Ecology* 9:523–532.
- Welsh, H.W., Jr., and L.M. Ollivier. 1998. Stream amphibians as indicators of ecosystem stress: a case study from California's redwoods. *Ecological Applications* 8:1118–1132.
- Zimmermann, B.L., and D. Simberloff. 1996. An historical interpretation of habitat use by frogs in a Central Amazonian forest. *Journal of Biogeography* 23:27–46.

Accepted: 16 November 2013
Associate Editor: Michael Freake
Editor: Brad Moon